

Pollination ecology of *Philodendron squamiferum* (Araceae)

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Abstract: In French Guiana, inflorescences of *Philodendron squamiferum* Poepp. (Araceae) were regularly visited by the scarab beetle *Cyclocephala simulatrix* Hölne and (Scarabaeidae, Coleoptera) occasionally by *Cyclocephala tylifera* Hölne. The flowering cycle lasted 2 days, and the protogynous inflorescence exhibited features typical of beetle pollination (floral chamber, food rewards, flower heating). The spadix temperature was measured during the entire flowering cycle in French Guiana and at the Montreal Botanical Garden. Both sets of measurements gave a similar temperature pattern. The spadix warmed up twice at the beginning of each evening with no notable heat production between the two peaks. These two temperature peaks were well synchronized with the arrival and departure of beetles.

Key words: beetle pollination, *Cyclocephala*, Dynastidae, floral traits, thermogenesis, French Guiana.

Résumé : En Guyane française, les inflorescences de *Philodendron squamiferum* Poepp. (Araceae) sont régulièrement visitées par *Cyclocephala simulatrix* Hölne (Scarabé-, Coléoptère) et occasionnellement par *Cyclocephala tylifera* Hölne. Le cycle de floraison dure 2 jours avec une inflorescence protogyne qui possède des caractères typiquement liés à la pollinisation par des coléoptères (chambre florale, ressource alimentaire, production de chaleur). La température du spadice a été mesurée durant toute la durée du cycle floral en Guyane française et au Jardin botanique de Montréal. Les deux types de mesures ont donné des résultats similaires. Le spadice chauffe par deux fois en début des deux soirées du cycle floral avec aucune production de chaleur entre ces deux événements. Ces deux pics de chaleur sont bien synchronisés avec d'une part l'arrivée, et d'autre part le départ des coléoptères de l'inflorescence.

Mot clés : pollinisation, *Cyclocephala*, Coléoptère, Dynastide, thermogénèse, traits floraux, Guyane française.

Introduction

Beetle pollination is prominent in several tropical or subtropical plant families: Annonaceae, Araceae, Arecaceae, Boweniaceae, Calycanthaceae, Cycadaceae, Cyclanthaceae, Eupomatiaceae, Magnoliaceae, Nymphaeaceae, and Zamiaceae (Bernhardt 2000). These taxa share some common features resulting from convergent evolutionary developments (Gottsberger 1990; Bernhardt 2000). Their inflorescences are generally protogynous and have a floral chamber. Beetle pollinators commonly stay in the floral chamber, where they mate. The flowers produce different kinds of nutritional rewards for the beetles: rich floral tissue

(e.g., petals, staminodia), pollen, and secretions (e.g., stigmatic exudate). Another characteristic feature of beetle pollination is the production of heat by the flowers. This increase in flower temperature is related to pollination, as it is not produced randomly during floral development. This phenomenon was first discovered by Lamarck (1778) on *Arum italicum* in France (Bay 1995). Heat production is generally associated with the emission of fragrance by the flower and the attraction of beetles (Meeuse 1975, 1978; Moodie 1976; Meeuse and Raskin 1988; Gottsberger 1990).

Among the Araceae, the pollination of the genus *Philodendron*, the second largest genus of Araceae with approximately 700 species (Mayo et al. 1997), is only known from three field studies (Gottsberger and Amaral 1984; Gibernau et al. 1999, 2000) and some observations (Madison 1979; Young 1987; Schatz 1990; Grayum 1996; Croat 1997). From these studies, *Philodendron* appears to be pollinated by dynastine scarab beetles, even if other insects can be found in the inflorescences. Inflorescences of *Philodendron* exhibit several floral features characteristic of beetle pollination and particularly the production of heat (Gottsberger 1990; Bernhardt 2000). Most studies show partial temperature records only during the maximum production of heat;

Received 28 August 2001. Published on the NRC Research Press Web site at <http://canjbot.nrc.ca> on 18 March 2002.

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continuous temperature records during the flowering cycle are less common (Gottsberger and Amaral 1984; Seymour 1999; Seymour and Blaylock 1999; Barabé and Gibernau 2000; Gibernau and Barabé 2000). The aim of this paper is to document the pollination ecology of *Philodendron squamiferum* Poepp. (subgenus *Philodendron*) and particularly the pattern of heat production by its inflorescences throughout the flowering cycle in the field and at the Montreal Botanical Garden.

Materials and methods

Philodendron squamiferum is an appressed hemiepiphytic climber. The inflorescence's spathe, 8–11 cm long, is red externally and white internally with vertical red lines within the floral chamber. The white spadix bears unisexual male and female flowers and is 7–10 cm long. The pistillate flowers occupy the proximal portion (3–4 cm) of the spadix, whereas the staminate flowers are located on its distal portion (3–5 cm). There is also a small intermediate zone (0.6–1.2 cm) of sterile male flowers.

Our study was conducted in July 1999 on one population of *P. squamiferum* in a valley at kilometre point 23 along the road to the Petit Saut dam (Kourou region) in French Guiana. Fifteen individuals of *Philodendron* were growing on erect or fallen trunks along a stream in a primary rain forest (voucher specimens: Barabé 59 (MT)). To complement the field study, the flowering cycle of *P. squamiferum* was observed in August 1999 at the Montreal Botanical Garden where three individuals flower regularly (No. 2201-1986 (two specimens) and No. 2365-1992).

Individuals of *Philodendron* were regularly monitored, and observations were made when an inflorescence opened. During this study, seven inflorescences opened in the field and three at the Montreal Botanical Garden. The number, sex, and species of insect visitors to inflorescences of *P. squamiferum* in French Guiana were recorded and voucher specimens were sent to R.P. Dechambre at the Museum of Natural History, Paris. Temperatures were recorded every 10 min with a Digi-Sense® DualLogR® thermocouple thermometer equipped with two probes (Type T). We recorded the temperature for the complete flowering cycle of one inflorescence in French Guiana and two inflorescences of different individuals at the Montreal Botanical Garden. To obtain the temperature of the spadix, one probe was inserted less than 5 mm deep into the spadix, in the middle of the fertile male zone. Ambient air temperature was measured with the other probe near the spadix (i.e., 10 cm away).

Results

Flowering cycle

The flowering cycle of each inflorescence studied lasted 2 days. The spathe began to open mid- or late morning on the first day. By the end of the afternoon, the spathe was open to two 1=1 thirds of its length, with the spadix protruding strongly forward. At dusk, the spadix began to warm up and a faint odor emanated from the inflorescence. Beetle visitors arrived at nighttime when the inflorescence was warm and more strongly odoriferous. During the next day,

the beetles remained at the base of the spadix and ate the sterile male flowers just above the female flowers. During the second day, the spathe blade had closed slightly and was open only above the constriction (half of the spathe length). In the afternoon, orange resin was secreted by the spadix along a gradient from the base to the top of the male zone. Resin drops were bigger at the base of the male zone than at the top. Hence, beetles crawling up the spadix were likely to be more or less coated with resin before reaching the pollen. This process may ensure a better "harvest" of pollen grains by the sticky insect cuticles. At dusk, the spathe blade closed by slowly wrapping around the spadix from the base to the upper part, thus forcing the beetles out of the inflorescence. At this time, the anthers released the pollen, which became stuck onto the resin coating the beetles.

Insect visitors

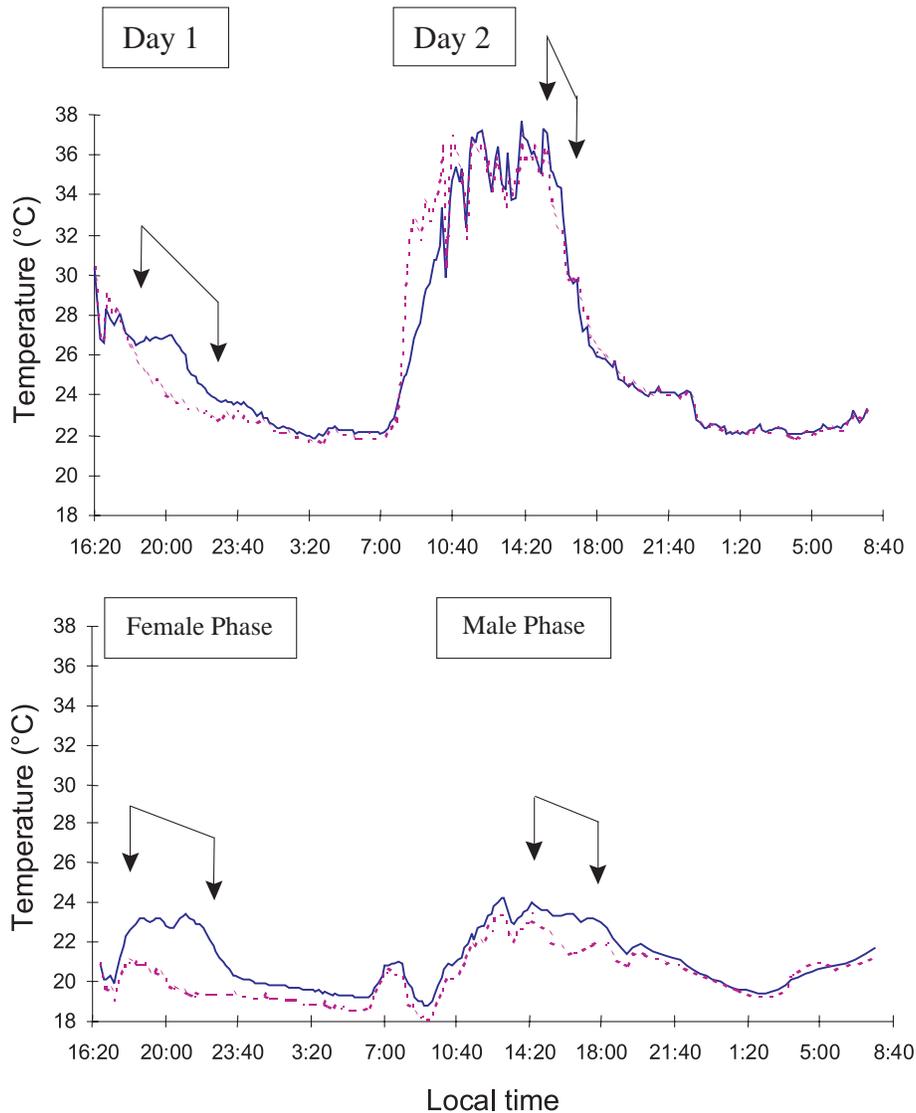
In French Guiana, we found only two insect species, both belonging to the subfamily Dynastinae (Scarabaeidae, Coleoptera), in inflorescences of *P. squamiferum*: *Cyclocephala simulatrix* Hölne (14–17 mm long) and *Cyclocephala tylifera* Hölne (14–16 mm long). One inflorescence had no insects, but the other six were each visited by one to five beetles. The six inflorescences were visited by a total of 10 *C. simulatrix* (six males and four females) and two *C. tylifera* (both females). The two *C. tylifera* were found in two different inflorescences always in association with *C. simulatrix*. *Philodendron squamiferum* thus appears to be pollinated by dynastid beetles.

In all of the inflorescences visited, the sterile male flowers (seven to nine rows) were entirely eaten by the second day but the ovaries and stamens were not damaged. Sterile male flowers thus appear to be a food reward for *Cyclocephala* visitors.

Spadix temperature

Inflorescences in French Guiana and the Montreal Botanical Garden behaved similarly in terms of their floral thermogenetic pattern. At the beginning of the first night, the spadix temperature increased and reached a plateau at 23°C (at the Montreal Botanical Garden) or 26°C (in French Guiana) for 3 h (19:00–22:00), whereas ambient temperature dropped to 19 or 22°C (Fig. 1). The spadix temperature was at this time 3–4°C above that of ambient air (Fig. 2). Then the spadix temperature decreased to near ambient temperature, and both temperatures followed the same variations. Important variations in temperature and negative temperature differences may be recorded during rains (Fig. 2, upper graph). At the end of the afternoon of the second day (15:40–17:00), although air temperature cooled, the spadix temperature increased and reached a second plateau (Fig. 1) 2–2.5°C higher than ambient air (Fig. 2). This second phase was clearer at the Montreal Botanical Garden than in French Guiana. Finally, the spadix temperature decreased and became similar to the ambient temperature as the spathe closed around the spadix. The maximum temperature differences were higher on the first night than on the second: 3.2 and 3.9 versus 2.4 and 2°C, respectively (3.5 versus 2.6°C for the third inflorescence (not shown)).

Fig. 1. Temperature curves of the spadix (solid line) and ambient air (dotted line) during 2 days of flowering for a specimen of *P. squamiferum* growing either in French Guiana (upper graph) or at the Montreal Botanical Garden (lower graph). Arrows indicate the heating periods.



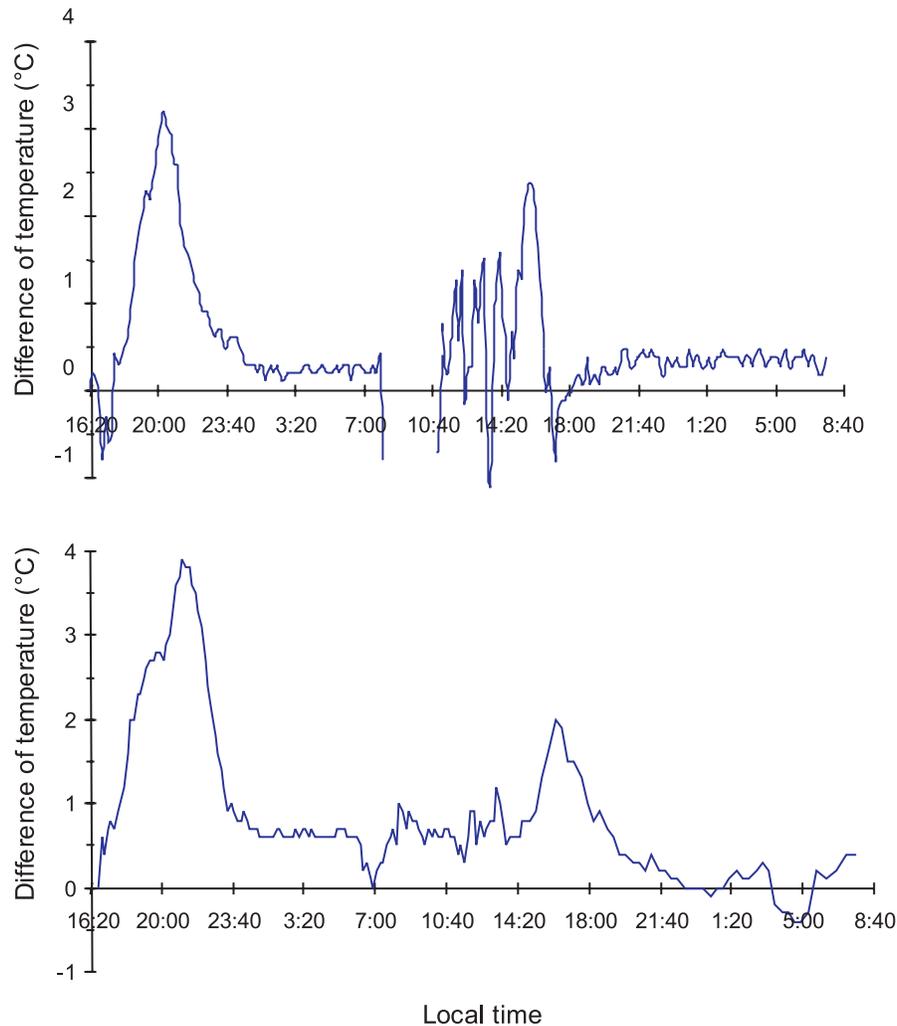
Discussion

Our field observations suggest that *P. squamiferum* is pollinated by dynastine scarab beetles, certainly by *C. simulatrix* and occasionally by *C. tylifera*. Interestingly, these two scarab species have not been mentioned as visitors of any other *Philodendron* inflorescences (Gottsberger 1986; Schatz 1990; Croat 1997). Like other known *Philodendron* species, *P. squamiferum* displays features characteristic of cantharophily, e.g., beetle pollination (Gottsberger and Amaral 1984; Gottsberger 1990; Dieringer et al. 1998; Gibernau et al. 1999, 2000). The inflorescence is protogynous, and the base of the spathe is more or less closed, forming a chamber around the female flowers where the beetles remain where copulations may take place as in *Philodendron solimoesense* (Gibernau et al. 1999). In *P. squamiferum*, the sterile male flowers appear to be the food reward, as they were entirely consumed in inflorescences containing *Cyclocephala* by the second day of the flow-

ering cycle. Resin was secreted along the male zone; hence, beetles crawling up the spadix are likely to be coated with resin. This process may ensure a better "harvest" of pollen grains by the sticky cuticle of the beetles.

Another floral characteristic of *Philodendron* is heat production. The flowering cycle of *P. squamiferum* was similar in French Guiana and at the Montreal Botanical Garden to that documented for other species of *Philodendron* (Gottsberger and Amaral 1984; Gibernau et al. 1999, 2000; Barabé and Gibernau 2000; Gibernau and Barabé 2000). This result suggests that the heating cycle is governed by endogenous processes (Meeuse 1978). The spadices of *P. squamiferum* warm up only at the beginning of two consecutive evenings of their flowering cycle (Fig. 2). Inflorescence heating in *P. squamiferum* is synchronized with pollination as in other Araceae (Bay 1995; Bermadinger-Stabentheiner and Stabentheiner 1995; Seymour and Blaylock 1999; Seymour and Schultze-Motel 1999) and is assumed to have at least two roles. First, volatile compounds

Fig. 2. Temperature difference between the spadix and ambient air for one inflorescence of *P. squamiferum* in French Guiana (upper graph) and one at the Montreal Botanical Garden (lower graph). Negative temperature differences in the field may be recorded during rains (upper graph).



are emitted by the male flowers, fertile and (or) sterile, and because heat production occurs at the site of production and storage of the odoriferous compounds, heating may help their volatilization (Meeuse 1975, 1978; Meeuse and Raskin 1988; Skubatz et al. 1995; Skubatz and Kunkel 1999). Second, this temperature increase may keep the spathe chamber warm for the beetles visiting during the first hours of the night (Seymour et al. 1983; Gottsberger and Silberbauer-Gottsberger 1991; Seymour 1999). Scarab beetles require a thoracic temperature of about 30–40°C to be active, and because they are endothermic, their body temperature costs less to maintain if they are in a warm place (Heinrich 1993; Dieringer et al. 1998). Warm beetles are more likely to be more active in the spathe chamber above the female flowers, increasing the probability of pollination (Seymour and Schultze-Motel 1997). The second peak of temperature is associated more with pollen dispersal. Heat may help to release the pollen from the anthers and to warm the beetles before they load pollen and leave the inflorescence. Similar multiple temperature phases can be observed in *Arum*, *Dracunculus*, and *Sauromatum*, in which the male zone is

divided into a fertile region inside the floral chamber and a distal appendix of sterile male flowers, which lies outside the floral chamber. The appendix warms up on the first day, emitting the odor, whereas the fertile male region heats only on the second day, when the pollen is shed (Meeuse and Raskin 1988; Bermadinger-Stabentheiner and Stabentheiner 1995; Seymour and Schultze-Motel 1999).

Despite the fact that measurements in the field showed variations, the pattern of spadix temperature fluctuation in *P. squamiferum* is similar to the patterns in *Philodendron acutatum*, *Philodendron melinonii*, and *Philodendron pedatum*, three other species of subgenus *Philodendron* (Gibernau and Barabé 2000; Gibernau et al. 2000). The spadix warms up on each of the two flowering nights, with no notable heat production between these two events. In contrast, the spadix heats up on the first night and then remains warm during the following day in *Philodendron* species of subgenus *Meconostigma* (Gottsberger and Amaral 1984; Seymour 1999; Gibernau and Barabé 2000). Within subgenus *Philodendron*, the spadix of *P. squamiferum* is shorter (7–10 cm) than that of *P. pedatum*, *P. melinonii*, and

P. acutatum (13–19 cm). Interestingly, the maximum temperature difference between the inflorescence and ambient air seems to increase with spadix length (3.5°C in *P. squamiferum* (7–10 cm), 12°C in *P. pedatum* (13–15 cm), and 13.5°C in *P. acutatum* (17–19 cm) and *P. melinonii* (13–15 cm)). Similarly, a significant positive correlation has been found between cone width and maximum temperature difference between the cone and ambient air in cycads (Tang 1987). Small cones (about 2 cm wide) exhibited a maximum temperature difference of 1–2°C, whereas big cones (10–12 cm wide) heated up to 8–10°C above ambient air (contrary in the genus *Cycas*). Thus, inflorescence size may have a direct impact on the quantity of heat produced and perhaps also on the ability of the inflorescence to attract pollinators.

Further studies are needed to enhance our comprehension of beetle pollination. In particular, an integrated approach (morphology, physiology, and ecology) is necessary in order to determine precisely the role of heat production and of the differentiation of fertile and sterile male flowers in this endogenous process.

Acknowledgements

This research was partly supported by grants from the Natural Sciences and Engineering Research Council of Canada (41794-98) and the Fonds pour la formation de chercheurs et l'aide à la recherche (Quebec) to D.B. We are grateful to the staff of the Environmental Laboratory at Petit Saut for technical support, Damien Labat for field assistance, and D. Charlebois, D. Lauzer, D. Morse, S. Mayo, and two anonymous referees for constructive comments on the manuscript.

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