Thermogenic Patterns in *Philodendron ornatum* and *P. grandifolium*: A Comparative Analysis

Denis Barabé
Institut de Recherche en Biologie Végétale
Université de Montréal
Jardin Botanique de Montréal
4101 rue Sherbrooke Est
Montréal (Québec), Canada H1X 2B2

Marc Gibernau
CNRS-UMR 8172 Écologie des Forêts de Guyane
BP 709, 97387 Kourou, France

ABSTRACT

Spadix temperature was measured in two species of *Philodendron* (subgenus *Philodendron*): *P. ornatum* Schott and *P. grandifolium* (Jacq.) Schott. Temperature differences between the spadix (male zone) and ambient air for *P. grandifolium* and *P. ornatum* showed the same pattern in both species. Two clear peaks appeared during two successive nights, and otherwise there was little or no difference between air and spadix temperatures. In *P. grandifolium* male flowers were 4.2–4.6°C warmer than ambient air during the first peak and 4.3–4.9°C during the second night. The temperature of female flowers remained more or less constant within the floral chamber (about 0.5°C above ambient air). In *P. ornatum* the male zone was 10.7°C warmer than ambient air during the first peak and 9.3°C during the second night. Applying heat model transfer based on inflorescence size, temperature differences in the spadix of *P. grandifolium* and *P. ornatum* should range respectively from 5.5 to 7.9°C and from 8.7 to 10.8°C, which is very close to our measurements. The present results confirm that the baseline pattern of thermogenesis may be fundamentally the same in the subgenera *Philodendron* ("two peak" pattern) and *Meconostigma* ("biphasic pattern"). The biphasic pattern can be seen as a variant of the "two peak" pattern, with a "plateau" phase between peaks. In the genus *Philodendron*, the quantitative differences between the patterns observed in both subgenera may be linked with the size of the spadix, which constitutes a physical constraint on the theoretical amplitude of the cycle.

KEY WORDS

Araceae, flowering cycle, flower temperature, thermogenesis, physical constraint.

INTRODUCTION

Thermogenesis in reproductive organs is common in Araceae species but also exists in Annonaceae, Cycadaceae, Cyclanthaceae, Magnoliaceae, Nymphaeaceae, Palmae and Zamiaceae (Gibernau *et al.*, 2005; Roemer *et al.*, 2005; Lamprecht *et al.*, 2006; Thien *et al.*, 2009). Inflorescences of Araceae are typically composed of a spadix onto which are inserted minute flowers, surrounded by a leafy organ, the spathe. The spadix temperature of certain species increases to 35–45°C during the first night of flowering, through a mitochondrial process called cyanide-insensitive respiration (Grabel'nykh *et al.*, 2006; Wagner *et al.*, 2008). Uncoupling protein is another mitochondrial factor involved in heat production (Vercesi *et al.*, 2006). The flowers of Araceae are interesting not only because

Corresponding author: marc.gibernau@ecofog.gf

they produce heat but also because some regulate their temperature by varying the rate of heat production inversely to ambient air temperature (Lamprecht *et al.*, 2006).

Heat production by floral structures is generally associated with emission of fragrances, arrival of pollinators and liberation of pollen, and it has been well documented in the subfamily *Aroideae* (Gibernau *et al.*, 2005; Ivancic *et al.*, 2005; Maia & Schlindwein, 2006; Chouteau *et al.*, 2007; Barthlott *et al.*, 2008, Seymour & Gibernau, 2008). In this subfamily (Mayo *et al.*, 1997), the spadix bears unisexual flowers arranged in sexual regions. Heat is generally produced by either the fertile and sterile male flowers or by a specialized sterile zone, the appendix, located above the male flowers (Gibernau *et al.*, 2005).

Numerous observations and experiments have been made on the production of heat by inflorescences of Araceae (e.g. 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; Seymour, 2004; Seymour & Gibernau, 2008). However, comparative analyses of spadix temperature patterns remain relatively scarce (e.g. Gibernau & Barabé, 2000; Barabé *et al.*, 2002; Gibernau *et al.*, 2005; Chouteau *et al.*, 2007, 2009). A quantitative comparison between thermogenesis cycles belonging to different species allows a better understanding of the relationship between biological and physical constraints during evolution (Gibernau *et al.*, 2005).

The inflorescences of *Philodendron* (over 700 species) are composed of female flowers in the lower part, male flowers in the upper part and sterile male flowers in the intermediate part. Data on thermogenic cycles 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 subgenus *Philodendron* for *P. acutatum*, *P. melinonii*, *P. pedatum*, *P. pterotum* and *P. squamiferum* (Barabé & Gibernau, 2000; Gibernau & Barabé, 2000; Gibernau *et al.*, 2000; Barabé *et al.*, 2002; Gibernau & Barabé, 2002; Seymour & Gibernau, 2008).

However, is the previously reported thermogenic pattern common to all species of *Philodendron*? The great number of species belonging to the genus *Philodendron* does not allow us to claim that the thermogenic cycle is similar for all species. For example, Mayo (1986, 1989) showed that there is great variability of anatomical characters between inflorescences in *Philodendron*. Therefore, although the overall thermogenic pattern of the inflorescence of *Philodendron* is consistent, one may expect to find some variability and alternate thermogenic patterns in a genus consisting of several hundred species.

In a previous study, a logarithmic relationship was found between the volume of the thermogenic spadix zone and the maximum temperature difference between the spadix and ambient air in the genus *Philodendron*. The increase in the temperature difference between the spadix and ambient air appeared to be physically constrained and to correspond to the value of a thermal model of heat conduction in an insulated cylinder with an internal heat source (Gibernau *et al.*, 2005). To test the value of this model, which was adjusted on 28 samples, one needs to predict the theoretical amplitude of the thermogenic species that are not included in the model, and compare it to empirical results. Therefore, the study of thermogenesis in *P. grandifolium* and *P. ornatum* will allow a better understanding of geometrical constraints linked with thermogenic patterns.

The specific goals of this study are: 1) to determine the relationships between the flowering cycle and the thermogenic pattern in two species of *Philodendron* subgenus *Philodendron* (*P. ornatum* and *P. grandifolium*); 2) to compare their thermogenic patterns to others known in the subgenera *Philodendron* and *Meconostigma*; and 3) to integrate the thermogenic pattern of these species into a general model linking the size of the inflorescence to the amplitude of heat peaks.

MATERIALS AND METHODS

Philodendron ornatum Schott (subgenus *Philodendron*) is a hemi-epiphyte usually growing below the tree canopy, but occasionally on logs or rocks. The spathe is greenish abaxially and pink to purplish in the adaxial basal part. The female flowers occupy the lower portion (3–4 cm) of the spadix, whereas the male flowers are located on its upper portion (12–13 cm). In between, there is a short intermediate zone (2–3 cm long) of sterile male flowers.

Philodendron grandifolium (Jacq.) Schott belongs to the subgenus *Philodendron*. This species is a climbing hemiepiphyte growing on trees. The spathe is green abaxially and white-cream adaxially. The pistillate flowers occupy the lower portion (4–5 cm) of the spadix, whereas the male flowers are located on the upper part (6–7 cm) of the inflorescence. An intermediate zone (ca. 1 cm) consists of sterile male flowers.

This study was conducted in French Guiana. Three individuals of *P. grandifolium* were observed, one at the Nouragues field station (GPS coord.: 04°05.196N-052°40.768W) in June 2008 and two near "Petit Saut" Dam in 2002 (GPS coord.: 04°49.43N-052°26.34W). Three individuals of *P. ornatum* were observed at the Nouragues field station in June 2008. Voucher specimens were deposited at Marie-Victorin Herbarium (MT): *Barabé 67, Barabé 374*.

Philodendron individuals were monitored regularly and flowering cycle temperatures were recorded during inflorescence opening. Temperatures of the spadix and ambient air were recorded every 10 or 20 min with two Digi-Sense® DualLogR® thermocouple thermometers. Probes were inserted about 5 mm deep into the spadix in the middle of the different zones under study (see Barabé *et al.*, 2002 for a detailed description of this procedure).

RESULTS

The flowering cycle of the two species studied mostly follows the same pattern described for other species of *Philodendron* (Gibernau *et al.*, 1999, 2000; Gibernau & Barabé, 2000; Barabé *et al.*, 2002). 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, and at dusk, the stigmata were receptive (female phase) and the spadix began to warm up.

During the second day of the flowering cycle, the spathe had closed slightly and in the afternoon, a brownish resin began to be produced by the spadix at the base of the male zone in both species. At dusk, the spathe closed by slowly folding around the spadix, from the base to the upper parts and the anthers released pollen (male phase).

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

In *P. grandifolium*, there was one temperature peak during each of the two consecutive evenings of the flowering cycle (Fig. 1). The temperature of the male zone peaked at 28–28.5°C (2143–2204 hours) during the first evening. The temperature of the sterile zone peaked at the same time as the male zone (2143 hours), but at a lower temperature, about 27°C. This increase in temperature occurred between 1950–2320 hours (Fig. 1A). Later, the male zone temperature decreased to 22–23°C, close to ambient temperature. During the same period, the temperature of the intermediate zone increased and peaked at 26.9°C, while the female zone remained cool (0.5 degrees above ambient air temperature). 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 approximately at the same temperature as the surrounding air. At dusk, while air temperature cooled down, the temperature of the male zone and the sterile male zone increased a second time.

This second temperature increase peaked about one hour earlier than the previous night. The temperature of the male zone peaked between 2030–2100 hours at 27.6–30°C. The temperature of the sterile zone peaked a bit earlier than the male zone, between 1940–2015 hours at 25.7–27.6°C. On the second day, there was still no significant temperature increase in the female zone. Subsequently, spadix temperature decreased to ambient level as the spathe closed around the spadix.

When looking at the temperature differences between the inflorescence zones and ambient air (Fig. 1B), the male flowers were 4.2–4.6°C warmer than ambient air during the first peak and 4.3–4.9°C during the second night. In one instance (Fig. 1C), the spadix (male zone) was 7.3°C warmer than ambient air during the second night. This indicates a certain degree of variability in the quantitative expression of the thermogenic cycle, even if the qualitative patterns remain stable among samples. The sterile male flowers were 3.2°C warmer than ambient air during the first night and 2.4–3.1°C during the second night. The temperature of the female flowers remained more or less constant within the floral chamber (about 0.5°C above ambient air).

In *P. ornatum* the thermogenic pattern of the inflorescence was similar to that of *P. grandifolium*, although the amplitude of the cycle was greater in the first species. The temperature of the male zone peaked at 34.5°C (2206 hours) during the first evening (Fig. 2). This temperature peak occurred between 1900–0030 hours (Fig. 2A). Later, the male zone temperature decreased to 24.6°C, close to ambient temperature (0.8–1°C above). The male zone and ambient temperatures followed approximately the same variations until late afternoon of the next day. At dusk, while air temperature cooled down, the temperature of the male zone increased a second time (2054 hours) to peak at 33.6°C. This second temperature increase peaked earlier than the previous night. Subsequently, spadix temperature decreased to ambient level as the spathe closed around the spadix. The temperature differences between the male zone and ambient air (Fig. 2B) were greater than in *P. grandifolium*. The male zone was 10.7°C warmer than ambient air during the first peak and 9.3°C during the second night.

Temperature differences between the spadix (male zone) and air for *P. grandifolium* and *P. ornatum* (subgenus *Philodendron*) showed the same pattern (Figs. 1B, 2B). Two clear peaks appeared during two successive nights, and otherwise there was little or no difference between air and spadix temperatures.

DISCUSSION

Previous works on Aroids have shown that the qualitative pattern of heat production (one-, two-, three-, or multi-phasic) is constant for a given species (Seymour, 1999; Barabé & Gibernau, 2000; Barabé *et al.*, 2002; Ivancic *et al.*, 2005; Chouteau *et al.*, 2007, 2009; Seymour & Gibernau, 2008). The study of thermogenesis in *P. grandifolium* and *P. ornatum* confirms that the pattern of the thermogenic cycle remains stable within a species and seems to be independent of external temperature. Although the qualitative patterns remain stable among samples, a certain degree of variability in the quantitative expression of the thermogenic cycle may be present, as in the case of *P. grandifolium* (Fig. 1C).

There are local variations in the temperature of the spadix, but they do not modify the thermogenic cycle, which depends on the increase of spadix temperature as compared to air temperature. The circadian thermogenic rhythm is an intrinsic characteristic of a species, as has been shown for other *Philodendron* species (Gibernau *et al.*, 2000; Barabé *et al.*, 2002). Therefore, we can assume that the thermogenic 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.

Our results show that the amplitude of the heating peak in *P. grandifolium* and *P.*

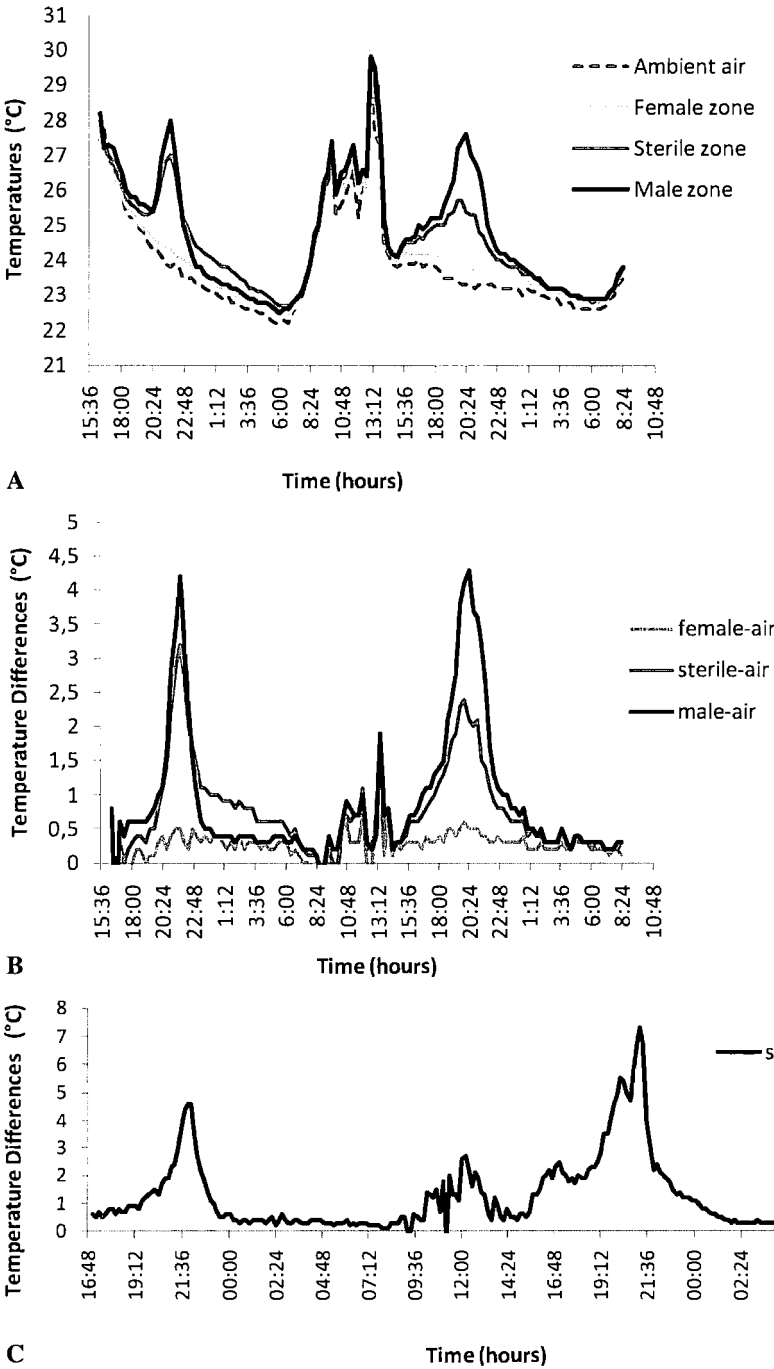

Fig. 1A. Temperature curves (°C) of the male zone, the male sterile zone, the female zone, and ambient air during two days of flowering for *P. grandifolium* (site of Petit-Saut). Fig. 1B. Curves of differences in temperature (°C) between the male zone, the sterile male zone and the female zone, and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

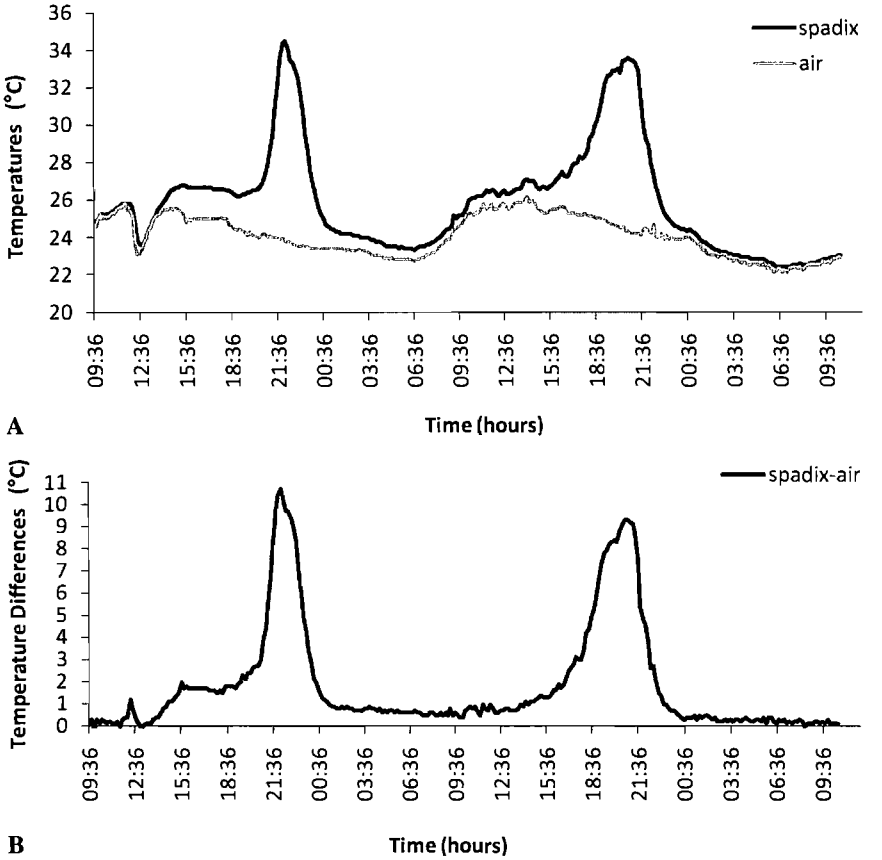

Fig. 2A. Temperature curve (°C) of the male zone and ambient air during two days of flowering for *P. ornatum* (site of Nouragues).
Fig. 2B. Curve of differences in temperature (°C) between the male zone and ambient air during two days of flowering for *P. ornatum* (site of Nouragues).

ornatum may be linked to the size of the spadix. The volume of the heating zone (e.g. male and sterile zones) in *P. ornatum* (mean ± SD: 14.2 ± 2.5 cm^3) is nearly twice the size of that in *P. grandifolium* (8.7 ± 2.5 cm^3). This size difference corresponds to a temperature differential in *P. ornatum* that is also more than twice that in *P. grandifolium*. This is not surprising, considering that in the genus *Philodendron* there is a quantitative relationship between the size of the spadix and the amplitude of the first peak, following a thermal model of heat conduction (Gibernau *et al.*, 2005). Applying the same heat model transfer based on the size of the inflorescence (Gibernau *et al.*, 2005), temperature differences in the spadix of *P. grandifolium* and *P. ornatum* should range respectively from 5.5 to 7.9°C and from 8.7 to 10.8°C. This is very close to our measurements, with the exception of the temperature minimum in *P. ornatum*, which is overestimated by the model by 1°C.

←

Fig. 1C. Difference between the temperature of the male zone and ambient air during the flowering cycle in an individual of *P. grandifolium* (site of Nouragues).

The spadix temperature of *P. grandifolium and P. ornatum* is very close (1°C or less warmer) to ambient air temperature between the two peaks, as in other species of the subgenus *Philodendron* (Barabé & Gibernau, 2000; Gibernau *et al.*, 2000; Barabé *et al.*, 2002; Gibernau & Barabé, 2002). Contrary to the subgenus *Philodendron*, in species from the subgenus *Meconostigma*, 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 several degrees above ambient air (around 30–35°C) until the second night (Seymour *et al.*, 1983; Gottsberger & Amaral, 1984; Mayo, 1991; Seymour, 1999; Barabé *et al.*, 2002). The "plateau" phase is not always very clear. The progressive decrease in the difference between 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). Despite the fluctuations in air temperature, spadix temperature remains higher, indicating the existence of a prolonged heating phase that persists until the second night. As ambient air temperature decreases at dusk, the temperature difference increases and a "second" heating peak may appear during the second night.

Qualitative differences in the pattern of heat production, a biphasic versus a "two peak" pattern, exist between the two subgenera (*Meconostigma* and *Philodendron*) but they can be seen as close heat production processes. In fact, in some cases, *Philodendron* species of the *Meconostigma* subgenus have a "second" peak even if there is a "plateau" phase (Mayo, 1991; Barabé *et al.*, 2002). Therefore, the thermogenic cycle is fundamentally the same between species of the genus *Philodendron*. However, some qualitative and quantitative differences exist between the subgenera *Philodendron* and *Meconostigma* (Gibernau & Barabé, 2000). Some *Philodendron* species of the subgenus *Meconostigma* have acquired the capacity to remain warm over a prolonged period between the first peak and the liberation of pollen. In *P. selloum* for example, 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). It has been shown that the male floret tissues of *P. melinonii* (subg *Philodendron*) possess the same thermoregulatory mechanism as species of the subgenus *Meconostigma*, but a combination of small spadix size, moderate thermogenic capacity, and slow reaction time result in poor and non efficient thermoregulatory performance (Seymour & Gibernau, 2008).

Consequently, the biphasic pattern present in the subgenus *Meconostigma* can be seen as a variant of the "two peak" pattern occurring in the subgenus *Philodendron*, with a "plateau" phase between peaks. In fact, the biphasic pattern can be seen as a derived two peak pattern that is possible only with inflorescences of a large size (which limits heat loss) and/or high thermogenic capacity (high heating rate) and/or fast reaction time (rapid physiological response to temperature changes). The present results confirm that the baseline pattern of thermogenesis is fundamentally the same in the subgenera *Philodendron* and *Meconostigma*, independent of the size of the inflorescence. In the genus *Philodendron*, the quantitative differences between the patterns observed in both subgenera may be linked with the size of the spadix, which constitutes a physical constraint on the theoretical amplitude of the cycle. Unfortunately, no species belonging to the third subgenus, *Pteromischum*, has been studied to date, to verify whether this spadix temperature pattern is a general characteristic of the genus *Philodendron*.

ACKNOWLEDGMENTS

We are grateful to the staff of the *Laboratoire environnement de Petit Saut* (*Hydreco*) for technical support. This research was supported in part by grants from the Natural Sciences and Engineering

Research Council of Canada, the programs Amazonie 1 ("BIG") and 2 ("2ID") of the CNRS (*Conseil National de la Recherche Scientifique, France*), and a research grant from the Nouragues CNRS field station.

LITERATURE CITED

Barabé, D. & M. Gibernau. 2000. Etude comparative de la production de chaleur chez quelques Araceae. *Adansonia* 22: 253–263.

———, ——— & F. Forest. 2002. Zonal thermogenetic dynamics of two species of Philodendron from two different subgenera (Araceae). *Bot. J. Linn. Soc.* 139: 79–86.

Barthlott, W., J. Szarzynski, P. Vlek, W. Lobin & N. Korotkova. 2009. A torch in the rain forest: thermogenesis of the Titan arum (*Amorphophallus titanum*). *Pl. Biol.* 11(4): 499–505.

Bermadinger-Stabentheiner, E. & A. Stabentheiner. 1995. Dynamics of thermogenesis and structure of epidermal tissues in inflorescences of *Arum maculatum*. *New Phytol.* 131: 41–50.

Chen, J. & B. J. D. Meeuse. 1975. Purification and partial characterization of two biologically active compounds from inflorescence of *Sauromatum guttatum* Schott (Araceae). *Pl. Cell Physiol.* 16: 1–11.

Chouteau, M., D. Barabé & M. Gibernau. 2007. Thermogenesis in *Syngonium* (Araceae). *Can. J. Bot.* 85: 184–190.

———, ——— & ———. 2009. Flowering and thermogenetic cycles in two species of *Monstera* (Araceae). *Bull. Soc. Hist. Nat. Toulouse* 145: 5–10.

Elthon, T. E., R. L. Nickels & L. McIntosh. 1989. Mitochondrial events during development of thermogenesis in *Sauromatum guttatum* (Schott). *Planta* 180: 82–89.

Gibernau, M. & D. Barabé. 2000. Thermogenesis in three *Philodendron* species (Araceae) of French Guiana. *Can. J. Bot.* 78: 685–689.

——— & ———. 2002. Flowering and pollination of *Philodendron squamiferum* (Araceae). *Can. J. Bot.* 80: 316–320.

———, ——— & D. Labat. 2000. Flowering and pollination of *Philodendron melinonii* (Araceae) in French Guiana. *Pl. Biol.* 2: 330–333.

———, ———, M. Moisson & A. Trombe. 2005. Physical constraints on temperature difference in some thermogenic aroid inflorescences. *Ann. Bot.* 96: 117–125.

Grabel'nykh, O. I., A. V. Kolesnichenko, T. P. Pobezhimova, V. V. Zykova & V. K. Voinikov. 2006. Mechanisms and Functions of Nonphosphorylating Electron Transport in Respiratory Chain of Plant Mitochondria. *Russ. J. Pl. Physiol.* 53(3): 418–429.

Gottsberger, G. & A. Amaral. 1984. Pollination strategies in Brazilian *Philodendron* Species. *Ber. Deutsch. Bot. Ges.* 97: 391–410.

Ivancic, A., O. Roupsard, J. Quero Garcia, V. Lebot, V. Pochyla & T. Okpul. 2005. Thermogenic flowering of the giant taro (*Alocasia macrorrhizos*, Araceae). *Can. J. Bot.* 83: 647–655.

Knutson, R. M. 1972. Temperature measurements of the spadix of *Symplocarpus foetidus* (L.) Nutt. *Amer. Midl. Nat.* 88: 251–254.

———. 1974. Heat production and temperature regulation in eastern skunk cabbage. *Science* 186: 746–747.

Lamprecht, I., C. M. Romero, L. B. Jaime & J. A. Teixeira da Silva. 2006. Flower Ovens and Solar Furnaces, pp. 385–404 In *Floriculture, Ornamental and Plant Biotechnology - Volume I.* J. A. Teixeira da Silva. Global Science Books.

Maía, A. C. D. & C. Schlindwein. 2006. *Caladium bicolor* (Araceae) and *Cyclocephala celata* (Coleoptera, Dynastinae): A well-established pollination system in the northern atlantic rainforest of Pernambuco, Brazil. *Pl. Biol.* 8: 1–6.

Mayo, S. J. 1986. Systematics of *Philodendron* Schott (*Araceae*) with special reference to inflorescence characters.

Unpubl. Ph.D. thesis, Univ. Reading, UK. 972 p.

———. 1989. Observations of gynoecial structure in *Philodendron* (*Araceae*). *Bot. J. Linn. Soc.* 100: 139–172.

———. 1991. A revision of *Philodendron* subgenus *Meconostigma* (*Araceae*). *Kew Bull.* 46(4): 601–681.

———, J. Bogner & P. C. Boyce. 1997. *The genera of Araceae.* Royal Botanic Gardens, Kew.

Nagy, K. A., D. K. Odell & R. S. Seymour. 1972. Temperature regulation by the inflorescence of *Philodendron*. *Science* 178: 1195–1197.

Raskin, I., A. Ehmann, W. R. Melander & B. J. D. Meeuse. 1987. Salicylic acid: a natural inducer of heat production in *Arum* lilies. *Science* 237: 1601–1602.

Roemer, R., I. Terry, C. Chockley & J. Jacobsen. 2005. Experimental evaluation and thermo-physical analysis of thermogenesis in male and female cycad cones. *Oecologica* 144: 88–97.

Seymour, R. S. 1999. Pattern of respiration by intact inflorescence of the thermogenic arum lily *Philodendron selloum*. *J. Exp. Bot.* 50: 845–852.

———. 2004. Dynamics and precision of thermoregulatory responses of eastern skunk cabbage *Symplocarpus foetidus*. *Pl. Cell Environm.* 27: 1014–1022.

——— & P. Schultze. 1998. Physiological temperature regulation by flowers of the sacred lotus. *Phil. Trans. R. Soc. London B* 353: 935–943.

——— & M. Gibernau. 2008. Respiration of thermogenic inflorescences of *Philodendron melinonii*: natural pattern and responses to experimental temperatures. *J. Exp. Bot.* 59: 1353–1362.

———, G. A. Bartholomew & M. C. Barnhart. 1983. Respiration and heat production by the inflorescence of *Philodendron selloum* Koch. *Planta* 157: 336–343.

Skubatz, H., T. A. Nelson, A. M. Dong, B. J. D. Meeuse & A. J. Bendich. 1990. Infrared thermography of *Arum* lily inflorescences. *Planta* 182: 432–436.

———, ———, B. J. D. Meeuse & A. J. Bendich. 1991. Heat production in the voodoo lily (*Sauromatum guttatum*) as monitored by infrared thermography. *Pl. Physiol.* 95: 1084–1088.

Thien, L. B., P. Bernhardt, M. S. Devall, Z-D. Chen, Y-B. Luo, J-H. Fan, L-C. Yuan & J. H. Williams. 2009. Pollination biology of basal angiosperms (ANITA grade). *Amer. J. Bot.* 96: 166–182.

Wagner, A. M., K. Krab, M. J. Wagner & A. L. Moore. 2008. Regulation of thermogenesis in flowering Araceae: The role of the alternative oxidase. *Bioch. Biophys. Acta* 1777: 993–1000.

Walker, D. B., J. Gysi, L. Sternberg & M. J. DeNiro. 1983. Direct respiration of lipids during heat production in the inflorescence of *Philodendron selloum*. *Science* 220: 419–421.

Young, H. J. 1986. Beetle pollination of *Dieffenbachia longispatha* (Araceae). *Amer. J. Bot.* 73: 931–944.