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Zonal thermogenetic dynamics of two species of *Philodendron* from two different subgenera (Araceae)

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Spadix temperature was measured in two species of *Philodendron*: *P. melinonii* (subgenus *Philodendron*) and *P. solimoesense* (subgenus *Meconostigma*). For each species, the temperature of the male zone, the sterile male zone and the female zone of the spadix were recorded. In both species, the temperature of the male zone warmed up at the beginning of each of the two flowering nights. In *P. melinonii*, the temperature of the male sterile zone increased the first day but remained not significantly different from that of the ambient air during the second day. The temperature of the male zone warmed up slightly on the second day. In *P. melinonii*, the temperature of the three zones was not significantly different from that of the ambient air between the two peaks. In *P. solimoesense*, the temperature of the male zone and sterile zone rose to above that of the ambient air during the first night and then progressively cooled down but remained 3–6°C above the ambient air temperature until the second peak. In both species the temperature of the female zones remained more or less constant during the entire flowering cycle, very close to the temperature of the ambient air. We suggest that the heat production and the spadix temperature patterns observed may reflect a general physiological process common to all species of *Philodendron*. The biphasic pattern present in the subgenus *Meconostigma* can be seen as a variant of the 'two peaks' pattern, occurring in the subgenus *Philodendron*, with a 'plateau' phase between them. The comparison of the different thermogenic cycles occurring in *Philodendron*, *Arum* and *Dracunculus* seems to indicate some clear evolutionary trends. *Botanical Journal of the Linnean Society,* 2002, **139**, 79–86.

ADDITIONAL KEYWORDS: flower temperature – flowering cycle – heating flower.

INTRODUCTION

Thermogenesis in reproductive organs is common in Araceae species but also exists in Annonaceae, Cycadaceae, Cyclanthaceae, Magnoliaceae, Nymphaeaceae, Palmae and Zamiaceae (Prance & Arias, 1975; Tang, 1987; Gottsberger, 1989, 1990; Seymour & Schultze-Motel, 1998; Azuma *et al.*, 1999; Dieringer *et al*., 1999). This particular physiological property of the flowers appears to be related to pollination. The production of heat is generally associated with the emission of fragrance and the liberation of pollen, and is linked with the arrival of pollinators (Moodie, 1976; Meeuse & Raskin, 1988; Seymour & Schultze-Motel, 1997, 1999).

Inflorescences of Araceae are typically composed of a spadix onto which are inserted minute flowers, surrounded by a leafy organ, the spathe. In the subfamily Aroideae (Mayo *et al.*, 1997), the spadix bears unisexual flowers and the heat is generally produced by the male flowers (fertile and sterile) or a specialized appendix (Meeuse, 1975, 1978; Skubatz *et al*., 1990, 1991; Bermadinger-Stabentheiner & Stabentheiner, 1995; Seymour, 1999). The spadix temperature increases to 35–45°C during the first night of flowering, through a mitochondrial process, called cyanide-insensitive respiration (Nagy *et al.*, 1972; Walker *et al*., 1983; Elthon *et al.* 1989; Skubatz

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et al., 1990). Uncoupling protein is another mitochondrial factor involved in heat production (Laloi *et al*., 1997; Ito, 1999). The flowers of Araceae 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 & Schultze-Motel, 1998; Seymour, 1999).

Although 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 & Meeuse, 1975; Seymour *et al*., 1983; Young, 1986; Raskin *et al*., 1987; Skubatz *et al*., 1990, 1991; Bermadinger-Stabentheiner & Stabentheiner, 1995). In the genus *Philodendron (*over 500 species), such data are available for *P. selloum*, *P. bipinnatifidum*, and *P. solimoesense*, which belong to subgenus *Meconostigma* (Gottsberger & Amaral, 1984; Seymour, 1999; Gibernau & Barabé, 2000), and in the subgenus *Philodendron* for *P. acutatum*, *P. melinonii*, *P. pedatum, P. pterotum* and *P. squamiferum* (Barabé & Gibernau, 2000; Gibernau & Barabé, 2000; Gibernau *et al.*, 2000; Gibernau & Barabé, 2002).

The inflorescences of *Philodendron* constitute of female flowers in the lower part, male flowers in the upper part and sterile male flowers in the intermediate part. In previous studies, the temperature of the spadix was recorded either in the male zone (subgenus *Philodendron*) or the sterile zone (subgenus *Meconostigma*). This method does not allow the comparison of the thermogenetic cycle in the three floral zones of the spadix simultaneously. The use of a measurement on only one part was based on the hypothesis that heat was mainly produced by the male sterile zone in subgenus *Meconostigma* and the male zone in subgenus *Philodendron*. But is this hypothesis justified? Is there a difference in heat production between the three floral zones of the spadix? Is there a real qualitative difference in the thermogenetic cycle between the subgenera *Meconostigma* and *Philodendron*? To answer these questions, we present here a detailed functional comparison of spadix heat production in the three zones of the inflorescences of *P. melinonii* and *P. solimoesense*. This study will also compare the qualitative variations of heat production (i.e. thermogenetic pattern) between species of the subfamily Aroideae in an evolutionary perspective.

MATERIAL AND METHODS

Philodendron melinonii Brongniart ex Regel (subgenus *Philodendron*, section *Philodendron*) is an epiphyte usually found growing below the tree canopy, but occasionally persists on logs or 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 long) 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 a third shorter than the spathe. The female flowers 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 (2–3 cm long) of sterile male flowers.

Philodendron solimoesense 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 and 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 descriptions see Mayo, 1991; Barabé & Lacroix, 1999; Gibernau *et al*., 1999; Gibernau & Barabé, 2000).

This study was conducted in July 2000 in French Guiana. *P. solimoesense* was studied along National Road #1 (97 km). The plants used were originally hemi-epiphytic individuals growing on trees that were cut down during the construction of the road in 1989 (Gibernau *et al*., 1999). *Philodendron melinonii* was studied at Petit Saut dam (Kourou region). Data were recorded on individuals growing on a large rock situated on the lakeside of Petit Saut dam, one hundred metres away from the forest and on specimens cultivated on the ground at the Environmental Laboratory of Petit Saut.

Philodendron individuals were regularly monitored and the flowering cycle temperatures were recorded during inflorescence opening. The temperatures of three inflorescences, belonging to three differents plants, were measured for *P. melinoni*, as were five inflorescences of *P. solimoesense* belonging to five different plants. Temperatures of the different zones of the spadix and the ambient air were recorded every 10 min with two Digi-Sense DualLogR thermocouple thermometers (Fluke Corporation, Everett, WA). The two probes of one thermometer were inserted about 5 mm deep into the spadix in the middle of the fertile male zone and the sterile male zones. One probe of the second thermometer was inserted into the middle of the female zone. The second one was used to record the ambient air temperature.

RESULTS

The flowering cycle of the two species follows mostly the same pattern as described previously (Gibernau *et al*., 1999, 2000; Gibernau & Barabé, 2000). Flowering appears to be asynchronous for the two species with inflorescences opening successively on the same individual. The flowering cycle was a two-day process: the spathe began to open in mid-morning or early afternoon of the first day of the flowering cycle. By the end of the afternoon, the spathe was wide open (1/2–2/3 of the spathe length), the spadix strongly protruding forward. At dusk, the spadix began to warm up and a distinctive odour emanated from the inflorescence. At this time, the stigmas were moist and appeared receptive.

During the second day of the flowering cycle, the spathe had closed slightly and only the upper part of the spathe was open (1/3–1/2 of the spathe length). In the afternoon, resin began to be produced by the inflorescence. In *P. solimoesense*, a brownish resin was secreted by the internal upper half of the spathe, as no resin canals are present in the spadix (Mayo, 1991; Barabé & Lacroix, 1999; Gibernau & Barabé, 2000). In *P. melinonii*, red resin was produced at the base of the male zone on the spadix (Gibernau *et al*., 2000). 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.

As the records were similar for individuals belonging to each species, only one temperature measurement is shown for each species (Figs 1, 2).

In *P. melinonii*, the temperature of the male zone peaked at 38.5°C (19h30) during the first evening. This temperature peak occurred between 18h00 and 21h20 (Fig. 1A). Later, the male zone temperature decreased to 25–27°C, close (2–3°C above) to ambient temperature. At the same time, the temperature of the intermediate zone increased and peaked at 32.5°C, while the female zone remained cool. The three zones of the spadix and ambient temperatures followed the same variations until late afternoon of the next day, but during the hottest hours of the day the inflorescence zones were cooler than the surrounding air. At dusk, while air temperature cooled down, the male zone temperature rose a second time to peak at 29°C. This second temperature increase peaked earlier than the previous night. On the second day, there was no significant temperature increase in the sterile male and female zones. Subsequently, the spadix temperature decreased to the ambient level as the spathe closed around the spadix.

When looking at the temperature differences between the inflorescence zones and the ambient air

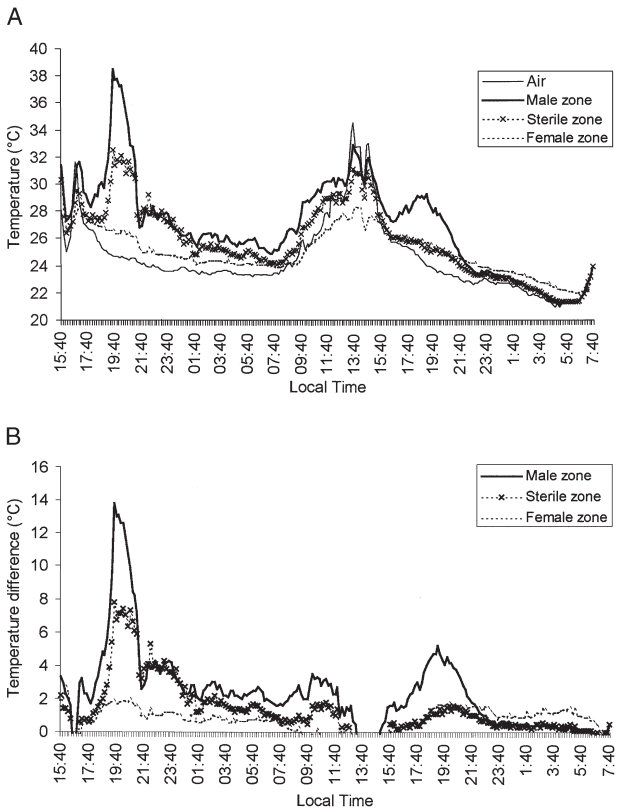

Figure 1. A. Temperature curves (°C) of the male zone, the male sterile zone, the female zone, and the ambient air during two days of flowering for *P. melinonii*. B. Curves of differences in temperature (°C) between the male zone, the sterile male zone and the female zone, and the ambient air during two days of flowering for *P. melinonii*.

(Fig. 1B), the male flowers were 14°C warmer than the ambient air during the first peak and only 5.2°C during the second night. The sterile male flowers were 8°C warmer than the ambient air during only the first night. The temperature of the female flowers remained more or less constant within the floral chamber (about 1–2°C above the ambient air). On the afternoon of the second day during the hottest hours (13h00–15h30), the temperature differences of the three zones were negative indicating that the inflorescence, particularly the female and sterile zones, was cooler than the ambient air (Fig. 1B).

In the inflorescence of *P. solimoesense,* the temperature started to increase first in the male zone and peaked at 41°C (19h40), and later (20h30) in the sterile male zone at 37.2°C (Fig. 2A), while the female zone remained cool. Although the temperature of the male sterile zone increased considerably at the beginning of the first night, it remained, in general, below the temperature of the male zone. However, in two of the five specimens, the temperature of the sterile male

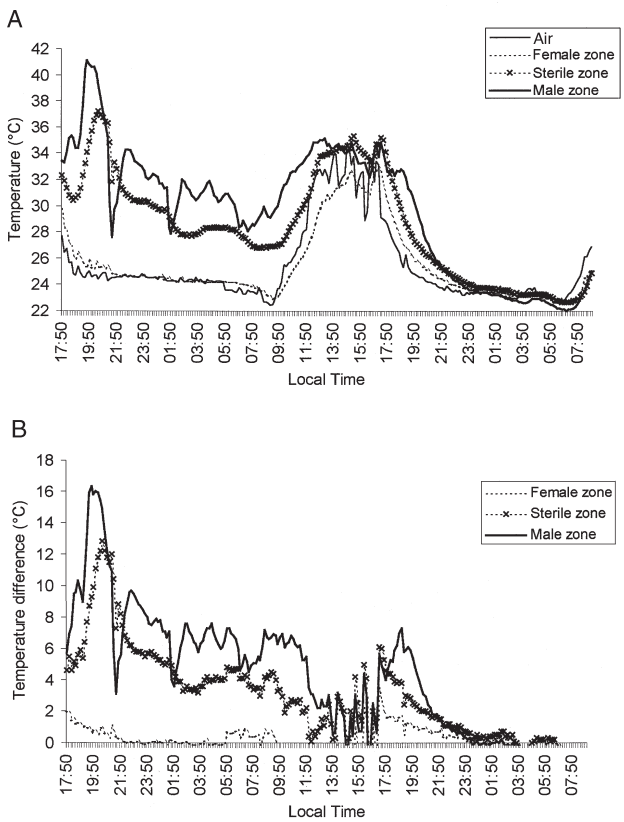

Figure 2. A. Temperature curves (°C) of the male zone, the sterile male zone, the female zone, and the ambient air during two days of flowering for *P. solimoesense*. B. Curves of differences in temperature (°C) between the male zone, the sterile male zone and the female zone, and the ambient air during two days of flowering for *P. solimoesense*. The fluctuations of temperature during the afternoon of the second day (13–17 h) are due to the presence of frequent and intermittent rains.

zone was as great as that of the male zone at the beginning of the first night. This indicates a certain degree of variability in the quantitative expression of the thermogenetic cycle even if the qualitative patterns remain stable among samples. The inflorescence temperature peaked between 19h10 and 21h30 during the first night then it decreased slowly but remained clearly higher than the ambient air temperature. During the following day, the spadix temperature of male and sterile male zones followed ambient temperature variations but remained a few degrees higher except during the hottest hours of the day (13h30–17h00) when the temperatures were similar. The second night, the temperatures of the male and sterile male zones increased slightly (17h20–21h00) while the ambient air temperature dropped and peaked at 17h20 for the sterile male zone and later at 19h00 for the male zone (Fig. 2A).

When looking at the temperature differences between the inflorescence zones and the ambient air (Fig. 2B), the male flowers were 16.3°C warmer than the ambient air during the first peak at 19h40 and about 1 h later (20h30) the sterile male flowers peaked 12.8°C above the ambient air. The temperature of these two zones decreased slowly but remained 4–7°C higher than the ambient air temperature, the male zone was warmer than the sterile male zone (Fig. 2B). The difference in temperature was maintained until the second night (19h00) except during the hottest hours of the day (13h30–17h00), giving the illusion of a second temperature peak. The temperature of the sterile male zone dropped before (17h20) that of the male zone (19h00). Later (after 21h30), the spadix temperature of both zone returned to ambient levels as the spathe closed around the spadix. The temperature of the female flowers remained more or less constant within the floral chamber during the entire flowering cycle and was the coolest zone of the inflorescence (Fig. 2B).

When comparing the temperature differences between the spadix and the air for *P. melinonii* and *P. solimoesense*, two different temperature patterns are revealed (Figs 1B, 2B). For *P. melinonii* (subgenus *Philodendron*), two clear peaks appeared during two successive nights, and the rest of the time, there was a small or no difference between air and spadix temperatures (Fig. 1B). On the other hand, for *P. solimoesense* (subgenus *Meconostigma*), the inflorescence temperature peaked only one time during the first night and then progressively declined but remained about 7°C higher than the air during the second day (Fig. 2B) until the second night except during the hottest hours of the day. The sterile male zone followed the same pattern except that the temperature difference with the ambient air was less than in the male zone; hence, the temperature pattern may be more similar to a 'two-peaks' pattern.

DISCUSSION

Our results show that the amplitude modulation of the thermogenetic cycle remains stable within a species and seems to be independent of the external temperature. Early studies on aroids (Seymour, 1999; Barabé & Gibernau, 2000; Gibernau & Barabé, 2000) show that the qualitative pattern of heat production (one-, two- or three-phasic) is constant for a given species. There are local variations in the temperature of the spadix but they do not modify the thermogenetic cycle which depends on the increase of the spadix temperature in comparison with air temperature. The circadian thermogenetic rhythm is an intrinsic characteristic of a species, as it has been shown for *Philodendron melinonii* (Gibernau *et al*., 2000). There-

fore, we can assume that the thermogenetic pattern is constant between individuals of the same species and constitutes an endogenous characteristic of the species. This regularity allows us to make comparisons between species.

In species from the subgenus *Meconostigma*, there is a biphasic pattern of heat production (Fig. 2B). A peak phase occurs after the first sunset followed by a plateau phase during which the temperature is maintained several degrees above ambient air (around 30–35°C) and lasts until the second night (Seymour *et al*., 1983; Gottsberger & Amaral, 1984; Mayo, 1991; Seymour, 1999). The 'plateau' phase is not always very clear. The progressive decrease in the difference between the air temperature and that of the spadix after the first peak can be related to a warming of the ambient air during the day (Gottsberger & Amaral, 1984; Mayo, 1991; Gibernau & Barabé, 2000). Such temperature decrease is not recorded in a controlled stable environment (Seymour *et al*., 1983; Seymour, 1999). Despite the fluctuations in air temperature, the spadix temperature remains higher indicating the existence of a prolonged heating phase persisting until the second night. As the ambient air temperature decreases at dusk, the temperature difference increases and a 'second' heating peak may appear during the second night. The fact that the inflorescence is warm during the second night is not related with pollinator attraction, since the pollinators are already in the inflorescence. It is possibly linked with the liberation/maturation of pollen. The sterile male zone is supposed to produce 70% of the inflorescence heat in *P. selloum*, as it represents about 55% of the male zone weight and has a doubled oxygen consumption rate (Nagy *et al*., 1972; Seymour, 1999). Our data from *P. solimoesense* show that the fertile male zone has a higher temperature than the sterile male zone during the entire flowering cycle, suggesting that heat production by this zone may not always be negligible. Further studies are necessary to assess if heat production (oxygen consumption rates) can vary among species in the same inflorescence zone.

In contrast to *P. solimoesens*e, the spadix temperature of *P. melinonii* matches the ambient air temperature between the two peaks as in other species of the subgenus *Philodendron* (Barabé & Gibernau, 2000; Gibernau *et al*., 2000). In the case of *P. melinonii* the temperature of the sterile male zone does not increase during the second day (Fig. 1B). Therefore, in this species, there seems to be no recordable diffusion of heat from the male zone to the sterile male zone when the second peak appears. Also, the length of the sterile male zone is probably too small to record any variation of temperature by the method used in this study.

Qualitative differences in the pattern of heat production, a biphasic vs. a 'two peaks' pattern, exist between the two subgenera (*Meconostigma* and *Philodendron*), but they can be seen as close heat production processes. In some cases, *Philodendron* species of the *Meconostigma* subgenus have a 'second' peak even if there is a 'plateau' phase (Mayo, 1991; this study). Therefore, it seems that the thermogenetic cycle is fundamentally the same between species of the genus *Philodendron* even if some qualitative differences exist between the subgenera *Philodendron* and *Meconostigma* (Gibernau & Barabé, 2000). This suggests that some *Philodendron* species have acquired the capacity to remain warm during a prolonged period. This property is probably due to the larger size of the inflorescences of the *Meconostigma* species that have been analysed, and consequently the physical constraints on its heat dissipation rate, but physiological and metabolism changes cannot be excluded. In *P. selloum*, the maximum temperatures of the spadices remain within a narrow range and are controlled by acute but reversible reductions in heat production as spadix temperature rises above ≈37°C (Seymour *et al*., 1983). The inhibition by high temperature of heat production 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 regulation of only the maximum spadix temperature, while the plateau phase demonstrates a true regulation around a mean of approximately 28°C (Seymour, 1999). Interestingly, the spadix temperature of *P. solimoesense* never drops below 27°C even if the ambient air is at about 20°C (Fig. 2A).

Subgenus *Meconostigma* is a small well-defined group with only 16 species out of the 500 *Philodendron* species. Such a biphasic pattern is also known from another Araceae: *Symplocarpus* (Knutson, 1974). Thus the 'two-peaks' pattern appears to be characteristic of many Araceae with female flowers in the basal part of the inflorescence and male flowers in the upper part, e.g. *Anubias*, *Culcasia*, and *Homalomena* (Barabé & Gibernau, 2000), and most of the *Philodendron* species. Consequently, the biphasic pattern present in the subgenus *Meconostigma* can be seen as a variant of the 'two-peaks' pattern occurring in the subgenus *Philodendron*, with a 'plateau' phase between them.

Other heating patterns exist within the Araceae with an appendix. In these species, the female and male flowers are enclosed in the floral chamber and the appendix, on the top of the inflorescence, lies outside the floral chamber. In *Arum maculatum* and *Dracunculus vulgaris*, the heat is produced by two distinct zones, the male flowers and the appendix,

but at different times (Bermadinger-Stabentheiner & Stabentheiner, 1995; Seymour & Schultze-Motel, 1999). Apparently, the female flowers do not produce heat. This pattern may be called triphasic, with first a minor episode of heating by the male flowers (floral chamber), then a major episode of thermogenesis in the appendix, and finally a long thermogenesis by the male flowers (floral chamber). Thus the inflorescence remains warm during its entire flowering cycle but due to different zones (Bermadinger-Stabentheiner & Stabentheiner, 1995; Seymour & Schultze-Motel, 1999). 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 (i.e. male zone and appendix).

When comparing the different thermogenetic cycles occurring in *Philodendron*, *Arum* and *Dracunculus,* some evolutionary trends clearly appear (Fig. 3). In all these genera, there is heat production by the male zone and sterile zone or the appendix in the case of *Arum* and *Dracunculus* (Fig. 3). In *P. melinonii*, the male zone starts to heat, followed by the sterile male zone during the first day. The increase in temperature is greater in the male zone than in the sterile male zone. However, no heating of the sterile male zone was detected during the second day. The same fundamental pattern occurs in *P. solimoesense.* The male zone heats first and more than the sterile zone, except that the spadix remains warm during the entire flowering cycle (Fig. 3). In *Arum* and *Dracunculus*, the male zone heats first and distinctly from the peak of the appendix whereas in *Philodendron* the two peaks of heat overlap even if fertile male flowers heat first. The appendice heats during the phase of pollinator attraction. Hours later, the fertile male flowers warm a second time before the second temperature peak of *Philodendron*, whereas the appendix remains cold. Given the fact that the tribe Areae (*Arum*, *Dracunculus*) is phylogenetically derived (French *et al*., 1995; Mayo *et al*., 1997) with respect to *Philodendron*, we postulate that there was a physiological modification of the thermogenetic cycle during the evolution of the family corresponding to a structural change. In the genus *Arum*, the heating of the sterile male zone occurring in the genus *Philodendron* was replaced by that of the appendix. This transfer of function corresponds to the appearance of a delay between the heating of the male zone and the appendix (Fig. 3). The heating of the male zone in *Arum* appears to be independent of pollinator attraction while the appendix function is directly linked with pollinator attraction. In this case, each zone is associated with different functions. On the contrary, in *Philodendron* both zones are synchronized and they participate together in the different functions.

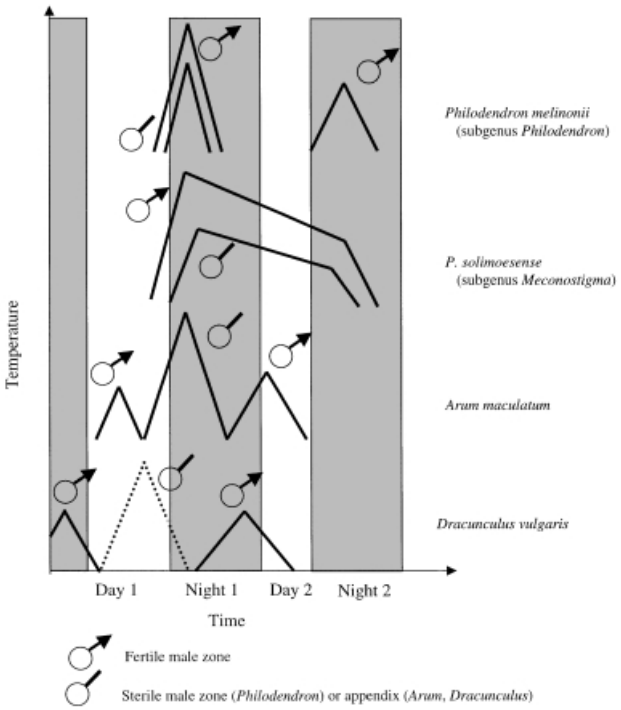

Figure 3. Schematic represention of the thermogenetic cycles of *Arum maculatum* (Bermadinger-Stabentheiner & Stabentheiner, 1995)*, Dracunculus vulgaris* (Seymour & Schultze-Motel, 1999), *P. melinonii* and *P. solimoesense* (this study). The first day is the time when the insects arrive at the inflorescence.

In *Alocasia odora*, another variant of heat patterning occurs. Here, the inflorescence is composed of four parts, from the top to the bottom: an appendix, a staminate zone, a sterile zone and a pistillate zone. The flowering cycle can last five days and thermogenesis was observed in three parts (appendix, staminate and pistillate zones) with a more or less definite synchronized circadian rhythmicity, but the male zone and the appendix were nevertheless the warmest (Yafuso, 1993). This indicates that thermogenesis patterns vary among species and may have evolved differently in different taxa. In all cases, thermogenesis function is linked with pollination (pollinator attraction, odour emission, liberation/maturation of the pollen). Further studies are needed to assess whether or not the different patterns observed in species from different taxa reflect different physiological processes.

The present results have shown that the baseline pattern of thermogenesis is fundamentally the same in the subgenera *Meconostigma* and *Philodendron*. It would be interesting to study species belonging to the third subgenus, namely *Pteromischum*, to verify if this pattern of spadix temperature is a general characteristic of the genus *Philodendron*. In this genus,

the quantitative differences between the patterns observed in both subgenera may be linked with the size of the spadix, which constitutes a physical constraint. This hypothesis can be tested by measuring, for example, the spadix temperature of *P. adamantinum* or *P. brasiliense* which have relatively small inflorescences for species from the subgenus *Meconostigma* (Mayo, 1991).

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