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Respiration and heat production by the inflorescence of *Philodendron selloum* Koch

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Abstract. During a 2-d sequence of anthesis, the spadices of the thermogenic arum lily, *Philodendron selloum,* regulated maximum temperature within a small range (37–44° C) by reversible thermal inhibition of respiratory heat production. This response protects the inflorescence and the attracted insects from thermal damage. Heat production by whole spadices, measured by O_2 respirometry, equalled heat loss, measured by gradient layer calorimetry, which confirmed the heat equivalence of O_2 consumption (20.4 J ml^{-1}). This also indicated that there was no net phosphorylation during thermogenesis, heat production being the primary function of high rates of respiration. The sterile male florets consumed about 30 ml g^{-1} h^{-1} and the average 124-g spadix produced about 7 W to maintain a 30° C difference between spadix and ambient temperature. Most of the energy for thermogenesis is present in the florets before anthesis. Despite high respiratory rates, thermogenesis is an energetically inexpensive component of the reproductive process.

Key words: *Philodendron* – Respiration and heat production – Spadix – Thermogenesis and thermoregulation.

Introduction

Philodendron, a chiefly protogynous, epiphytic genus of the arum lily family (Araceae), contains several species with large inflorescences (spadices) that achieve temperatures near 40° C and respiratory rates approaching those of the most active animal endotherms (Nagy et al. 1972). Heating is thought to increase volatilization of chemicals that attract insect pollinators (Smith and Meeuse 1966; Chen and Meeuse 1971). In some *Philodendron* species, the pollinators are beetles (Hubbard 1885).

Previous work on the occurrence and biochemistry of heat production in arum lilies has been directed mainly at a cellular and subcellular level (see reviews by Meeuse 1975; Henry and Nyns 1975; Laties 1982). Our approach focuses on the interaction between the inflorescences and their surroundings during the flowering sequence with regard to gas exchange, heat production, heat loss, and temperature.

The maximum temperature developed during the flowering sequence of *Philodendron selloum* is nearly independent of ambient temperature (Nagy et al. 1972). The spadix warms to 38–46° C in ambient temperatures ranging from 4–39° C. Heat production by whole spadices is inversely related to ambient temperature in a way strikingly similar to the picture in homeothermic animals. A lower ambient temperature produces greater heat loss which is nearly matched by greater heat production. A similar relationship occurs in eastern skunk cabbage, *Symplocarpus foetidus* (Knutson 1974). This response has been termed "temperature regulation" and a model for it has been proposed for *P. selloum* (Nagy et al. 1972). The model proposes an acute inhibition of respiration when spadix temperature exceeds approx. 37° C. Thus, the warmer the spadix becomes, the more it reduces its heat production. Unfortunately, most of the data supporting the model were calculated indirectly. Moreover, if *Philodendron* truly regulates its temperature, not only should the spadix reduce heat production at high ambient temperature, it should increase it again if the ambient temperature drops. We wished to determine if *Philodendron* could recover its heat-producing capacities after experiencing inhibition at high temperature.

Published estimates of heat production in arum

lilies have been based on indirect calorimetry. That is, CO_2 production or O_2 consumption ($\dot{V}_{O_2}$) have been measured with the assumption that rates of oxidative metabolism are directly related to heat production. To verify this, we simultaneously measured O_2 consumption and heat fluxes of isolated whole spadices in a gradient layer calorimeter. This permitted us to assess the importance of dry and evaporative heat losses and heat storage in the thermodynamics of warm-up.

Material and methods

Plants. Experiments were performed during the peak of the flowering season in June, 1979, on plants from the extensive beds of *Philodendron selloum* Koch on the campus of the University of California at Los Angeles. Laboratory experiments were begun within 30 min of the time the flowers were cut on the first evening of major heat production.

Temperatures of outdoor inflorescences. The temperature of the spadices at the level of the sterile male florets was recorded in situ from 15 flowers during the natural sequence of anthesis of plants in an outdoor bed. Long hypodermic needles were pushed through the spathe into the core of the spadix a day or two before warm-up. After inserting a fine thermocouple (0.18 mm wire) to the point, the needle was withdrawn and the termocouple was left implanted in the spadix with enough free wire to prevent movements of the spathe dislodging it. The thermocouples were attached by copper-constantan leads to a six-channel potentiometric recorder inside the building. Temperatures were recorded every 30 s. Flowers in their warming sequence were compared with ambient air and with adjacent inactive buds exposed to similar environmental conditions.

Bomb calorimetry. To help establish the location of the substrate for thermogenesis, samples of sterile male florets at three stages of anthesis were analyzed for total content of chemical potential energy. Florets were cut from outdoor plants at about noon on days 1, 3 and 4, weighed, dried at 70° C to constant weight, and powdered with a mortar and pestle. The powder was pelletized, redried and burned in a Phillipson microcalorimeter calibrated with standard benzoic acid pellets. The output of the calorimeter was recorded on a flatbed recorder.

Heat production and heat loss in whole spadices. Heat production was measured by open-flow respirometry and heat loss was measured directly by gradient layer calorimetry. Small spadices (51–79 g) were cut off at the base approx. 30 min before the peak of warm-up. The cut end was sealed with bee's wax to prevent water loss. Fine thermocouples (0.12 mm wire) were placed at selected locations within the spadix and temperature was recorded every 30 s. Each spadix was placed in a gradient layer calorimeter (internal dimensions: $100 \cdot 135 \cdot 98$ mm^3) fabricated by H.T. Hammel of the Scripps Institution of Oceanography, La Jolla, Cal., USA. The calorimeter measures the integrated difference in temperature across all walls of the enclosure; this difference is proportional to the heat loss from the spadix. Dry air was passed through the chamber at 800 ml min^{-1}, metered by a mass flow controller (model 5840; Brooks Instrument Division, Emerson Electric Co., Hatfield, Pa., USA). Incurrent and excurrent air temperatures were monitored with thermocouples suspended in the inlet and outlet ports and attached to an electronic thermometer (model BAT8; Bailey Instruments Co., Saddle Brook, N.J., USA). Water evaporated from the spadix was collected in two tubes of anhydrous $CaSO_4$ which were alternately placed in the excurrent line and weighed at intervals during the experiments. A sample of the dried excurrent air was drawn into an oxygen analyzer (model S-3A; Applied Electrochemistry, Sunnyvale, Cal., USA). Fractional concentration of oxygen in the excurrent air measured by the oxygen analyzer and total heat loss registered by the calorimeter were recorded simultaneously on a flatbed recorder. Instantaneous $\dot{V}_{O_2}$ was calculated by using the method of Bartholomew et al. (1981) and was converted to heat production by multiplying by 20.43 J ml^{-1} (Bartholomew 1977). This arrangement allowed us to partition heat loss into an evaporative component and a dry (radiant, conductive and convective) component, and simultaneously, to measure instantaneous rates of heat production and heat storage.

Respiration of isolated florets: effect of temperature. Respiration by isolated sterile male florets was measured at selected temperatures in closed respirometers consisting of airtight 250-ml lucite syringes, containing 250 mg of florets spread loosely on an aluminum-foil tray. When the respirometers reached thermal equilibrium, they were flushed with isothermal air and sealed. After 20 min, the chamber gas was stirred and a fraction of it was injected through a desiccant and a CO_2 absorbant into a paramagnetic O_2 analyzer (model E-2; Beckman Instruments, Irvine, Cal., USA). $\dot{V}_{O_2}$ was calculated from the fractional change in O_2 volume of the air in the syringe (Hoyt et al. 1978).

The reversibility of heat inactivation of respiration was tested in a two-channel, open flow system. Sterile male florets were spread on cotton-gauze platforms suspended inside 400-ml containers. Humidified air was metered with the mass-flow controller through the chambers at 300 ml min^{-1}. The excurrent air was passed through desiccants and CO_2 absorbants and delivered to an O_2 analyzer (model G-2; Beckman). Floret temperature was controlled in two constant-temperature cabinets and was recorded by placing fine thermocouples with the florets. Because $\dot{V}_{O_2}$ of isolated florets was not constant, it was necessary to compare the changes in $\dot{V}_{O_2}$ during high-temperature exposure in one sample of florets with the changes in a control sample held at a constant lower temperature. To achieve this, 6–10 g of florets were cut from a single spadix, mixed and divided into two equal subsamples. The control sample was maintained at 39° C while the experimental sample was exposed first to 39° C, then to a higher test temperature for 4–9 min and finally to 39° C again. Instantaneous $\dot{V}_{O_2}$ of the control and experimental samples was measured until the rates of both dropped to low values.

All statistics are 95% confidence intervals (CI) for means or differences between means.

Results

Floral anatomy. The inflorescence of *P. selloum* consists of a spadix surrounded by a green spathe (see Nagy et al. 1972). The mean mass of 30 randomly selected mature spadices was 123.5 g ($\pm$14.5 CI). Three types of florets are tightly packed in distinct regions on the central stalk. Sterile male florets (accounting for about half of the floral mass) form a region separating the fertile male florets at the apex from the female florets at the base. Because the sterile male florets account for approx. 70% of the heat production of the

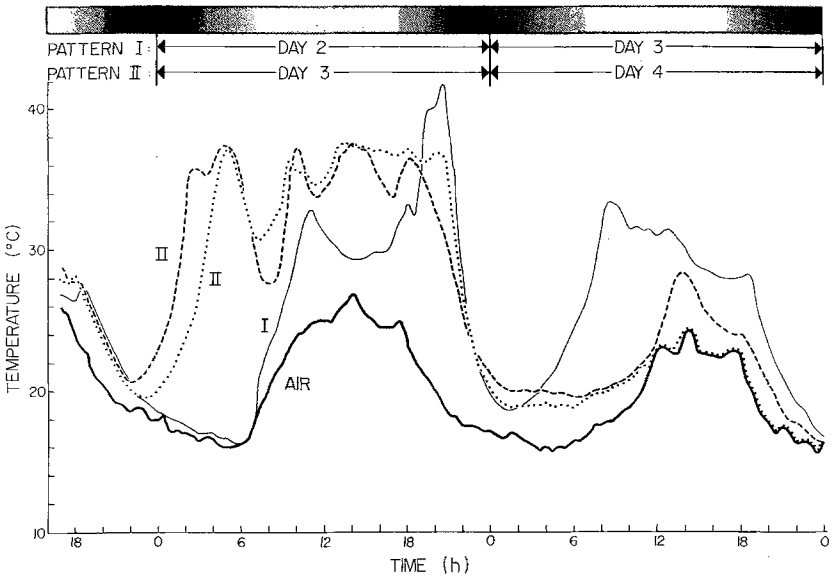

Fig. 1. Temperatures of three spadices of *Philodendron selloum* and nearby ambient air in an outdoor garden, 14–16 Jun 79. One spadix shows pattern I and two show pattern II. Note that day 1 for the pattern-I spadix is day 2 for the pattern-II spadices

entire spadix (Nagy et al. 1972), we did not study the other florets. Consequently, all of the present data refer to whole spadices or to sterile male florets cut from the stalk.

Flowering sequence. The major thermogenesis of the flowering sequence occurred over a 2-d period, but for the present analysis we include a day before and a day after the event.

On *day 1* the green spathe loosened and pulled slightly away from the spadix, but no warm-up occurred. On *day 2* the spathe gradually opened revealing the creamy-white spadix and inner surface of the spathe. The onset and sequence of warming in outdoor plants was not consistent with time of day but fell into two rather distinct patterns (Fig. 1). Of 15 flowers that were examined, nine exhibited pattern I and six exhibited pattern II.

Pattern-I spadices began to warm during daylight on day 2 and temperature peaked between 19:00 and 21:00 h. Thereafter spadix temperature decreased to approx. 4–6° C above ambient between about 00:00 and 03:00 of *day 3*. During this period of reduced temperature, the spathe loosely closed around the spadix. On day 3, between 03:00 and 05:30, a second episode of thermogenesis began and spadix temperatures gradually rose to a maximum of about 10–15° C above ambient by 12:00. Spadix temperature decreased during the afternoon and evening of day 3, when the spathe again opened exposing the fertile male florets which shed their pollen. Spadix temperatures returned to ambient levels by midnight and did not rise appreciably above ambient again. On *day 4* the spathe had closed and did not again reopen.

Pattern-II spadices did not begin thermogenesis until after 22:00 on day 2, at which time spadix temperature rose and usually peaked before dawn of day 3. Following a brief dip after sunrise, spadix temperature was maintained between 36 and 42° C until about 20:00 when it slowly began to approach ambient. Because pollen was shed in the evening of day 2 in spadices of both patterns, it appears that the main difference between the patterns is the delayed onset of thermogenesis in pattern II.

We do not know the causes of the two patterns. They were not obviously related to previous ambient temperatures, to time of lunar month, to time of thermocouple placement or to individual plants. On different days flowers from the same plant sometimes showed both patterns.

Maximum temperatures. There were two main temperature maxima recognisable in all inflorescences, presumably associated with the fertility of the female and male florets. However, there were slight differences between the two patterns of warming (Fig. 2). The first maxima of pattern I ranged from about 39–42.8° C and correspond to maxima measured in severed spadices examined by Nagy et al. (1972). The peak temperatures of pattern-II spadices during the first warm-up were 4–5° C lower (34.8–37.8° C). The second temperature peaks were substantially lower than the first in pattern-I spadices but were about the same as the first peak in pattern-II spadices. Regulation of maximum

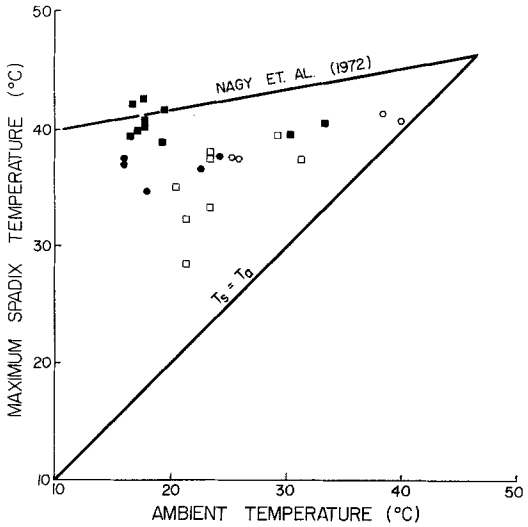

Fig. 2. Maximum spadix temperatures in outdoor *Philodendron selloum*. Sequence pattern I is shown with squares, pattern II by circles. First and second peaks are indicated by dark and light symbols, respectively. The regression line for maxima of severed spadices incubated in the laboratory at 4–39° C (Nagy et al. 1972) is also shown

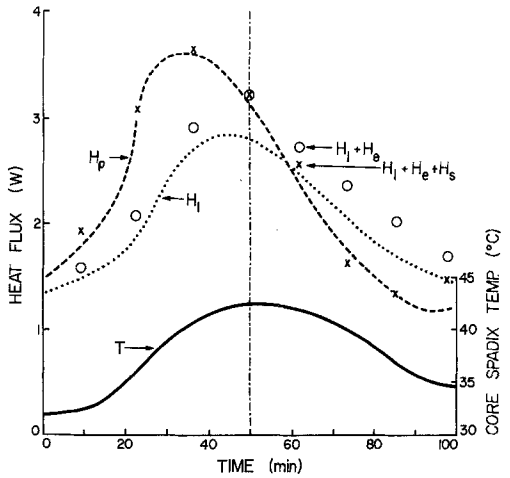

Fig. 3. Continuous measurement of core temperature (T), metabolic heat production (H_p) and combined heat loss by convection, conduction and radiation (H_l) in spadices of *Philodendron selloum*. Evaporative heat loss (H_e), calculated periodically from water loss, is added to H_l (o). Heat storage (H_s) was calculated from spadix weight (71.4 g), specific heat capacity (2.49 J g^{-1} $°C^{-1}$, Nagy et al. 1972) and temperature. Total heat loss and storage (X) closely approximates heat production

Table 1. Total chemical-potential-energy content of sterile male florets of *Philodendron selloum* cut from outdoor spadices during the flowering sequence

	Day	*N*	Energy content[a] J mg^{-1}
	1	6	22.77±1.96
	3	4	19.67±1.93
	4	10	19.32±0.95
Difference			
	1–3		3.10±2.18[b]
	3–4		0.35±1.67
	1–4		3.45±1.70[b]

[a] Mean±95% CI
[b] Significant, $P<0.01$

Table 2. Summary of direct and indirect calorimetry of four whole spadices of *Philodendron selloum* weighing 51–79 g. Data are means±95% CI

Variable	Units	Maximum	at T_{max}
Spadix temperature	°C	42.3 ±1.8	–
Air temperature	°C	–	26.8 ±1.2
O_2 consumption	ml min^{-1}	10.57±0.50	8.46±0.97
Heat production (H_p)	W	3.60±0.17	2.88±0.33
Dry heat loss (H_l)	W	2.57±0.54	2.48±0.60
Evaporative heat loss (H_e)	W	0.39±0.28	0.37±0.31
H_p–H_l–H_e	W	–	0.03±0.69

spadix temperatures is evident in the virtual independence of spadix temperature and ambient temperature during the first warm-up in all spadices. A limited degree of regulation also appears in the second warm-up of pattern-II spadices.

Temperature excess and energy expenditure. In 12 inflorescences for which complete temperature records were obtained, we summed the hourly temperature differences between thermogenic spadices and nearby spadices which had not yet begun to warm. We used inactive spadices rather than ambient air to minimize the effects of solar heating during the day. The total integrated temperature excess of each inflorescence was reasonably consistent, averaging 255 degree-hours (±25 CI). There was no significant difference between the total temperature excesses of the two patterns (266 degree-hours for pattern I and 230 for pattern II; difference = 36±50 CI).

Total content of chemical potential energy of sterile male florets decreased significantly between day 1 and day 3, but not between days 3 and 4 (Table 1). This is consistent with the temperature records of outdoor plants which showed that most of the heat had been produced by the middle of day 3.

Heat production and heat loss in cut spadices. Spadices cut from the plant in the evening of day 2 were usually warmer than air temperature. How-

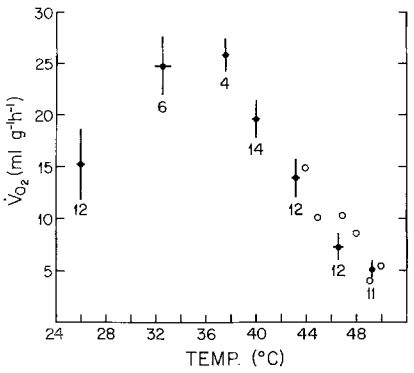

Fig. 4. Effect of temperature on $\dot{V}_{O_2}$ by isolated sterile male florets of *Philodendron selloum* severed from the spadix during the first episode of thermogenesis. Points represent means during 20-min periods of exposure to constant temperature; number of trials and 95% confidence intervals are indicated. Open circles show $\dot{V}_{O_2}$ during short-term exposure to high temperature in experiments demonstrating reversibility of heat inhibition

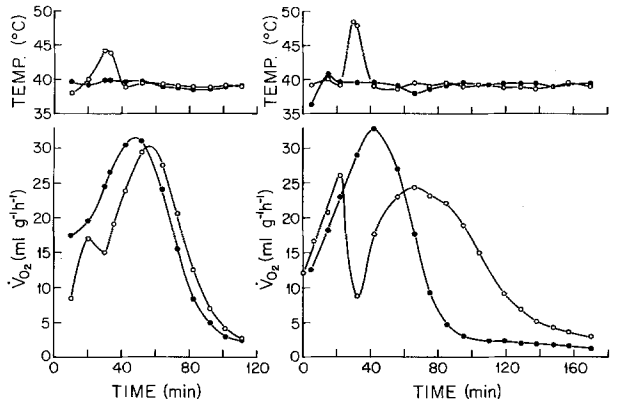

Fig. 5. Two examples of changes in $\dot{V}_{O_2}$ of isolated sterile male florets of *Philodendron selloum* exposed continuously to approx. 39° C (●) or exposed briefly to temperatures of 44 and 48° C (○)

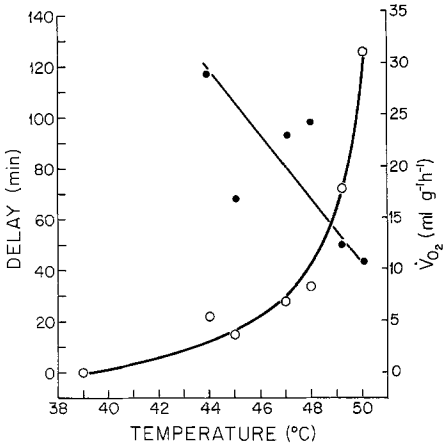

Fig. 6. Duration of delay before recovery of isolated florets of *Philodendron selloum* from heat inhibition by high temperature (○). The delay is the interval between minimum $\dot{V}_{O_2}$ during exposure to inhibiting temperature and the attainment of maximum $\dot{V}_{O_2}$ after being returned to 39° C. Maximum post-exposure $\dot{V}_{O_2}$ is also related to the temperature used for thermal inhibition (●)

ever, cutting seemed to trigger a rapid burst of heat production which peaked after about 20–30 min. This response also occurred in sterile male florets when severed from the spadix. High temperatures in cut spadices were short-lived compared with outdoor flowers, and after only 1.5–2 h, heat production decreased sharply (Fig. 3).

Four cut spadices examined in the gradient layer calorimeter showed similar patterns of heat production and loss (Fig. 3, Table 2). Metabolic heat production (H_p), measured from instantaneous $\dot{V}_{O_2}$ assuming 20.43 J ml^{-1}, was already high when the spadices were first monitored. Nevertheless H_p rapidly increased and peaked at about 3.6 W. This was followed by a dry (non-evaporative) heat loss (H_l) maximum of about 2.6 W. Spadix temperature peaked after H_p and H_l had started to decline. Evaporative heat loss (H_e), calculated from evaporative water loss (2.424 J mg^{-1}), increased with spadix temperature in an exponential fashion such that it was about 70 mW at 30° C and 300 mW at 45° C. The rate of heat storage (H_s) was calculated from the instantaneous change in average spadix temperature and the specific-heat capacity of whole spadices (2.49 J g^{-1} °C^{-1}; Nagy et al. 1972). Thus the rate of heat storage was zero when maximum temperature was reached. Theoretically, total heat loss equals heat production at this time. In our experiments, total heat loss was within 16% of heat production when spadix temperatures peaked; the mean difference was 0.03 W. This agreement between direct and indirect calorimetry validates the initial assumption that the heat equivalent of $\dot{V}_{O_2}$ is the same in *Philodendron* spadices as in animals.

Respiration of isolated florets: effect of temperature. The maximum $\dot{V}_{O_2}$ of isolated sterile male florets in closed respirometers occurred at about 37° C (Fig. 4). Rates at this and lower temperatures were similar to data presented by Nagy et al. (1972). At higher temperatures $\dot{V}_{O_2}$ declined steeply. When briefly exposed to high temperature in open flow respirometers, isolated florets quickly decreased $\dot{V}_{O_2}$ to levels similar to those of 20-min measurements in the closed respirometers (Fig. 4).

The reversibility of thermal inhibition of respiration during transient exposure to high temperature may be observed by comparing $\dot{V}_{O_2}$ of control samples of florets held at 39° C with that of experimental samples from the same spadix held first

at 39° C, then raised to a higher test temperature, and subsequently returned to 39° C (Fig. 5). The onset of thermal inhibition closely tracked floret temperature, but the recovery was not complete until many minutes after the florets returned to 39° C; the higher the maximum temperature they were exposed to, the longer the delay (Fig. 6). The magnitude of the maximum post-exposure $\dot{V}_{O_2}$ was inversely related to the temperature during thermal inhibition (Fig. 6). Despite the period of thermal inhibition and the reduction in maximum post-exposure $\dot{V}_{O_2}$, the total volume of O_2 consumed by the florets during the experiments was similar to that of the controls. The high-temperature exposure caused $\dot{V}_{O_2}$ to exceed control values during the latter period of measurement (Fig. 5).

Discussion

Differences between cut and intact spadices. The facility with which cut spadices and florets undergo thermogenesis in the laboratory is convenient for study but certain differences between cut and intact flowers should be recognised. Severed whole spadices examined during the evening of day 2 reached similar temperatures as did pattern-I spadices at the same time in the field (compare Figs. 2, 3). Temperature maxima from pattern-II spadices in the field were always lower than those of cut spadices at the same ambient temperatures. In contrast, the spadices of *Symplocarpus foetidus* start to cool immediately when severed from the plant (Knutson 1972) and severed spadix clubs of *Arum maculatum* break down starch at half the rate of intact clubs (ap Rees et al. 1976, 1977).

Cutting or slashing the spathe of *Sauromatum guttatum* can trigger a thermogenic episode, but only after a lag of about 34.2 h (Buggeln et al. 1971). In *Philodendron,* on the other hand, the peak metabolic activity of the spadix occurred within 30–60 min after excision (Figs. 3, 5). The variability in warming patterns of intact flowers of *Philodendron* is substantial (Fig. 1), but cutting off the whole spadix or excising the florets promptly triggers a maximal, yet regulated, thermogenic episode. The duration of this episode in severed spadices or florets is similar to those of the first thermogenesis of pattern-I flowers in the field (Fig. 1), showing that sufficient substrate is present in severed sterile male florets to support considerable thermogenesis.

Temperature regulation. This study demonstrates that the temperature maxima of *Philodendron* spadices remain within a narrow range (Fig. 2) and are controlled by acute but reversible reductions in heat production as spadix temperature rises above approx. 37° C (Fig. 4). At higher ambient temperatures, heat loss diminishes and the rising spadix temperature is accompanied by a diminution in heat production until heat production equals heat loss. This mechanism should prevent the flower from becoming hot enough to damage its own tissues or harming pollinating insects.

The inhibition of heat production by high temperature is reversible and the spadix may remain warm during a drop in the ambient temperature. Inactivation of enzyme activity by high temperatures may be caused by reversible changes in protein structure or from disruption of arrays of membrane-bound enzymes as a result of increased fluidity of the lipid matrix (Somero 1978). The respiration in slices of *P. selloum* spadices may be mediated largely by the cytochrome pathway during thermogenesis and an equally powerful but apparently little used cyanide-insensitive pathway exists in this species (Theologis 1979). The effect of temperature on the rates of these two pathways in unknown in *Philodendron* but the cyanide-insensitive pathway, known to be important in thermogenesis in other arum lilies (Meeuse 1975; Henry and Nyns 1975; Laties 1982), is inhibited by high temperature. For example, respiration in *Arum maculatum* and *A. italicum* mitochondria is severely reduced after exposure to 40–45° C (Chauveau et al. 1978).

Thermal inhibition of the cyanide-insensitive pathway can occur at relatively low temperatures. The rate of O_2 consumption by cyanide-insensitive wheat mitochondria decreases linearly with increasing temperature above 17.5° C and this has been linked with changes in membrane lipids (McCaig and Hill 1977). Such low temperatures are not usually associated with protein denaturation. Thus, the temperature regulation between 15 and 24° C in spadices of *Symplocarpus foetidus* (Knutson 1974), which rely almost entirely on the cyanide-insensitive pathway for heat production (Bendall and Bonner 1971), may be the consequence of membrane changes that occur above about 15° C.

The reversibility of thermal inhibition in our experiments was not immediate. The time delay between the cessation of high-temperature exposure and the post-inhibition peak in $\dot{V}_{O_2}$ increased with magnitude of the inhibiting temperature (Fig. 6). This delay may represent the time required to reorganize the enzyme systems after their disruption. Our data are insufficient to determine whether or not thermal inactivation is totally re-

versible at all experimental temperatures. Maximum post-inhibition $\dot{V}_{O_2}$ decreased with higher inhibiting temperatures (Fig. 6) but it may have been limited by the same factor or factors that caused the control $\dot{V}_{O_2}$ to decrease (Fig. 5). In any case, the recovery is rapid and $\dot{V}_{O_2}$ is essentially normal following exposure to 44° C (Figs. 5, 6). Because normal florets are unlikely to experience temperatures as high as 44° C (Fig. 2; see also Nagy et al. 1972), thermal inactivation under natural conditions appears to be completely reversible.

Heat production and spadix size. The spadix of eastern skunk cabbage, *Symplocarpus foetidus,* can generate temperatures as high as 35° C above ambient for periods of days or weeks (Knutson 1972, 1974). As in *Philodendron,* spadix temperature is partly regulated by increases in heat production as ambient temperature drops. The mass of the spadices of *Symplocarpus* is less than 4% the mass of the spadices of *Philodendron.* Consequently their surface:volume ratio is about three times that in *Philodendron* and they should lose heat faster. This size difference (Table 3) permits an allometric comparison of heat production in arum lilies. The heat produced to maintain a 30° C difference between spadix and air temperatures is related to spadix mass raised to the 0.71 power; $H_p = 0.23\ M^{0.71}$ where H_p is watts (W) and M is grams (g). Knutson (1974) calculated a similar exponent (0.73) for *Symplocarpus* spadices with masses between 2.5 and 9.5 g. The 95% confidence intervals for these exponents cannot be defined satisfactorily, but they can reasonably be assumed to include both the exponent (0.67) that relates surface area to mass in similarly shaped objects, and the exponent (0.75) that approximately related metabolic rate to body mass in many kinds of animals (Hemmingsen 1960). The spadices or appendices of arum lilies range in mass from 1.5 g in *Arum maculatum* (Lance 1972), to many kilograms in *Amorphophallus titanum* (Meeuse 1966). The opportunity exists to relate heat production to mass in morphologically similar inflorescences differing in size by many orders of magnitude.

Symplocarpus foetidus blooms in the winter in temperate regions where the ambient temperature may drop considerably below freezing. It has been suggested that heat production in this plant prevents damage to frost-sensitive tissues (Knutson 1974). Our comparison shows that *Symplocarpus* and *Philodendron* have similar surface-specific thermal conductances (Table 3). Thus both plants appear adapted to liberate heat to the environment rather than to retain it in the spadix. If frost prevention were the exclusive function of heat production in *Symplocarpus,* one would expect a much better insulated inflorescence and temperature regulated just above 0° C rather than at 15–20° C. The odor associated with thermogenesis in arum lilies indicates that attracting insect pollinators is important (Meeuse 1966). However, thermogenesis and odor production are not necessarily coincidental in some species (El-Din 1968). Although the idea of a "warm shelter" alone may be untenable as an insect attractant (Faegri and van der Pijl 1979), high temperatures within the spathe may be helpful for insects to feed, digest, breed or initiate flight.

Table 3. Comparison of heat production in two species of Araceae maintaining a temperature excess of 30° C. Values for heat production are calculated from regressions of $\dot{V}_{O_2}$ on ambient temperature in Nagy et al. (1972) and Knutson (1974)

	Philodendron selloum	*Symplocarpus foetidus*
Spadix mass (g)	123.5	4.5
$T_{spadix}-T_{air}$ (°C)	40–10	15 to −15
$\dot{V}_{O_2}$ (ml g^{-1} h^{-1})	10	26
Heat production (mW)	7,010	660
Thermal conductance		
Total (mW $°C^{-1}$)	234	22
Surface (mW $g^{-0.67}$ $°C^{-1}$)	9.28	8.03

Conservation of energy. The concordance between the heat production that we measured directly in the gradient layer calorimeter and that we calculated from $\dot{V}_{O_2}$ indicates that all the energy released by oxidation during thermogenesis appears as heat and there is no conservation of energy. Because the cytochrome and cyanide-insensitive pathways form a branched respiratory chain and share the same dehydrogenases before the point of branching near coenzyme Q, some phosphorylation of ADP may occur in mitochondria employing either of the pathways (Bonner et al. 1972; Lance 1974; Laties 1982). However, uncoupling of phosphorylation may occur and ATP may be hydrolysed by endogenous ATPase (see Meeuse 1975). Therefore, heat production is almost certainly the primary function of the high rates of respiration in arum lilies and does not appear to be incidental to any other metabolic activity.

Cost of thermogenesis. It is of interest to compare the decrease in chemical potential energy over the entire flowering sequence with an estimate of the energetic cost of temperature elevation in outdoor flowers. Assuming the average equivalent thermal conductance (0.43 ml O_2 g^{-1} h^{-1} $°C^{-1}$) from lab-

oratory spadices (Nagy et al. 1972) and the energy equivalence (20.43 J ml^{-1}) of O_2 consumed, the conductance becomes 8.78 J g^{-1} h^{-1} $°C^{-1}$. From the relative proportions of heat production by the sterile and fertile male florets (see note 14 of Nagy et al. 1972), we calculate a conductance of 21.7 J g^{-1} h^{-1} $°C^{-1}$ for the sterile male florets alone. This value, multiplied by the mean total temperature excess of the 12 spadices of the present study (255 °C·h), yields a total energy expenditure of 5.54 J mg^{-1} for the sterile males alone. The value from bomb calorimetry is 3.45 J mg^{-1}, or 62% of the predicted. There are several plausible reasons for this discrepancy: energy-producing substrates may move into the florets during the course of thermogenesis; the spathe in intact plants may insulate the spadix and reduce thermal conductivity; solar radiation may have heated active flowers more than inactive ones.

Over the entire flowering sequence, the direct energy cost of thermogenesis expenditure of the sterile male florets (5.54 J mg^{-1}) is less than 25% of their total energy content prior to thermogenesis (22.8 J mg^{-1}). Considering (1) that these florets produce most of the heat, and (2) that the plant must expend large amounts of energy synthesizing the 125-g spadix, it appears that two days of thermogenesis is an energetically inexpensive component of the reproductive process. However the two-week-long episodes of thermogenesis in *Symplocarpus* require relatively much more energy (Knutson 1974).

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