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From leaves to inflorescences: Gall induction of *Iatrophobia brasiliensis* Rübsaamen, 1915 on inflorescences of *Manihot caerulescens* Pohl (Euphorbiaceae) during the dry season

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A B S T R A C T

Gall-inducing insects are highly specialized herbivores as they have the ability to control and redirect the development of host plants to obtain food and shelter. The distribution of galls on plants can be influenced by seasonality and phenological events, which determines the reproductive success of these insects. The species *Manihot caerulescens* Pohl (Euphorbiaceae) has a great diversity of gall-inducing insects in the Cerrado of Western Bahia. Our study aimed to (1) study the fauna associated with *M. caerulescens* Pohl (Euphorbiaceae) and (2) evaluate the phenological events of this host plant species. We performed gall collections between July 2018 and June 2020 and monitored 30 individuals of the host species to study the phenology in the Serra da Bandeira, Bahia, Brazil. The emerged insects in the laboratory were mounted on permanent slides and identified. We found galls on the stems, leaves and inflorescences. Stem galls were induced by lepidopterans (Alucitidae), and leaf and inflorescence galls by *Iatrophobia brasiliensis* Rübsaamen, 1915 (Cecidomyiidae). Further, we showed that *I. brasiliensis* preferentially induced galls on the leaves, however during the dry season, galls were induced on the inflorescences. Although the induction of galls on the leaves by *I. brasiliensis* has already been reported in the literature, here for the first time we record the presence of galls on the inflorescences induced by the same gall-inducing species. Our study constitutes an important contribution towards the knowledge of the insect-plant interaction between *M. caerulescens* and *I. brasiliensis* in the Cerrado of Bahia.

Introduction

The distribution of herbivorous insects in tropical environments is mainly influenced by host plant diversity (Kuchenbecker and Fagundes, 2018; Araújo et al., 2019;). Many endophagous insects use host plants for feeding, nesting and development, as is the case with gall-inducing insects (Cornell, 1989; Araújo et al., 2019;). Gall-inducing insects are able to control and redirect host plants to their benefit (Coelho et al., 2017), and are therefore considered the most sophisticated herbivores in nature. These insects have high specificity with the plant and host organ for oviposition (Carneiro et al., 2009a; Guedes et al., 2018; Araújo et al., 2019; Fagundes et al., 2019), however, when a given gall-inducing insect interacts with more than one plant species, they are usually phylogenetically related (Santos-Silva and Araujo, 2020).

Insect galls are developed from tissue hyperplasia and cell hypertrophy (Isaias et al., 2013; Martini et al., 2019) due to abnormal differentiation in mechanical and chemical response of inducers, resulting in characteristic growth that harbor gall-inducing insects (Santos-Silva and Araujo, 2020). The plant tissues form a capsule that totally or partially shelters the gall-inducing insect (Araújo et al., 2019), offering food, protection against natural enemies (Coelho et al., 2017) and protection (Stone and Schönrogge, 2003).

Many factors can influence the distribution of galls on host plants, including the seasonality of the rainfall that can change the availability of water and nutrients in the soil, which affects plant development (Oliveira and Scareli-Santos, 2018; Menezes et al., 2023). At the beginning of the rainy season, most plants emit new leaves and branches, which increases the availability of food resources, favoring the development and survival of gall-inducing insects (Pinheiro et al., 2002; Araújo, 2013). Thus, it can be noted that the behavior of the plant is closely connected to abiotic factors, which drive phenological events (Novaes et al., 2020).

In addition to seasonality, the synchrony or asynchrony of phenological events also determines the reproductive success of gallers (Yukawa, 2000). The timing of phenological events, such as budding, flowering and fruiting in plant species, may vary in plant species (Fagundes et al., 2018).

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These changes in ecological variation include differences in temperature, photoperiod, moisture and soil quality (Campos et al., 2010). Plant phenology can reduce herbivore actions by using the host's satiation mechanism or by producing resource parts that vary over time (Fagundes et al., 2018). In contrast, herbivores try to synchronize their life cycle with the appearance of target organs in the plant to ensure greater offspring performance (Thompson and Gilbert, 2014).

Iatrophobia Rübsaamen, 1916 (Cecidomyiidae) is a monotypic genus and considered oligophagous. Studies have shown that many species of the genus *Manihot* Mill. (Euphorbiaceae) have galls induced by *Iatrophobia brasiliensis* Rübsaamen, 1915. Carneiro et al. (2009a) compiled biological and taxonomic data of 196 species of cecidomyids in 128 plant species in Brazil, among them, the induction of galls by *I. brasiliensis* on *Manihot dichotoma* Ule (Euphorbiaceae), *Manihot palmata* Müll.Arg. (Euphorbiaceae), *Manihot tripartita* (Spreng.) Müll. Arg. (Euphorbiaceae) and *Manihot esculenta* Crantz (Euphorbiaceae).

Gall-inducing insects deal with the mechanical and chemical defenses of plants (Ramos et al., 2019). Thus, gallers tend to be highly specialized in their host plants, due to the high degree of intimacy of gall-inducing insects and their interactions with the host (Carneiro et al., 2009a; Araújo et al., 2019;). Generally, each insect species has a unique gall morphology (Price, 2005). The gall morphotype, therefore, can be considered as part of the inducer's extended phenotype (Bourg and Hanson, 2014).

The selection of a particular plant by a gall-inducing insect is not a matter of chance, given that the insect encounters several plant taxa in a natural and heterogeneous environment. However, gall-inducing insects preferentially feed on plant organs, or specific plant parts. Thus, phenology and plant quality are essential factors in plant selection (Miller and Raman, 2019). Furthermore, pregnant females play a key role in site selection for oviposition (Raman, 1991; Miller and Raman, 2019).

Here, to shed light on different ecological aspects related to insect-plant interactions, we (1) study the fauna associated with *Manihot caerulescens* Pohl (Euphorbiaceae) and (2) evaluate the phenological events of this host plant species.

Material and methods

Study area

The study was carried out in an area of Cerrado stricto sensu located in Serra da Bandeira in the municipality of Barreiras-BA (12°10'38.04"S, 44°99'59.37"W). The Cerrado biome is characterized by a seasonal climate, with two well-defined seasons, a rainy one (October to March) and a dry one (April to September). The average annual rainfall in this biome is 1,500mm and temperatures are generally mild throughout the year, varying between a minimum of 20.3º and a maximum of 31.5º C (Nascimento and Novais, 2020).

Insect galls collection

We sampled a total of 24 collections between the months of July 2018 and June 2020 to study the reproductive and vegetative phenology. In the field, 30 individuals of the species *M. caerulescens* were randomly selected and inspected monthly. All plant organs along the trail were analyzed and photographed, and the galls characterized. For the characterization and analysis of the galls, collections were carried out between the months of May 2018 and February 2019, five leaves of each host plant were selected, totaling 1,500 leaves, and also 1 inflorescence per plant, totaling 90 inflorescences. The collected plant organs were stored in plastic containers, identified and taken to the Entomology Laboratory of the Federal University of Western Bahia (UFOB).

Part of the galls were dissected using tweezers and analyzed under a stereomicroscope to identify the associated fauna (Lima and Calado, 2018). Larvae and pupae were preserved in 70% alcohol and placed in identified micro tubes. The remaining galls were placed in plastic containers, covered with a fine screen and lined with moistened filter paper to obtain the adult phase, being examined daily until the possible emergence of the adults. The cecidomyids that emerged from the plastic containers were mounted on slides and identified using the keys (Gagné, 1994). Inducer mosquitoes and associated fauna were deposited in the collection of the UFOB Entomology Laboratory. Inquilines were identified following Luz and Mendonça Júnior (2019). The identification of the host plant was carried out using an optical microscope, consulting the original description of the species and comparing with specimens from the Herbarium of the Federal University of Western Bahia (UFOB).

Host plant phenology

The phenological events related to *M. caerulescens* were observed and recorded in the field, using notebooks and a digital camera. The same host plants used to characterize the galls and associated fauna were monitored for studies of phenological events. The observed vegetative and reproductive phenophases were: flowering, when the flowers were open; fructification, when the fruits were present or not; budding, which is the appearance of leaf shoots to the expansion of new leaves and leaf fall (Morellato et al., 1989). The presence of mature leaves was also assessed.

Results

Gall characterization and associated fauna

We found galls on the stems (Fig. 1a), leaves (Fig. 1b) and inflorescences (Fig. 1c-1d) of *M. caerulescens*. Stem galls were induced by lepidopterans of the Alucitidae family. Leaf galls and inflorescences were induced by *I. brasiliensis* belonging to the Cecidomyiidae family. Galls induced by *I. brasiliensis* had a cylindrical shape, absence of trichomes and variable color according to the senescence stage. The galls were green in the early stages, lilac in the mature stage and brown when senescent. Insect galls have been found to traverse the leaf blade and perianth, expanding from the adaxial to the abaxial surface. Internally, the galls presented only one larval chamber, with one or several larvae of the inducing insect per locule.

Additionally, we noticed other invertebrates associated with the insect galls. The inducers were represented by dipterans and lepidopterans. The parasitoids found belonged to the orders Hymenoptera, while the successors were represented by the orders Collembola¸ Acarina, Coleoptera, Araneae, Hemiptera and Thysanoptera. As for the occurrence of galls on plant organs, the number of galls per organ was variable, with a minimum of 1 (isolated) and a maximum of 20 galls occurring grouped on a single leaf. With regard to galls induced in reproductive structures, we collected 365 flower buds, of which 127 (34.79%) had galls. The presence of gall-inducing insects was observed in buds of different sizes and a variable number of galls per bud, with a minimum of 1 and a maximum of 8.

Figure 1 Galls induced by *I. brasiliensis* on *M. caerulescens* (a) galls on the stem; (b) galls on the leaves and (c-d) galls on the inflorescences found in the Serra da Bandeira, Barreiras, Bahia, Brazil.

Phenological characterization of *M. caerulescens* and gall occurrence

Regarding the vegetative and reproductive phenological events in *M. caerulescens*, we observed that the presence of leaves was constant in the two years of sampling. Leaf senescence began in May, coinciding with the beginning of the dry season. The percentage of individuals with leaves, buds and fruits was higher in the rainy season in both years, while the flowering period was represented by the months of July to November, with higher averages during the dry season (Fig. 1). Further, we noted that the highest percentage of individuals hosting galls was recorded from December 2019 to February 2020, comprising the rainy season in the Cerrado. Here, we also highlight that in the months of greatest leaf senescence (dry season), *I. brasiliensis* induced galls on the inflorescences, an event for the first time reported for this species of cecidomyid.

Discussion

Our findings show that *I. brasiliensis* primarily induce galls on the leaves, however we noticed that during the months with greater leaf senescence of *M. caerulescens* (dry season), galls were induced on the inflorescences, a pattern never reported in the literature. According to Mani (1964), nearly 70% of Neotropical galls have preference for leaves, which is similar to other studies, dealing with *Iatrophobia* galls (Carneiro et al., 2009b; Saito and Urso-Guimarães, 2012; Scareli-Santos et al., 2018). Here, the stem-inducing insects belonged to the order Lepidoptera (Alucitidae), a result also found by Brito et al. (2018) and Maia (2006).

Insect galls can occur on any host plant organ, from roots to reproductive structures, but they are more common on aerial structures of host plants, especially on the leaves (Santos and Ribeiro, 2016; Soares et al., 2021). Scareli-Santos et al. (2018) noted that this may be related to the fact that leaves occupy the same environment as most insects and also because it is an organ that is more exposed when compared to others, in addition to presenting high morphological plasticity and its important role for photosynthesis (Mani, 1964; Maia, 2013b; Santana et al., 2020).

There are no records of studies towards the induction of galls by *Iatrophobia* on the inflorescences, which generates a high specificity for *M. caerulescens* in situations where responsive tissues are available. Studies on alternative plant organ inductions were carried out by Oliveira and Isaias (2009), where gall-inducing insects induced galls on young and mature leaves. Campos et al. (2010) also observed on *Copaifera langsdorffi* Desf. (Fabaceae) that the inducers laid eggs more frequently on young leaves, however these insects also established themselves on mature leaves. Further, Guedes et al. (2018) observed on *Calophya rubra* Blanchard, 1852 that galls are generally induced on the leaves, however when the diapause period takes place, induction occurs on flowers, which implies a suitable period of availability of plant resources. Due to the short duration of the adult stage of gall-inducing insects, females that do not locate suitable structures probably deposit their eggs in non-preferred locations (Campos et al., 2010; Weis et al., 1988). Studying *Rollinia laurifolia* Schltdl. (Annonaceae), Gonçalves et al. (2009) observed that the crawlers leave the galls even before the leaves fall and go to the stems, where they induce a second gall morphotype and enter dormancy throughout the dry season. Therefore, we hypothesize that galls induced by *Iatrophobia* on the inflorescences during leaf senescence might be related to the search for food resources as well as suitable oviposition sites for gall induction, which seems to be a successful survival strategy for the completion of its life cycle.

In addition to gall-inducing insects, we observed a diversity of insect fauna associated with galls. These arthropods vary in their eating habits and can be classified as: parasitoids, predators, tenants and successors (Maia, 2001). The arthropod fauna associated with *M. caerulescens* galls belonged to eight orders: Acarina, Araneae, Coleoptera, Collembola, Diptera, Hemiptera, Hymenoptera and Thysanoptera. Parasitoids have been considered the most frequent natural enemies of gall-inducing insects in different Brazilian formations (Lima and Calado, 2018; Santos et al., 2018; Soares et al., 2021) and were induced by Hymenoptera, considered the order with the highest number of natural enemies of gall inducers (Lima and Calado, 2018; Maia, 2013b). The tenants were represented by cecidomyids, which was observed by Urso-Guimarães et al. (2017), who recorded the tenant *Camptoneuromyia* Felt, 1908 (Cecidomyiidae) in galls of *M. tripartita* in the Cerrado of Mato Grosso do Sul. The successor fauna was composed by Collembola, Acarina, Coleoptera, Araneae, Hemiptera and Thysanoptera – represented by the organisms that occupy the gall after being abandoned by the inducers (Maia, 2013a; Mani, 1964).

Regarding the vegetative phenology of *M. caerulescens*, the senescence phenophase began in the dry season, with few leaves falling over the course of the year (Allem, 2001). According to Novaes et al. (2020), one of the factors related to leaf fall in the dry season is the lower availability of water, presence of wind and increased temperature. In the absence of rain and in the presence of heat and wind, caducity can help the plant to reserve water; otherwise, the release of water vapor into the atmosphere through evapotranspiration may compromise plant vital activities during the dry season (Tomlinson et al., 2013).

The budding phenophase was more frequent in the rainy season (Allem, 2001). According to Araújo and Santos (2009), leaf sprouting provides greater availability of resources, thus favoring the colonization of gall-inducing insects and increasing the abundance of galls. Fully developed leaves were present in the dry and rainy seasons, but less so at the end of the dry season, when leaf senescence and leaf budding occur. Novaes et al. (2020) observed this pattern in the Cerrado for *Aspidosperma tomentosum* Mart. & Zucc. (Apocynaceae), *Dalbergia miscolobium* Benth. (Fabaceae) and *Peixotoa tomentosa* A.Juss. (Malpighiaceae). According to Yukawa (2000), the gall-inducing insects that attack young leaves are more sensitive to the phenological variation of the plant when compared to those that feed on mature leaves, thus, the time and place of oviposition are crucial for the well-developed development of galls (Fagundes et al., 2018). The fruiting phenophase extended from the end of the dry season to the rainy season, comprising a long period of time. This fruit adaptation probably occurs to increase the chances of seeds ripening and thus dispersing in a period when wind conditions are favorable to dispersal, which can increase reproductive success (Novaes et al., 2020). Flowering of *M. caerulescens* was more frequent in the dry season. Flowering in the dry season can be an adaptation to provide floral resources at a time when this product is scarce, increasing the chances of attracting pollinators and herbivorous insects (Novaes et al., 2020). Thus, flowering in the dry season can be advantageous, as it reduces florivory and increases pollinator activity (Silva et al., 2017).

Gall infestation on *M. caerulescens* occurred in both seasons, with the highest occurrence concentrated in the rainy season for both years. Scareli-Santos et al. (2018) described leaf gall infestation on *Manihot esculenta* Crantz (Euphorbiaceae), and evaluated the impacts on plant architecture and productivity in a cultivated area in the state of Tocantins. They observed that gall infestation was significantly higher in the rainy season. Similar results were also obtained by Araújo and Santos (2009) who studied the abundance of galls on *Piper arboreum* Aubl. (Piperaceae) and found that the highest infestation occurred in the rainy season. One of the factors that could justify this pattern is that rain prevents the vegetation from drying out and becoming deciduous, making the environment more favorable to the development and survival of herbivorous insects, as well as favoring the growth of young leaves, which allows for a greater occurrence of oviposition (Araújo and Santos, 2009; Oliveira and Scareli-Santos, 2018).

Despite several studies corroborating this hypothesis, this pattern is not always observed. Luz et al. (2012) recorded higher rates of galls in the dry season, in xeric environments (Cerrado and Dry Forest), mainly induced by insects of the order Diptera (Cecidomyiidae). Santos et al. (2018) found that the morphotypes of the three species of the genus *Copaifera* L. (Fabaceae) were more abundant in the dry season. Oliveira and Scareli-Santos (2018) observed gall infestation on *Ouratea spectabilis* (Mart.) Engl. (Ochnaceae), and showed that the leaves had a higher infestation in the dry season. According to Araújo and Santos (2009) and Oliveira and Scareli-Santos (2018), this behavior may be related to water scarcity, as they provide physiological and hormonal changes in the plant, thus altering metabolism and development and consequently makes them more susceptible to herbivory.

The richness and abundance of free-living herbivorous insects are influenced by temperature, humidity and precipitation (Araújo and Santos, 2009). According to the hygrothermal stress hypothesis (Fernandes and Price, 1988), gall-inducing insects are more abundant in xeric environments (high temperatures, low humidity and nutrient-poor soils) than in mesic environments (low temperatures, high humidity and nutrient-rich soils). Therefore, the xeric environments that harbor plant species from the Cerrado have large concentrations of defense compounds such as tannin, which provide gall-inducing defenses against predators and pathogens (Fernandes and Price, 1988; Luz et al., 2012; Coelho et al., 2017).

In conclusion, although short-term gall inventories help us understand and estimate the diversity of gall-inducing insects, long-term assessments similar to this one allows us to better understand ecological patterns of gall inducers. Throughout our two-year evaluation, we clearly noticed that *I. brasiliensis* induced galls preferentially on the leaves, however, during the months of greatest senescence peaks in the dry season, galls were induced on the inflorescences. This pattern is reported for the first time here in our study, and reinforces the need for long-term and specific assessments of interactions between host plants and gall-inducing inducers.

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Conflicts of interest

The authors declare no conflicts of interest.

Author contribution statement

ATBS, DCC conceived the study; ATBS, RRM, DCC, VPL analyzed the data and ATBS led the writing with contributions from all the authors. All authors approved the final version of this paper.

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