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Implications of the Floral Herbivory on Malpighiacea Plant Fitness: Visual Aspect of the Flower Affects the Attractiveness to Pollinators

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Abstract

The Malpighiaceae family is species-rich and is abundant in Brazil. Malpighiaceae flowers provide oil and pollen to pollinating bees and serve as food for herbivorous insects, which damage the floral structures. Although common in the Cerrado, florivory is still poorly studied. In the present study, we evaluated the effect of florivory in one of the most common genera of Malpighiaceae in the Cerrado (*Banisteriopsis*) and the impact of florivory on fruiting. The florivory rate was quantified in flowers of *B. malifolia* belonging to two morphotypes and in flowers of *B. variabilis*. Additionally, a petal-removal experiment was performed, which simulated the presence of damage in the flowers. The manipulation involved a control group with intact flowers, a group without the standard petal and a group of flowers without common petals. The florivory in the petals (floral area lost) differed between the species, and *B. malifolia* was the most damaged. The experimental manipulation revealed that intact flowers had a higher fruiting rate compared with the remaining flowers. These results reinforce the concept that florivory renders flowers less attractive to pollinating bees, which negatively affects the fruiting rate and the reproductive success of plants. We suggest that basic studies (such as the present investigation) be extended to further elucidate the effect of interactions between pollinators, plants, and herbivores on the general structure of communities.

Introduction

Interactions among organisms have occurred since the origin of life on Earth, and all species are involved in this process (Thompson, 2010). Among the relationships that occur between plants and animals, pollination is essential because it increases the adaptive value of plants in relation to the environment, provides resources to animals, and occurs in 87.5% of angiosperms (Ollerton et al., 2011). Insects, especially winged social Hymenoptera (bees and wasps), are among the main pollinators in nature (Gullan & Cranston, 2006). Conversely, herbivory is one of the most important antagonistic relationships because it harms angiosperms and reduces their fitness (Strauss et al., 1996, 1997; Price et al., 2011). Herbivores can consume photosynthetic tissues, storage organs, and reproductive structures (Romero & Vasconcellos-Neto, 2007; Del-Claro et al., 2013), thereby compromising the growth, reproduction, and survival of plants (Torezan-Silingardi, 2011). Florivory, or the consumption of floral structures, negatively affects pollination (Krupnick et al., 1999; McCall & Irwin, 2006), either by destroying the internal structures of the buds and/or by reducing the attractiveness of flowers to the pollinators. For example, flower damage recorded for *Sanicula arctopoides* causes a reduction in the number and weight of the seeds produced (Lowenberg, 1994), illustrating reproductive losses for the species. Therefore, florivory may affect the maintenance of plants in natural environments (Torezan-Silingardi, 2007, 2011).

The signaling of the production and provision of resources, by coloration, size, scent, shape, and texture (Gumbert, 2000; Miller et al., 2011), serves as a cue for floral visitors. Several studies have demonstrated that bees respond to these signals by visiting mainly the flowers that offer cues of more profitable rewards such as a greater amount of pollen,

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nectar, scent, or inflorescences that are larger, more conspicuous, or more numerous (Waser & Price, 1981; Krupnick et al., 1999; Irwin & Strauss, 2005). Similarly, these signals are attractive for other types of visitors and directly affect the reproduction of plants (Torezan-Silingardi, 2007; Alves-Silva et al., 2012).

The family Malpighiaceae is very common in the Brazilian Cerrado (Ratter et al., 1997; Giulietti et al., 2005), and the genus *Banisteriopsis*, one of the largest genera of the family, comprises approximately one half of the species that occur in this biome (Mabberley, 1997). *Banisteriopsis* flowers supply oil and pollen for pollinating bees (Anderson, 1979, 1990; Vogel, 1974, 1990; Sigrist & Sazima, 2004; Gaglianone, 2005). However, its flowers, fruit, and leaves are also sought by animals from various taxa (Torezan-Silingardi, 2011; Oki, 2005; Diniz et al., 2000; Alves-Silva et al., 2013). Therefore, the main objective of the present study was to investigate the hypothesis that florivory in *Banisteriopsis* significantly reduces the reproductive potential (i.e., fruit formation). The specific objectives were (1) to determine the proportion of damage by floral herbivory in the species *B. malifolia* and *B. variabilis* and (2) to describe the effect of florivory on the attractiveness of flowers and on the reproductive success of *B. malifolia*.

Materials and Methods

Study site

The study was performed in an area of cerrado *strictu senso* (a savanna-like vegetation that is the main physiognomy of the Cerrado biome) at the legal reserve area of the Clube de Caça e Pesca Itororó de Uberlândia (CCPIU), located at 18° 59' S and 48° 18' W, with an altitude of 863 m and a total area of 640 ha. According to the Koppen classification, the climate of the region is type AW, with two well-defined seasons: the dry season from May to September and the rainy season from October to April, with a mean annual temperature of 22°C and a mean rainfall of 1,500 mm (Bachtold et al., 2012). The vegetation in the reserve includes the following physiognomies: grassland (campo limpo), shrubland (campo sujo), cerrado *strictu senso*, woodland (cerradão), palm swamps (veredas), and small patches of mesophyllous forest (see Réu & Del-Claro, 2005, for details on the area).

Species

B. malifolia variety *malifolia* (Ness & Martius) G. Gates and *B. variabilis* B. Gates are extremely similar species (Fig. 1). Their flowers are complete and conspicuous, with a slightly zygomorphic symmetry and five fimbriated petals, the standard petal has a size and insertion angle that is different from the remaining four petals. *B. malifolia* exhibits two types of shrubs that vary in the coloration of the flowers at the moment of anthesis and in the intensity of the scent: one type has flowers with an intense pink coloration and a strong scent (B. mali IP - morphotype 1), and the other type produces light pink flowers and a mild scent (B. mali LP - morphotype 2). *B. variabilis* produces only shrubs with white flowers and no scent.

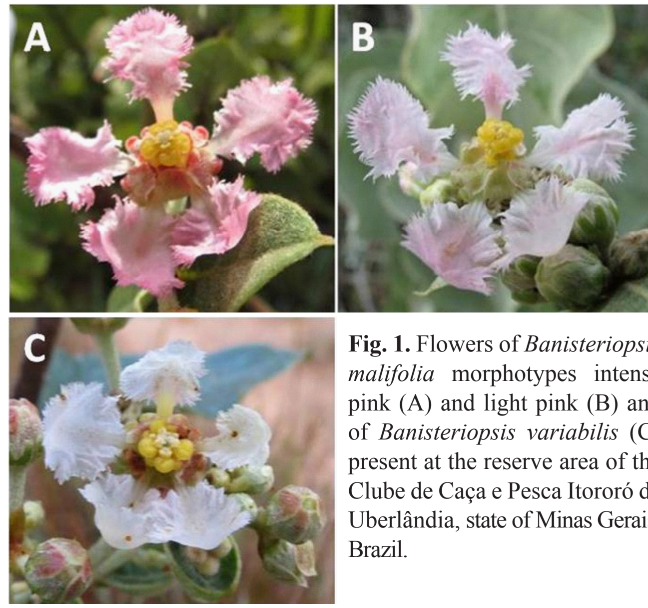

Fig. 1. Flowers of *Banisteriopsis malifolia* morphotypes intense pink (A) and light pink (B) and of *Banisteriopsis variabilis* (C) present at the reserve area of the Clube de Caça e Pesca Itororó de Uberlândia, state of Minas Gerais, Brazil.

Data collection

B. malifolia and *B. variabilis* shrubs of similar size and phenological state were monitored throughout the flowering period, particularly between April and July. For quantifying the floral herbivory, the flowers of 15 individuals of *B. malifolia* morphotype 1 (B. mali IP), *B. malifolia* morphotype 2 (B. mali LP), and *B. variabilis* were collected, photographed, and measured. In total, 45 flowers were analyzed with the Photoshop CS6 software, by measuring the total floral area and the floral area lost. For the experiment of simulated florivory, the inflorescences of 30 shrubs of *B. malifolia* (morphotype 2: light pink), divided in three groups of 10 individuals, were isolated at the pre-anthesis period and were subsequently manipulated using gloves and fine-tip tweezers. The manipulations were always performed before 07:00 to avoid the timepoint at the beginning of pollinator activity. In total, 150 flowers were manipulated (five per shrub), and each individual was submitted to one of the following treatments: (1) control, the flowers remained intact without the simulation of herbivory; (2) herbivory was simulated by removing only the standard petal, with the common petals intact; (3) herbivory was simulated by removing four common petals, with the standard petal intact.

Statistical analysis

After determining the normality of the data, a one-way analysis of variance (ANOVA) was used to evaluate whether the florivory differed between the *B. malifolia* and *B. variabilis* species and morphotypes. We also assessed whether there was variation in the fruiting rate among the different treatments of the damage-simulation experiment. The analyses were performed with the Systat 10.1 software.

Results

The flowering period occurred between the months of April and July 2012 (Fig. 2). *Banisteriopsis malifolia* was the first species to exhibit flowers (at the beginning of April), followed by *B. variabilis*, which had its first flowers recorded at the end of the same month and in the beginning of May. The flowering overlap encompassed approximately 20 days and resulted in a high number of available flowers, which attracted different groups of floral visitors.

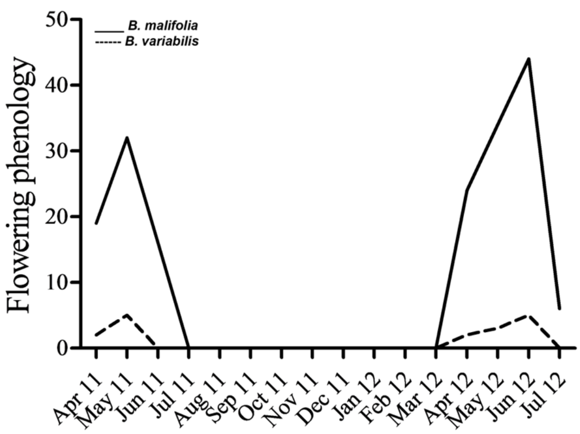

Fig. 2. Flowering phenology of the species of *Banisteriopsis variabilis* and *Banisteriopsis malifolia* from the reserve area of the Clube de Caça e Pesca Itororó de Uberlândia, state of Minas Gerais, Brazil.

The flowers began the process of anthesis between 06:15 and 10:00 in the morning, with a small delay on cloudy and rainy days. During this period, pollinators and other groups such as herbivores, predators, and parasitoids were recorded exploring the resources offered by both species. The signs of floral herbivory were easily recognized, and herbivores were found mainly at the onset of flowering, between the months of April and May. Herbivores belonging to the orders Coleoptera, Lepidoptera, Hemiptera, Orthoptera, Hymenoptera, and Thysanoptera were recorded in flowers of both species studied - the most common ones being the Curculionidae beetles (present mainly at the bud stage) and Lycaenidae butterflies and small Thysanoptera (in the buds and flowers).

The results demonstrated variations in the floral area, number of damaged flowers, and florivory rate. The number of damaged flowers was higher in *B. malifolia* than in *B. variabilis* (Table 1 and 2). The floral area was higher in *B. malifolia* (2,95±0.76; N= 45), mainly in flowers of the light-pink morphotype (df $_{2,42}$=14.307; P<0.001) (Fig. 3). Of the *B. malifolia* morphotypes, the light-pink one exhibited a higher number of damaged flowers; however, intensely pink flowers suffered a higher loss of floral tissue area. The florivory percentage differed significantly between the species (0.03±0.13; N= 45). *B. malifolia* suffered a greater loss of floral area than did *B. variabilis* ($F_{2,42}$=4.86; P=0.013) (Fig. 4), and there was no significant difference in these values between the *B. malifolia* morphotypes. Regarding the site of the damage, both species had damaged flowers with signs of herbivory in the central area of the petals, the margin of the petals and in both parts.

The results of the simulated florivory revealed that the visual aspect of the flower affects the attractiveness to pollinators because there was a significant difference among the fruiting rates in the different treatments (2,93±1,38; N= 30). The group of intact flowers (control) had the highest fruiting rate of all three treatments ($F_{2,27}$= 35,413; P<0.001) (Fig. 5).

Table 1. Estimate of the floral damage and its percentage recorded for the study species and the different morphotypes of *Banisteriopsis malifolia*.

Species /Damage	Number of flowers	Total area of the petal (cm²)	Number of damaged flowers (%)	Damaged area in cm² (%)
B. malifolia IP	80	42.75	32 (40%)	2.80 (6.5%)
B. malifolia LP	70	53.90	36 (51%)	2.08 (3.7%)
B. variabilis	15	36.42	03 (20%)	0.24 (0.6%)

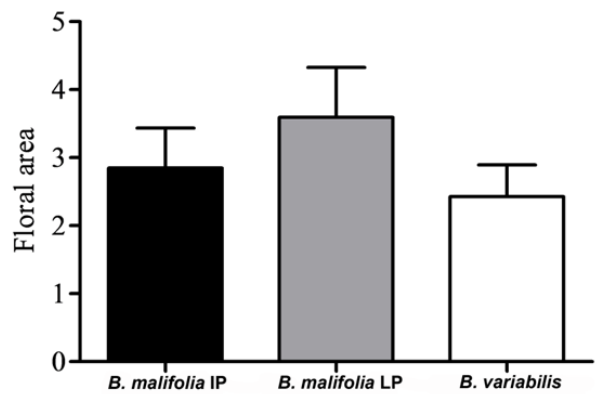

Fig. 3. Floral area of *Banisteriopsis variabilis* and of *Banisteriopsis malifolia* and its morphotypes from the reserve area of the Clube de Caça e Pesca Itororó de Uberlândia, state of Minas Gerais, Brazil. IP and LP refer to the two morphotypes of *Banisteriopsis malifolia:* intense pink and light pink, respectively.

Discussion

The results of the floral-manipulation experiments and quantification of the natural florivory and the fruiting rate revealed that florivory negatively affects the reproduction of plants by the genus *Banisteriopsis* in the Cerrado.

Table 2. Contingency data based on the presence and absence of floral damage recorded for both morphotypes of *Banisteriopsis malifolia* and for both species of *Banisteriopsis*.

	Presence	Absence	Total
B. malifolia IP	36	44	80
B. malifolia LP	32	38	70
Total	68	82	150
	Presence	Absence	Total
B. malifolia	68	82	150
B. variabilis	3	12	15
Total	71	9	165

These findings thus corroborate the central hypothesis of the present study. Plants have developed several strategies to attract the service of pollinators, and this investment favors the maintenance of the species in the ecosystem (Stout, 2000). However, florivory may directly reduce the quality and quantity of the available resources (Karban & Strauss, 1993) by alterations in the floral traits, such as shape and size of the petals (Fraze & Marquis, 1994), and by reductions of the visual and olfactory cues (Krupnick & Weis, 1999; Krupnick et al., 1999). The damage recorded in the flowers of both species of *Banisteriopsis* is directly related to the use of buds for egg-laying by endophytic florivores (Torezan-Silingardi, 2011) or to the use of petals for feeding by exophytic herbivores (Alves-Silva et al., 2013), both in the juvenile and adult stages (Torezan-Silingardi, 2007). The use of petals and of the remaining internal bud structures has been associated with a reduction in the overall attractiveness of flowers to their effective pollinators and to the consequent decrease in fruiting success (Leavitt & Robertson, 2006).

The flowers of *B. malifolia* displayed a more extensive floral area, a higher number of flowers attacked, and a greater proportion of damage. The herbivores responsible for the reported damage might be attracted by the same cues identified by pollinators to find the flowers, such as the coloration, intensity of scent, size of the flowers and density of flowers per area, which are more evident in *B. malifolia* than in *B. variabilis*. Therefore, the coloration and size of the flower appear to be important characteristics for explaining the preference of floral herbivores. Irwin and Strauss (2005), Frey (2004), and Salomão et al., (2006) discuss similar results in which the attraction cues (such as size, color, shape, and scent) that are recognized by the pollinators and can also be identified by floral herbivores.

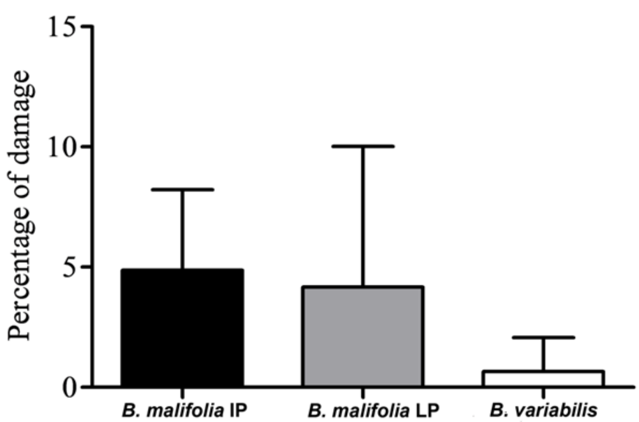

Fig. 4. Percentage of damage by florivory in the flowers of *Banisteriopsis variabilis* and of *Banisteriopsis malifolia* and its morphotypes from the reserve area of the Clube de Caça e Pesca Itororó de Uberlândia, state of Minas Gerais, Brazil. IP and LP refer to the two morphotypes of *B. malifolia:* intense pink and light pink, respectively.

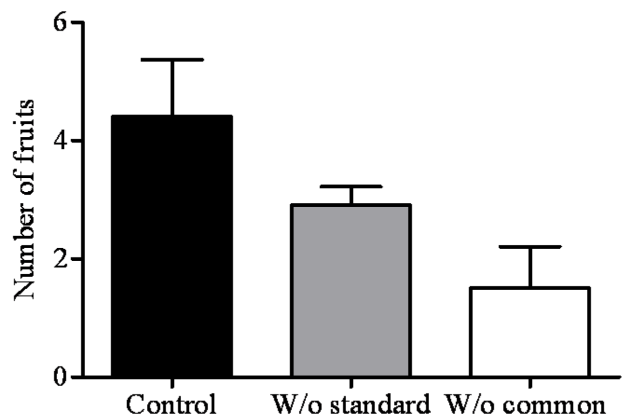

Fig. 5. Mean number of fruits produced during the simulated-florivory experiment in *Banisteriopsis malifolia* (morphotype 2: light pink) at the reserve area of the Clube de Caça e Pesca Itororó de Uberlândia, state of Minas Gerais, Brazil.

The results obtained in the experiment of simulated florivory reinforce the importance of floral attractiveness in the selection of resources by the pollinator because a reduced number of petals negatively affected the production of fruits. Flowers with damaged structures or eaten petals may indicate a deficit or absence of resources, causing the bees to refuse them. Furthermore, the olfactory cues that act together on the floral attraction of pollinators may influence the process of selection. Salomão et al. (2006) studied the effects of the floral-area size and of the floral herbivory in *Trichogoniopsis adenantha* (Asteraceae) and reported that large bushes and flowers undamaged by herbivory produce a higher proportion of seeds. The authors also noted that, just as pollinators prefer to visit larger bushes, herbivores may also respond in the same manner and cause greater damage in larger flowers, thereby reducing their attractiveness to pollinators. Sober et al. (2010) studied the floral herbivory in *Verbascum nigrum* and reported results similar to the present findings, in which the visitation rate was negatively correlated to florivory.

The presence of herbivorous insects on the *Banisteriopsis* flowers studied was responsible for the change in the floral traits, and such damage negatively affected the flower-pollinator interactions, causing a significant reduction in the fruit and seed production. This lower fruiting rate may be the first sign of a reduction in fitness, considering that the majority of interactions with herbivores cause similar losses. Hendrix and Trapp (1989) tested the hypothesis that the responses to floral herbivory in *Pastinaca sativa* L. (Apiaceae) may compensate or even increase the fitness of the individuals attacked. The authors found that, despite the compensatory responses generated, the reduced fitness is a result of damage by herbivory, and the species cannot compensate for this reduction. Therefore, future investigations (e.g., Byk & Del-Claro, 2010) will be important for describing the responses of plant species to floral damage over time.

Studies of the interactions that occur between organisms are critical for the survival and reproduction of the species involved. Furthermore, the different forms of interactions generate ecological diversity and enable the formation of rich ecosystems, which are composed of species that have coevolved (Thompson, 2012). We can conclude that the species *B. malifolia* and *B. variabilis* are damaged by floral herbivores in different proportions and that this phenomenon directly affects the floral attractiveness, resulting in lower fruit production; furthermore, the higher the damage that is caused, the lower are the visitation rate and the reproductive success. The study of these effects in the interactions between floral herbivores, flowers, and pollinators elucidates how these species relate to the environment and may support future investigations regarding the selection of areas for conservation of the local biodiversity.

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