

SHORT COMMUNICATION

Pollination ecology of *Monstera obliqua* (Araceae) in French Guiana

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(Accepted 2 July 2007)

Key Words: *Colopeterus*, floral chamber, nitidulid, pollination, thermogenesis, floral cycle

Data on pollination ecology of Araceae are still scarce and most concern species belonging to the subfamily Aroideae (García-Robledo *et al.* 2004, Gibernau 2003, Ivancic *et al.* 2004, 2005; Maia & Schlindwein 2006). In this subfamily, inflorescences consist of unisexual flowers: female flowers are located in the lower portion and the male flowers are in the upper portion of the inflorescence (Mayo *et al.* 1997). In the documented neotropical Aroideae, pollinators are nocturnal beetles and pollination mechanisms take place within a floral chamber during a short flowering cycle (generally 24–48 h) with floral rewards (sterile flowers rich in proteins and/or lipids) for the beetle pollinators, the secretion of resin to secure pollen on the pollinator, and the production of heat and odours (Chouteau *et al.* 2007, García-Robledo *et al.* 2004, Gibernau & Barabé 2002, Gibernau *et al.* 1999, 2000, 2003; Maia & Schlindwein 2006, Young 1986).

However, the pollination ecology of the neotropical genera bearing bisexual flowers is poorly known and is mostly based on observations and a few studies (Croat 1980, Franz 2007, Kraemer & Schmitt 1999, Montalvo & Ackerman 1986, Ramirez & Gomez 1978, Schwerdtfeger *et al.* 2002). The bisexual flowers generally consist of a whorl of stamens surrounding a pistil, with (e.g. *Anthurium*) or without (e.g. *Monstera*) a perianth (Mayo *et al.* 1997) and in some species a basal sterile zone is present (e.g. *Monstera*). In the documented species (i.e. *Anthurium*, *Spathiphyllum*) pollination mechanisms appear relatively simple (a long flowering cycle, the lack of a floral chamber), pollinators are believed to be diurnal bees and thermogenesis has never been documented. The genus *Monstera*, ubiquitous throughout the neotropical

rain forest, is composed of up to 40 species (Mayo *et al.* 1997). In *Monstera deliciosa* diurnal *Trigona* bees attracted to the gums produced by the flowers were common visitors to the inflorescences (Ramirez & Gomez 1978) and it was therefore supposed that these bees were pollinators, like in other members of the Monsteroideae family. In this study we document the pollination ecology of *Monstera obliqua* by a nitidulid beetle.

This study was conducted in July 2006 at one population location of *M. obliqua* downstream of the Petit-Saut Dam in French Guiana (05°04'02 N, 53°03'12 W). The population was composed of about 30 stems growing on 12 supporting trees which were 3–25 m apart. Voucher specimens were deposited at the Montreal Botanical Garden for *M. obliqua* (Chouteau 23) and at the California Department of Food & Agriculture CDEA, Sacramento, California (Dr Cline) for the nitidulid beetles.

Monstera obliqua Miquel is a neotropical understorey hemi-epiphytic climber growing near freshwater habitats (i.e. temporary ponds and river margins). Our observations (n = 14) showed that at maturity the stems (7.1 ± 0.6 mm in diameter) bear ovate leaves (22.0 ± 3.4 cm × 11.4 ± 1.9 cm) with tear-drop-shaped perforations. The bisexual inflorescences, 1–3 per axil, have very thin peduncles (7.4 ± 1.2 cm × 3.9 ± 0.3 mm) and are usually produced at 1.6 m above the ground or more. The inflorescences are 4.3 ± 0.6 cm long, bear 58.2 ± 12.5 fertile flowers and a few (3–7) sterile flowers at the base, and they are enclosed in a green spathe (6.1 ± 0.3 cm long) which became white and yellowish with maturation.

The flowering cycle was observed on 20 inflorescences several times per day (e.g. spathe opening, flower maturation, insect presence, fragrance by smelling). During the female phase of 15 inflorescences, insect

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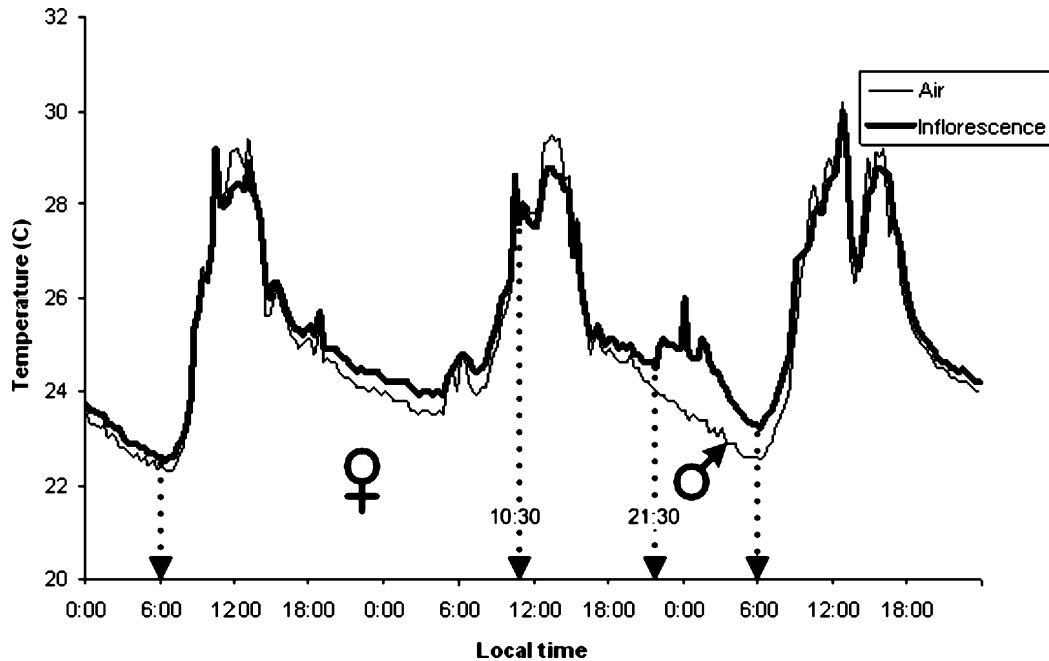


Figure 1. Temperature curves of the spadix (thick line) and ambient air temperature (thin line) during 3 consecutive days of the flowering cycle for *Monstera obliqua* inflorescences in French Guiana. The beginning and ending times of female and male phases are indicated by arrows. The more distant the two curves are, the greater is the temperature difference between the inflorescence and ambient air, and thus the inflorescence is heating up. During the male phase, the inflorescence is clearly warmer than ambient air.

visitors were collected in a bag using a paint brush and quickly frozen prior to counting. Moreover, all collected insects were observed under a dissecting microscope to check for the presence or absence of pollen on their bodies. Self-pollination was tested by bagging 15 other inflorescences prior to their opening. In addition, 28 non-manipulated infructescences were monitored in order to determine the frequency of abortion. If inflorescences fruited, the numbers of fruits and aborted fruits were counted.

The temperature of five inflorescences, growing on four plants, was recorded during different days every 20 min during the complete flowering cycle using Digi-Sense® DualLogR® thermocouple thermometers. One probe was inserted approximately 5 mm into the middle of the spadix and another probe was used to record the ambient air temperature 20 cm from the inflorescence.

Flowering appeared to be asynchronous in *Monstera obliqua*, since only one inflorescence at anthesis per stem was observed at any given time during this study. The mean lapse of time between two successive anthesis on a given stem was 6.7 d with a minimum of 4 d. Interestingly, half of the 20 inflorescences opened (female phase) when at least one other inflorescence was still dispersing pollen (male phase). The flowering and thermogenic cycle was a 48-h process spread out over 3 d (Figure 1). Before flowering began, the green spathe was tightly folded around the spadix, preventing access to the flowers.

The flowering cycle started on the first morning around 6h00. At this time, stigmas were wet, turgescient with stigmatic droplets and supposedly receptive (beginning of female phase, Figure 1 first arrow), fragrances were produced and the spathe began to slightly unfold, creating a floral chamber between the spadix and the spathe. On the second morning (10h00–11h00), the stigmas were dry (end of the female phase, Figure 1 second arrow) and appeared to be no longer receptive. The fragrance continued to be produced and the spathe began to open widely (0.66–0.75 of its length) until nightfall (Figure 1). Around 1h00, the pollen started to be released from all flowers synchronously (male phase, Figure 1 third arrow). Around 3h00, the flowering cycle ended: the pollen ceased to be released, but stayed on the flowers, and the fragrance was no longer emitted.

Temperature records showed small differences ($0.6^{\circ}\text{C} \pm 0.1^{\circ}\text{C}$) between the inflorescence and ambient air early on the second morning ($5\text{h}36 \pm 15$ min) when ambient temperatures dropped to $23.4^{\circ}\text{C} \pm 0.7^{\circ}\text{C}$ (Figure 1). On the second night of the flowering cycle ($21\text{h}33 \pm 1$ h 42 min to $9\text{h}03 \pm 37$ min), as ambient air temperatures dropped, the spadix temperature rose gradually until it reached $25.2^{\circ}\text{C} \pm 0.5^{\circ}\text{C}$ ($2^{\circ}\text{C} \pm 0.4^{\circ}\text{C}$ above air temperature) at $1\text{h}11 \pm 1$ h 37 min and was coupled with the release of pollen (male phase, Figure 1).

All of the 242 insect visitors found in the inflorescences of *M. obliqua* were *Colopeterus amputatus* Erichson

(Nitidulidae). Using a dissecting microscope, we recorded small amounts of pollen wedged in small clusters in the ventral area of 83% of the collected beetles. Arrival of *C. amputatus* on all inflorescences was observed during daylight (morning, midday and afternoon) of the first and second day of flowering (during the female and female-male interphase). They remained tightly packed inside the floral chamber and copulation was observed. At the end of the female phase (10h00–11h00 of the second day), floral chambers were sheltering 3–25 individuals (mean \pm SD: 16.1 ± 6.9). Later, when the spathe had opened wider, the beetles present in the inflorescences hid between the spadix and the spathe. On the third day, in the early morning hours (around 3h00), released pollen stuck to the beetles which then left the inflorescences at daybreak. *Colopeterus amputatus* beetles were also observed eating pollen after its release (during the night). After 6h00, the inflorescences were empty and virtually no pollen was left on the flowers.

All the 15 bagged inflorescences aborted within 1 wk and hence *M. obliqua* is considered to be unable to self-pollinate. Moreover, of the 28 non-manipulated inflorescences, 20 (e.g. 71%) aborted naturally after 2 wk. Of the eight inflorescences in which fruiting was observed, $84.1\% \pm 9.7\%$ of flowers produced fruits. Each berry contained three or four seeds.

Until now, pollination ecology in the genus *Monstera* had not been documented except for observations of resin harvest by bees on *Monstera deliciosa* (Ramirez & Gomez 1978). *Colopeterus amputatus*, a small (4–5 mm) nitidulid, was the only insect visitor attracted to *M. obliqua* inflorescences. The presence of pollen on their bodies when arriving at a new inflorescence coupled with the fact that they stayed inside the inflorescence during the entire flowering cycle suggests that *C. amputatus* was the only pollinator of *M. obliqua* in the studied population in French Guiana. Gum production by the sterile flowers, as documented in *Monstera deliciosa* (Ramirez & Gomez 1978), was never observed in *M. obliqua*.

In addition, our results show that *M. obliqua* exhibited a short flowering cycle and a floral chamber, two floral traits unique for a neotropical species bearing bisexual inflorescences. The 48-h flowering cycle of *M. obliqua* contrasts with other taxa with bisexual flowers, such as *Anthurium* and *Spathiphyllum*, whose flowering cycles last from 10 d to 30 d (Croat 1980, Franz 2007, Montalvo & Ackerman 1986, Schwerdtfeger *et al.* 2002), but is comparable with neotropical beetle-pollinated Araceae of the Aroideae subfamily which also possess a floral chamber (Chouteau *et al.* 2007, García-Robledo *et al.* 2004, Gibernau & Barabé 2002, Gibernau *et al.* 1999, 2003; Maia & Schlindwein 2006, Young 1986). In *M. obliqua*, the pollinating *C. amputatus* arrived on the first and second day before the spathe was completely open and they used the floral chamber as a mating site and as a

shelter. The inflorescences did not offer pollinator rewards in the form of protein-rich flowers as has been described in other neotropical beetle-pollinated Araceae (Gibernau & Barabé 2002, Gibernau *et al.* 2003, Young 1986) until the release of pollen which was subsequently eaten.

Heat production by floral structures is generally associated with the emission of fragrances, the arrival of pollinators and the liberation of pollen and this has been well documented in the aroid family (Gibernau *et al.* 2003, Gottsberger 1990, Meeuse & Raskin 1988). However, unlike other neotropical beetle-pollinated species (Chouteau *et al.* 2007, García-Robledo *et al.* 2004, Gibernau & Barabé 2000, 2002; Gibernau *et al.* 1999, 2000, 2003; Maia & Schlindwein 2006, Young 1986), *M. obliqua* produced limited heat during the female phase. Pollinators appeared to be attracted to the sweet scent which was produced during the 48-h of the flowering cycle albeit a small increase of the spadix temperature was recorded during the female phase. Heating occurred mainly at the time of pollen release (i.e. male phase) as in other beetle-pollinated genera such as *Philodendron* subgenus *Philodendron* (Gibernau & Barabé 2002, Gibernau *et al.* 1999, 2000), *Caladium* (Maia & Schlindwein 2006), *Xanthosoma* (García-Robledo *et al.* 2004), *Dieffenbachia* (Young 1986), *Montrichardia* (Gibernau *et al.* 2003) and *Syngonium* (Chouteau *et al.* 2007), and is believed to aid in releasing pollen from the stamens and also in increasing the body temperature of the beetles prior to flight activity (Gibernau & Barabé 2002, Seymour *et al.* 2003).

Our results suggest that *M. obliqua* is unable to self-pollinate due to protogyny (temporal separation of sexes). The fruit set was low – only about 30% of the inflorescences set fruit – but when pollination did occur, fruit production was high with 84% of the berries reaching maturity. These results suggest that fruiting is more limited by resource availability than by pollination efficiency. Firstly, all receptive inflorescences were visited. Secondly, inflorescences were visited by numerous nitidulids almost always loaded with pollen. Thirdly, very few inflorescences flowered in synchrony, increasing the probability of cross-pollination. Another explanation could be that many of the inflorescences were in fact self-pollinated since they could grow on different stems that were genetically similar. In the studied population, vegetative reproduction was common: numerous independent, rooted sections of *M. obliqua* could be observed on the forest floor, suggesting it is an important mode of reproduction.

In conclusion, although *M. obliqua* is phylogenetically close to *Spathiphyllum* and *Anthurium*, it displays a very different flowering cycle. The flowering cycle of this species is similar to that commonly found in taxa with inflorescences consisting of unisexual flowers that are pollinated by beetles. The results of this study demonstrate

that although inflorescences of bisexual flowers appear earlier in the evolution of Araceae (Barabé *et al.* 2004), they can display a pollination mechanism similar to those present in more recent taxa.

ACKNOWLEDGEMENTS

The authors would like to thank Philippe Cerdan and the staff from the Environmental Laboratory HYDRECO (French Guiana) for providing the facilities and the equipment for this study. We are grateful to Alain and Andréa Dejean for their support in the field, to Andy Cline (California Department of Food & Agriculture Cdfa, Sacramento, USA) for nitidulid identification, and to Denis Barabé for his constructive comments on the manuscript. And finally, a special thank you is due to Dorian Noel and Greg Lamarre for their precious aid during fieldwork.

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