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SHORT COMMUNICATION

# Reproductive biology of *Montrichardia arborescens* (Araceae) in French Guiana

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Data on the pollination biology of neotropical aroids are still scarce and concern only a few species (Beath 1999, Croat 1997, Gibernau *et al*. 1999, 2000; Mayo *et al*. 1997 and references cited therein). It appears from these studies that *Anthurium*, *Monstera* and *Spathiphyllum* are on the whole pollinated mainly by bees (but see Kraemer & Schmitt 1999), whereas *Dieffenbachia*, *Homalomena*, *Syngonium*, *Philodendron* and *Xanthosoma* are generally beetle-pollinated. Although araceous inflorescences may be visited by several insect taxa (Madison 1979), only a few are the legitimate pollinators for each species (Seres & Ramirez 1995, Valerio 1984, Young 1986).

Previous observations have suggested various modes of pollination in the genus *Montrichardia*. The first published report indicated that *M. arborescens* (L.) Schott is pollinated by bees (Madison 1979), while later observations in Costa Rica suggest pollination by dynastine scarab beetles (Grayum 1986). The latter hypothesis was confirmed by Ramirez & Brito (1992) who mentioned that *M. arborescens* is pollinated by the dynastine beetle *Cyclocephala gravis* in Venezuela, a species that has also been found in inflorescences of *Philodendron grandipes* in Costa Rica (Croat 1997). In this study, we document precisely the pollination ecology of *M. arborescens* and measure characters linked with its pollination and reproduction. Moreover, we identify the volatile compounds emitted by the inflorescences that may be implicated in beetle attraction.

*Montrichardia arborescens* is an erect arborescent (up to 4 m in height) evergreen herb growing in fresh-water habitats (swamps) and along river margins where it forms dense populations. Inflorescences, 1–2 per axil, are 10–15 cm long. The spathe is externally yellow (greenish) and internally white. The pistillate flowers are located on the lower portion (3–4 cm) of the spadix, whereas the male flowers, situated directly above, occupy all the rest of the spadix (7–12 cm). In contrast to *Philodendron*, there are no sterile flowers at all. The spathe and the male zone of the spadix are deciduous and fall after anthesis. Flower and inflorescence development have been previously described (Barabé & Lacroix 2001, Boubes & Barabé 1997).

This study was conducted in July 1999 on two dense populations of several hundred *M. arborescens* established along National Road No. 1 in French Guiana. The first population was situated just outside the city of Kourou (Kilometric Point 60.5) in open swamps, the second population was located at a boat ramp (degrad Sinnamary) on the outskirts of Sinnamary (Kilometric Point 120) along the river bank close to the forest.

Every 3 d, each population of *Montrichardia* was checked and open inflorescences were observed (sexual stage, insect visitors). Voucher specimens were taken and deposited at the Montreal Botanical Garden for *M. arborescens* (Barabé 127 MT) and at the Natural History Museum of Paris for the insects. The flowering cycle was observed on 17 inflorescences over 5 consecutive days. Self-pollination was tested by bagging 12 other inflorescences from 12 individuals in organdy bags prior to their opening, thus preventing pollination by wind or small insects (e.g. thrips). Moreover, 72 non-manipulated infructescences were marked in order to see whether abortion was frequent.

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We recorded the spadix temperature every 10 min using a Digi-Sense® DualLogR® for the complete flowering cycle of two inflorescences. Previous studies have shown that the thermogenetic pattern is stable for a given species (Barabé & Gibernau 2000, Gibernau & Barabé 2000, Gibernau *et al*. 2000, Seymour 1999). In order to obtain the temperature of the spadix, one probe of the thermometer was inserted less than 5 mm deep into the spadix, in the middle of the fertile male zone. Ambient air temperature was measured 10 cm from the spadix with the other probe.

Volatile compounds emitted by two inflorescences were collected using the adsorption–desorption (headspace) technique. One inflorescence from each population was enclosed in a polyethylene terephtalate (Nalophan®) bag. Air was drawn by a pump out of the bag through Tygon tubing over a Porapak®Q (25 ng, 80–100 mesh) collection trap. Volatile compounds were collected on 7 and 13 July 1999 between 18h30 and 20h00, during the period of thermogenic inflorescence activity, on two consecutive nights (female and male phases). Samples were desorbed with 5 ml of hexane. Gas Chromatographic–Mass Spectrometric (GC–MS) analyses were performed with a Finnigan GC8000$^{TOP}$ chromatograph and a MD800 mass spectrometer using a 30-m SPB-20 (0.53 mm i.d.) high-resolution column (Chemistry Department, University of Montréal). The ion source was operated in the electron-impact mode (EI, 70 eV, 180 °C). Full-scan mass spectra (m/z 35–535; 0.49 s/scan, resolution M/—M= 500) were recorded. The temperature of the column was programmed as follows: 40 °C, 5 °C min$^{-1}$ to 240 °C, then 20 min at 240 °C. Tentative compound identifications were performed according to the mass spectrum library and correspond to the best fits to known mass spectra (fit factors > 90%).

The flowering cycle of *M. arborescens* can be summarized as follows. There is only one inflorescence at anthesis on a plant at one time. The spathes of young inflorescences, not yet open, were green. Their stamens were light green and the stigmas pink. The reproductive cycle of the inflorescence lasted 2 d, but as the inflorescence did not close after the beetles departed, its flowering cycle appeared longer (3–4 d). The spathe began to open at mid- or late morning of the first day. The stamen and stigmas were white at this time. By the end of the afternoon, the spathe was open to 2/3–3/4 of its length, with the spadix protruding outside the spathe, but the inflorescences (n = 40) were not visited by beetles before nightfall. At dusk, the stigmas were moist, the spadix began to warm up and an odour emanated from the inflorescence attracting the beetles. During the second day, the spathe had closed slightly (to 1/2 of the spathe length), and the spadix was then erect within the spathe. Beetles remained at the base of the inflorescence and the female flowers bore signs of having had their stigmas chewed. There was no production of resin on the spathe or spadix. At dusk, the spadix warmed up again and the anthers released the pollen, whose grains are extruded in sticky strands, beetles usually leaving at this time. During the third day, the spathe remained open with pollen accumulated at the bottom of the floral chamber, a few beetles were still present in 9 out of the 40 open inflorescences. The spathe began to wilt, its colour changing from yellow to brown, and fell during the third or fourth day after anthesis.

While checking for beetle presence every three mornings in all open inflorescences (n = 141) we noted that 60 of them had not been visited, 53 sheltered dynastine beetles (1–6 individuals; mean ± SD: 1.95 ± 1.34) and 28 presented signs of having been visited (chewed stigmas) but the beetles were absent. Almost all the visited inflorescences had damaged (chewed) stigmas; we believe that in the absence of sterile flowers in this species, the stigmas provide a nutritional reward for the pollinators.

Almost all of the 98 visitors noted in the inflorescences of *M. arborescens* were *Cyclocephala colasi* (Endrödi). Exceptions were one *C. vestita* (Höhne), one *C. varians* (Burmester), one *Aspidolea quadrata* (Endrödi) and four *Erioscelis proba* (Sharp). Using a stereomicroscope, we noted pollen presence on all these collected beetles, but we did not quantify it as part of the pollen was deposited on the stigma during the previous night. Moreover, an undetermined tenebrionid beetle was regularly found in old inflorescences which had shed their pollen (third day), but never in receptive inflorescences (first or second day). During the day, some ants regularly walked all over inflorescence at all stages and even entered inside open spathes. Flies, wasps and *Trigona* bees were often seen on buds or immature inflorescences collecting water or nectar on the exterior of the spathe but never on or in mature inflorescences or infructescences.

All the 12 bagged inflorescences produced infructescences of which four aborted after 2 wk. Hence *M. arborescens* inflorescences are able to produce seeds by self-pollination or apomixis. Moreover, of the 72 non-manipulated infructescences, 31 aborted naturally after 2 wk, suggesting that fruit abortion may be common in this species. These two abortion frequencies are not significantly different ($\chi^2 = 0.4$; df = 1; P = 0.53). Unfortunately, seed viability was not tested as the fruits were not fully mature at the end of the experiment.

*Montrichardia arborescens* exhibits typical features of plants pollinated by beetles (Gottsberger 1990, Schatz 1990) as noted for *Philodendron* species (Gibernau & Barabé 2000, Gibernau *et al*. 1999, 2000; Gottsberger & Amaral 1984). The inflorescences are protogynous and have a floral chamber where most beetle pollinators remain for about 24 h and some for 36 h. The inflorescence produces stigmatic secretions and nutritional rewards for the beetles, but unlike *Philodendron* species, *M. arborescens* does not have sterile flowers (rich floral

tissue). It appears that in this species, as a consequence of the absence of sterile flowers, pollinators often eat stigmas since the female flowers appear to have been chewed by the beetles. However, their ovaries seem to remain undamaged. The fact that the stigmas are chewed by the beetles may play an important role in flower abortion, but this hypothesis remains to be tested.

In *Philodendron* species, pollen is extruded in sticky strands, mixed with a resin secretion, or extruded in amorphous masses (Mayo *et al*. 1997). In *M. arborescens*, pollen is extruded in sticky strands, but without the production of resin. As dynastid beetles are mostly hairless pollinators, there are strong selective pressures to enhance pollen adhesion on their cuticle, so that in beetle-pollinated plants, two major mechanisms have been developed: sticky pollen grains and pollen grains mixed with resin.

The most frequent visitor, *Cyclocephala colasi*, is known to be the pollinator of *Philodendron solimoesense* and *P. melinonii* which flower at the same time in the adjacent forests surrounding the populations of *Montrichardia* (Gibernau *et al*. 1999, 2000). *Erioscelis proba* has been collected in Costa Rica from the inflorescences of *P. brevispathum*, a species not present in French Guiana (Croat 1997). The other beetle species recorded in this study (*C. vestita*, *C. varians* and *Aspidolea quadrata*) have never been collected before in Araceae inflorescences. Further studies are needed to assess if the same population of *C. colasi* indiscriminately pollinates *Montrichardia* and *Philodendron* or if there is some kind of ecological (forest vs. swamp) or behavioural (odour discrimination) isolating factor (Schatz 1990). The lack of specialization in *Cyclocephala* visiting several species has already been documented in several Araceae genera (Croat 1997, Pellmyr 1985, Schatz 1990, Valerio 1984, Young 1986). Moreover, the pollinator of *M. arborescens* in French Guiana (*C. colasi*) is different from that noted in Venezuela (*C. gravis*) (Ramirez & Brito 1992). Such geographical variations of pollinators visiting the same Araceae in different locations have also already been documented (Beath 1999, Croat 1997, Gottsberger 1986).

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. At the beginning of the first night, the spadix heated up whereas the ambient temperature dropped to 24–25 °C (Figure 1). The spadix temperature is higher than ambient air for about 8 h (17h30–00h30) resulting in a maximum difference of 10–11 °C. Then the spadix temperature decreased to near ambient temperature by roughly midnight, and both temperatures followed the same variations during the day (rains may cause important variations in temperature; Figure 1 upper graph). At the end of the second afternoon (around 17h00), whereas the air temperature had cooled down to 22–24 °C, the spadix temperature remained around 32 °C and peaked at 34 °C at about 19h30, 9–9.5 °C higher than the ambient air (Figure 1). The spadix temperature again decreased and by midnight had become similar to the ambient temperature, following the ambient temperature variations.

The pattern of heat production in *M. arborescens* is similar to that of *Philodendron* species of the subgenus *Philodendron* (Gibernau & Barabé 2000, Gibernau *et al*. 2000). The spadix warms up on each of the two nights of the flowering cycle, with no noticeable heat production between these two events. Nevertheless, in *Montrichardia*, the two heating phases are of the same intensity (temperature difference of about 10 °C), whereas in *Philodendron* subgen. *Philodendron* the second heating phase is less intense than the first one (Gibernau & Barabé 2000, Gibernau *et al*. 2000).

The production of heat by the flower is generally associated with the volatilization of fragrant compounds which are implied in beetle attraction (Gottsberger 1990, Meeuse & Raskin 1988). The floral odour of *M. arborescens* inflorescences is composed principally of jasmone and 1,3,5-trimethoxy benzene, with some additional compounds (Table 1). Odour differences appear to be mainly quantitative variations of the same compounds during the second day emission (Table 1). In *Peltandra virginica*, the floral odour changes between female-stage inflorescences and male-stage ones (Patt *et al*. 1995). The floral odour of *Montrichardia* also shows some changes between these two stages (Table 1) but they are not strongly discernible to the human nose. Pollinator attraction could thus also occur during the second night as the inflorescence remains open, emits odoriferous compounds and warms up intensely. This may explain the presence of beetles during the third day in some inflorescences. More precise studies are needed to assess the odour variability among floral stages, individuals or populations. Nevertheless, the odour of the *Montrichardia* inflorescence appears to be dominated by a cyclopentenone derivative (jasmone) and a few benzenoid derivatives (methyl benzoate, methyl salicylate, 1,3,5 trimethoxy benzene, 2-pentenyl-oxy-benzene). The latter compounds are commonly emitted by flowers/inflorescences of many beetle-pollinated taxa (*Eupomatia*, *Encephalartos*, *Liriodendron*, *Magnolia*, *Michelia*, *Nelumbo*, *Victoria*, *Zamia*), sometimes as major compounds, and may be implicated in beetle attraction (Azuma *et al*. 1997, Kite *et al*. 1991, Knudsen *et al*. 1993). On the contrary, the cyclopentenone derivative appears to be a compound peculiar to *Montrichardia*.

Further studies are needed to compare the floral odour of *Montrichardia* and *Philodendron* species sharing *C. colasi* as a pollinator to assess if individuals of this dynastine beetle species respond indiscriminately to these aroids or if there is some kind of specificity (Schatz 1990).

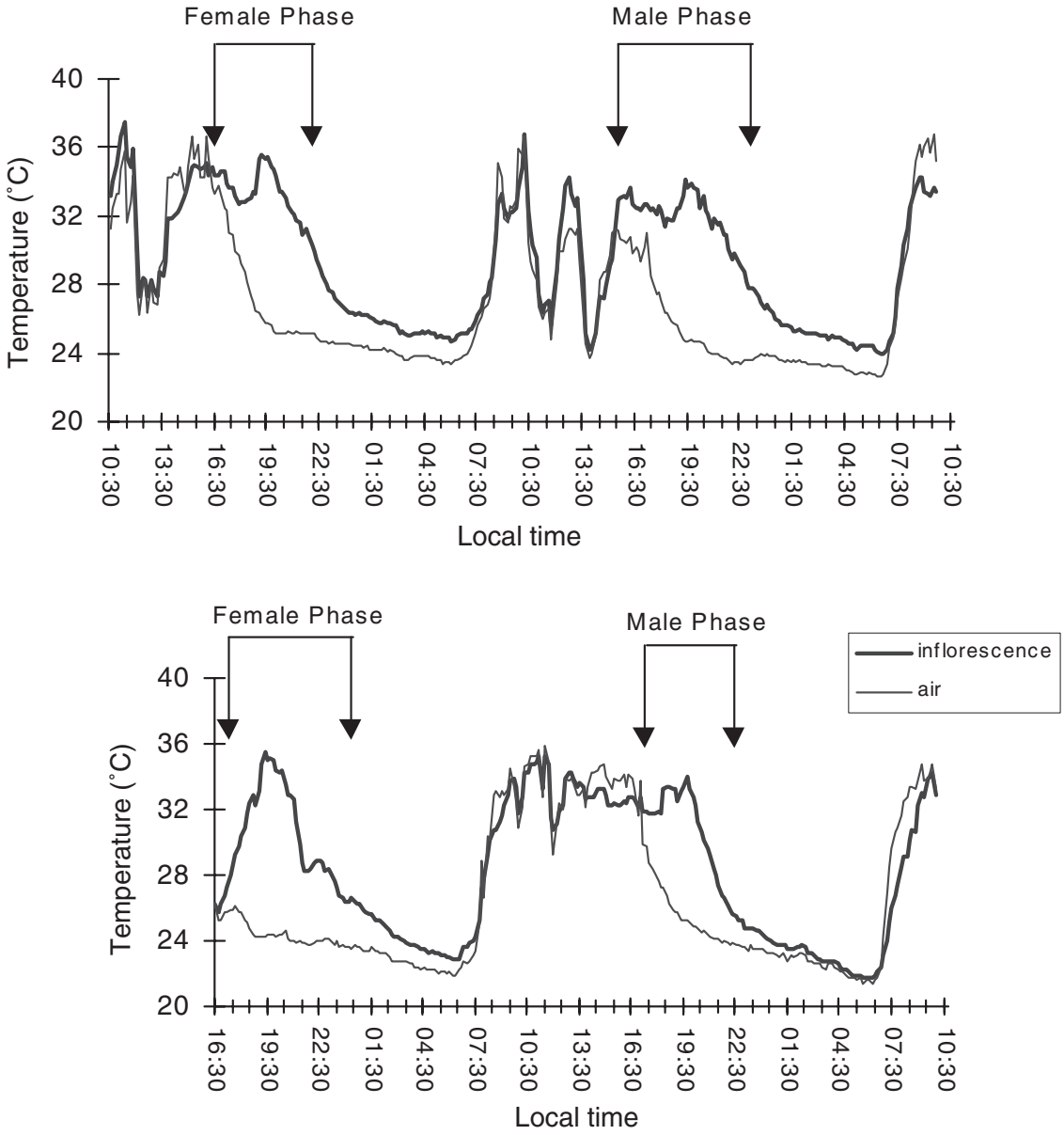


**Figure 1.** Temperature curves of the spadix (thick line) and ambient air (thin line) during 2 consecutive days of the flowering cycle for two *Montrichardia arborescens* inflorescences in French Guiana. The arrows indicate the two periods of heat production (female and male stages).

**Table 1.** Percentages of the major volatile compounds in the fragrant blend emitted by two inflorescences of *Montrichardia arborescens* on two consecutive days in 1999. Compounds are named after tentative identifications according to the mass spectrum library (fit factors > 90%). These six compounds represent between 87 and 95% of all the volatile compounds emitted.

| Compound | Individual 1 | | Individual 2 | |
|---|---|---|---|---|
| | 7 July (%) | 8 July (%) | 13 July (%) | 14 July (%) |
| Methyl benzoate | 1.3 | 0.6 | 4.2 | 17.2 |
| Methyl salicylate | 4.2 | 2.9 | 6.2 | 21.9 |
| 2-pentenyl-oxy-benzene | 6.0 | 11.7 | 8.3 | 7.7 |
| Jasmone | 42.9 | 58.4 | 21.9 | 23.7 |
| 1,3,5 trimethoxy benzene | 39.5 | 11.7 | 39.6 | 11.7 |
| 2,6-ditert-butyl-4-methylphenol | 1.3 | 2.3 | 6.8 | 10.9 |

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