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Leaf herbivory in *Miconia albicans* (Melastomataceae): an evaluation of leaf position and age

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Abstract: Leaf herbivory in *Miconia albicans* (Melastomataceae): an evaluation of leaf position and age – Abstract: Herbivory represents a critical interaction between insects and plants, involving physical defenses like trichomes that enhance plant resistance to herbivorous attacks, while galls—plant tumors—can drain nutrients from healthy tissues. This study aimed to assess foliar herbivory rates and analyze gall incidence in *Miconia albicans* in a cerrado stricto sensu area near Uberlândia, Minas Gerais, Brazil. From December 2013 to March 2014, herbivory rates were documented biweekly using a digital camera, with subsequent analysis performed using ImageJ software. A Wilcoxon signed-rank test was used to determine significant differences in herbivory rates between young and old leaves, while a GLMM test with beta error distribution followed by a Wald chi-square test examined variations in herbivory rates between high and low leaves. Fifteen plants were selected, marking one young and one old leaf, alongside one high and one low leaf. The incidence of galls was assessed across 50 randomly chosen plants, and the average number of galls per leaf was quantified in another 20 plants. The difference between galled and non-galled branches was analyzed using the Mann-Whitney test. Findings indicated no significant difference in herbivory rates between young and old leaves; however, higher leaves exhibited reduced herbivory rates compared to those in the lower strata, suggesting that leaf position significantly influences herbivory. Galls averaged 19 ± 9 per leaf, predominantly on older leaves. The shaded microclimates of lower strata likely contribute to increased herbivorous insect abundance, underscoring the impact of leaf position on herbivory rates.

Key words: phytophagy, galls, plant-insect interactions, cerrado ecosystem, leaf age, trichomes

Introduction

Herbivory is one of the main forms of interaction between insects and plants. In this relationship, insects feed on several plant structures, the leaf being one of the most attacked parts (Coley & Barone, 1996). Given such strong selective pressure imposed by insects, plants have developed different strategies of defense against herbivory, which may be chemical, biotic, and/or physical (mechanical) (Ruttan & Lortie, 2014; Fürstenberg-Hägg et al., 2013). Herbivory also plays a key role in shaping vegetation structure, particularly in savanna ecosystems, where herbivores significantly reduce the biomass of grasses by 57% and of trees by 30.6% (Staver et al., 2021). The magnitude of this reduction is directly related to herbivore abundance, with more grazing herbivores leading to greater reductions in grass biomass, and more browsing herbivores causing larger decreases in tree biomass (Staver et al., 2021). Additionally, recent studies suggest that climate change, including rising temperatures and altered stoichiometric balances in plants, may intensify herbivory (Swain et al., 2024), potentially leading to more pronounced vegetation changes in contemporary ecosystems. Long-term studies have also shown that insect herbivores can significantly influence plant populations and community dynamics by limiting plant population growth and altering competitive abilities, though the full extent of these effects often takes years to manifest, while the relative importance of factors such as herbivore specialization and plant productivity remains unclear (Agrawal & Maron, 2022). Such enduring impacts underscore the importance of understanding herbivory not only in short-term interactions but also in the broader context of plant community structure and ecosystem dynamics.

Chemical defenses act by reducing the damage and palatability of plant parts (Corrêa et al., 2008; Ruttan & Lortie, 2014), such as through the presence of toxic compounds including phenols, tannins, and alkaloids. These are present at almost twice the concentration in young leaves than in old leaves (Coley & Aide, 1991; Marquis, 2012). According to the optimal defense theory, plants allocate defensive compounds in a way that maximizes their fitness, concentrating defenses in tissues most critical for survival and reproduction (Gershenzon & Ullah, 2022; Hunziker et al., 2021). For instance, high concentrations of glucosinolates in younger leaves of *Arabidopsis thaliana* protect these vital tissues by guiding herbivores toward older, less valuable leaves (Hunziker et al., 2021).

Biotic defenses are those made by animals to protect the plant in a mutualistic relationship, such as ants (Fagundes et al., 2017; Rico-Gray & Oliveira, 2007; Del-Claro & Torezan-Silingardi, 2012) and arachnids (Nahas et al., 2016). In this way, plants offer food resources or nesting sites and receive protection against herbivore attack in return (Calixto et al., 2018). Finally, physical defenses are constituted by cuticular deposits, thickened epidermis, the abundance of crystals, trichomes or fibers in the leaves, all of which operate as a mechanical barrier against biotic and abiotic action (Bovendorp, 2009; Calixto et al., 2015; Marquis, 2012; Sousa-Lopes et al., 2019). For example, trichomes represent an excellent defense strategy as they render insect oviposition on leaves challenging (Bovendorp, 2009; Sousa-Lopes et al., 2019). Several groups of plants have a dense hairy indumentum that can protect the leaves against evapotranspiration, such as in *Verbascum Thapsus* (Woodman & Fernandes, 1991), or that can preclude the action of phytophagous insects, as in *Miconia albicans* (Paleari & Santos, 1998). In addition to these defensive characteristics, the location of the structures or the plants themselves in the environment are delimiting factors in herbivory.

On the other hand, plant growth and the production of meristematic tissues, which are often the most vulnerable phases of plants, are directly related to the attractiveness of herbivores (Marquis, 2012). Herbivory can reduce plants' competitive ability, with negative implications for growth and development (Corrêa et al., 2008; Lehndal & Ågren, 2015). Herbivory impacts plant species differently depending on their traits and the diversity of the surrounding plant community. For instance, forbs experience greater damage from herbivores than grasses, with factors such as leaf dry matter content and biomass influencing herbivore preference (Bröcher et al., 2023). The loss of herbivores can also reduce plant diversity, as increased plant cover diminishes light availability in the understory, driving competitive exclusion (Eskelinen et al., 2022). Conversely, higher plant diversity has been shown to reduce herbivore impacts, as diverse plant communities enhance predator populations and reduce herbivore food quality, ultimately lowering herbivory levels (Barnes et al., 2020). Moreover, herbivory patterns differ significantly between island and mainland ecosystems, where insular plants may experience higher mammalian herbivory pressure due to the introduction of exotic herbivores, potentially driving an increase in physical defenses, while chemical defenses remain unaffected (Moreira et al., 2020). These findings highlight the complex dynamics between herbivory, plant defenses, and environmental context, emphasizing the importance of location and diversity in shaping plant-herbivore interactions.

Highly specialized herbivores such as galling insects can stimulate the onset of plant tumors, known as galls. These changes are caused by pathogens or parasites that develop within certain plant structures, promoting anomalous growth in cell volume (cell hypertrophy) and/or the number of cells (hyperplasia) (Costa et al., 2018; Raman et al., 2005). The negative effects of galling insects on the growth and fitness of their host plants are evident, as the galls act as physiological drains of nutrients, which are displaced from the healthy tissues to the galled tissue (Santos et al., 2012), affecting plants' abilities to reproduce and flower (Fernandes & Santos, 2014). In summary, the evolutionary relationships that exist between herbivores and the plants they attack have resulted in numerous adaptations, such as specific defense mechanisms in the latter, and responsive evolutions in the former (Coley & Barone, 1996; Marquis, 2012).

Several studies of herbivory exist regarding the genus *Miconia* (e.g. Rebouças et al., 2002; Souza et al., 2002), but few of *M. albicans* (e.g. Oki et al., 2002; Paleari & Santos, 1998). Therefore, the main objective of this study is to analyze whether there is variation in the foliar herbivory rate of *M. albicans* considering the age and position of the plant's leaves, and to evaluate gall indexes in the leaves and branches. The main hypotheses guiding the work are that (i) the young leaves will present lower rates of herbivory due to the presence of the hairy indumentum, which acts as physical defense; (ii) leaves located in the lower extracts will have higher rates of herbivory due to the presence of more favorable microclimates (greater humidity and shading) for herbivorous insects; and (iii) branches will be less affected by the galls than the leaves.

Study area

The field study was developed in the Reserva Ecológica do Clube de Caça e Pesca Itororó de Uberlândia, Minas Gerais, Brazil (18º59'S, 48º18'W), from December 2013 to March 2014. The predominant vegetation is the Cerrado, with about 400 ha, of which 230 ha are characterized by cerrado stricto sensu, a type of vegetation dominated by an open field, with numerous grasses and scrub shrubs. The area also includes the vegetation of Campo Sujo and Vereda, with patches of mesophyll forest (Marques & Del-Claro, 2010). The climate is characterized by Aw-type Köpen, with well-defined wet and dry seasons: a hot and humid season from October to March, and a cold and dry season from April to September (Vilela et al., 2017).

Materials and Methods

Study species

The plant species used was *Miconia albicans* (Sw.) Triana (Melastomataceae), which is common in tropical regions, including the Cerrado. It is a shrub that can reach up to approximately 2.5 m in height, averaging 1.30 to 2 m. Its leaves are coriaceous with the adaxial face tomentose (hairy, Fig. 1), possessing five basal veins. It has pentamer flowers (five petals), with white petals, grouping in inflorescences of panicle type. Its fruiting occurs in the rainy season (from October to March), red when young and jade green when mature (Carreira, 2004). Its dispersion is facilitated by birds, rodents, and ants, and the leaves are mainly attacked by phytophagous insects. The younger leaves differ from older counterparts in terms of the presence of a hairy indumentum (Paleari & Santos, 1998).

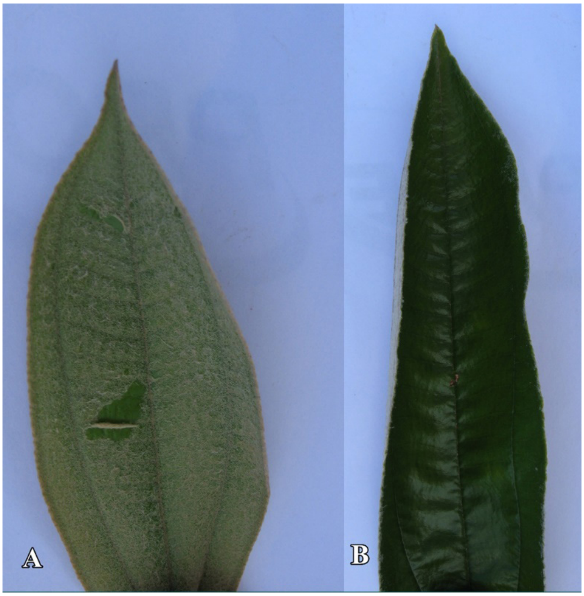


Fig. 1: Young (A) and old leaves (B) of *Miconia albicans*, showing the difference in the hairy indumentum between them.

Leaf herbivory

To analyze whether there is variation in the foliar herbivory of *M. albicans* regarding the age and location of its leaves, 15 individuals were selected, at least 4 meters apart. In each plant, both one young and one old leaf were marked. Young leaves were considered close to the apical bud and with a hairy indumentum (trichomes), and old leaves those that were distant from the apical bud and without a hairy indumentum. Were also selected one leaf located in higher parts (above 100 cm in height) and one located in the lower parts (15-50 cm in height), constituting a total of 30 leaves similar in age, shape, and size.

The loss of leaf area was calculated for all leaves. This procedure was performed during the four months of the study, always on the same leaves. The herbivory was recorded biweekly using a digital camera (Canon® PowerShot A560), through which images of the leaves were recorded. Thus, no damage was made to the plants, because it was not necessary to remove leaves. The percentage of herbivory was analyzed using ImageJ software (Image Processing and Analysis in Java). To compare the herbivory rate between young and old leaves, we used a Wilcoxon signed-ranks test. To analyze whether the herbivory rate varied between leaves located at lower and higher parts and over time, we used a GLMM test with beta error distribution using the "glmmTMB" package (Brooks et al., 2017), followed by a Wald chi-square test with the "car" package (Fox & Weisberg, 2011). The interaction between leaf location and time of collection as a fixed factor was used, and the time of nested collection in plant individuals (1 plant/collection time) was used as a random effect to control temporal measures. All tests were analyzed using R Studio software (version 3.51).

Incidence of galls

To evaluate the incidence of galls, 50 plants of *M. albicans* were randomly selected, and the presence or absence of galls was inspected in each branch of each shrub. To compare the number of branches of *M. albicans* with and without galls, the Mann-Whitney test was used, as the data did not present normality and homogeneity of variance. To quantify the average number of galls present in the leaves of *M. albicans*, 20 other plants were randomly selected and only one leaf containing the presence of gall was quantified in each plant. Fig. 2 shows some leaves and branches of *M. albicans* with high gall rate. The test was analyzed using Statistica software (version 12.0).

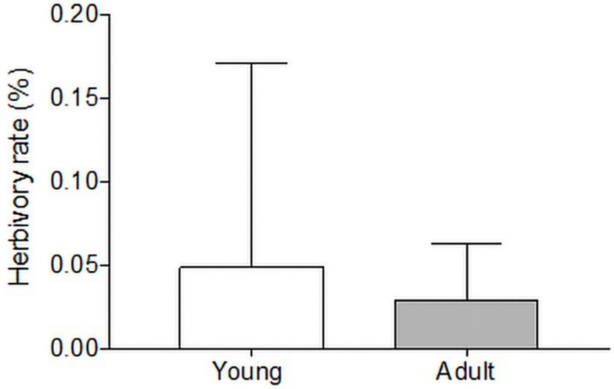
Fig. 2: Images of *Miconia albicans* (Melastomataceae) representing: A) presence of galls in branches; B) and C) detail of branches taken by galls; D) galls in leaves and branches.

Results

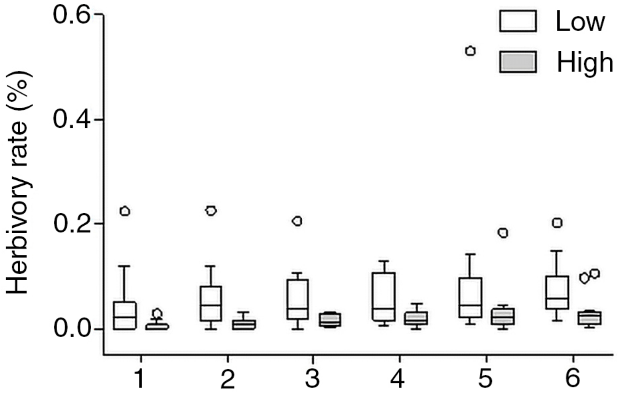
Our results showed that young and old leaves did not present significant differences in herbivory rates ($Z = 1.223$, $p = 0.239$). Young leaves had a mean herbivory rate of 0.048 ± 0.122% (mean ± SD) and old leaves of 0.028 ± 0.034% (Graph 1).

Both the height (GLMM: $\chi2 = 39.071$, $p < 0.001$) and the time (GLMM: $\chi2 = 36.160$, $p < 0.001$) presented a significant difference in the herbivory rate of the leaves (Graph 2). However, the interaction of these factors was not significant ($\chi2 = 1.130$, $p = 0.951$). Lower leaves (0.06 ± 0.07%, mean ± SD) had a higher rate of herbivory than the highest leaves (0.01 ± 0.02%, mean ± SD).

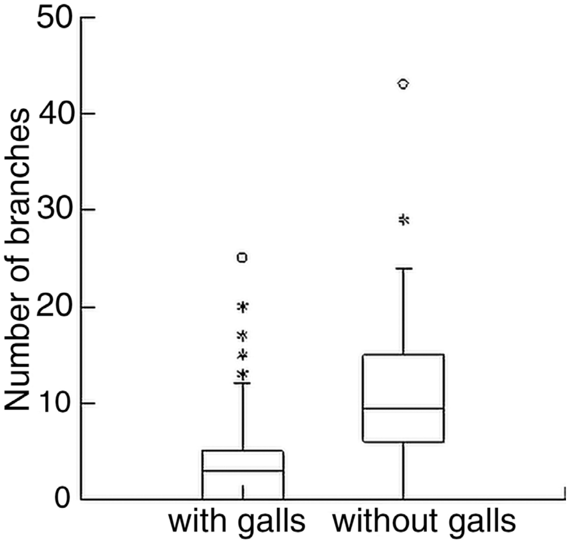
The results also demonstrated that there were fewer branches with galls than branches without galls ($U = 487.0$, $p < 0.001$, mean ± SD, Graph 3), while the average number of galls per leaf was 19 ± 9 (X ± SD).



Graph 1: Average herbivory rate between young and old leaves, demonstrating that there was no significant difference in this variable.



Graph 2: Mean herbivory rate between high and low leaves over time, showing that there was a significant difference in this variable, both in relation to height and in relation to time.



Graph 3: Galls in branches of *Miconia albicans*, demonstrating that there were more branches without galls than branches with galls.

Discussion

Leaf herbivory in *M. albicans* varies, primarily due to leaf position. Lower leaves, which are better shaded, suffered more from the action of herbivores than those exposed to the sun. However, there was no significant variation in herbivory between young and old leaves, refuting the initial hypothesis stating that young leaves would be significantly less herbivorous than older counterparts.

Our results did not corroborate the findings of Paleari and Santos (1998). These authors conducted an experiment to test whether there were differences in herbivory between young and old leaves in *Miconia albicans*, and in some young leaves the hairy indumentum was artificially removed. As a result, young leaves had lower herbivory rates, except for leaves with artificially removed hairy indumentum, which had herbivory rates like those of old leaves (without hairy indumentum). Throughout the experiment, the young leaves that were naturally losing the hairy indumentum (through the expansion and growth of the leaves) faced more attacks than the young ones. Given these results, the authors concluded that the hairy indumentum plays an important role in protecting against herbivory in the species.

Additionally, fluctuating asymmetry, which has been associated with developmental stress, may also play a role in how leaves respond to herbivory. Dodonov et al. (2022) assessed leaf fluctuating asymmetry in *Miconia albicans* and found that while there was no clear relationship between plant size and fluctuating asymmetry, larger leaves tended to show lower relative fluctuating asymmetry. This suggests that leaf developmental conditions, rather than overall plant size, influence asymmetry. These developmental stresses may affect leaf susceptibility to herbivory, particularly as fluctuating asymmetry has been linked to stress factors such as pollution and fire, both common in Cerrado ecosystems. Thus, it is possible that fluctuating asymmetry in leaves, along with the presence of the hairy indumentum, could modulate herbivory rates in *M. albicans*.

In general, plants that did not have galls were younger (less than one meter), while those with more galls were older (more than 1.5 meters), perhaps indicating the preference of gall makers for older plants. Older leaves had numerous galls, while younger leaves (with more hairy indumentum) had practically no galls, potentially indicating the higher preference of gall makers for older leaves. Both Maruyama et al. (2012) and Uesugi et al. (2016) concluded that arthropod diversity is greater in galled parts of plants, as these structures are richer in nutrients essential for the survival of these organisms and provide shelter. Maruyama et al. (2012) found that galled infructescences had a 20% higher nitrogen rate compared to non-galled ones, while Uesugi et al. (2016) emphasized the role of gall-inducing organisms as ecosystem engineers, modifying plant microhabitats to increase arthropod abundance and diversity.

Further studies on galls induced by *Ditylenchus gallaeformans* on *Miconia* species in the Brazilian Cerrado have demonstrated the complex interactions involved in gall formation and nutrient dynamics. Arriola et al. (2020) showed that galls in *Miconia* accumulate lower concentrations of aluminum (Al) compared to non-galled tissues, with Al being compartmentalized between apoplast and symplast, while phenolics act against Al toxicity. This suggests that galls not only modify plant tissues to serve as nutrient-rich sinks but also regulate harmful elements such as Al, thus creating a more suitable microenvironment for the gall-inducing organisms. In another study, Arriola et al. (2021) highlighted the indeterminate growth potential of galls induced by *D. gallaeformans* on different *Miconia* species, which ensures continuous nutrient supply and protection for the nematode colonies. These galls adapt structurally to maintain homeostasis and protect against environmental stressors, particularly in the Cerrado ecosystem. Additionally, Santos et al. (2021) demonstrated that plant ontogeny influences susceptibility to herbivore and pathogen damage, with adult *Miconia albicans* being more vulnerable to nematode gall formation, while juvenile plants were more susceptible to insect herbivores and fungal pathogens. This is consistent with the present study, which also found significantly more galls in older individuals of *Miconia albicans* compared to younger plants, emphasizing that older plants or their structures tend to have more galls than younger ones. This ontogenetic variation adds another layer of complexity to the interactions between plants, herbivores, and pathogens, further emphasizing the dynamic nature of these relationships in the Cerrado.

In another study of galls, Fernandes et al. (1988) identified their abundance in Leguminosae. Moreover, these authors argued that the leaves were the most galled structures, followed by stems and branches, consistent with the present study in which a high abundance of leaf galls was found (mean of 19.15 galls per leaf), followed by the branches (average of 4.28 galled branches). In our study, there were also more branches without galls than branches with galls, again indicating that the branches are not as significantly affected by the galls as the leaves. The leaves that had galls were almost all old, without hairy indumentum, as the young rarely presented such structures. The plants with the most galled branches were also older (higher). For this reason, the hairy indumentum may also be related to galls' protection. Young leaves and plants, as well as hairy indumentum, may also have more secondary protective substances, and gall makers may demonstrate greater preference for more mature parts.

Finally, a recent study by Xu et al. (2023) demonstrated that herbivory plays a significant role in reducing the success of vegetation restoration in degraded ecosystems, both terrestrial and aquatic. Through a global meta-analysis, which included 2,594 experimental tests from 610 articles, the authors found that herbivores in restoration areas reduced vegetation abundance by an average of 89% and suppressed plant diversity more intensely than in relatively undisturbed ecosystems. These effects were more pronounced in regions with higher temperatures and lower precipitation. Additionally, the study suggested that strategies such as temporarily excluding herbivores or reintroducing predators could significantly enhance restoration efforts, surpassing even traditional management techniques like plant competition or facilitation. This highlights the importance of herbivory control as a promising strategy for effectively restoring ecosystems.

Conclusions

Our study indicates that in *M. albicans,* the rate of herbivory is affected by the position of leaves, but not the age. The leaves in the higher strata presented a much lower herbivory rate than those in the lower strata, implying that the lower parts of the plant present a microclimate more favorable to herbivores. For herbivory between young and old leaves, the difference was not significant. The analyzed leaves showed a high gall index, while more branches were counted without galls than branches with galls in each analyzed plant, suggesting that the branches are less affected by the galls than are the leaves. Older plants and leaves were those with the highest gall indexes, indicating that young counterparts are better protected from the attack of gall makers, most likely because they have superior chemical defenses, including through hairy indumentum in the leaves. This may additionally indicate that the gall makers prefer older parts of the plants. These results highlight the importance of studies in the field of ecology, especially concerning the impacts of herbivory and gall makers, as they help to understand the dynamics of plant-herbivore interactions and their implications for the sustainability of ecosystems.

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