



***Thalia geniculata* L. (MARANTACEAE): A PLANT THAT PRODUCES A PSEUDANTHIUM WITH TWO FLOWERS, TWO OVARIES BUT JUST ONE FRUIT**

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Abstract: *Thalia geniculata* L. (Zingiberales, Marantaceae) has inflorescences with two simultaneously opening, hermaphroditic, single-day flowers, which form a pseudanthium. The species has an irreversibly explosive pollination mechanism. In one population of *T. geniculata* we verified that in 98.5% of the pseudanthia, only one flower from each pair set fruit. We assessed whether this fruit-set pattern could be linked to pollinator behavior, testing if pollinators only visit one flower in each pseudanthium, which would decrease visitation probability of the other flower in the pseudanthium. In the morning, less flowers were visited than in the afternoon, and we observed higher pollinator activity in the afternoon. In the morning, most of the visited pseudanthia had only one flower visited, while in the afternoon most pseudanthia had both flowers visited, the opposite of what we predicted. We concluded that single fruit set in the pseudanthia is not caused by pollinator behavior. It might be caused by pollen limitation during pollinator visits or even resource limitation to support two fruits per pseudanthia.

Keywords: floral display; inflorescence mechanisms; Pantanal; pollinator behavior; reproduction.

Floral display is strongly correlated with reproductive success of animal pollinated plants (Goulson *et al.* 1998). Display can affect reproduction by increasing the number of floral visitors or by improving visitor fidelity to a given plant species (Ratchke 1983). Floral signals to attract pollinators have evolved in individual flower traits or even floral arrays in inflorescences. For example, pseudanthia present sets of flowers organized to resemble a single flower, which

can make the entire display more attractive to pollinators than individual flowers. Angiosperms have had multiple independent pseudanthia evolutions in at least 40 families (Claßen-Bockhoff 1990). Pollinator selective pressure plays an important role in evolution of floral traits in natural populations (Benitez-Vieyra 2014, Caruso *et al.* 2018). Therefore, floral signals could be an outcome of plant-pollinator interactions and an evolutionary consequence of pollinator behavior.

However, to be effectively pollinated, pollinators must be able to efficiently perceive floral signals (Brito *et al.* 2014).

A curious floral display is found in *Thalia geniculata* L. (Zingiberales, Marantaceae), an herbaceous plant that grows in dense populations in tropical wetland areas with seasonal climates (Kirchhoff 1986, Silva *et al.* 2000, Hawkeswood & Sommung 2016; Supplementary Material 1-3). When these plants bloom, they resemble gramineous spikes within grassland environments (Supplementary Material 1a). The inflorescences consist of panicles of pseudanthia (Kirchhoff 1986, Ley & Claßen-Bockhoff 2009), *ca.* 2 m tall with 60 to 340 pseudanthia (Figure 1c-d). Each pseudanthium is a fascicule of two small hermaphroditic flowers subtended by a single bract (approx. 15 mm corolla wide and 8 mm long fleshy staminode). Although each flower is asymmetrical, the resulting pseudanthium resembles a single flower with bilateral symmetry in color and structure (Supplementary Material 1), as the two flowers are mirror images of each other (two blossoms and one flower) (Andersson 1981, Kirchhoff 1986, Claßen-Bockhoff 1990, 1991). Besides the pseudanthium, *T. geniculata* also attracts pollinators with its conspicuous petaloid staminodes and highly concentrated nectar (Claßen-Bockhoff 1990, Ley & Claßen-Bockhoff 2009). The flowers bloom for one day and stamens deposit pollen onto a stylar depression behind the stigma before anthesis (Supplementary Material 2c), characterizing secondary pollen presentation. An explosive pollination action is performed by a cucullate (hooded) staminode, which holds the style, and is released under pollinator pressure (Claßen-Bockhoff 1991). Such explosive style movement is only present in Marantaceous flowers and, for structural reasons, are obligately cross pollinated (Andersson 1981, Claßen-Bockhoff & Heller 2008). Interestingly, autogamous reproduction has been reported in *T. geniculata* (Davis 1987). When the floral mechanism is triggered, the style is catapulted around the front of the flower, bringing the stigma in contact with the pollinator, capturing any previously deposited pollen from the pollinator's body, while simultaneously depositing its own pollen on the pollinator's mouth parts (for details about the mechanism see <https://youtu.be/uFXI1IXqtk4>

and Jerominek *et al.* 2018). This style movement is irreversible, so each flower has only one chance of being pollinated (Claßen-Bockhoff 1991). *Thalia geniculata* is considered a locked flower, since the trigger appendage completely obstructs the flower entrance and only certain visitors can trigger the style (Ley & Claßen-Bockhoff 2009). Triggered flowers change their morphology and are easily recognized by the change of style position.

Thalia geniculata is regularly visited by carpenter bees *Xylocopa* spp. (Hymenoptera, Apidae) and less frequently by hummingbirds and skipper butterflies (Davis 1987). Bees always trigger the styles, while hummingbirds occasionally do and butterflies never trigger them (Hawkeswood & Sommung 2016). Large bees are forced into the same position when perching on staminodes, therefore, pollen is deposited precisely onto their proboscis fossa (Ley & Claßen-Bockhoff 2009). The symmetry of triggered flowers also changes in the pseudanthium, which acts as a visual signal for bees to distinguish between visited and unvisited pseudanthia.

In the field, we observed that each pseudanthium produces only a single arillate seed-fruit, even though each has the potential to produce two fruits, as both flowers are functional. Such pattern has been previously recorded for *T. geniculata* in Costa Rica (Davis 1987) and in Indonesia (Claßen-Bockhoff 1991). Observing such fruit set pattern in a population of *T. geniculata* in Pantanal wetland flowers, we asked if pollinator behavior could explain why two flowers with two functional ovaries produced one single fruit per pseudanthia. This question is based on two statements: I) It is known that bumble bees present an innate preference for flowers with bilateral symmetry (Rodríguez *et al.* 2004). The pseudanthium of *T. geniculata* resembles a single flower with bilateral symmetry which could be perceived by bees as a single flower, at least from far distances. Additionally, due to optimal foraging, we expect bees to avoid immediately revisiting flowers, since floral nectar would just have been consumed (Best & Bierzychudr 1982). If the bee perceives the pseudanthium as one single flower, we can hypothesize that it will only visit and drink the nectar of the first flower, thus leaving the second flower unvisited; II) It is known that bees use visual signals besides color when exploiting flowers (Giurfa *et al.* 1996). We hypothesized that

foraging bees will perceive and visually detect the loss of symmetry when the first flower of a pseudanthium has been triggered, moving to another unvisited pseudanthium to increase their chances of obtaining nectar instead of visiting the second flower in the same pseudanthium, as pseudanthium looks like only one flower. From this hypothesis, we predicted that bees' foraging activity in the population of *T. geniculata* will result in only one triggered flower in each visited pseudanthia. We expect that it would generate a correlation between pollinator visitation in pseudanthium and single fruit set.

To test if single fruit set was linked to pollinator behavior, we sampled the pollination success of the pseudanthia by recording if both flowers were unvisited (0/0), if only one flower was visited (1/0), or if both flowers were visited (1/1). We directly tested whether the probability of a flower to be visited depended on the visitation of the other flower in the pseudanthium. According to our hypothesis, if one flower in the pair was visited, the probability of the second flower being visited would be lower. We calculated the probability

of a flower receiving a visit in the population (P_i = number flowers triggered/total number of flowers) and used that probability to determine the expected values in each of the cases. According to our hypothesis, if the probabilities were linked, we would expect higher values for 1/0 case. By chance, each case probability would be P_i^2 , for 1/1, $2*[P_i*(1-P_i)]$ for 1/0 or 0/1, and $(1-P_i)^2$ for 0/0 is. It is important to state that we did not tested the effect of maternal resources on fruit-set for all flowers produced in the panicle of the plant, but rather we tried to determine if the mechanism by which a pseudanthium of two functional flowers produces only one fruit was linked to pollinator behavior.

We conducted this study in April 2017 using a population of *T. geniculata* located near the Pantanal Field Station (BEP-UFMS) in Passo do Lontra Miranda-Abobral region, state of Mato Grosso do Sul, Brazil (Figure 1a-b). This region is characterized by a warm, seasonal climate with a dry winter (average temperature 21°C) and a marked precipitation regime in the summer (Nov-March; average temperature 32°C) (Cadavid-Garcia 1984). This plant occurs in flooded fields with

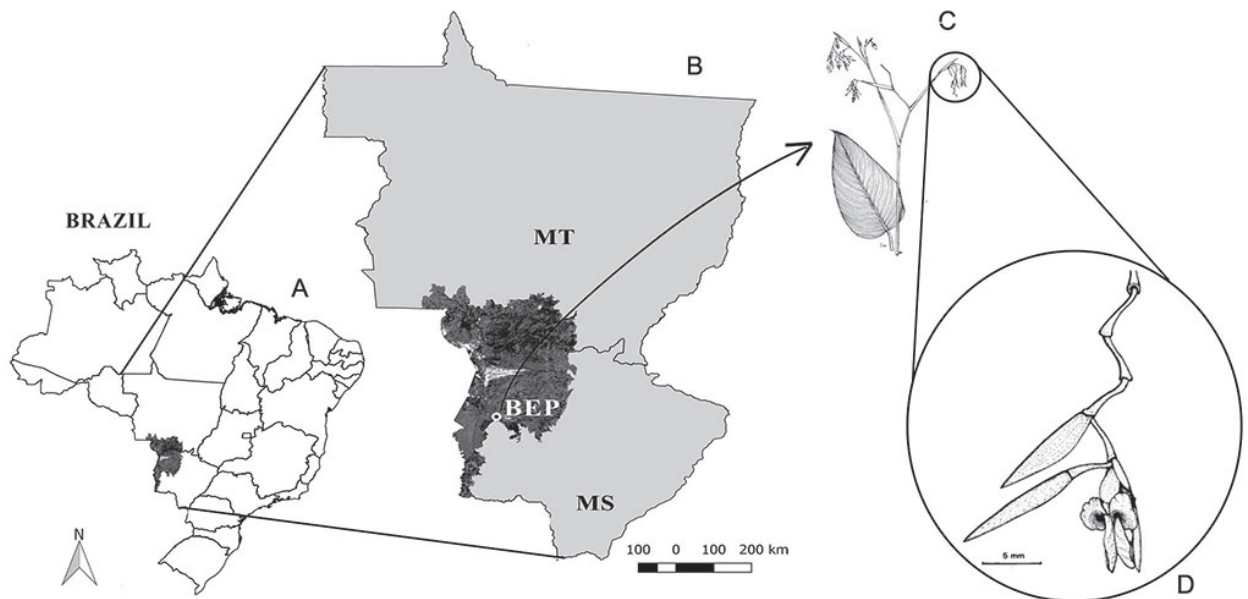


Figure 1. (a) Map of Brazil with the location of the Pantanal, Brazil; (b) The two states that comprise the Brazilian Pantanal wetland (dark area on the map; MT = Mato Grosso State; MS = Mato Grosso do Sul State) and Base de Estudos do Pantanal (BEP; Pantanal Field Station) located in state of Mato Grosso do Sul State, South-West of the Pantanal area. (c) *Thalia geniculata* (Zingiberales, Marantaceae), an herb that is approx. 2 m tall and grows in dense populations in wetlands. This species presents massive blooms. *Thalia geniculata* has panicles of pseudanthia, each of which has a pair of small, hermaphroditic flowers subtended by a single bract. Each pair of flowers presents bilateral symmetry both in color distribution and structure. Illustration (d) adapted from Andersson (1981).

prolonged periods of soil-water saturation and is restricted to the western portion of the Pantanal, near the Paraguay River.

To describe the single fruiting pattern of the pseudanthium (Davis 1987, Claßen-Bockhoff 1991), we performed a one-day census of 998 pseudanthia (pairs of flowers) within an ~1 km² area of swamp. In each individual, all the pseudanthia were counted. The next day we conducted two censuses to record the pollination state of the pseudanthia. We used whether the flower's style was "triggered" as a proxy for visitation. The first census was conducted using 260 pairs of pseudanthia beginning at anthesis and lasting for two hours (aprox. 10:00 to 12:00 h). The second census was conducted six hours after the first census in the same plant population, using different transect trajectories. In the afternoon, we counted 279 pairs of flowers. We analyzed the pollination state of the pseudanthia data in each census using Chi-squared tests, performed in R

Studio (v.3.5.0). Additionally, we studied pollinator activity by recording pollinator type and period in which the visitation occurred during the two days. To record visitation data, five independent observers conducted 20 observation hours. The pollinator visitation data was expressed as a rate of visitation (number of visits per unit of time) calculated in morning and afternoon censuses.

Both flowers in the pseudanthium of *T. geniculata* opened around 9:40-10:00 h. In our studied population, only 15 of the 998 pseudanthia produced two seeds, confirming the single seeded-fruit pattern production of *T. geniculata*. In the first, morning census, a high percentage of pseudanthia were unvisited (63%; N = 260). Our data from the first census also indicated that the visitation pattern was not different from what we would expect if pollinators visit the flower as a single unit ($\chi^2 = 1.257$; df = 1; p = 0.261; N = 520) (Figure 2). Conversely, in the second/afternoon census, the opposite was

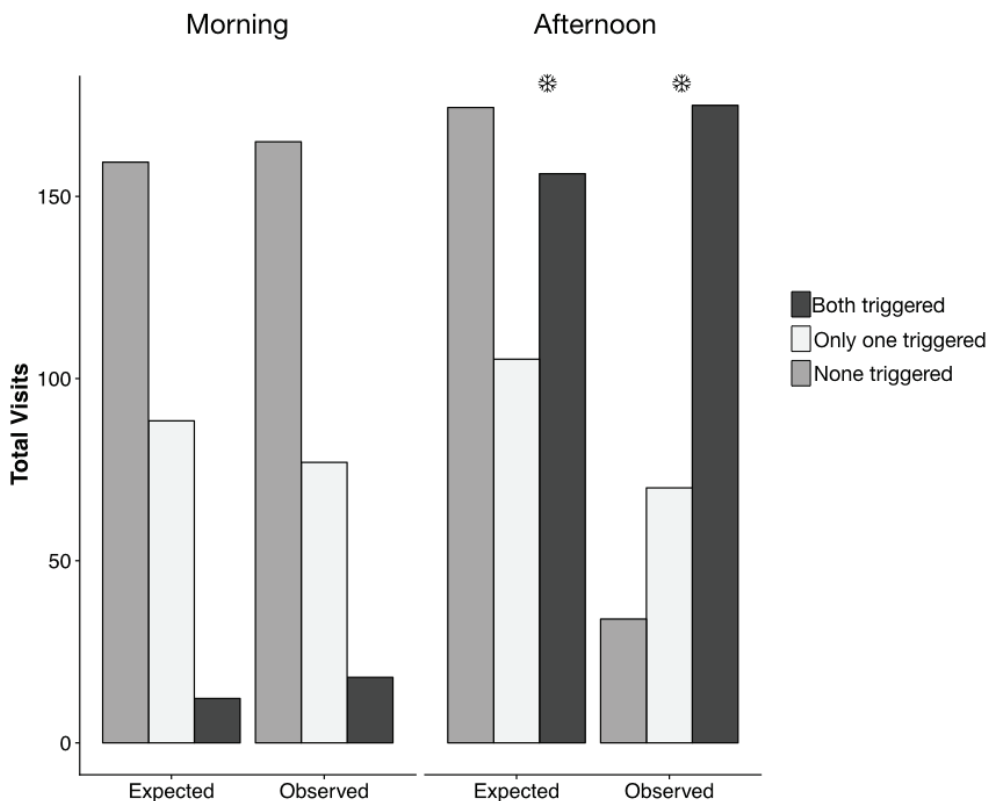


Figure 2. The morning census was similar to that expected under visitation probabilities not linked between the flowers in the pseudanthia (1st census - left side of the graph). In the morning census, most of the pseudanthia had not been visited and most of the visited pseudanthia had only one flower triggered (very few inflorescences had two flowers triggered). In the afternoon (2nd census – left side of the graph), the visitation pattern contradicted the morning pattern, with most pseudanthia having both flowers triggered. In the afternoon, few pseudanthia remained unvisited. 0/0 (dark gray bars) - no flowers were triggered; 0/1 - only one flower was triggered, as our hypothesis suggests (light gray bars); 1/1 - both flowers were triggered (black bars).

found with most pseudanthia in the population visited and only 12% of them unvisited ($N = 279$), and higher pollinator activity recorded at this time of the day. We also found in the second census that more pseudanthia presented both flowers triggered than what was expected by random visitation ($\chi^2 = 7.139$; $df = 1$; $p = 0.00752$). There were about twice as many pseudanthia with both flowers triggered than pseudanthia with only one flower triggered (Figure 2).

Bees, butterflies and hummingbirds visited the flowers. We observed two groups of bees based on their morphology (*Bombus* sp. – Hymenoptera, Apidae - and *Xylocopa* sp.; Supplementary Material 3), and two groups of butterflies, as well as one hummingbird species that sporadically visited flowers. We did not register visitation by *Apis mellifera* (Hymenoptera: Apidae: Apini). Additionally, pollinator activity was lower in the morning (2.1 visit/min*population) than in the afternoon (7.4 visit/min*blossom).

According to our hypothesis, pollinators would only trigger one flower in the pseudanthium (each pair), leaving the other flower unvisited. Also, if pollinators could distinguish between triggered and untriggered pseudanthia, they would avoid revisiting previously visited pseudanthia. From these two statements, we expected the probability distribution of pseudanthia with just one triggered flower (1/0) to be much higher than pseudanthia with both flowers visited (1/1) in the population.

Our results from the morning census showed that there were more pseudanthia with only one flower triggered in the population. This pattern could be generated by our first statement, that bees perceive the pseudanthium as a single unit and do not visit the second flower even though pollinators should behave like that according to the optimal foraging theory (Best & Bierzychudr 1982): time and energy intake are optimized when foragers leave the flower from which they have just consumed nectar, to visit a new flower with a higher probability of containing nectar.

Results from our second census showed that the probabilities of finding pseudanthia with one (0/1 or 1/0) or two flowers triggered (1/1) in the population was not random (Figure 2). According to our hypothesis, we expected the probability of finding two flowers triggered to be lower than the probability of finding a single triggered flower,

therefore, we rejected our hypothesis that the single fruit set pattern is a product of insufficient pollinator visitation or pollinator behavior. In our second statement, we proposed that the change in bilateral symmetry of the pseudanthium, caused by the triggered style, might be playing a key role in the pollination system of *T. geniculata*, generating a pattern of one visited flower per pseudanthia. However, our findings indicate that triggered styles do not act as a floral cue for pollinators and do not cause them to avoid visiting the pseudanthium, as both flowers were ultimately visited by the end of the day. It is possible that the same pollinator returned to the same pseudanthium later in the day or that other pollinators visited the second flower in the pseudanthium in the afternoon. Furthermore, we also observed hummingbirds visiting *T. geniculata*. Normally, hummingbirds do not trigger the styles, however, triggering mechanism is more sensitive later on in the day, when hummingbirds might trigger them. Furthermore, it is possible for even small insects or rain drops to trigger the style in the afternoon. Davis (1987) also observed more hummingbirds visiting *T. geniculata* later in the day.

These results refute our hypothesis and showed that the single seeded-fruit pattern of *T. geniculata* was not a consequence of not receiving visits in both flowers of the pseudanthium. However, if both flowers are triggered: Why does a plant produce two energetically costly flowers with viable ovules if only one flower will produce fruit? There are alternative explanations for the single-seed pattern. Since style movement is irreversible, and each blossom only has a single chance of being pollinated, it is possible that some pollinators do not have pollen on their bodies during visits (Leite & Machado 2007). Consequently, the mechanism is triggered, but the stigma may not receive any pollen and the ovule cannot be fertilized. In this scenario, having two flowers would double the chances of flowers being pollinated, acting as an insurance mechanism, similar to that occurring in semelparous flowers with vegetative bulbil formation (Arizaga & Ezcurra 1995). However, we would not expect such scenario to happen often enough to explain the prevalence of the single fruit-set pattern registered here.

Given that i) pollinator visitation rates can vary greatly in time and space, leading to a high

uncertainty of cross-pollination for flowers; ii) reproductive assurance has been demonstrated in *T. geniculata* in the absence of pollinators (Davis 1987); and iii) populations of *T. geniculata* can present a higher proportion of clones due to vegetative reproduction (Claßen-Bockhoff 1991). Therefore, presenting two flowers that only produce one fruit could be a strategy to increase pollinator attraction, disperse male gametes and mitigate ecological and evolutionary costs of forming fruits with endogamous seeds (Austerlitz *et al.* 2012). Since floral reproductive success also occurs through male reproductive success, through pollen dispersal (Cruden 2000), producing two flowers doubles the chances of pollen dispersal, *i.e.*, pollen exportation, as the trigger mechanism is irreversible and only deposits pollen onto a single visitor (Harder & Wilson 1994). This could be functioning as enantiostyly (Fenster *et al.* 1995, Jesson & Barrett 2002, Jesson & Barrett 2003). Notwithstanding, whether this plant can select one ovary to develop the seed, through the temporal triggering of styles or female choices based on gametophyte quality remains unknown (Stephenson & Bertin 1983).

In this short communication, we tested whether the pattern of single fruit production in pseudanthia of *T. geniculata* was related to pollinator visitation patterns and, consequently, was pollinator limited. We concluded that the process behind this pattern is not related to pollinator behavior. It could be linked to a strategy to disperse more pollen but only invest energy in producing one seed, if maternal resource is limited or related to decreased endogamy risk. Future studies may be conducted to determine the mechanism behind the single fruit set in *T. geniculata* pseudanthia and comprehend if there is a mechanism selecting which of the flowers will develop the seed.

ACKNOWLEDGEMENTS

We would like to thank all professors at the Workshop in Ecology and Evolution of Plant Reproduction for sharing their knowledge during lectures, and for their encouragement and support to conduct this research project; Nicolay Leme da Cunha for his effort in organizing the workshop; Diego Finatti for his participation in obtaining data; Joice Iamara and Catalina Zuluaga for their help producing Figure 1; Hannah Doerrier and

Laura L. Figueroa for English review. Marcelo Aizen for statistical advice. PSC acknowledges University of São Paulo and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) (process number: 140232/2018-4) for support. MAM acknowledges the Universidad Nacional de Colombia for support and PMMP the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 001 and the Departamento Administrativo de Ciencia, Tecnología e Innovación – Colombia (Colciencias) Finance Code 568 for support.

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Supplementary Material 1. *Thalia geniculata* L. (Marantaceae). a) Plants at Pantanal grow in open spaces in swamps. Each plant has ca. 2 m

with 60-340 pseudanthia. b) Both flowers in the pseudanthium are structurally organized to look like a single flower with bilateral symmetry.

Supplementary Material 2. *Thalia geniculata* L. (Marantaceae) flower. **a)** A cucullate (hooded) staminode holds the style which is released under pollinator pressure. **b)** Each flower in the pseudanthium has an ovule with the potential to produce a single-seed fruit. **c)** Stamens deposit pollen onto a stylar depression (arrow pointed) behind the stigma, characterizing secondary pollen presentation.

Supplementary Material 3. *Thalia geniculata* L. (Marantaceae) being visited by a carpenter bee (*Xylocopa* spp.).

Submitted: 11 October 2018

Accepted: 18 July 2019

Published online: 16 December 2019

*Associate Editors: Camila Aoki, Gudryan J. Barônio
& Arnildo Pott*