

Flowering and Pollination of *Philodendron melinonii* (Araceae) in French Guiana

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Abstract: The pollination ecology of *Philodendron melinonii* was studied at two locations in French Guiana. Inflorescences of *P. melinonii* were regularly visited by *Cyclocephala colasi*, a scarab beetle also found in inflorescences of *P. solimoense* in the same area. The flowering cycle lasted two days and the inflorescence exhibited features typical for beetle pollination (e.g., floral chamber, food rewards, flower heating). The flowering process is well synchronized with the night activity of *Cyclocephala* visitors. The spadix temperature was measured during the entire flowering cycle in the field in French Guiana and in greenhouse conditions at the Montreal Botanical Garden. Both measurements gave a similar temperature pattern with a two hour delay at the Botanical Garden. The spadix warmed up twice during the flowering period and its temperature was not significantly different from that of ambient air between the two peaks. These two temperature peaks are also well synchronized with the arrival and departure of the beetles on two consecutive nights.

Key words: *Cyclocephala*, Dynastinae, heat production, pollination specificity.

Introduction

Beetles are important or exclusive pollinators in tropical and subtropical species in only a few families of Cycadales (Cycadaceae, Zamiaceae), dicotyledonous angiosperms (Annonaceae, Calycanthaceae, Eupomatiaceae, Magnoliaceae, Nymphaeaceae) and monocotyledonous angiosperms (Araceae, Arecaceae, Cyperaceae) (Gottsberger, 1986^[7], 1989a^[8], 1990^[10], 1991^[11]; Henderson, 1986^[16]; Young, 1986^[29]; Irvine and Armstrong, 1990^[17]; Eriksson, 1994^[3]; Momose et al., 1998^[22]; Beath, 1999^[1]). All these beetle-pollinated species have some common floral characters that can be seen as convergent evolution (Gottsberger, 1989b^[9]; 1990^[10]). Pollination may be diurnal or crepuscular, according to the insect taxa (Gottsberger, 1989b^[9]). Flowers or inflorescences are generally protogynous, they often have a floral chamber where beetles can remain hidden; they offer food rewards (secretions, food bodies). They attract beetles through odour emissions which

are often accompanied by the production of heat (Gottsberger, 1990^[10]).

In general, beetle-pollinated flowers are visited either by a few related species or by numerous insects belonging to different orders (Diptera, Coleoptera, Hymenoptera). However, in some taxa, beetle pollination can be specific (Gibbs et al., 1977^[4]; Gottsberger and Amaral, 1984^[12]). Moreover, in cases where several insect species are visitors, differences in pollination efficiency may occur (Young, 1986^[29]).

Little is known about the pollination of Araceae, a family of 3300 species, for which only about 20 species have been studied (Grayum, 1990^[14]; Mayo et al., 1997^[20]). Principal pollinators of Araceae flowers are beetles, flies and bees (Grayum, 1990^[14]). Similarly, the pollination biology of *Philodendron*, the second largest genus of Araceae with 700 species, is poorly documented with only two field studies (Gottsberger and Amaral, 1984^[12]; Gibernau et al., 1999^[5]) and some observations (Madison, 1979^[18]; Young, 1987^[30]; Schatz, 1990^[24]; Grayum, 1996^[15]; Croat, 1997^[2]). It appears from these studies that *Philodendron* inflorescences are pollinated by dynastid scarabs, even if other insects can be found in the inflorescences.

The aim of this paper is to document the pollination ecology of *Philodendron melinonii* in French Guiana and the pattern of heat production of its inflorescence.

Materials and Methods

The species

Philodendron melinonii Brongn. ex Regel (subgenus *Philodendron*, section *Philodendron*) is an epiphyte, usually growing below the tree canopy, but occasionally persisting on logs or on rocks. The inflorescences are situated at the base of the leaves in the middle of a mass of dried bracts. Although they have a long peduncle (9–10 cm), only the upper half of the spathe (20–25 cm) emerges from the bract mass. The spathe is light pink–yellow below the constriction, white–pink on the back above it, and white–green around the opening. Some red spots (extra-floral nectaries) are present on the side opposite the spathe, opening in two zones at the level of the constriction and on the top of the spathe. The spadix (13–15 cm) is whitish and about one third shorter than the spathe. The female flow-

ers occupy the lower portion (3–4 cm) of the spadix, whereas the male flowers are located on its upper portion (7–8.5 cm). In between, there is a short intermediate zone (2.5–3 cm long) of sterile male flowers.

Study sites

This study was conducted in July 1999 at two locations in French Guiana. On the lakeside of Petit Saut dam (Kourou region), four individuals bearing several inflorescences were growing on a huge rock, several hundred meters from the forest. A few flowering individuals were also growing in the shadow of a tree-fall gap along National Road #1 (PK101). These few individuals were established 30–60 m from a large population of *Philodendron solimoesense* A. C. Smith (about 40 individuals). The flowering cycle of *P. melinonii* was also studied under greenhouse conditions at the Montreal Botanical Garden in August 1999, where two individuals regularly flower (#2246–1986 and #3564–1987). Voucher specimens: *Barabé & Savoie 142* (MT), *Barabé & Savoie 143* (MT), *Barabé & Gibernau 144* (MT).

Observations and temperature measurements

During this study, four inflorescences opened in the field (two along the National road and two on the lakeside) and two at the Montreal Botanical Garden. The flowering process was observed at different times of the day. The number, gender and species of insect visitors of *P. melinonii* inflorescences in French Guiana were recorded and voucher specimens for identification were taken. The length of the different spadix zones (female, male sterile and male) was also measured.

Temperatures of the spadix and the ambient air were recorded with a Digi-Sense® DualLogR® thermocouple thermometer every 10 min. To obtain the temperature of the spadix, the thermometer was inserted, to about 5 mm depth, in the spadix, in the middle of the fertile male zone. We recorded temperature for the complete flowering cycle on one inflorescence in French Guiana and one at the Montreal Botanical Garden.

Results

Pollination biology

The flowering cycle of *P. melinonii* was similar to that of other known *Philodendron* species (Gottsberger and Amaral, 1984^[12]; Gibernau et al., 1999^[5]). Flowering appeared to be asynchronous, with a delay of several days in the opening of two successive inflorescences on the same individual. The flowering cycle lasted two days with the spathe beginning to open in the middle or late morning of the first day. By the end of the afternoon (16:30–17:00), the spathe was wide open (2/3 of the spathe length), with the spadix strongly protruding forward. At 18:00–18:30, the spadix began to warm up and an odour emanated from the inflorescence. At this time, the stigmas were moist and appeared receptive. Visiting beetles arrived during the night after 19:30 when the inflorescence was warm and odoriferous. They remained throughout the next day at the base of the inflorescence above the female flowers and fed on the sterile male flowers.

During the morning of the second day, the spathe closed slightly, with only the upper half remaining open. In the afternoon, a reddish resin was secreted by the upper sterile male flowers and the fertile male flowers. Resin drops of a diameter of 1–2 mm were present on the male zone of the spadix, mostly at the base and in the middle. At dusk (18:30), the spathe started to slowly close by wrapping around the spadix, from the base upwards. At about 20:00, the anthers released the pollen which stuck to the resin covering the beetle's cuticle before the beetles flew away.

Insect visitors

Inflorescences of *P. melinonii* were visited by a dynastid, *Cyclocephala colasi* (Scarabaeidae, Coleoptera) at the two locations and by one species of an unidentified staphylinid at the lakeside. The two inflorescences along the National road were, respectively, visited by two and 13 *C. colasi* while the two inflorescences at the lakeside contained, respectively, two and 10 *C. colasi* (overall mean \pm SD: 6.75 ± 5.6). Beetle copulation took place in the floral chamber. In all the visited inflorescences, the 950–1000 sterile male flowers were more or less eaten (up to 55%) by the second day, depending on the number of occupying beetles. On one occasion, the stigmas also seemed to be damaged but the ovaries were intact.

Spadix temperature

The ambient air temperature range was similar in French Guiana and in greenhouse conditions at the Montreal Botanical Garden. At the beginning of the first night, the spadix temperature clearly increased for 3.5 h, whereas ambient temperature dropped to 22 °C (Fig. 1). The temperature peaked at 37 °C (13.5 °C above air) for 30 min in French Guiana (at 19:30) and at 35 °C (10.1 °C above air) in the Botanical Garden (at 21:20). Then the spadix temperature decreased sharply to just above ambient temperature and both temperatures followed the same variations until the next evening. During the second evening (18:50 or 21:00), whereas air temperature cooled, the spadix temperature reached a plateau (in French Guiana) or peaked a second time (at the Botanical Garden), both at about the same temperature of 32 °C (6 °C above air, Fig. 1). After this, the spadix temperature decreased to a level similar to ambient as the spathe closed around the spadix. There was a clear delay of 2 h between the temperature patterns in French Guiana and at the Montreal Botanical Garden.

Discussion

The flowering and pollination cycle of *P. melinonii* is typical of beetle-pollinated flowers: a 2-day flowering period, heat production plus emission of a strong odour, presence of a floral chamber where pollinators copulate and shelter during a night and a day, protogynous inflorescences, offering of food rewards (stigmatic secretions, male sterile flowers), and closure of the inflorescences with pollinator exclusion. The consumption of sterile flowers can be significant (up to 55%) when the inflorescence is visited by numerous individuals of *Cyclocephala colasi* (up to 13). A positive correlation between the number of scarab visitors and the proportion of sterile flowers eaten has also been found in *Philodendron solimoesense* (Gibernau et al., 1999^[5]).

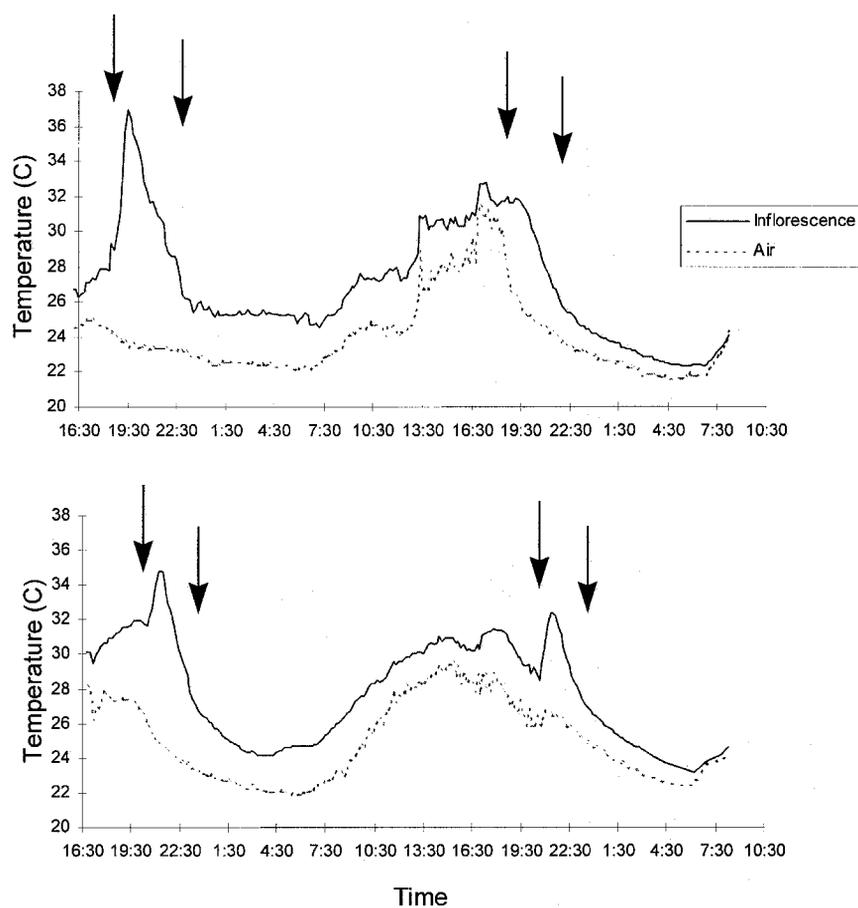


Fig. 1 Temperature curves of the spadix (full line) and ambient air (dotted line) during two days of flowering for *P. melinonii* in French Guiana (upper graph) and in greenhouse conditions at the Montreal Botanical Garden (lower graph). The arrows indicate the periods of heating.

Inflorescences of specimens in French Guiana and at the Montreal Botanical Garden behave similarly in their flowering cycles and floral temperature patterns. Such a comparison was possible because the temperature in the greenhouse was comparable to the ambient temperature in French Guiana. The inflorescence of *P. melinonii* heated up twice during two successive evenings. These spadix temperature increases are linked to pollination and well-synchronized with *Cyclocephala* activity. The first phase of thermogenesis corresponds to the attraction and the arrival of *Cyclocephala* and may help to volatilize odoriferous compounds present in the spadix (Meeuse and Raskin, 1988^[21]; Gottsberger and Silberbauer-Gottsberger, 1991^[13]; Skubatz et al., 1995^[27]; Skubatz and Kunkel, 1999^[26]). The second temperature peak corresponds to pollen release and departure of the pollen-loaded *Cyclocephala*.

The pattern of the spadix temperature in *P. melinonii*, with two heating peaks on consecutive flowering nights, is typical for species of the subgenus *Philodendron*: *P. acutatum*, *P. pedatum* and *P. squamiferum* (Gibernau and Barabé, 2000^[6], unpub.). This pattern contrasts with species of subgenus *Meconostigma*: *P. selloum*, *P. solimoense*, in which the spadix heats up on the first night and then remains warm during the following day (Gottsberger and Amaral, 1984^[12]; Seymour, 1999^[25]; Gibernau and Barabé, 2000^[6]).

Inflorescences of *P. melinonii* were visited by a dynastid scarab, *Cyclocephala colasi*, which has been described as a pollinator of *P. solimoense* (Gibernau et al., 1999^[5]). Inflorescences of *P. melinonii* were visited by less beetles than those of *P. solimoense*

(6.75 ± 5.6 versus 21 ± 12). This difference may be due to a shorter male zone in *P. melinonii* (10–12 cm) than in *P. solimoense* (20–25 cm), since the male zone plays an important role in pollinator attraction through the production of heat and the emission of odour (Skubatz et al., 1995^[27]; Seymour, 1999^[25]; Gibernau et al., 1999^[5]). In the first sample from the National Road, *P. melinonii* individuals were growing near a flowering population of *P. solimoense*, but at the lakeside site, *P. melinonii* individuals were isolated by several hundred meters from the forest and thus from conspecifics or *P. solimoense*. Whilst in the first case (15 beetles), “visit error” might have been due to the proximity of flowering *P. solimoense*, the second case (12 beetles) indicates that *C. colasi* visit inflorescences of isolated *P. melinonii*. Our sample size was small, but it seems likely that *C. colasi* is the main pollinator of *P. melinonii* in this area.

Our observations indicate that *P. melinonii* and *P. solimoense* may synchronously share the same pollinator. Since these two species can flower at the same time in adjacent populations, the probabilities of pollen exchange are likely to be high. *Cyclocephala* switching from one species to others in flower have been documented in several *Philodendron* species and other genera, such as *Caladium*, *Dieffenbachia*, *Homalomena*, *Syngonium* and *Xanthosoma* (Valerio, 1984^[28]; Pellmyr, 1985^[23]; Young, 1986^[29]; Croat, 1997^[2]). Geographical variations of pollinators (*Cyclocephala* species) visiting the same plant have also been documented (Gottsberger, 1986^[7]; Croat, 1997^[2]; Beath, 1999^[11]).

Philodendron species have few, if any, genetic barriers to cross pollination, and unrelated species readily cross pollinate and produce intermediate offspring in controlled conditions (Mayo, 1991^[19]; Croat, 1997^[21]). However, although hybrids can be readily produced under greenhouse conditions, there is little evidence of hybridization in wild populations (Schatz, 1990^[24]) and no hybrids of *P. melinonii* and *P. solimoense* have been observed. For this reason, prevention of cross pollination by such mechanisms as odour discrimination, ecological or phenological isolation, must thus be critical for preventing interspecific hybridization (Gottsberger, 1990^[10]; Schatz, 1990^[24]; Croat, 1997^[21]).

From this perspective, further studies will be necessary to determine whether *Cyclocephala colasi* pollinates *P. solimoense* and *P. melinonii* indiscriminately or if these two *Philodendron* species are incompatible.

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