



How galling herbivores share a single super-host plant during their phenological cycle: the case of *Mimosa gemmulata* Barneby (Fabaceae)

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Abstract

The success of the galling insects sharing the same microhabitat depends both on the synchrony of their life cycles with the leaf flushing of the super-host plant and to the asynchrony among their life cycles. The asynchrony of the multivoltine life cycles of *Lopesia* spp. (Diptera—Cecidomyiidae) is favored by the constant leaf flushing in *M. gemmulata*, and favors the non-overlapping of gall induction periods. Peculiarly, the univoltine life cycle of the galling Lepidoptera on its stem galls is synchronized to the availability of mature host leaves during the rainy season, which is important for the water potential in host stem branches. The abundance of the *Lopesia* gall morphotypes follow the phenology of *M. gemmulata*, which obeys the seasonal pattern of water availability in the neotropical savanna climate.

Keywords Gall abundance · Gall-induction overlapping · Multivoltinism · Plant-interaction · Phenological synchronism · Seasonality

Introduction

Galls are sophisticated relationships between specialist herbivores, which include mites, nematodes, fungi, and more extensively insects, and their host plants (Stone and Schönrogge 2003; Shorthouse et al. 2005). The guild of galling insects include six orders, Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera, and Thysanoptera (Fernandes and Santos 2014; Miller and Raman 2018; Ferreira et al. 2019) with a global estimation of 211,000 species in the last century (Espírito-Santo and Fernandes 2007). In face of the high specificity of this host plant-galling arthropod interaction, both richness and abundance of the galling insects can

be estimated in nature by the distinct structural features of gall morphotypes (Carneiro et al. 2009; Isaias et al. 2013). Structural features, such as pubescence, shape, and size, as well as gall coloration are tools for the interpretation of gall developmental stages (Dias et al. 2013; Carneiro et al. 2013; Oliveira et al. 2013; Costa et al. 2018), and can be used to estimate the life cycles of the galling insects.

The life cycles of the galling insects can be defined by the type of voltinism, which indicates the number of generations of an organism within a one-year time (Yukawa 2000). Galling insects can have univoltine, bivoltine or multivoltine cycles (Yukawa 2000; Oliveira et al. 2016). Univoltine galling insects have only one generation throughout one-year time (Magalhães et al. 2014; Pfeffer et al. 2018; Guedes et al. 2018a, b), while the bivoltine and the multivoltine galling insects have two (Carneiro et al. 2013) or more generations over a year (Mendonça and Romanowski 2012; Dias et al. 2013; Costa et al. 2018), respectively. The periodicity of their cycles demands different and efficient strategies of the galling insects to exploit the resources during the host plant phenology (Oliveira et al. 2016).

The plant phenological pattern depends on environmental factors such as seasonality, precipitation, and temperature, as well as on the water potential of the plants (Lemos-Filho and Mendonça-Filho 2000; Franco et al. 2005; Garcia et al. 2017; García-Núñez et al. 2019). These abiotic and

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physiological variables can impose constraints to the host plant species and, consequently, to the life cycles of the gall-forming insects, and to gall abundance (Oliveira et al. 2013). Several studies demonstrated strategies of phenological synchronism between gall-forming insects and the phenology of their host plants in temperate (Yukawa 2000; Tokuda 2012), tropical (Oliveira et al. 2016), and mediterranean (Guedes et al. 2018a, b) climatic conditions. Based on that, the seasonal leaf flushing of Neotropical plant species, that occur at the end of the dry season or early rainy season (Garcia et al. 2017; García-Núñez et al. 2019), can provide a large amount of resources for gall-forming insect exploitation (Oliveira et al. 2016). One of the most efficient strategies of the gall-forming insects is ovipositing in young tissues (*sensu* Weis et al. 1988). Nevertheless, the oviposition is not exclusive on the young tissues. Gall-forming insects can induce their galls in mature leaves, whose cells keep the capacity for re-differentiation (Oliveira and Isaias 2009; Oliveira et al. 2013). The ability to exploit both young and mature tissues is important for the success of the gall-forming insects, which widens the opportunities of gall-forming insects to synchronize their life cycles with the phenology of their host plants (Oliveira et al. 2013). The synchronization between gall-forming insects and their host plants is a critical event for the first, because a time lag synchronization determines the quality and quantity of available food resources, and the abundance of population dynamics of gall-forming herbivores (Yukawa 2000; Mendonça 2001; Oliveira et al. 2013, 2016). Interactive systems involving a super-host plant and several gall-forming insects can reveal peculiar temporal strategies involving niche overlapping during gall induction by generations of gall-forming insects (Weis et al. 1988; Toma and Mendonça 2014), which share the same induction site. The niche overlapping refers to the use of the same resources or conditions by two or more species, and the greater the number of resources shared by the species, the greater the overlapping (Pianka 1974). *Mimosa gemmulata* Barneby is a super-host Fabaceae, the mean host family of gall-forming herbivores in the Neotropical region (Fernandes and Santos 2014). This species occurs in Venezuela and Brazil (Bahia, Minas Gerais, Goiás, Pernambuco, and Piauí), and grows naturally in areas of Caatinga, Savanna, and Campos Rupestres vegetation (Santos-Silva et al. 2015). *Mimosa gemmulata* hosts five leaf gall morphotypes induced by five species of *Lopesia* Rübsaamen, 1908 (Diptera—Cecidomyiidae, Maia and Carvalho-Fernandes, personal communication), and one fusiform stem gall induced by a Lepidoptera (Costa 2016; Silva et al. 2018). The five leaf galls on *M. gemmulata* share the same induction microsite, i.e., the pinna-rachis (Costa 2016), a peculiarity of the galls associated with this super-host plant.

The first approach toward the six gall morphotypes associated with *M. gemmulata* deals with the host plant phenology and the life cycles of the six associated gall-forming insects.

Currently, the life cycles of the six gall-forming insects are evidenced by the developmental stages of their specific gall morphotypes (Carneiro et al. 2009; Isaias et al. 2013), herein referred as the life cycles of the galls. We hypothesize that the gall-forming insects alternate their phenological synchrony with that of the host plant, and asynchrony among their life cycles as strategies to share the same microsite of induction. All processes involving this super-host plant-galling herbivore systems are directly influenced and dependent on climatic factors, which directed the following questions: (1) how are the gall life cycles distributed along a one-year period? (2) Do the periods of gall induction and leaf flushing on *M. gemmulata* overlap for the five gall-forming herbivores? And (3) what are the abiotic and physiological factors that best relates to gall abundance?

Materials and methods

Study area

This study was carried out in Serra Geral of Caetité (14°04' 36. 8" S, 42°29'59" W), state of Bahia, northeast Brazil. The area has 974 m of altitude with the vegetation comprising a savanna, where the individuals of *M. gemmulata* may be isolated or grouped in low density populations. According to the Köppen system, the climate of the region is classified as Aw (tropical with dry winters, and rainy summers; Alvares et al. 2013), with marked seasonality. The rainy season ranges from November to April, when monthly rainfall is > 60 mm, and dry season ranges from May to October, when monthly rainfall is < 60 mm (Fig. 1). The mean annual rainfall is 608 mm and the mean temperature is above 23 °C (Fig. 1). The data of precipitation and of mean temperature were obtained from the meteorological station of Caetité, and from the meteorological station of Lençóis, Bahia state, respectively. The second station is the nearest (~ 350 km) and with climate (Aw) similar to that of the study

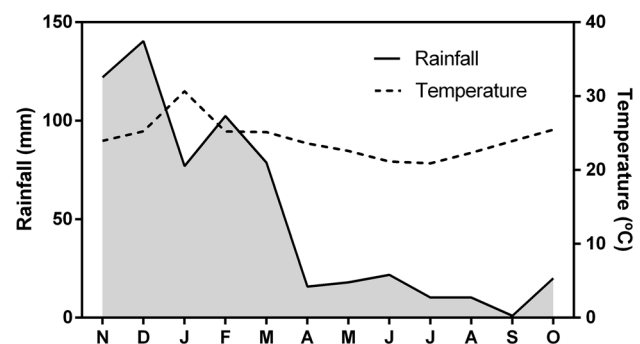


Fig. 1 Climatic diagram with mean annual rainfall (mm) and temperature (°C) during the year of study: from November 2017 to October 2018

site (Alvares et al. 2013; meteorological data for the years 1961–1990; INMET 2019).

Super-host plant phenology

The phenology of *M. gemmulata* (voucher specimens: herbarium of the Universidade do Estado da Bahia, HUNEB-25044) was monitored every 15-day intervals from November 2017 to October 2018 on individuals ($n = 12$) selected by order of appearance along trails previously traced (cf. Eça-Neves and Morellato 2004). The vegetative phenophases (leaf flushing, mature leaves, and leaf falling) and the reproductive phenophases (inflorescence buds, inflorescence anthesis, immature, and mature fruits) were monitored according to the methods proposed by Fournier (1974) in each *M. gemmulata* individual. This method is semi-quantitative, ranking five categories of phenophases (0 = absence of the phenophase; 1 = 1–25%; 2 = 26–50%; 3 = 51–75%; and 4 = 76–100% intensity of the phenophases). The presence and absence of the vegetative and reproductive phenophases were evaluated for each plant, and phenological synchrony was estimated (Bencke and Morellato 2002). Leaf flushing was considered valid from the beginning of the first leaves until their complete expansion (Pedroni et al. 2002) with light green leaflets (Fig. 2A, B). Mature leaves were considered as those with dark green leaflets (Fig. 2C), and leaf falling was considered when the leaflets are yellowish and fell off the branches easily (Fig. 2D). The phenophase of inflorescence buds referred to the presence of inflorescences with flower buds (Fig. 2E), and the phenophase of inflorescence anthesis referred to the presence of inflorescences with flower in anthesis (Fig. 2F). The phenophase of immature fruits referred to the presence of fruits with green collar (Fig. 2G), while the phenophase of mature fruits referred to the presence of fruits with brown collar (Fig. 2H). The observation of the phenology was based on the percentage categories for the canopy covering.

Life cycles of the galls

The definition of the life cycles was based on the most abundant of the developmental stages for the six galls in each field observation period throughout the year (Arduin et al. 1994; adapted). Terminal branches ($n = 4$) were randomly marked on each individual of *M. gemmulata* ($n = 12$), in a total of 48 branches. At each branch, the presence and abundance of each morphotype were counted every 15-day intervals from November 2017 to October 2018. The life cycles of the six galling insects were differentiated in the field based on structural features such as, the gall shape, and size, and color (Isaias et al. 2013). Galls stages were later registered as gall induction, growth and development, maturation and senescence (Fig. 2 I-B', Table 1). For the five

leaf galls, the induction stage was characterized as a small intumescence on the pinna-rachis. The induction stage of the stem gall could not be observed in field conditions. The growth and development stage was determined by the higher dimensions of the intumescence (1–3 mm of height, and 0.1–0.4 mm of width) or color. The mature stage was determined by the gall shape and color, and the senescent stage was determined by the presence of the open galls, pupal exuviae, or scape channel of the galling insects. Samples of mature leaf galls ($n = 24$ for each gall morphoespecies) were collected and opened on the stereomicroscope to obtain the fauna associated with the galls. The stem gall induced by a Lepidoptera was not collected due to its low abundance.

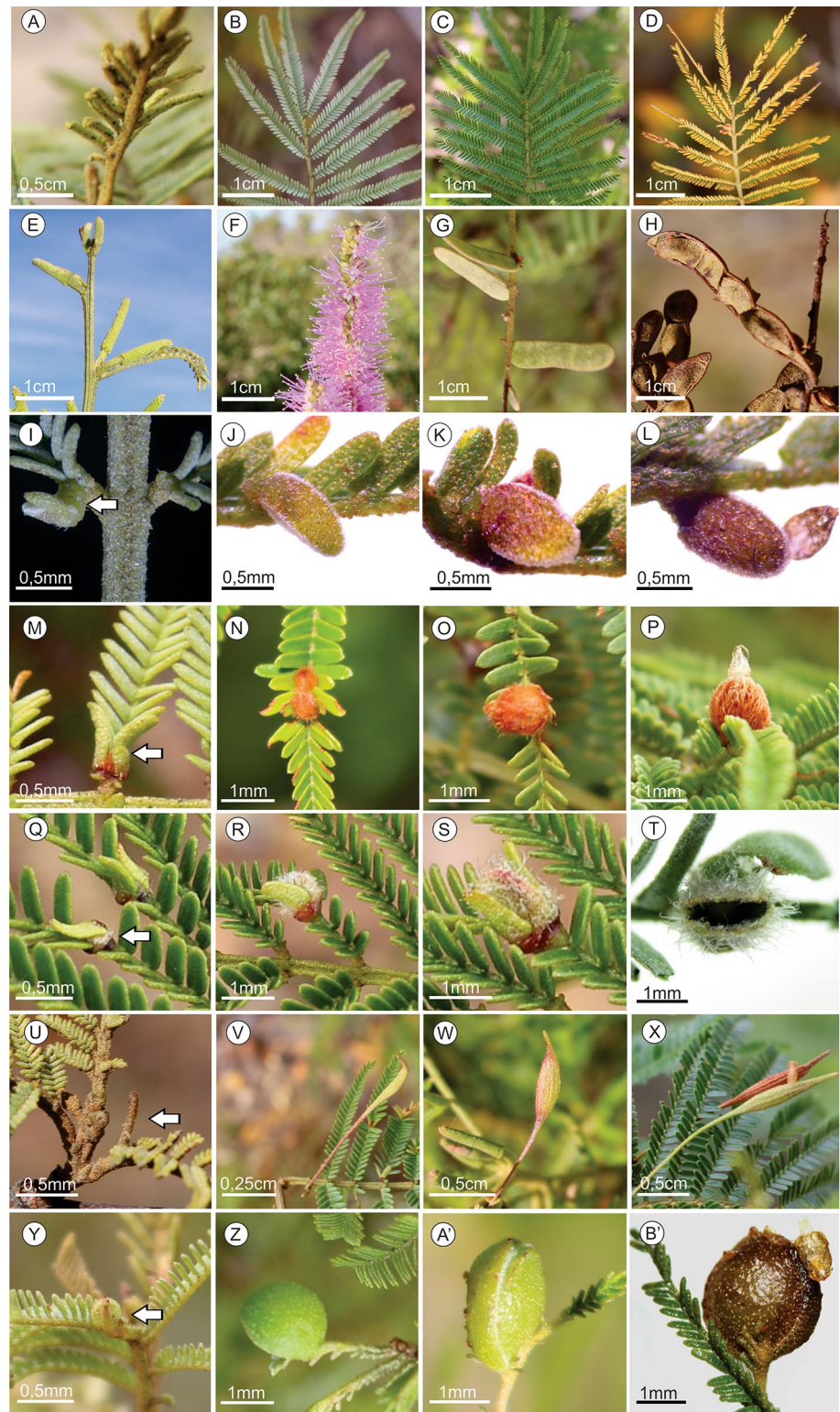
Water potential measurements

The water potential (Ψ) of terminal branches sectioned about 10 cm from the apex of the individuals ($n = 6$) of *M. gemmulata* (Scholander et al. 1965) was determined using a pressure chamber (Model 600 PMS, EUA). The water potential was measured at the predawn (Ψ_{PD} 05:00 a.m.), and mid-day (Ψ_{MD} 12:00 p.m.). The measurements were taken in the rainy season (November and December 2017, and January and April 2018), and in the dry season (July, September and October 2018).

Data analysis

The phenological data of the six-gall morphotypes was organized in histograms evidencing the annual gall life cycles. The stem gall induced by a Lepidoptera was not subjected to the analyses of distribution, overlapping, and correlation due to its low abundance. We tested the distribution and overlapping of the phenophases of *M. gemmulata* and the life cycles of five leaf gall morphotypes using the circular analysis (Agostinelli and Lund 2017), and the Pianka index (Pianka 1974). To circular analyses of the abundance of the gall life cycles, and the phenophases of the host plant, the Watson-Wheeler test was made using von Mises distribution. The mean angles of the induction of the five leaf gall life cycles and leaf flushing was compared. The data were standardized for adjusting the unities and create evenness on the variance. The overlapping of gall inductions and leaf flushing, and within gall morphotypes per month were quantified (Pianka 1974). To compare the overlapping of gall induction and leaf flushing, gall values were transformed in percentages. The overlapping was compared to a stochastic distribution of the data using the null model with Pianka metric and Ra3 algorithm running 5000 randomizations. The Pianka index ranged from 0 (no overlap) to 1 (complete overlap), which overlap was classified as high (> 0.6), intermediate (between 0.4 and 0.6) or low (< 0.4). To verify

Fig. 2 Phenology of *Mimosa gemmulata* Barneby (Fabaceae) and the *Lopesia* gall life cycles (Diptera–Cecidomyiidae). **A, B** Leaf flushing. **C** Mature leaves. **D** Leaf falling. **E** Inflorescence buds. **F** Inflorescence anthesis. **G** Immature fruit. **H** Mature fruit. **I–L** Lenticular bivalve-shaped gall. **I** Induction (arrow). **J** Growth and development. **K** Maturation. **L** Senescence. **M–P** Brown lanceolate bivalve-shaped gall. **M** Induction (arrow). **N** Growth and development. **O** Maturation. **P** Senescence. **Q–T** Green lanceolate bivalve-shaped gall. **Q** Induction (arrow). **R** Growth and development. **S** Maturation. **T** Senescence. **U–X** Clavate gall. **U** Induction (arrow). **V** Growth and development. **W** Maturation. **X** Senescence. **Y–B'** Globoid bivalve-shaped gall. **Y** Induction (arrow). **Z** Growth and development. **A'** Maturation. **B'** Senescence



the relationships between water potential (predawn and midday) and abundance of leaf gall morphotypes, we performed a generalized linear mixed model (GLMM), using the plant water potential as fixed variable and the gall morphotypes as random effect. The correlation between

the abundance of the five leaf gall morphotypes with climatic factors (temperature, and rainfall), water potential, and plant phenophases were evaluated using a canonical analysis of principal coordinates (Legendre and Anderson 1999), based on Euclidian distance and standardized

Table 1 General features of the six gall morphotypes induced by insects on *Mimosa gemmulata* Barneby (Fabaceae) at Serra Geral, Caetité, Bahia state, Brazil

Morphotypes at MG	Inducing-insect	Host organ	Attachment at MG	Color at GD and MG	Size ($n=5$ galls) of GD (height and width; mm)
Lenticular bivalve-shaped gall	<i>Lopesia</i> sp. (Cecidomyiidae)	Pinna-rachis	Extralaminar	Green	1.24 ± 0.20 ; 0.54 ± 0.32
Brown lanceolate bivalve-shaped gall	<i>Lopesia</i> sp. (Cecidomyiidae)	Pinna-rachis	Extralaminar	Brown	1.96 ± 0.23 ; 0.93 ± 0.69
Green lanceolate bivalve-shaped gall	<i>Lopesia</i> sp. (Cecidomyiidae)	Pinna-rachis	Extralaminar	Green	1.72 ± 0.12 ; 0.86 ± 0.04
Clavate gall	<i>Lopesia</i> sp. (Cecidomyiidae)	Pinna-rachis	Pedunculated	Green	1.67 ± 0.25 ; 0.80 ± 0.02
Globoid-shaped bivalve gall	<i>Lopesia</i> sp. (Cecidomyiidae)	Pinna-rachis	Extralaminar	Green	3.30 ± 0.40 ; 1.41 ± 0.53
Fusiform gall	Lepidoptera	Stem	Intralaminar	Green (GD) and Brown (MG)	–

Values are mean—mm \pm standard deviation. The number of samples was insufficient to average the size of the fusiform gall
GD growth and development, MG mature gall

data. All analyses were made using the R software (R Core Team 2020), with EcoSimR and Vegan packages (Oksanen et al. 2007).

Results

General features of the galls

Mimosa gemmulata hosts five gall morphotypes induced by five species of *Lopesia* (Cecidomyiidae) on the pinna-rachis, four of these galls are bivalve-shaped and one is clavate (CG), a sixth gall morphotype is fusiform (FG) and is induced on stems by a Lepidoptera. The bivalve-shaped galls are: (1) the lenticular bivalve-shaped (LG); (2) the brown lanceolate bivalve-shaped (BLG); (3) the green lanceolate bivalve-shaped (GLG); and (4) the globoid bivalve-shaped (GG) (Fig. 2I–B', Table 1). The *Lopesia* larvae of the LG, GLG, and BLG can be parasitized by *Eupelmus* sp. (Hymenoptera – Eupelmidae), while the *Lopesia* larvae of the CL and GG can be parasitized by *Torymus* sp. (Hymenoptera–Torymidae).

Life cycles of the galls

The lenticular bivalve-shaped gall had six generations over the year, each one of about 2 months (Fig. 3A). The induction stage was observed on the second fortnights of December, February, April, June, August, and October. The growth and development stage lasted about 15 days, and the maturation stage lasted about 30–45 days. The BLG, the GLG, and the CG had at least four generations over a year of about 3 months each (Fig. 3B–D). The induction of the BLG was

observed on the second fortnights of December and February, on the first fortnight of May, and on the second fortnight of August (Fig. 3B). The induction of the GLG was observed on the second fortnight of December, on the first fortnight of March, on the second fortnight of May, and on the first fortnight of August (Fig. 3C). The induction of the CG was observed on the second fortnight of December, on the first fortnight of April, and on the second fortnights of June and September (Fig. 3D). The growth and development stage of these three gall morphotypes lasted approximately 30 days, and the maturation stage lasted 45–60 days. The life cycle of the GG lasted approximately 4 months, with three generations over a year (Fig. 3E). The induction was observed on the second fortnights of December and April, and on the first fortnight of August; the growth and development stage lasted 45–60 days, and the maturation stage lasted 60–75 days. The FG had one generation a year, which lasted about 5 months, beginning on the first fortnight of January and getting final development in May, when the gall reached senescence (Fig. 3F).

Phenology of the super-host plant

Mimosa gemmulata is a semi-deciduous host plant with all its vegetative, and reproductive phenophases synchronized (100%). The vegetative phenophases were distributed during the year, and the reproductive phenophases occurred at specific periods (Fig. 4A). The leaf flushing had the maximum intensity on the first fortnight of November (48%), and on the second fortnight of December (62%) with the mean vector directed to November. The intensity of leaf flushing decreased from March (15%) to October. At the second fortnight of February, the mature leaves intensity

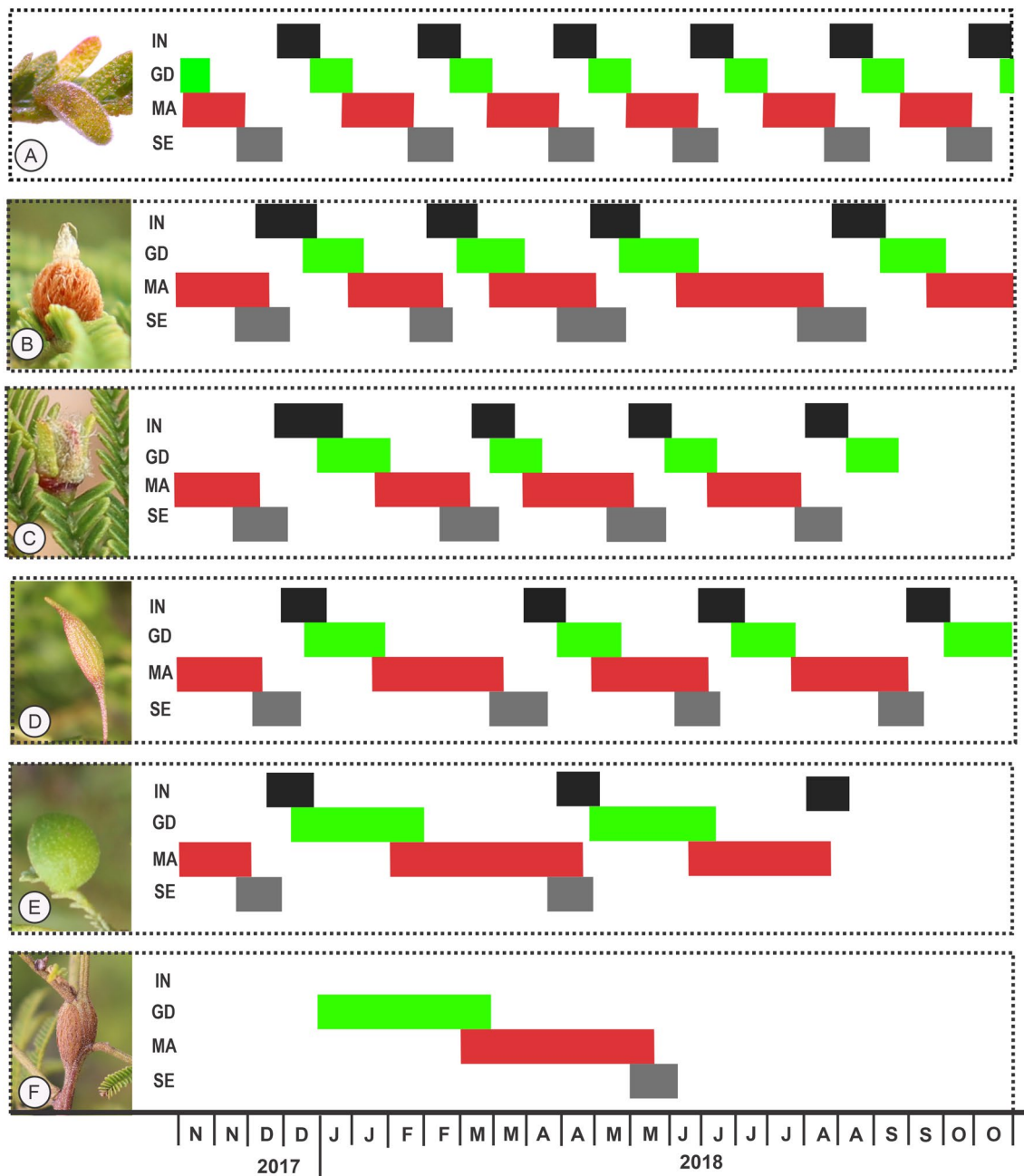


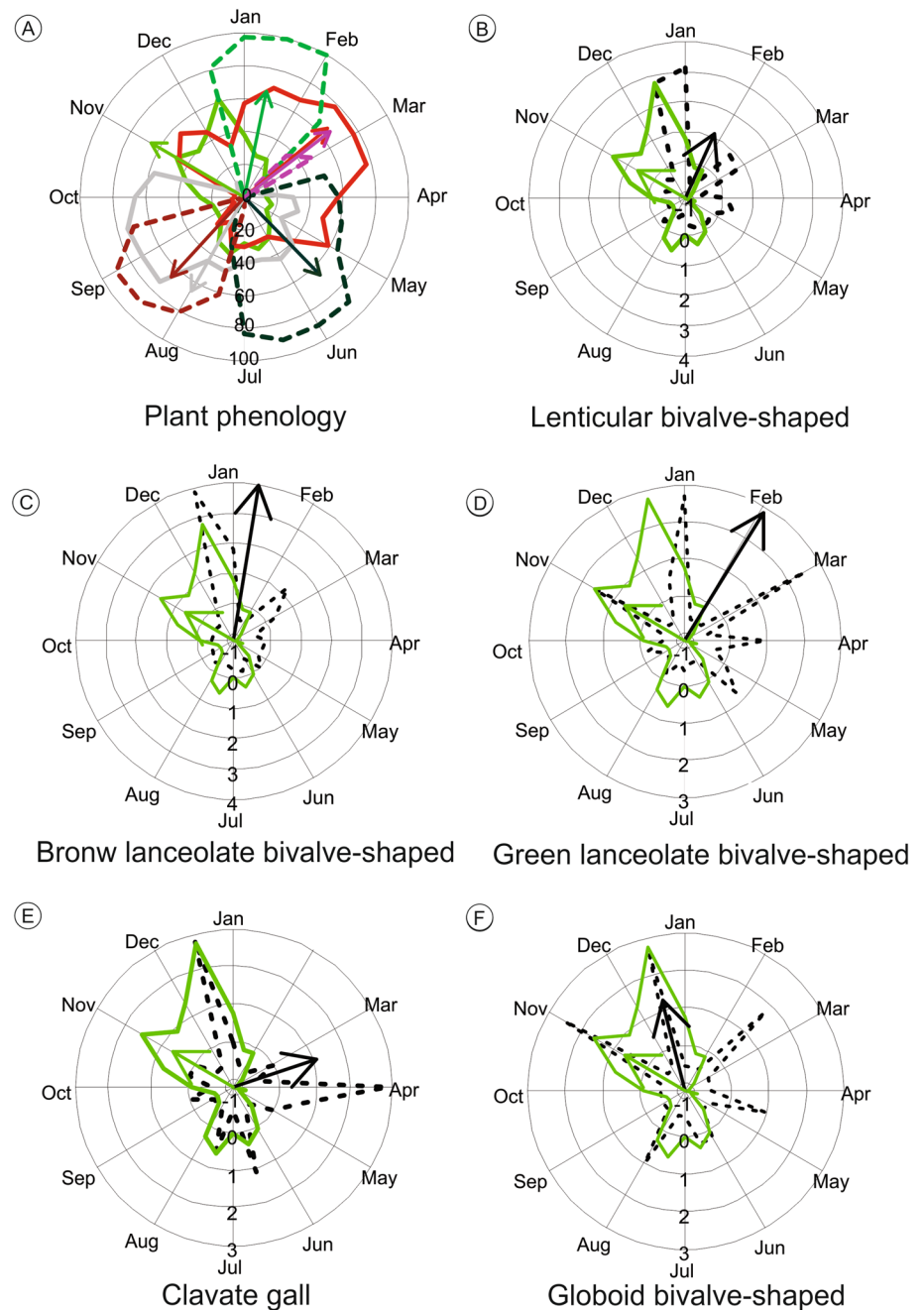
Fig. 3 Diagram of the life cycles of the gall morphotypes induced by insects (*Lopesia* spp.–Diptera–Cecidomyiidae and Lepidoptera) on *Mimosa gemmulata* Barneby (Fabaceae). **A–E.** Leaf galls induced by five *Lopesia* spp.. **A** Lenticular bivalve-shaped gall. **B** Brown lanceolate bivalve-shaped gall. **C** Green lanceolate bivalve-shaped gall.

D Clavate gall. **E** Globoid bivalve-shaped gall. **F** Stem fusiform gall induced by Lepidoptera. The bars indicate to the specific temporal window of the stages of gall development: Induction (IN) (■); Growth and development (GD) (■); Maturation (MA) (■) and Senescence (SE) (■).

increased and was constant throughout March (76%). The mean vector directed to concentration between February and March. The leaf falling occurrence increased from June (46%) to October (66%), and was more intense in September (73%) with the mean vector directed to August. The inflorescence buds occurred from December to February and had the maximum intensity in January (100%)

with the mean vector pointed to January. At the second fortnight of February to the first fortnight of March, the vector pointed to the mean concentration of the inflorescence anthesis. The immature fruits occurred from March to August with the maximum intensity in July (90%), and the direction of the mean vector pointed between May and June. The mature fruits occurred from July to September

Fig. 4 Circular analysis of index of intensity of the vegetative and reproductive phenology of *Mimosa gemmulata* Barneby (Fabaceae) and induction of the five leaf galls induced by five *Lopesia* spp. from November 2017 to October 2018. **A** Phenology [Immature fruit (dark green); Inflorescence anthesis (pink); Inflorescence buds (light green); Leaf falling (gray); Leaf flushing (fluorescent green); Mature leaves (red); Mature fruit (brown)]. **B** Lenticular bivalve-shaped gall. **C** Brown bivalve-shaped gall. **D** Green bivalve-shaped gall. **E** Clavate gall. **F** Globoid bivalve-shaped gall



with the intensity peak in August (90%), observed by the direction of the mean vector.

Relationship between the induction of the leaf gall morphotypes and leaf flushing

The galling insects induce their galls throughout the year by the time of the leaf flushing. However, more events of gall induction than peaks of leaf flushing were observed

(Fig. 4A). The Watson-Wheeler test showed different mean angles of inductions of the five leaf gall morphotypes comparing to leaf flushing (P values < 0.001). The LG had the highest peaks of induction along the second fortnight of December and first fortnight of January with the mean vector direction pointing to February (Fig. 4B). The highest peak of induction events of the BLG was observed on the second fortnight of December, with the mean vector pointing to January (Fig. 4C). The peaks of induction of the GLG were observed on the first fortnights of January and March, with the mean vector direction pointing to February (Fig. 4D).

The CG had the highest peaks of induction on the second fortnight of December, and on the first fortnight of April, with mean vector direction pointing to March (Fig. 4E). The highest peak of inductions of the GG was observed on the second fortnight of December, which coincided with the direction of the vector (Fig. 4F). The inductions of the five leaf gall morphotypes decreased from May to October. The highest overlapping occurred between the leaf flushing and the induction of the BLG (Pianka index = 0.74), and there was an intermediate overlapping between leaf flushing and the induction of GG (Pianka index = 0.40). However, there was no significant overlapping between the inductions of the three leaf galls (LG, GLG, CG) with leaf flushing. The overlapping between the events of induction was significant only for the BLG and the LG (Pianka index = 0.94). There was no significant difference in the values of overlapping of the induction events among the GLG, CG, and the GG, when compared to the null-model.

Gall morphotypes abundance versus abiotic and physiological factors

The six gall morphotypes co-occurred on *M. gemmulata* from January to May, during the rainy season. The numbers of gall morphotypes decreased in September and October, during the dry season, when the GLG, the GG, and the FG were not observed. The total abundance of the galls was higher from November to April, during the rainy season, with the highest abundance (2197) in January (Fig. 5A, B). In this month, the BLG was the most abundant (1135), followed by the LG (992), the GLG (39), the CG (21), the GG (9), and the FG (1). The seasonal pattern of the gall morphotypes was concomitant with the intensity of the leaf flushing (November to January) and mature leaves (February and March), and with the highest values of water potential (−0.3 MPa at predawn and −0.5 MPa at midday) during the rainy season (Fig. 5). Gall abundance decreased from May to October, and the lowest gall

abundance was observed in September (185) and October (144). There was a positive correlation between the total gall abundance and the increasing of the water potential (Fig. 6) at predawn ($R^2 = 0.24$, P values < 0.001), and mid-day ($R^2 = 0.25$, P values < 0.001).

The Canonical analysis of the principal coordinates showed the five leaf gall morphotypes clustered in an environment with water potential, rainfall, temperature, mature leaves, inflorescence buds, inflorescence anthesis and no leaf falling, immature, and mature fruits. The eigenvalues were 3.305 for the axis 1 and 0.306 for axis 2, with a total of 82 and 7% of the total explained variance of abundance of the five galling Cecidomyiidae in the rainy season, respectively (Fig. 7, Supplementary table S1). The abundance of the LG was more correlated to the occurrence of mature leaves. The abundance of the BLG and GLG were correlated with the temperature. The CG and GG were more correlated with the rainfall, and the water potential. The flowering phases were positively correlated with the five leaf galls. The leaf falling, and immature and mature fruits were negatively correlated with the distribution of the five gall morphotypes.

Discussion

The distribution of the five gall morphotypes induced by five *Lopesia* spp. (Diptera—Cecidomyiidae) along the one-year cycle confirmed different strategies of synchronizing to *M. gemmulata* leaf flushing. The five species of galling *Lopesia* had a peculiar asynchronism among them, which favored the sharing of the same microsite of induction on host plant. This asynchronism was peculiar for the five multivoltine species of *Lopesia*, while the univoltine Lepidoptera exploited another site of induction on the same host species, the stem. The strategies of synchronism were influenced by seasonal water availability during the dry and the rainy seasons in neotropical savanna of Brazil, which defined the abundance and presence of the different gall morphotypes.

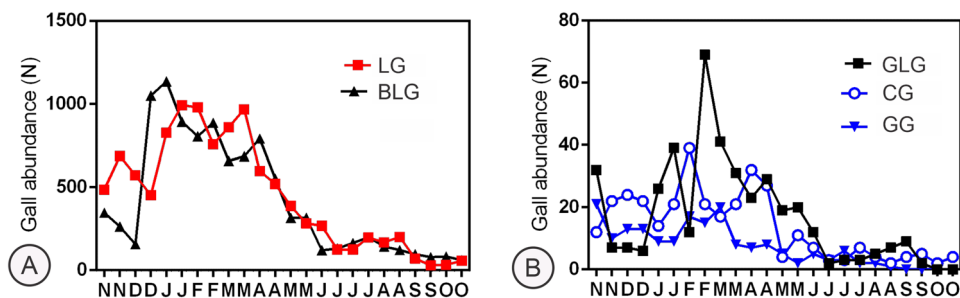


Fig. 5 Abundance of *Lopesia* galls (Diptera-Cecidomyiidae) on *Mimosa gemmulata* Barneby (Fabaceae) from November 2017 to October 2018. **A** Lenticular bivalve-shaped gall (LG) and Brown

lanceolate bivalve-shaped gall (BLG). **B** Green lanceolate bivalve-shaped gall (GLG), Clavate gall (CG) and Globoid bivalve-shaped gall (GG)

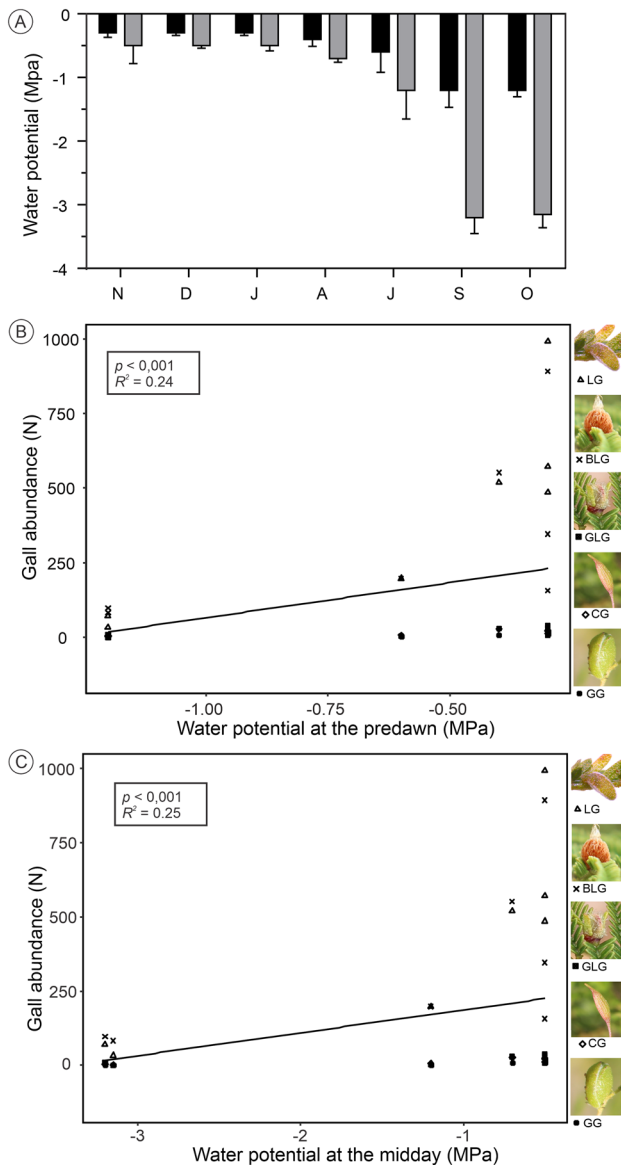


Fig. 6 Relationships between water potential (predawn and midday) and abundance of the five leaf *Lopesia* galls (Diptera–Cecidomyiidae) on *Mimosa gemmulata* Barneby (Fabaceae). **A** Leaf water potential (MPa) at predawn (■) and midday (▒) in the *M. gemmulata* population on rainy (November and December 2017, and January and April 2018), and dry (July, September, and October 2018) seasons. **B** Relation of the predawn with gall abundance. Clavate gall (CG). Brown lanceolate bivalve-shaped gall (BLG). Globoid bivalve-shaped gall (GG). Green lanceolate bivalve-shaped gall (GLG). Lanceolate bivalve-shaped gall (LG)

Univoltinism versus multivoltinism

The Lepidoptera stem gall on *M. gemmulata* had a univoltine life cycle. In the Neotropical region other galls induced by Lepidoptera have been reported, as the *Tibouchina trichopoda* (DC.) Baill. (Melastomataceae)-*Palaeomysetella beckeri* Moreira and Basilio 2015 (Momphidae) and

Schinus weinmannifolius Mart. ex Engl (Anacardiaceae)-*Cecidonius pampeanus* Moreira and Gonçalves 2017 (Cecidosidae) systems (Basilio et al. 2015; Moreira et al. 2017). The stem galls synchronized the growth and development and maturation phases with the high intensity of mature leaves during the rainy season. Such synchronization favored a high nutritional support to gall development due to the allocation of photoassimilates (Castro et al. 2012, 2013; Oliveira et al. 2017; Zorić et al. 2019), and water supply favoring the development of the Lepidoptera larvae.

The generations of the five leaf gall morphotypes on *M. gemmulata* revealed multivoltine life cycles for the *Lopesia* spp. (Cecidomyiidae). Generally, the Cecidomyiidae have univoltine or bivoltine life cycles, and rarely multivoltine life cycles in the Temperate region, despite the synchronism with deciduous plants (Tokuda 2012; Yukawa et al. 2015, 2019). In the Neotropical region, the Cecidomyiidae have univoltine life cycles as observed in the *Copaifera langsdorffii* Desf. (Fabaceae)-Cecidomyiidae systems (Oliveira et al. 2013; Carneiro et al. 2017), bivoltine life cycles as observed in the *Aspidosperma spruceanum* Benth. ex Müll.Arg. (Sapindaceae)-Cecidomyiidae system (Campos et al. 2010) or multivoltine life cycles, as described for *Eugenia uniflora* L. (Myrtaceae)-*Eugeniomyia dispar* Maia, Mendonça and Romanowski, 1996 system (Mendonça and Romanowski 2012; Rezende et al. 2018).

The multivoltine life cycles are the most common for the galling Cecidomyiidae in the Neotropical region (Hawkins and Gagné 1989), because of the evergreen or semi-deciduous habits that frequently provide sites of inductions in the neotropical savanna (Dalmolin et al. 2015; Garcia et al. 2017; Camargo et al. 2018; García-Núñez et al. 2019). Although the strategies of synchronism with their host plants are not completely clear for the galling insects with multivoltine life cycles (Mendonça and Romanowski 2012; Toma and Mendonça 2014; Oliveira et al. 2016), the multivoltine *Lopesia* spp. associated with *M. gemmulata* had peculiar strategies of synchronism. The continuous leaf flushing during the year support the multivoltine life cycles. *Mimosa gemmulata* is a semi-deciduous shrub, with periods of leaf flushing and leaf falling related to the contrasting periods of drought and raining in the neotropical savanna climate. The periods of leaf flushing were continuous throughout the year, but with main peaks in the rainy season, which coincided with the main peaks of Cecidomyiidae gall induction. Such synchronization indicated an advantage over the best windows of opportunity (Mendonça 2001; Yukawa 2000; Tokuda 2012; Oliveira et al. 2016). The induction phase of the five leaf gall morphotypes synchronized with the semi-deciduous habit of *M. gemmulata*, which was discussed herein based on the overlapping of resources.

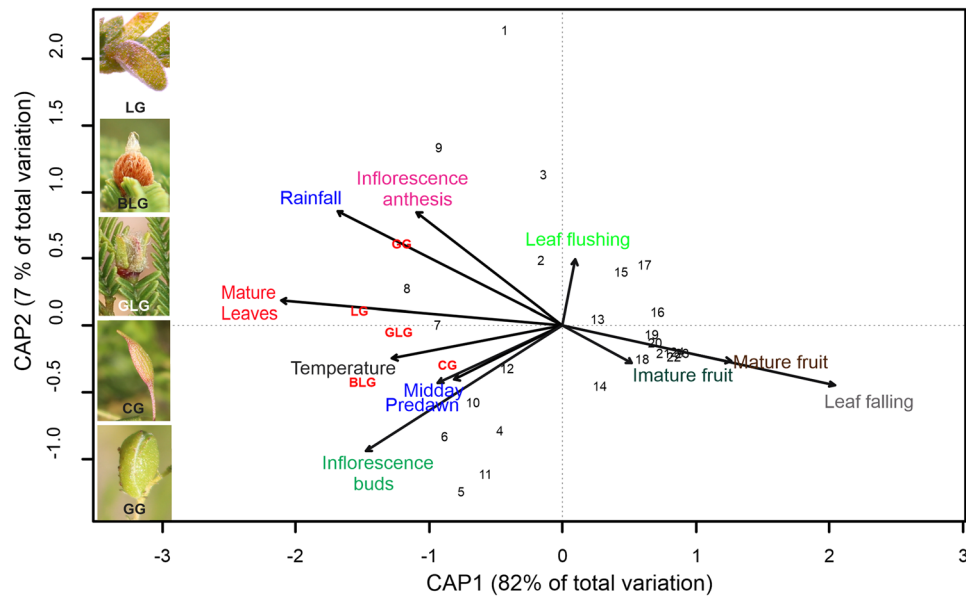


Fig. 7 Canonical analysis of principal coordinates (CAP) of the five leaf *Lopesia* galls (Diptera-Cecidomyiidae) on *Mimosa gemmulata* Barneby (Fabaceae). Vectors represent explanatory variables derived from host physiology: water potential at predawn (blue) and midday (blue); from host phenology: immature fruit (dark green), inflorescence anthesis (pink), inflorescence buds (light green), leaf falling (gray), leaf flushing (fluorescent green), mature leaves (red), mature

fruit (brown), and from climatic factors: temperature (black) and rainfall (blue). Numbers represent each data collected from November 2017 (1) to October 2018 (24). Clavate gall (CG). Brown lanceolate bivalve-shaped gall (BLG). Globoid bivalve-shaped gall (GG). Green lanceolate bivalve-shaped gall (GLG). Lanceolate bivalve-shaped gall (LG)

Temporal strategies of multivoltine galling insects

The success of galling insects depends on the selection of the host plant, the most vigorous organ (quality of resources), and the number of oviposition sites (abundance of resources) available for their development (Höglund 2014; Oliveira et al. 2016). In addition, the parasitoids are the main causes of the death of gall-inducing insects, and can affect the life cycle and abundance of galls on their host plants (Rezende et al. 2019), as is true for *Eupelmus* sp. and *Torymus* sp., parasitoids of *Lopesia* larvae in galls on *M. gemmulata*. The abundance of gall inductions in the rainy season revealed the performance of the five galling *Lopesia* spp. in synchronizing with the best quality of resources and water availability in *M. gemmulata*. Our results suggested that, despite the non-synchronism among the multivoltine gall life cycles and the host plant over the year, the abundance of gall inductions followed the dry and rainy seasonal of the neotropical savanna climate imposed to the phenology of *M. gemmulata*. Herbivores that share host plants sometimes use leaves at different ages (Oliveira and Isaias 2009; Condon et al. 2014; Nakadai et al. 2018) or different microsites on the same leaves (Oliveira et al. 2013). The nine leaf galls on *Copaifera langsdorffii*, for example, are induced by Cecidomyiidae species on distinct microsites of young or mature leaves,

such as leaf bud, petiole, lamina, and midrib (Oliveira and Isaias 2009; Oliveira et al. 2013; Carneiro et al. 2017). This is a spatial–temporal strategy for the co-occurrence of the galling insects, and the avoidance of the overlapping in the use of resources. Differently, the five *Lopesia* spp. associated with *M. gemmulata* had temporal strategies to the induction of the five leaf-gall morphotypes, and shared the same microsite of induction, i.e., the pinna-rachis. The multivoltine galling *Lopesia* spp. emerged and induced their galls in distinct temporal scales in the pinna-rachis, as evidenced by the overlapping dynamics of the induction phases.

The high overlapping of the induction between the most abundant gall morphotypes, the LG, and the BLG, were explained by the temporal adjustments with the leaf flushing. The species of *Lopesia* associated with the LG had the strategy that better adjusted to the availability of leaf flushing, evidenced by the short life cycles and six gall generations throughout the year. The induction of the BLG had the highest overlapping with the leaf flushing peaks, and consequently the highest chance of finding available microsites of induction. For the inducers of the GLG, the CG, and the GG, the overlapping is not completely clear. We believed that the gall induction in different temporal scales was an adaptive strategy to avoid the overlapping of inductions in the pinna-rachis of *M. gemmulata*. These strategies of synchronism with seasonal availability of resources during the

leaf flushing of *M. gemmulata* promoted the temporal partitioning of resources and the success of the multivoltine life cycles of the galling *Lopesia* spp.

Seasonal abundance of insect galls and climatic factors, water potential, and plant phenology

The presence and abundance of each *Lopesia* gall morphotype were related to the phenological behavior of the host *M. gemmulata*, which was regulated by the seasonal climate of the neotropical Savanna. We could distinguish seasonal patterns of gall abundance in a year-time, which resembled a wave pattern with the abundance rarely decreasing to zero in the dry season, as proposed for free-living insects (Wolda 1988; Kishimoto-Yamada and Itioka 2015). We assumed that this pattern was true for the galling insects associated with *M. gemmulata*. In the neotropical savanna climate, the rainfall is one of the environmental factors that most influences the seasonal dynamics in the populations of the tropical free-living insects (Kishimoto-Yamada and Itioka 2015), and influence the abundance of the galling Cecidomyiidae on *M. gemmulata*, as well. The high rainfall values increased the amount of water available in the soil, which led to better water conditions for *M. gemmulata*, as evidenced by the values of water potential in many other plants (Franco et al. 2005; Garcia et al. 2017). As a response to the excellent water status, the highest intensity of leaf flushing and mature leaves in *M. gemmulata* favored the total abundance of galls. The pattern of abundance of galls on *M. gemmulata* differed from the pattern on the super-host *Copaifera langsdorffii* (Oliveira et al. 2013). For *C. langsdorffii*, the hygrothermal stress defined the pattern of gall richness (Fernandes and Price 1988) during the dry season, while the abundance of the nine gall morphotypes of Cecidomyiidae were distributed by seasonal syndromes during the rainy and the dry season. Similarly to *M. gemmulata*, *C. langsdorffii* is a semi-deciduous host plant, but with the peak of leaf flushing at the end of the dry season. The galls on *C. langsdorffii* could be induced on young or mature leaves, while on *M. gemmulata* the leaf flushing was continuous, but the induction occurred only on young leaves. These phenological patterns evidenced that the water availability, which the host plants were exposed to, directly influenced gall abundance and richness in each system.

The specific abundance of the five *Lopesia* leaf gall morphotypes in the rainy season on *M. gemmulata* could be explained by the rainfall, water potential, temperature and mature leaves, as evidenced by the canonical analysis of principal coordinates. The GG, and the CG were more associated with the rainfall, and water potential. These were the two largest leaf galls on *M. gemmulata*, so they probably

required large quantities of water for their cellular developmental and physiological processes (Tyree and Jarvis 1982; Gall et al. 2015). The water stress in the dry season seemed to be a limiting factor for the development of the GG, and could result in the interruption of the gall life cycle. The temperature was more associated with the abundance of the BLG and the GLG. In the BLG, the redifferentiation and hypertrophy of the non-glandular trichomes conferred protection against natural enemies, as well as against unfavorable environmental factors, such as temperature (Stone and Schönrogge 2003; Costa et al. 2018; Ferreira et al. 2019). Additionally, the trichomes could be related to the maintenance of an internal stable microclimate for the development of the Cecidomyiidae larvae (Dias et al. 2013; Carneiro et al. 2017; Costa et al. 2018), which could also occur due to the non-glandular trichomes of the GLG. The abundance of the LG was more influenced by the occurrence of mature leaves. As the LG had more generations throughout the year, its associated Cecidomyiidae adjusted better to the higher available photoassimilates of mature leaves, as proposed by Castro et al. (2013), Carneiro et al. (2014), Oliveira et al. (2017), and Zorić et al. (2019) for other gall systems. The increase on the production of photoassimilates due to the maximum intensity of mature leaves, and the abiotic variables in the rainy season were responsible for modulating the flowering in *M. gemmulata*. This result evidenced that the flowering phase did not affect the life cycles of the five leaf *Lopesia* gall morphotypes, and that the development of the galls and the flowering phase shared temporal photoassimilated resources.

For the *M. gemmulata-Lopesia* systems, leaf falling, and low water potential were direct strategies for reducing future losses to the nutrient sinks, and the investment in fruit development. These phenological responses were indirect strategies to the potential increasing in the mortality risk imposed to the populations of the galling Cecidomyiidae, and the low gall abundance (Williams and Whitham 1986). We believe that the abundance of the populations of the five galling *Lopesia* spp. were adjusted to the phenology of *M. gemmulata*, and to the seasonal water availability of the Neotropical climate.

Conclusions

As expected, water availability both in the environment and inside plant body was determinant for plant phenology and consequently for the gall life cycles, and for the patterns of gall abundance. The continuous leaf flushing of *M. gemmulata* favored the asynchrony among the *Lopesia* gall life cycles. This asynchronism indicated a temporal strategy for the multivoltine galling *Lopesia* spp. sharing the pinna-rachis as the microsite for their gall establishment.

The univoltine Lepidoptera gall cycle seemed to benefit from the peaks of mature leaves in *M. gemmulata* and the high production of photoassimilates drained to the stem gall. Altogether, current results evidenced peculiar phenological dynamics within a super-host plant toward guaranteeing favorable microsites for the success of their associated galling herbivores.

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Declarations

Conflict of interest The authors declare no conflict of interest.

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