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POLLINATION OF *PHILODENDRON ACUTATUM* (ARACEAE) IN THE ATLANTIC FOREST OF NORTHEASTERN BRAZIL: A SINGLE SCARAB BEETLE SPECIES GUARANTEES HIGH FRUIT SET

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Philodendron acutatum (Araceae) is a hemiepiphyte common to the Atlantic Forest of northeastern Brazil. In two localities, we studied the species' breeding system and associations with flower-visiting insects, along with an analysis of its floral scent composition. The fruit set of self-incompatible *P. acutatum* was high, more than 90%, and inflorescences were exclusively pollinated by one species of scarab beetle, *Cyclocephala celata* (Scarabaeidae, Dynastinae). Pollinators are drawn toward the inflorescences at dusk by strong floral fragrances given off during the female phase of anthesis, along with endogenous heating of the spadix, whose temperatures were recorded at more than 11°C above ambient air. Two other species of flower-visiting *Cyclocephala* were also consistently recovered in blacklight trappings during the flowering period of *P. acutatum*. The fact that only *C. celata* was found in association with *P. acutatum* suggests a local reproductive dependence of the plant to this scarab beetle species. Dihydro-β-ionone and 2-hydroxy-5-methyl-3-hexanone, a rare volatile molecule so far unreported as a floral compound, together accounted for more than 97% of the unique scent composition of *P. acutatum* and might be involved in specific attraction of *C. celata*.

Keywords: Cyclocephala, floral volatiles, pollination specificity, reproductive success, thermogenesis.

Introduction

Scarab beetles (Coleoptera, Scarabaeidae) constitute an unusual group of pollinating insects (Barth 1991; Endress 1996; Richards 1997; Gottsberger and Silberbauer-Gottsberger 2006). Morphological adaptations toward anthophily—readily recognizable among many bees, flies, butterflies, moths, birds, and bats (Müller 1873; Vogel 1954)—are apparently absent in these insects. Thus, it has frequently been concluded that they are unspecialized pollinators and that if they do effectively pollinate a plant species, it is only by chance, since they indiscriminately visit flowers to feed on pollen and/or fertile floral tissues (Buchmann and Nabham 1996). Nevertheless, in tropical and subtropical ecosystems, several Magnoliaceae, Annonaceae, Cyclanthaceae, Arecaceae, Nymphaeaceae, and Araceae rely solely on scarab beetles (Dynastinae, Cyclocephalini) as their effective pollinators (Gottsberger 1986; Bernhardt 2000). According to Schatz (1990), the diverse cyclocephaline scarabs (>500 species) are pollinators of more than 900 plant species in the Neotropics alone. Although not all of the 14 known genera exhibit flower-visiting species, *Cyclocephala* (>350 species), *Erioscelis* (5 species), and *Ruterolyctes* (2 species) are predominantly anthophilous (Endrödi 1985).

Angiosperms pollinated by cyclocephaline scarabs show specialized floral assembly and physiology, generally understood as the result of convergent evolution (Gottsberger 1990; Bernhardt 2000). Their flowers present nocturnal anthesis and are protogynous, which render them functionally self-incompatible as a result of a rigorous temporal partitioning of stigma receptivity (female phase) and pollen release (male phase; Grayum 1990; Mayo et al. 1997). Floral structures are robust and often modified into floral chambers, which function as shelter and mating aggregation sites for the beetles (Gottsberger and Amaral 1984; Bernhardt 2000). Food rewards are available in the form of abundant pollen, nutritious sterile floral tissues (e.g., petals and staminodes) and floral exudates, which entice a prolonged stay of the pollinators and ensure effective pollen transfer (Bernhardt 2000). The large flowers of the Annonaceae and the funnel-shaped inflorescences of the Araceae may host dozens, sometimes hundreds of night-active cyclocephaline scarabs at a time, attracted by floral scents given off during anthesis (Gottsberger 1986). These fragrances are strong and their dispersion is facilitated by flower thermogenicity, a physiological process during which carbohydrates or lipids stored in specific floral tissues are burnt to raise their temperatures above that of the surrounding air, thus enhancing volatilization (Seymour et al. 1983; Gottsberger 1990). Endogenous temperatures of some thermogenic flowers are the highest ever recorded in plants and exceed 45°C (Gottsberger and Amaral 1984; Seymour 1999).

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The large Neotropical genus *Philodendron* (Araceae) might be regarded as the archetype of cyclocephaline scarab-pollinated angiosperms. It is believed that most of its more than 700 species are exclusively pollinated by this particular group of insects, a relationship that likely played a crucial role in the radiation of both the plants and the insects (Schatz 1990; Croat 1997; Gibernau et al. 1999, 2000). These evergreen herbs are found in a wide array of habitats, from forests and wetlands to rock outcrops and open savannas, along a geographic range that stretches from the West Indies to a southernmost limit at the Rio de La Plata region in Uruguay (Mayo et al. 1997). In tropical forests, they often represent a dominant element of the vegetation, and their abundant, juicy infructescences probably constitute an important food resource to birds, bats, and tree-dwelling mammals (Croat 1997; Mayo et al. 1997). Currently, there is detailed published information on the pollination biology of a handful of *Philodendron* species, mainly from studies conducted in the Cerrado and Atlantic Forest of southeastern Brazil (Gottsberger 1986; Gottsberger and Amaral 1984) and the Amazon rain forest of French Guiana (Gibernau et al. 1999, 2000; Gibernau and Barabé 2002). From the diverse but highly impacted Atlantic Forest of northeastern Brazil, however, no species of this genus has been studied so far.

Philodendron acutatum Schott thrives as an ubiquitous and widespread hemiepiphyte, found from north South America to southeastern Brazil (Sakuragui 2001). Easily adaptable to disturbed areas, it is commonly found in gaps and along the edges of forest fragments that portray the severely disjointed landscape of the Atlantic Forest of northeastern Brazil (Ranta et al. 1998). In its northernmost limits, where forest loss percentages may be more than 95% (Silva and Casteleti 2003; Ribeiro et al. 2009), vast sugarcane monoculture fields are predominant, and few forested patches endure in locations where the steep terrain hindered agricultural use and human occupation (Silva et al. 2007). Here, we examine the reproductive biology of *P. acutatum* and address the following questions: (1) How diverse are the pollinating insects? (2) What is the level of reproductive success? (3) What is the composition of the floral scent, and how original is it?

Material and Methods

Studied Species

Philodendron acutatum has sagittate dark-green leaves with long petioles and funnel-shaped inflorescences, composed of an 18–19-cm-long white spadix and an 18–20-cm spathe, which is externally green and internally white above the constriction and red and with vertical dark red striations below. The spadix is composed of staminate flowers (upper 12–13 cm), pistillate flowers (lower 6–7 cm), and a short transition zone between the two (0.4–0.6 cm) comprised of sterile staminate flowers (fig. 1*f*; Gibernau and Barabé 2000). Vouchers of *P. acutatum* are deposited at the Herbário UFP–Geraldo Mariz, Universidade Federal de Pernambuco (UFPE), Recife, Brazil.

Study Sites

The study was conducted in two localities in the Atlantic Forest of the northern coastal region of the state of Pernambuco, northeastern Brazil. The first locality, hereafter referred to as Goiana, is situated in the municipality of Goiana (7°38′S, 34°57′W; altitude ~90 m) and consists of ~100 climbing individuals of *P. acutatum* growing in association with sapodilla trees (*Manilkara zapota* L., Sapotaceae) in an old orchard, observed from January through April 2005. The area is adjacent to a native forest fragment of ~20 ha present in a sugarcane plantation, neighboring the BR-101 north road. The second locality, hereby referred to as Igarassu, is 40 km distant from *Goiana* and consists of a private Atlantic Forest reserve on the grounds of the Usina São José S/A sugarcane company (USJ) in the municipality of Igarassu (7°49′S, 35°02′W; altitude ~110 m). In this area, which represents a total of 66 km^2 of highly scattered forest fragments situated in a sugarcane monoculture matrix (Trindade et al. 2008), populations of *P. acutatum* are commonly found along forest edges and were thus easily accessible for observations taken between January and August 2007.

The region presents a seasonal pluviometric regime with distinct rainy and dry seasons. More than 80% of the average annual precipitation (~1800 mm) falls between February and August, whereas in the drier months from September to January, monthly precipitation is commonly <100 mm. Mean monthly temperatures vary only slightly, between 26°C in March and 23°C in August (Schessl et al. 2008; ITEP 2009).

Flowering Biology

We have addressed the flowering cycle, self-pollination capacity, and fruit set of *P. acutatum* at two sites. Three inflorescences from each site were observed throughout their entire flowering cycle to determine the sequence of events of the anthesis, as well as the behavior of insect visitors. Female and male phases were defined as the beginning of stigma receptivity (determined by the addition of H_2O_2; Kearns and Inouye 1993) and anther dehiscence (pollen release), respectively. Daily observations took place March 9–23, 2005, at Goiana and April 4–16, 2007, at Igarassu at 3-h intervals and at 10-min intervals during the consecutive evenings of floral thermogenic activity. Spontaneous self-pollination was tested by bagging a total 60 inflorescences in organdy bags before the opening of the spathe, preventing access to all insect visitors (Goiana, $n = 20$; Igarassu, $n = 40$). We marked 220 nonmanipulated inflorescences to determine fruit set under natural conditions (Goiana, $n = 20$; Igarassu, $n = 200$). Developing infructescences were also examined for physical evidence of insect visitation, typified as chewed up floral tissues (Igarassu, $n = 40$) in order to assess whether they had been visited by insects.

Floral thermogenesis was also measured to determine the floral temperature patterns during anthesis. Measurements from both the spadix and ambient air were taken at regular 5-min intervals with a portable logging thermocouple thermometer (accuracy 0.1°C; Hanna Instruments). Data were recorded from two intact inflorescences for 39 h during the entire flowering cycle from different individuals chosen randomly at Goiana. For each, one of the thermometer's probes was inserted ~3 mm into the middle of the sterile staminate zone of the spadix, carefully avoiding damage to the deeper

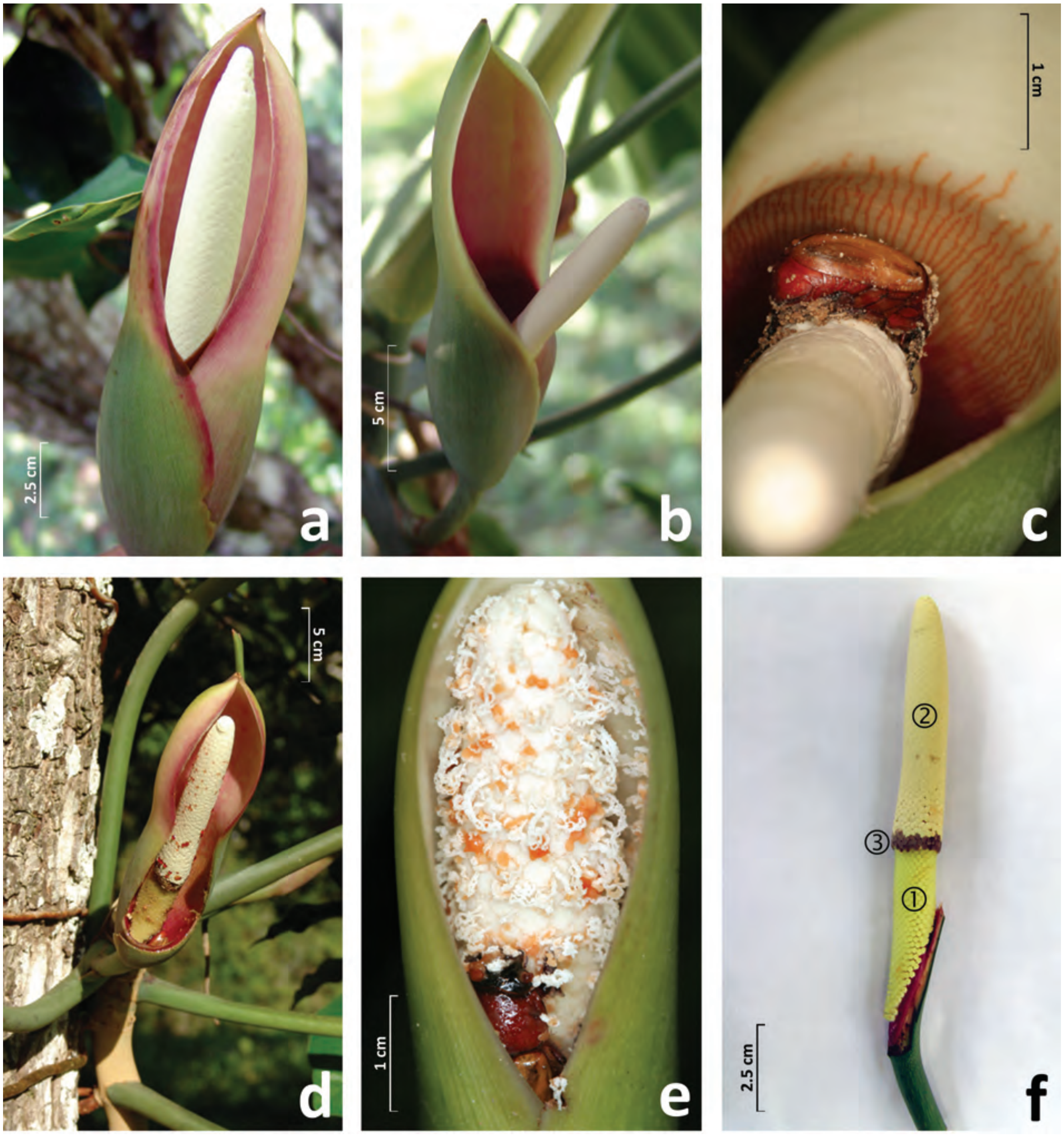

Fig. 1 *Philodendron acutatum*. *a*, Partially opened inflorescence on the morning of day 1 of anthesis. *b*, Fully opened inflorescence late in the afternoon of day 1 of anthesis, moments before the beginning of thermogenic episode. *c*, Pollen-covered *Cyclocephala celata* (Scarabaeidae) arriving at a fragrant inflorescence. *d*, Cross section of the spathe of an inflorescence on day 2 of anthesis, showing beetles at the bottom of the floral chambers and resin droplets over the spadix. *e*, *Cyclocephala celata* exiting inflorescence on the evening of day 2 of anthesis, covered with resin and pollen. *f*, Detail of the spadix of an early day 2 inflorescence: *1*, pistillate zone; *2*, staminate zone; *3*, transition zone bearing sterile staminate flowers. Photographs by A. C. D. Maia and H. Teichert.

tissues of the axis. The other one was kept ~50 cm distant from the inflorescence.

Insect Visitors

Flower-visiting insects were collected in inflorescences of *P. acutatum*, and their visiting frequencies were determined. During the second day of anthesis, between 0900 and 1700 hours, a total of 42 inflorescences were manually opened to quantify and identify insect visitors inside the floral chambers (Goiana, $n = 12$; Igarassu, $n = 30$).

Moreover, at Igarassu, the diversity of night-active cyclocephaline scarabs was surveyed by sampling specimens attracted to light during the flowering period of *P. acutatum*.

Battery-operated blacklight sources were installed monthly between 1730 and 2100 hours on four consecutive nights at different spots (~8-km radius) from April to August, in areas in which populations of *P. acutatum* were found. The surface of the individuals attracted to blacklight was screened under a stereomicroscope for adhering pollen grains and mounted on glass lamins with fuchsin-stained glycerin gelatin (Louveaux et al. 1978; Wittmann and Schlindwein 1995). In the same period, insects were collected within inflorescences. Collected specimens are deposited at the entomological collection of Universidade Federal de Pernambuco (UFPE) and Coleção Entomológica Padre Jesus Santiago Moure (DZUP), Curitiba, Brazil.

Floral Odor

Floral scent samples were collected in situ at Igarassu through dynamic headspace extraction from five female phase and two male phase inflorescences during thermogenic episodes. The inflorescences were enclosed within PET film oven bags (Toppits Bratschlauch, Melitta) from which scented air was drawn for 30 min by a battery-operated membrane pump (ASF Thomas) at a constant flow rate of ~200 mL min^{-1} through sorbent traps containing a 1 : 1 mix of Tenax TA (80/100 mesh, Macherey-Nagel 706318) and Carbopack X (20/40 mesh, Supelco 1–0435). Blanks were simultaneously collected from empty bags. The traps were eluted with 150 μL acetone (p.a. grade), which was kept under −24 °C refrigeration until analysis.

The trapped volatiles were analyzed by combined gas chromatography-mass spectrometry (GC-MS) on a Thermo Finnigan Voyager Mass Spectrometer coupled with a Thermo Trace GC 2000 (Thermo Fisher Scientific), equipped with a CP-Wax 52CB column (Varian; 30 m × 0.25 mm i.d., 0.25-μm film thickness). For each sample, 0.6 μL of the elution was injected on column. GC oven temperature was set at 60°C for 3 min, then increased by 2.5°C min^{-1} to 240°C, and then held steady for 10 min. Helium carrier gas flow was maintained at a constant pressure of 100 kPa. The MS interface was 200°C, and mass spectra were taken at 70 eV (in EI mode) with a scanning speed of 0.5 scan s^{-1} from m/z 20–350. Compounds were identified by comparison of their mass spectra and retention times with those of authentic reference samples available from the Givaudan SA reference compound collection with the Xcalibur 2.0 software (Thermo Fisher Scientific). The peak areas on the chromatograms were integrated for the total ion current signal, and their values were used to determine the relative amounts of each compound.

Results

Flowering Biology

Philodendron acutatum individuals were first observed to be flowering at both sites by early January, whereas the last opened inflorescences were seen by late April at Goiana and by early June at Igarassu, following the arrival of yearly heavy seasonal rainfall. Each flowering individual bore several inflorescences at different stages of maturation disposed in a spiral pattern, but only a single mature inflorescence was open at a time.

Inflorescences are born erect with the spathe fully enclosing the spadix. They exhibit a 2-d flowering cycle and are protogynous, undergoing a female and male phase on consecutive evenings. In the morning of the first day of anthesis, from 0930 to 1030 hours, the spathe slowly opens from the apex down to expose the spadix, which also gradually protrudes outward throughout the day (fig. 1*a*). By late afternoon, the spathe is open to its fullest and the spadix is tilted at a 45° angle (fig. 1*b*). At dusk, around 1730 hours, the stigmas at the base of the spadix are moist and receptive. The inflorescences begin to emanate an intense sweet odor, following perceptible heating of the spadix (fig. 1*c*). Temperatures rapidly rise and reach their peak in ~1 h, being recorded at a maximum of 38.6° or 38.1°C, 11.6° or 11.9°C above the ambient air temperature (fig. 2). From that point on, the spadix slowly cools down, and the detectable thermogenic episode is over in ~5 h. During the remainder of the evening and following day, the spadix begins to slowly retract toward the spathe. Early in the afternoon on the second day of anthesis, around 1400–1530 hours, the inner surface of the spathe and both fertile and sterile staminate zones of the spadix produce droplets of a viscous, sticky orange resin (fig. 1*d*). Also, the spathe slowly encloses the spadix from the base up. A second thermogenic episode, more discrete than that of day 1, takes place between 1615 and 1715 hours, during which temperatures reach 34.1° or 33.5°C, 4.7° or 4.1°C above the ambient air temperature. During this interval, there is no perceivable odor emission, and pollen is abundantly released from the upper portion of the spadix, now only partially exposed (fig. 1*e*). One to three hours later, the spathe is completely closed, and a mix of pollen and sticky resin functions as a cement, sealing the edges.

Reproductive success was evident 5–8 d after the end of anthesis by discrete enlargement of the ovaries. The spathe bulges to accommodate the developing berries until they are fully ripe (45–60 d later), when it eventually withers and exposes the sweet scented infructescence.

At both sites, fruit set was high for nonmanipulated inflorescences accessible to flower visitors, averaging 91.8% (Goiana, 95.0%; Igarassu, 91.5%). In contrast, only one of the inflorescences bagged for self-pollination developed into infructescences (1.7%). Nonpollinated inflorescences dried out within 2–5 d following anthesis.

Insect Visitors and Effective Pollinators

At both sites, the inflorescences of *P. acutatum* were frequently visited by scarab beetles of the species *Cyclocephala celata* Dechambre, 1980. At Igarassu, no other flower visitors occurred, and at Goiana we recorded stingless bees of an undescribed species of *Trigona* (Apidae, Meliponini) and individuals of an unidentified rove beetle species (Staphylinidae). The bees were observed in two inflorescences during the male phase, gathering droplets of sticky resin at the upper spadix and chewing on staminate flowers. We did not see them venture toward the pistillate flowers, nor did we observe pollen adhered to their bodies. The minute rove beetles (total body length = 1.0–1.5 mm) were frequently seen inside

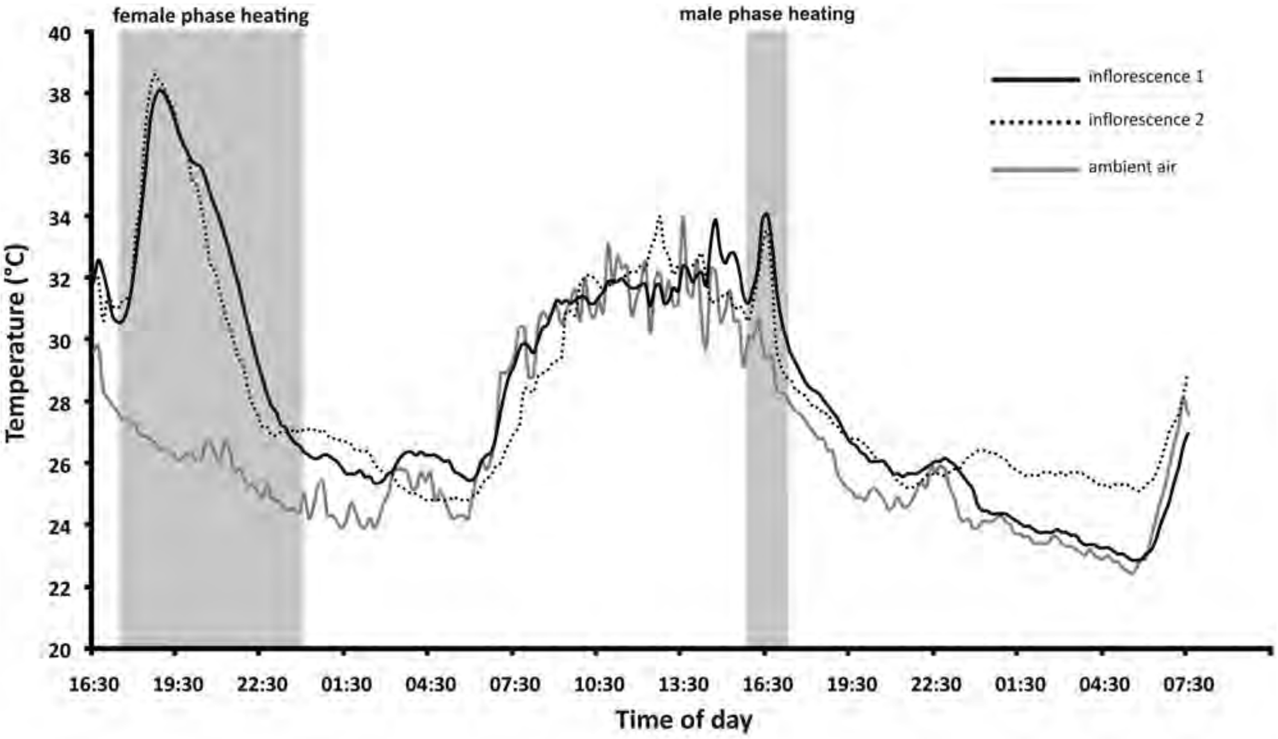

Fig. 2 Temperature curves of the ambient air (gray line) and sterile staminate zone of the spadices of two inflorescences (solid and dotted lines) during the biphasic flowering cycle of *Philodendron acutatum* (Araceae). Vertical gray bands represent the heating intervals during the female phase (day 1) and male phase (day 2).

the floral chambers of manually opened inflorescences (58.3%), sometimes numbering hundreds of individuals. They arrived at the inflorescences during the female phase of anthesis, even hours before thermogenic activity or odor emission. On inspection, no pollen grains were attached to their body surfaces, and they mostly never left the inflorescences, even after total enclosure of the spathe at the end of day 2. Thus, neither *Trigona* bees nor rove beetles were effective pollinators.

All inflorescences opened at day 2 of anthesis bore *C. celata* individuals inside their floral chambers (total body length = 1.5–1.8 cm). The mean number of beetles found per inflorescence was 3.8 ± 2.2 (SD) and 14.6 ± 8.0 (SD) at Goiana and Igarassu, respectively. The highest number of beetles recorded inside a single inflorescence was 9 and 33 at Goiana and Igarassu, respectively.

With the strong odor emission at dusk and early evening (~1700–1930 hours), the scarabs were seen flying around and rapidly entering the inflorescences, with their bodies covered with a thick coating of sticky resin and pollen (fig. 1*c*). Once inside, they agglomerated at the bottom of the warm floral chambers, where they remained highly active, copulating and feeding on the oil-bearing sterile staminate flowers (fig. 1*f*). Activity was less intense during sunlight hours on the following day. Early on the second evening, with the closing of the spathe, the part-time tenants were reluctantly expelled through the narrow exit left by the closing spathe—in this process, their bodies became encrusted with a resin and pollen mix with which they flew away toward receptive female phase inflorescences (fig. 1*e*).

Blacklight collecting at Igarassu revealed the presence of four different species of night-active cyclocephaline scarabs during the last half of the flowering period of *P. acutatum*, all belonging to the genus *Cyclocephala*: *C. celata*, *Cyclocephala distincta* Burmeister 1847, *Cyclocephala latericia* Höhne 1923, and *Cyclocephala vestita* Höhne 1923. Both *C. distincta* and *C. vestita* were consistently abundant every month (table 1), whereas *C. celata* was collected only from April through June and in significantly lower quantities than the other two species. *Cyclocephala latericia* specimens were recovered in low quantities only during the month of April.

Floral Odor

During the female phase of anthesis, inflorescences of *P. acutatum* give off a sweet fruity aroma with yeasty reminiscents, so intense it can be easily perceived by the human nose 5–10 m apart from the source. Chemical analysis of the total fragrance blend revealed it to be comprised of 20 volatile compounds. These can be classified into four out of the seven major classes proposed by Knudsen et al. (2006) regarding structure and biosynthesis of scent constituents. These included aliphatics (6), benzenoids and phenylpropanoids (2), terpenoids (11), and nitrogen-containing compounds (1; table 2). Two compounds alone accounted for more than 97% of the scent composition of *P. acutatum*, dihydro-β-ionone (an irregular terpene) and 2-hydroxy-5-methyl-3-hexanone (an aliphatic acyloin). They represent 74.41% ± 6.63% (SD) and 23.11% ± 7.15% (SD), respectively of the total blend.

Table 1

Night-Active Cyclocephaline Scarabs (Scarabaeidae, Dynastinae) Collected with Blacklight Traps

Species	Blacklight collectings (no. individuals) April	May	June	July	August	Other known plant associations
Cyclocephala celata	1–10	1–10	1–10	. . .	. . .	*Caladium bicolor* (Araceae), NE Brazil;[a] *Taccarum ulei* (Araceae), NE Brazil[b]
Cyclocephala distincta	10–30	10–30	>30	10–30	>30	*Attalea funifera* (Arecaceae), NE Brazil[c]
Cyclocephala latericia	1–10	. . .	. . .	. . .	. . .	*Annona crassiflora* (Annonaceae), central Brazil[d]
Cyclocephala vestita	>30	>30	>30	10–30	10–30	*Annona muricata* (Annonaceae), NE Brazil;[b,e] *Montrichardia arborescens* (Araceae), French Guiana[f]

Note. Collectings conducted from April to August 2007 at Usina São José S/A, municipality of Igarassu, northeastern Brazil. Ellipses indicate no blacklight collectings. For other known plant associations, refer to the literature cited.

[a] Maia and Schlindwein 2006.

[b] A. C. D. Maia, C. Schlindwein, and M. Gibernau, unpublished data.

[c] Voeks 2002.

[d] Cavalcante et al. 2009.

[e] Cavalcante 2000.

[f] Gibernau et al. 2003.

Moreover, 2-hydroxy-5-methyl-3-hexanone is a rare natural volatile molecule, so far unreported as a floral compound.

Discussion

Cyclocephala celata was identified as the only effective pollinator of native populations of *Philodendron acutatum* in the northern coastal region of the state of Pernambuco, northeastern Brazil. In the same region, Maia and Schlindwein (2006) have reported this cyclocephaline scarab in exclusive association with sympatric and coflowering populations of another aroid, *Caladium bicolor* (Aiton) Vent. Cyclocephaline scarabs are commonly acknowledged as indiscriminate toward floral host choice (Schatz 1990). Many species will promptly switch from flowering individuals of one species to the next not only within the same genus, as is known for *Dieffenbachia* (Young 1986) and *Philodendron* (Gibernau et al. 1999, 2000; Gibernau and Barabé 2002), but also within different genera, tribes, or even families (Gottsberger 1986; Schatz 1990). Often, the observed scenario in a given ecosystem consists of an assembly of locally available cyclocephaline scarab species that function as pollen vectors of the associated flora. For instance, inflorescences of *Dieffenbachia longispatha* Eng. & K. Krause (Araceae) populations in La Selva, Costa Rica, are visited by nine different species of *Cyclocephala* and one species of *Erioscelis* (Young 1986). Two of these beetle species, *Cyclocephala atripes* Bates 1888 and *Cyclocephala conspicua* Sharp 1877, are also the main pollinators of sympatric *Cyclanthus bipartitus* Poit. ex A. Rich (Cyclanthaceae; Beach 1982). All four *Annona* species studied by Gottsberger (1986) in the *Cerrado* vegetation of the state of São Paulo, southeastern Brazil, were visited by the same three species of *Cyclocephala*, also recovered inside inflorescences of coflowering geophytic aroid *Xanthosoma striatipes* (Kunth & C.D. Bouché) Madison.

At least three other species of flower-visiting *Cyclocephala* (*Cyclocephala vestita*, *Cyclocephala distincta*, and *Cyclocephala latericia*) were also present at Igarassu during the flowering period of *P. acutatum*, two of them recovered at a higher frequency than that of *C. celata* in blacklight trappings. Populations of *C. vestita* are associated with both native and introduced *Annona* species in northeastern Brazil (Cavalcante 2000), and it is likely that *C. distincta* is an effective pollinator of at least one species of Arecaceae at Igarassu, since a pollen morphotype of this family was recurrently recovered from the body surfaces of collected specimens (A. C. D. Maia, personal observation). Also, Voeks (2002) reports this species as a frequent flower visitor of the piassava palm (*Attalea funifera* Mart. ex. Spreng., Arecaceae) in the state of Bahia. In contrast to the more generalistic plant-pollinator interactions aforementioned, *C. celata* was found in tight association with *P. acutatum*, out of four syntopic *Cyclocephala* species. This suggests a more specialized relationship. Gottsberger and Amaral (1984) considered the pollinator specificity observed in upland Atlantic Forest populations of *Philodendron bipinnatifidum* Schott ex Endl. (previously referred to as *Philodendron selloum* K. Koch; Gonçalves and Salviani 2002) an effective strategy to increase its reproductive success. Relying on a specialized pollen vector can significantly decrease the risk of interspecific pollen flow and improve the rate of successful visitations, since the visitors most probably carry only conspecific pollen (Faegri and van der Pijl 1979). Additional field work is required to elucidate how coflowering sympatric populations of *P. acutatum* and *C. bicolor* species both share the same pollinator and maintain a high fructification rate (>90%). Nonetheless, populations of the latter are greatly outnumbered by those of *P. acutatum* and bloom for a shorter and slightly delayed period. In such a case, it seems unlikely that interspecific pollen flow would affect the reproductive success of *P. acutatum*.

The "two peaks" thermogenic pattern of *P. acutatum* is characteristic of species of the subgenus *Philodendron* (Gibernau and Barabé 2000, 2002; Gibernau et al. 2000). The heating intervals on two successive nights are synchronized with the floral cycle and are associated first with attraction of pollinating beetles by aiding the emission of scented volatiles and, second, with pollen release on beetle departure. Floral thermogenesis may also function as an important reward for visiting

Table 2

Chemical Composition of the Floral Scent of *Philodendron acutatum* (Araceae) and Relative Amounts of Compounds

Compound	mw	Relative amounts ± SD (%)
Aliphatics:		
Acetic acid[a]	60	.03
Propionic acid[a]	74	.07
Isobutyric acid[a]	88	.01
2-Hydroxy-3-hexanone[a]	116	.04
2-Hydroxy-5-methyl-3-hexanone	130	23.11 ± 7.15
3-Hydroxy-5-methyl-2-hexanone	130	.02 ± .01
Benzenoids and phenylpropanoids:		
4-Vinylanisole	134	.01 ± .01
Methyl salicylate	152	.02 ± .01
Nitrogen-containing compounds:		
2-Methoxy-3-isopropylpyrazine[b]	152	.34 ± .40
Terpenoids:		
(E)-Ocimene	136	.02 ± .01
(E)-4,8-Dimethyl-1,3,7-nonatriene[b]	150	.28 ± .13
(Z)-4,8-Dimethyl-1,3,7-nonatriene[b]	150	.19 ± .11
Linalool	154	.03 ± .03
4-Terpinenol[b]	154	.02 ± .01
Dehydrodihydro-β-ionone	192	.01 ± .01
Dihydro-β-ionone	192	74.41 ± 6.63
β-Ionone	192	.79 ± 1.37
Dihydro-α-ionone	194	.20 ± .13
Dihydro-β-ionol	194	.14 ± .11
Dihydro-β-ionone epoxide[c]	208	.02 ± .01

Note. mw = molecular weight. Odor samples recovered by dynamic headspace from fragrant inflorescences during the female phase of anthesis ($n = 5$). Footnotes indicate relative amounts.

[a] Present in only one of the samples.

[b] Present in only four of the analyzed samples.

[c] Present in only three of the analyzed samples.

cyclocephaline scarabs, which take advantage of heated floral chambers to reduce the energetic expenditure of their intense activity inside the inflorescences (Seymour et al. 2003, 2009).

Floral odors appear to be an important element of pollinator selectivity (Schiestl and Ayasse 2002; Jürgens 2009). Both Gibbs et al. (1977) and Gottsberger (1986) in Brazil observed that the distinctly sweet-scented flowers of *Magnolia ovata* (A. St.-Hil.) Spreng. (Magnoliaceae) were visited by a single species of *Cyclocephala*, even though other flower-visiting scarabs were actively flying in the same area. According to Gottsberger and Amaral (1984), the cyclocephaline scarab *Erioscelis emarginata* Mannerheim 1829 was found only in association with inflorescences of biogeographically restricted populations of *P. bipinnatifidum*, and such species-specific relationship are probably explained by the particular floral fragrance given off by this aroid during anthesis.

The floral odor of *P. acutatum* is dominated by ionones (mainly dihydro-β-ionone), which give it its characteristic floral notes. These irregular terpenoids are widespread in floral scents and commonly associated with insect attraction (Knudsen et al. 2006). For instance, β-ionone has been effectively used as a fragrant bait for male euglossine bees in several Neotropical environments (Dodson et al. 1969; Darrault et al. 2005; Milet-Pinheiro and Schlindwein 2005). The other major constituent in the odor blend of *P. acutatum* is the rare acyloin 2-hydroxy-5-methyl-3-hexanone, accompanied in smaller amounts by an isomer, 3-hydroxy-5-methyl-2-hexanone. Neither compound is known in floral scents (Knudsen et al. 2006). Along with the ionones, they account for the very distinctive odor of *P. acutatum*. The role of these compounds in the attraction of *C. celata* is yet to be clarified. Some acyloins, nonetheless, are indeed bioactive and have been identified as sex pheromones of longhorn beetles (Cerambycidae; Schröder et al. 1994; Lacey et al. 2009).

Methoxylated benzenoids have been associated with scarab beetle attraction and are present as major flower constituents in *Victoria* and *Nymphaea* species (Nymphaeaceae), *Montrichardia arborescens* (L.) Schott and *Homalomena propinqua* Schott (Araceae), and *Phytelephas* species (Arecaceae; Kite et al. 1991; Ervik et al. 1999; Ervik and Knudsen 2003; Gibernau et al. 2003; Kumano and Yamaoka 2006; Kumano-Nomura and Yamaoka 2009). According to Dobson (2006) and Knudsen et al. (2006), many compounds belonging to this particular chemical subclass are among the most widespread fragrant floral constituents and are acknowledged attractants of insects. Schiestl and Roubik (2003) showed that five benzenoid derivatives are major attractants of male euglossine bees.

We have found very low relative amounts of benzenoids in the floral odor of *P. acutatum*. Methyl salicylate and vinyl anisole accounted for less than 0.05% of the total blend concentration. Such is also the case for the floral scent of beetle-pollinated *Magnolia tamaulipana* Vázq. Avila, which is entirely constituted of terpenoids (Azuma et al. 1997). Inflorescences of *C. bipartitus*, whose floral scent is mainly a mix of several terpenoids, are attractive to cyclocephaline scarabs and derelomine weevils (Curculionidae; Schultz et al. 1999). Of course, further elucidation of this theme can be attained only through controlled odor attraction assays with these beetles, so far still lacking.

Our field observations suggest that the pollination and reproduction of *P. acutatum* is not limited by the common environmental consequences of habitat fragmentation in northeastern Brazil. However, *P. acutatum* has evolved locally to strict dependency on a single species of pollinating beetle. The beetles find optimal mating sites and food for a period of at least 4 mo in the abundant inflorescences of the aroid, whereas the numerous beetles ensure that the reproductive strategy adopted by the plant is rewarded. Because *P. acutatum* shows a wide distribution in South America (Sakuragui 2001), it would be of great interest to verify the reproductive dependence of the species to cyclocephaline scarabs in other regions, for example, southeastern Brazil and the Amazon basin.

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