

Thermogenesis in three *Philodendron* species (Araceae) of French Guiana

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Abstract

Spadix temperature was measured in three species of *Philodendron*: *P. acutatum*, *P. pedatum* and *P. solimoense*. These species showed two different patterns of spadix temperature during their flowering cycle. In *P. acutatum* and *P. pedatum* (subgenus *Philodendron*), the spadix warmed up twice during the beginning of each flowering night with a temperature not significantly different from that of ambient air between the two peaks. In *P. solimoense* (subgenus *Meconostigma*), the spadix temperature rose up to 14°C above that of ambient air during the first night, then it progressively cooled down but remained 3-6°C above ambient air temperature. We propose that the heat production and the spadix temperature patterns observed may reflect different physiological processes and have a taxonomic significance in the genus *Philodendron*.

Keywords: Araceae, flowering cycle, flower temperature, heating flower.

Résumé

Nous avons mesuré la température du spadice chez trois espèces de *Philodendron*: *P. acutatum*, *P. pedatum* et *P. solimoense*. Deux types de courbe de température des spadices ont été observés. Les spadices de *P. acutatum*, *P. pedatum* (sous-genre *Philodendron*) produisent deux pics distincts de chaleur lors des deux soirs de la floraison. Entre ces pics de chaleur, la température du spadice n'est pas différente de celle de l'air ambiant. Le spadice de *P. solimoense* (sous-genre *Meconostigma*) produit un pic de chaleur le premier soir puis reste chaud, de 6 à 3°C au dessus de l'air ambiant jusqu'au soir suivant. Nous suggérons que ces différentes courbes de température des spadices peuvent être dues à des processus physiologiques différents et avoir une signification taxonomique dans le genre *Philodendron*.

Mot-clés: Aracées, biologie florale, température florale.

Introduction

Floral thermogenesis is common in Araceae species but also exists in Annonaceae, Cycadaceae, Cyclanthaceae, Magnoliaceae, Nymphaeaceae and Zamiaceae (Prance and Arias 1975; Tang 1987; Gottsberger 1990; Dieringer et al. 1999). This particular physiological property of the flowers appears to be linked with pollination. The production of heat is associated with the arrival of pollinators (beetles or flies), the emission of fragrance and the liberation of pollen (Moodie 1976; Meeuse and Raskin 1988; Gottsberger 1990; Gottsberger and Silberbauer-Gottsberger 1991; Gibernau et al. 1999).

Inflorescences of Araceae are typically composed of a spadix on which are inserted minute flowers, surrounded by a leafy organ, the spathe (Fig. 1). In Araceae, the heat is generally produced by a part of the spadix, the male flowers (fertile or sterile) or the appendix (Skubatz 1990, 1991; Bermadinger-Stabentheiner and Stabentheiner, 1995; Seymour 1999). The spadix temperature increases up to 35-45°C during the first night of flowering, through a mitochondrial process, called the cyanide-insensitive respiration (Nagy et al. 1972; Walker et al. 1983; Elthon et al. 1989; Skubatz et al. 1990). These flowers are interesting not only because they produce heat but also because they regulate their temperature by

varying the rate of heat production inversely to the ambient air temperature (Knutson 1974; Seymour et al. 1983; Seymour and Schultze-Motel 1998; Seymour 1999).

If numerous observations have been made on the production of heat by inflorescences of Araceae, data on spadix temperature measurements are scarce (Nagy et al. 1972; Knutson 1972, 1974; Chen and Meeuse 1975; Young 1986; Raskin et al. 1987; Skubatz et al. 1990, 1991; Seymour et al. 1993; Bermadinger-Stabentheiner and Stabentheiner; 1995). For the genus *Philodendron* (over 500 species), such data are available for only two closely related species, *P. selloum* and *P. bipinnatifidum* (Gottsberger and Amaral 1984; Seymour 1999). We report here measurements of spadix temperature on 3 new *Philodendron* species: *P. acutatum*, *P. pedatum* and *P. solimoense*. The temperature of the spadix was recorded during the entire flowering cycle in contrast to a previous study on *P. solimoense*, where the temperature was measured only during the first flowering night (Gibernau et al. 1999). *P. acutatum* and *P. pedatum* belong to the subgenus *Philodendron* whereas *P. solimoense* belongs to the subgenus *Meconostigma* as *P. selloum* and *P. bipinnatifidum*. We present in this study a functional comparison of spadix heat production in these two *Philodendron* subgenera.

Material and methods

Philodendron acutatum Schott belongs to the subgenus *Philodendron* section *Philodendron*. This hemi-epiphyte has sagittate leaves, narrowly ovate with a long yellow-orange petiole. The inflorescence is composed of a white spadix (18-19 cm long) and a spathe (18-20 cm in length when opened). The spathe is green externally and white internally above the constriction and red with vertical dark red lines below. The inflorescence peduncle is 19-21 cm long. The pistillate flowers occupy the lower portion (6-7 cm) of the spadix, whereas the male flowers are located on its upper part (12-13 cm). In the middle of the spadix, there is a small intermediate zone (0.4-0.6 cm) consisting of sterile male flowers.

P. pedatum (Hooker) Kunth belongs to the subgenus *Philodendron* section *Schizoplacium*. This species is a hemi-epiphytic vine or an appressed climber on rocks with long stems. Its leaf blades have

3-5 deep lobes and a large anterior one, with a long green petiole. The inflorescence is composed of a white spadix (13.5-15 cm long) and a spathe (16-18 cm long when opened). The spathe is clear green externally and creamy internally. The inflorescence peduncle is 6-8 cm long. The pistillate flowers occupy the lower portion (5-6 cm) of the spadix, whereas the male flowers are located on the upper part (7-8 cm) of the inflorescence. These two zones are separated by a small median zone (0.8-1 cm) consisting of sterile male flowers.

P. solimoense A. C. Smith belongs to the subgenus *Meconostigma*. This species is a hemi-epiphyte or terrestrial on sandy soils. The spadices are white and their length varies between 23-29 cm when open. The pistillate flowers occupy the lower portion (7-9 cm) of the spadix, whereas the male flowers are located on the upper part (7-9 cm) of the inflorescence. In the median portion of the spadix, there is a prominent intermediate zone (9-12 cm) consisting of sterile male flowers (for further description see Barabé and Lacroix 1999; Gibernau et al. 1999).

This study was conducted in July 1999 in French Guiana. *P. solimoense* was studied along National Road # 1. The plants used originated from hemi-epiphytic individuals growing on trees cut down during the construction of the road in 1989, and successfully reproducing since (Gibernau et al. 1999). *P. pedatum* was studied at Petit Saut dam (Kourou region). Three individuals bearing several inflorescences were appressed climbers on a large rock situated on a lakeside several hundred meters away from the forest and conspecifics. *P. acutatum* was studied just outside Cayenne (Leblond cross-roads) along the road to Kourou where the species grew in dense populations covering entire trunks of trees.

Philodendron individuals were regularly followed and the flowering cycle was observed when an inflorescence opened. The temperature of two inflorescences were measured for *P. acutatum* and *P. solimoense* and one for *P. pedatum*. Temperatures of the spadix and the ambient air were recorded every 10 minutes with a Digi-Sense® DualLogR® thermocouple thermometer. To obtain the temperature of the spadix, the thermometer was inserted about 5 mm deep into the spadix, in the middle of the fertile

male zone (*P. acutatum*, *P. pedatum*; Fig. 1) or the sterile male zone (*P. solimoense*).

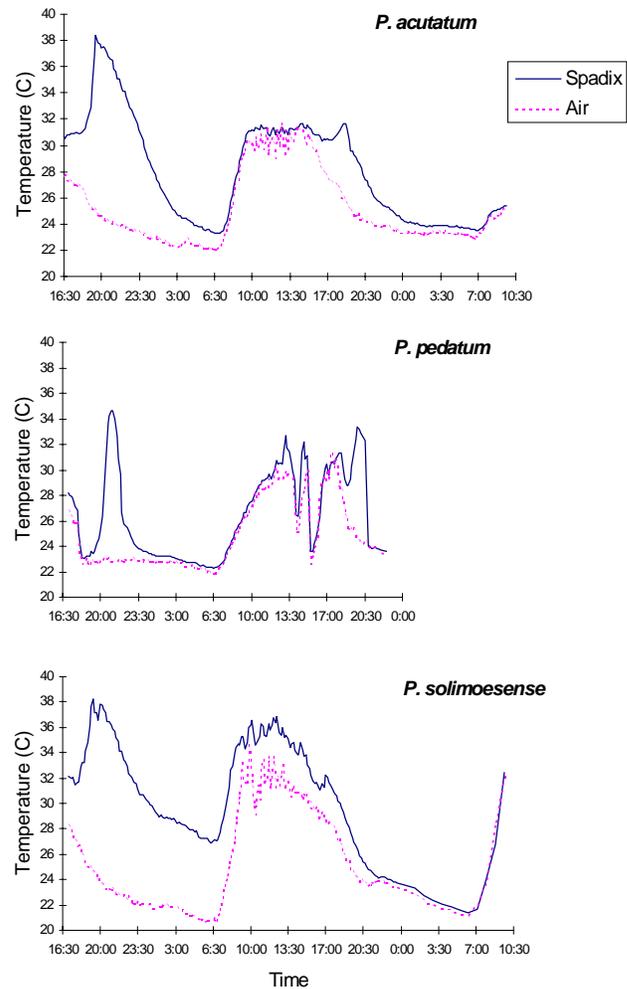
Results

Flowering cycles - The flowering cycle of the three species follows mostly the same pattern as already described for *P. solimoense* (Gibernau et al. 1999). Flowering appears to be asynchronous for the three species with inflorescences opening successively on different individuals. The flowering cycle was a two-day process: the spathe began to open in the mid morning or early afternoon of the “first day”. By the end of the afternoon, the spathe was widely open (1/2 to 2/3 of the spathe length), the spadix strongly protruding forward. At dusk, the spadix began to warm-up and a distinctive odor emanated from the inflorescence. At this time, the stigmas were moist and appeared receptive.

During the “second day”, the spathe had slightly closed and only the upper part of the spathe was open (1/3 to 1/2 of the spathe length). In the afternoon, resin began to be produced by the inflorescence (Fig. 1). In *P. solimoense*, a brownish resin was secreted by the internal upper half of the spathe, no resin canals are present in the spadix (Mayo 1991; Barabé and Lacroix 1999). In *P. pedatum*, red resin was produced on the spadix by the male zone that began to appear at the base of this zone. In *P. acutatum*, resin drops were located along the red lines (resin canals) on the inner lower surface of the spathe (below the constriction) and on the male lower portion of the flower zone of the spadix (Fig. 1). At dusk, the spathe closed by slowly folding around the spadix, from the base to the upper parts. At this time, the anthers released massive quantities of pollen that became sticky in contact with the resin covering the spathe and/or the spadix.

Temperature patterns - Two different patterns of spadix temperature variation were observed, the first in *P. acutatum* and *P. pedatum*, and the other in *P. solimoense*. Only one temperature measurement is shown for *P. acutatum* and *P. solimoense* as the two records were similar, except that in the second inflorescence of *P. acutatum*, the first temperature peak was narrower (faster decrease of temperature after the peak).

Fig. 2. Temperature curves of the spadix (full line) and ambient air (dotted line) during two days of flowering for *P. acutatum* (upper graph), *P. pedatum* (middle graph) and *P. solimoense* (lower graph).



In *P. acutatum* and *P. pedatum*, the spadix temperature peaked at 38.4°C and 34.5°C respectively. The increase occurred in the beginning of the first night between 19h20-20h00 for *P. acutatum* and 20h30-21h30 for *P. pedatum* (Fig. 2). Later the spadix temperature decreased to 23-24°C close to ambient temperature. Spadix and ambient temperatures followed the same variations until late afternoon of the next day (rains may cause important variations in temperature). At dusk, while air temperature cooled down, the spadix temperature rose a second time to peak at 31.8°C in *P. acutatum* and at 33.5°C in *P. pedatum* (Fig. 2). The second temperature increase peaked earlier than the previous night and the two heating periods overlapped (Fig. 2). Subsequently, the

spadix temperature decreased to the ambient level as the spathe closed around the spadix.

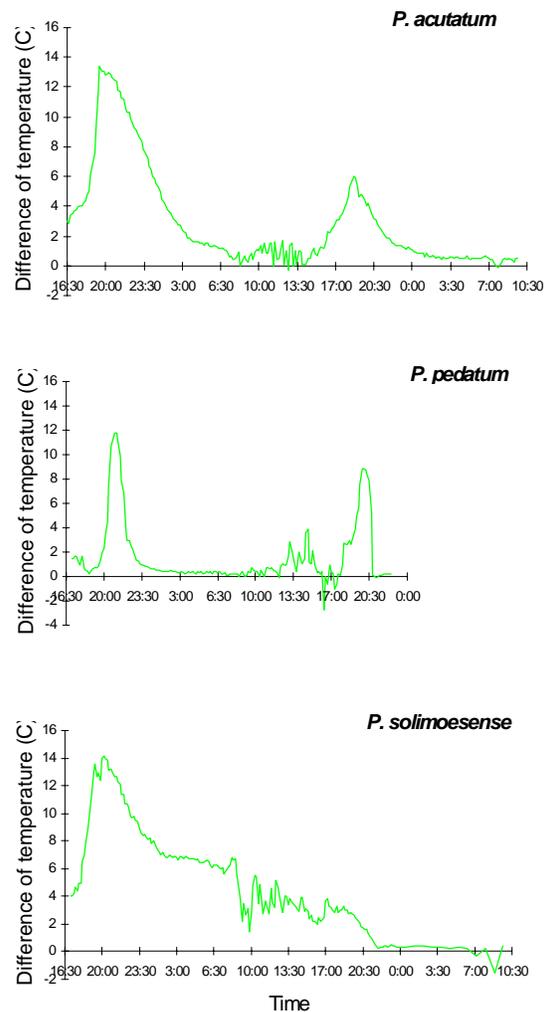
The spadix temperature of *P. solimoense* peaked at 38.2°C in the beginning of the first night between 19h00-21h00 (Fig. 2), and it decreased but remained higher than 27°C whereas ambient air was around 20°C. During the following day, the spadix temperature followed ambient temperature variations but remained a few degrees higher. At the end of the second afternoon (17h00), the spadix temperature increased slightly a few degrees above ambient air during the early night (Fig. 2). Later (after 21h30), the spadix temperature returned to ambient levels as the spathe closed around the spadix.

When looking at the difference of temperature between the spadix and the air, two clear peaks appeared for *P. acutatum* and *P. pedatum* during the two successive nights, indicating a higher increase of the spadix temperature in comparison to air temperature (Fig. 3). During the rest of the time, there was a small or no difference between air and the spadix, showing that the spadix temperature matched that of ambient air (Fig. 3). The temperature differences were higher in the first night than in the second for both species: 13.5 vs. 9°C in *P. acutatum* and 12 vs. 9°C in *P. pedatum*. On the other hand, in *P. solimoense*, the difference of temperature between the spadix and the air peaked in the first night (14°C) and then progressively declined to level at 3-6°C higher than the air during the second day (Fig. 3). It was not possible to clearly recognize the presence of a second temperature peak in this species.

Discussion

Measurements of spadix temperature and heat production in *Philodendron* are only known for two species, *P. selloum* and *P. bipinnatifidum* (Gottsberger and Amaral 1984; Seymour et al. 1983; Seymour 1999). These two species, like *P. solimoense*, belong to the subgenus *Meconostigma*. It is interesting to note that the temperature pattern of these three species is similar. In *P. selloum* and *P. bipinnatifidum*, there is a biphasic pattern of heat production. A peak phase occurs after the first sunset followed by a plateau phase during which the temperature is maintained around 30-35°C and lasts until the second night (Gottsberger and Amaral 1984; Seymour et al. 1983; Mayo 1991).

Fig. 3. Difference of temperature between the spadix and ambient air for *P. acutatum* (upper graph), *P. pedatum* (middle graph) and *P. solimoense* (lower graph).



However, in the case of *P. solimoense* the temperature of the spadix does not appear to be as well regulated as in *P. selloum* and *P. bipinnatifidum*. There is a progressive decrease of the difference between the air temperature and that of the spadix after the first peak. Even if the temperature of the spadix remains 3-6°C above ambient air, it follows directly the fluctuations of air temperature.

The species of subgenus *Meconostigma* (*P. solimoense*, *P. selloum* and *P. bipinnatifidum*) present a different pattern of heat production from species of subgenus *Philodendron*. In *P. acutatum* and *P. pedatum* as well as in *P. squamiferum* (Gibernau et al. unpub.) and *P. melinonii* (Gibernau and Barabé

unpub.), the spadix warms twice on the two consecutive flowering nights with no temperature difference between these two events. This pattern may suggest that these *Philodendron* species are unable to remain warm during a prolonged period.

It is striking that for the three species, the two heating periods during the two successive nights are synchronized and overlapped (Fig. 2). This character is a floral adaptation for pollination by dusk- or night-active beetles (Gottsberger 1990). Temperature increase in "second day" inflorescences stimulates the beetles but they will not leave the inflorescence until it closes and the pollen is released (Gottsberger and Silberbauer-Gottsberger 1991; Gibernau et al. 1999). At this time "first day" inflorescences are fully heating and odoriferous and the beetles will fly directly from "second day" towards "first day" inflorescences (Gottsberger and Amaral, 1984; Young 1986; Gibernau et al. 1999).

Some flowers are known to regulate their temperature in particular *Philodendron* (Seymour 1997). In *P. selloum*, temperature maxima of spadices remain within a narrow range and are controlled by acute but reversible reductions in heat production as spadix temperature rises above approx. 37°C (Seymour et al. 1983). The inhibition of heat production by high temperature is reversible with a time delay and the spadix may remain warm during a drop in the ambient air temperature. Thus temperature regulation exists during the two phases at different levels. The peak phase represents only regulation of maximum spadice temperature, while the plateau phase demonstrates true regulation around a mean of approximately 28°C (Seymour 1999). Interestingly, the spadix temperature of *P. solimoense* never drops below 27°C even if ambient air is at about 20°C (Fig. 2).

Flower temperature has been measured on other taxa, but few studies have produced continuous measurements. A biphasic pattern (i.e. a peak phase followed by a plateau phase) is or is likely to be present in *Nelumbo* (Nelumbonaceae), *Victoria* (Nymphaeaceae), *Magnolia* (Magnoliaceae) and *Symplocarpus* (Araceae) (Valla and Cirino 1972; Knutson 1974; Prance and Arias 1975; Seymour and Schultze-Motel 1998; Dieringer et al. 1999). In cycads, both patterns are present, a circadian pattern of thermogenesis (1 or 2 peaks) is produced by cones of Zamiaceae and Boweniaceae species whereas all

Cycadaceae species, except one, heat weakly but continuously (Tang 1987). In Annonaceae and Cyclanthaceae, two heating periods have been recorded during two successive nights (Gottsberger 1989, 1990). In *Arum maculatum*, heat is produced by two distinct zones, the male flowers and the appendix, but at different times. Thus the inflorescence of *Arum* remains warm during its entire flowering cycle (Bermadinger-Stabentheiner and Stabentheiner; 1995). This thermogenesis pattern might be considered functionally similar to a biphasic pattern, but it appears more highly evolved because it results from the specialization and complementarity of two spadix parts.

Thermogenesis pattern varies among species and may have evolved differently in the different taxa. In all cases, thermogenesis function is linked with pollination but its exact role may vary among taxa. Further studies are needed to assess whether the different patterns observed in species from different taxa reflect different physiological processes. In particular in *Philodendron*, it will be interesting to study species belonging to the third subgenus, namely *Pteromischum*, to verify if the patterns of spadix temperature have some taxonomic or phylogenetic signification. Is there a relationship between the phylogeny of *Philodendron* subgenera and the pattern of heat production? A phenetic analysis of 15 species of *Philodendron* representing the three subgenera indicates that the subgenus *Meconostigma* is primitive in comparison to subg. *Philodendron* (Mayo 1988). Is then the two-peak pattern present in the subgenus *Philodendron* a derived character? To answer these questions one needs a comparative analysis of the inflorescence morphology and physiology in relation with the phylogeny.

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