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Analysis of heat production in a thermogenic arum lily, *Philodendron selloum*, by three calorimetric methods

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Abstract

Rates of heat production and heat loss have been measured during flowering by direct (gradient-layer) calorimetry, indirect (respirometric) calorimetry, and bomb calorimetry. The inflorescences produce a heat flux of about 7 W, and can maintain a 35 °C temperature elevation. Concordance between the direct and indirect methods indicates that the heat equivalence of oxygen consumption is 20 J ml^{-1}, that there is no net phosphorylation, and that thermogenesis occurs specifically to warm the inflorescence. All energy substrates (chiefly lipid) exist in the inflorescence before thermogenesis and are not imported.

INTRODUCTION

Compared with animals, rates of respiration and heat production in plants are generally quite low. Exceptions to this rule occur among several species of the arum lily family (Araceae) and certain water lilies (Nymphaeaceae). Their flowers produce so much heat that some species are able to raise the temperature of the inflorescence as high as 35 °C above the environmental temperature [1,2]. Explanations for this phenomenon include volatilisation of insect attractants [3], promotion of flowering in cold weather while protecting the flowers from frost damage [2], and provision of a warm environment for insect pollinators [4].

Our work involved the inflorescence of the epiphytic arum lily, *Philodendron selloum* Koch (Fig. 1), which is a common ornamental plant originally from Brazil [4]. It produces a conspicuous 120 g spadix that is creamy-white and phallic in shape, consisting of hundreds of tiny florets of three morphological types. Female florets at the base of the spadix are separated from male florets at the apex by a band of sterile male florets in the middle. The inflorescence undergoes a two-day flowering sequence. On the first day, the green spathe opens and exposes the spadix. The first episode of thermogenesis occurs, and pollen-bearing insects are attracted to fertilise the receptive female florets. The spathe then closes loosely around the spadix, but partly opens again on the second day when the female florets are no longer

Fig. 1. Inflorescence of *Philodendron selloum* Koch during the first day of heating. The green spathe has opened, partly revealing the creamy-white 15 cm spadix. Fertile male florets are seen at the top of the spadix, and a few infertile male florets are distinguishable just above the overlap of the spathe. Female florets are concealed by the spathe at the base of the spadix.

receptive, and the male florets release their pollen onto the escaping insects. There is also a minor episode of thermogenesis at this time.

Our initial study revealed that the sterile male florets produced most of the heat, and that their rates of respiration were exceptionally high, approaching those of flying birds [1]. We also discovered that the maximum temperature of the spadix was relatively constant, varying between 38 °C and 46 °C while ambient temperature varied between 4 °C and 39 °C. This degree of homeothermy was achieved by progressively increasing the rate of heat production at lower ambient temperature. The pattern was so similar to that of a thermoregulating bird or mammal that we became interested in the mechanisms of temperature regulation [4] and respiratory gas exchange

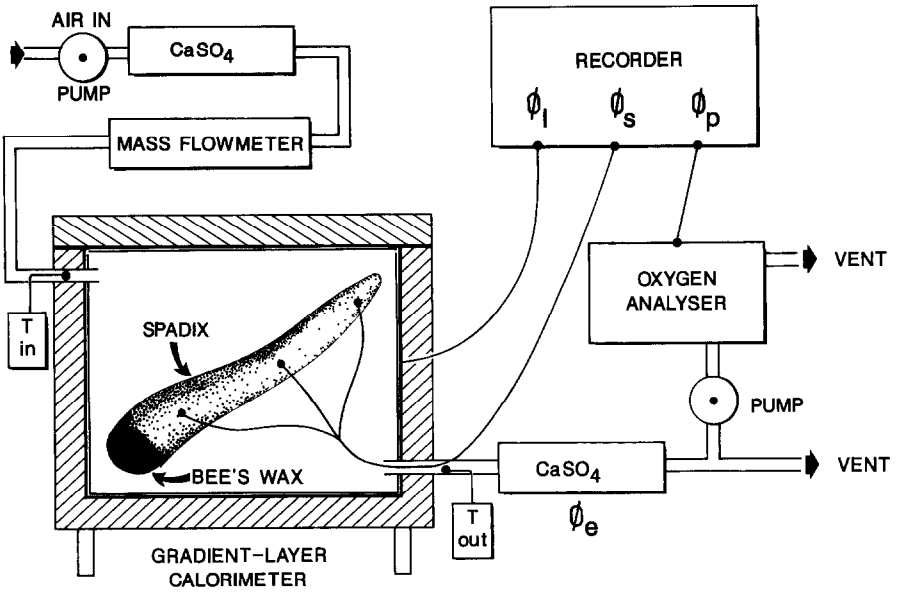

Fig. 2. Apparatus for simultaneous measurement of rates of respiratory heat production (ϕ_p), heat loss by convection, conduction and radiation (ϕ_l), evaporative heat loss (ϕ_e) and heat storage (ϕ_s) in the severed spadix of *Philodendron selloum*.

during thermogenesis [5]. We basically transferred techniques designed for animals to the flower.

We used direct calorimetry (measuring heat loss in a gradient-layer calorimeter), indirect calorimetry (measuring heat production by oxygen consumption), and bomb calorimetry (measuring changes in chemical potential energy of the florets throughout the flowering sequence). We thus examined the energetics of flowering from three directions, an approach that allowed us to evaluate the energy equivalent to oxygen consumption, to partition avenues of heat flux, and to observe the origin of the energy liberated during thermogenesis.

This short paper focuses on our calorimetric methods, their results and the implications. Other aspects of the study, including results statistics, may be found in the original publications.

METHODS

We carried out direct and indirect calorimetry simultaneously on whole spadices immediately after cutting from the plant during the first episode of heating. After covering the severed end in beeswax to prevent evaporative heat loss from the cut, we inserted fine thermocouples to measure core temperature, and placed the spadix in the apparatus (Fig. 2).

Heat loss rates due to the combined effects of convection, conduction and radiation (ϕ_l) were measured in a gradient-layer calorimeter. This consisted

of a thick aluminium case of $100 \times 135 \times 98$ mm^3 internal dimensions, supported on four legs in a constant temperature enclosure. The entire inside of the case was lined with a double-layered thermopile which gave an output voltage of 0.5025 μV mW^{-1}. Calibration of the calorimeter was performed by burning measured amounts of ethyl alcohol in a small lamp (heat of combustion = 29.68 J mg^{-1} at 25 °C). A small amount of heat (ca. 1%) was lost to the air flowing through the chamber, and this was calculated from mass flow rate, temperature difference, and the specific heat capacity of the air.

Evaporative heat loss rate (ϕ_e) was evaluated by multiplying the latent heat of vaporisation at spadix temperature (2.42 J mg^{-1}) by the mass of water vapour collected in two tubes of desiccant that were alternately placed in the excurrent line and weighed at intervals.

Heat production rate (ϕ_p) was measured by open-flow respirometry. Dry air was pumped through a mass flow controller at a rate of 800 ml min^{-1} into the calorimeter. A subsample of the dried excurrent air was pumped into an Applied Electrochemistry (S-3A) oxygen analyser. The instantaneous rate of oxygen consumption was calculated continuously with a technique that accounts for temporal lag as the gas flows through the system [6]. The rate of oxygen consumption (ml s^{-1} STPD) was converted into a rate of heat production (W = J s^{-1}) by multiplying by 20.43 J ml^{-1} [7], the value appropriate for the measured respiratory quotient of 0.82 [5].

The rate of heat storage (ϕ_s) was calculated from changes in mean core spadix temperature, spadix mass, and measured specific heat capacity of whole spadices (2.49 J g^{-1}K^{-1} [1]).

Total caloric content of the sterile male florets was measured by cutting the florets, weighing them, drying at 70 °C, grinding with a mortar and pestle, pelletising, redrying, weighing and combusting in a Phillipson microcalorimeter [8]. The florets were sampled three times: the day before thermogenesis, after the first episode of thermogenesis, and after the second episode.

RESULTS

The spadices had started the first episode of warming when cut for calorimetry. Cutting appeared to stimulate a rapid rise in oxygen consumption, which was coupled with further heating of the spadix (Fig. 3). The four small spadices that would fit in the calorimeter weighed 51–79 g and produced 2.9 W, to achieve a temperature excess (spadix minus ambient temperature) of 15.5 °C. Field spadices were usually about twice as large (124 g), and produced about 7 W to maintain an excess of 30 °C [1]. For an unknown reason, the duration of heating in severed spadices lasted only 1–2 h, whereas intact spadices on the plant stayed warm for several hours. However, the maximum levels of respiration were similar.

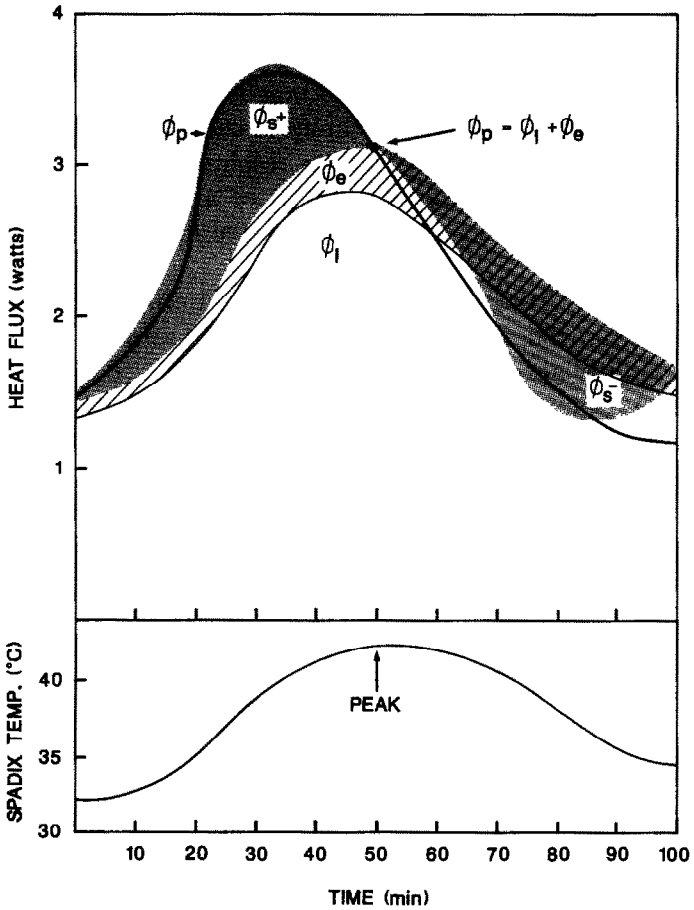

Fig. 3. Instantaneous rates of heat production (ϕ_p), heat loss rates by convection, conduction and radiation (ϕ_l), evaporative heat loss rate (ϕ_e) and heat storage rate (ϕ_s) during a thermogenic episode in a 71.4 g spadix of *Philodendron selloum*. ϕ_e and ϕ_s are added to the curve for ϕ_l, and the total approximates ϕ_p. At peak spadix temperature, ϕ_s is zero, and $\phi_p = \phi_l + \phi_e$ at the indicated point.

Most of the heat produced was lost by convection, radiation and conduction (ϕ_l); ϕ_e accounted for less than 10% of the total heat production. Calculated ϕ_s was positive as spadix temperature increased, negative when it decreased. The sum of ϕ_l, ϕ_e and ϕ_s was close to ϕ_p (Fig. 3).

Before the first episode of thermogenesis, the sterile male florets had a total energy content of 22.8 J mg^{-1} (dry mass). This decreased to 19.67 J mg^{-1} after the first episode, and to 19.32 J mg^{-1} after the second episode. At the same time, water content (mg of water per mg dry mass) increased from 1.35 to 1.79 to 2.23 mg mg^{-1}, respectively. However, it was apparent that the florets lost an unmeasured amount of total mass.

DISCUSSION

I am unaware of any other studies which simultaneously applied direct and indirect calorimetry to plant tissues. Our techniques show that all of the heat energy released from the flower originates from respiratory catabolism, and that heat production is not an incidental product of anabolic activity. Apparently spadix warming is the only adaptive function of heat production in arum lilies.

The concordance of direct and indirect calorimetry also confirms that the heat equivalence of oxygen consumption (20 J ml^{-1}) is the same in these flowers as in animals. Unlike animals, however, the arum lilies employ a dual respiratory chain. A cyanide-insensitive oxidative pathway branches from the cytochrome pathway near ubiquinone, and both pathways may be thermogenic [9]. In any case, net ATP production is prevented by uncoupling of phosphorylation or hydrolysis of ATP by endogenous ATPase.

Changes in heat production and loss reflect core spadix temperature (Fig. 3). During the warming phase, ϕ_p increases exponentially by a self-reinforcing feedback loop. Because ϕ_p is greater than $\phi_l + \phi_e$, ϕ_s is positive, and the rising spadix temperature further increases ϕ_p exponentially [1]. When the temperature reaches 37 °C, ϕ_p is maximal. Above 37 °C, ϕ_p begins to decrease due to reversible thermal inactivation of the heat producing pathways [4]. Nevertheless, ϕ_p remains higher than $\phi_l + \phi_e$ and temperature continues to rise. When spadix temperature reaches a peak of 42 °C, ϕ_p has decreased to about 80% of the maximum value and it now equals $\phi_l + \phi_e$ (see point on Fig. 3). The decrease in ϕ_p after this point is an artifact attributable to severing the spadix, because temperature and ϕ_p remain high for several hours in intact plants. Cooling of a laboratory spadix is shown in Fig. 3 as a decrease in temperature and negative ϕ_s. Again, ϕ_p is similar to the total ϕ_l, ϕ_e and ϕ_s.

Bomb calorimetry shows that the energy density (J mg^{-1}) decreases over the period of warming, but the change in the total amount of energy in the florets is not directly known. It is likely, however, that all of the energy used during thermogenesis is present in the florets before warming, and not imported from other parts of the plant. This conclusion is based on continuous measurements of the temperature excess during the course of thermogenesis in the field [4]. The integrated temperature excess in 12 inflorescences is 255 "degree-hours." With measurements of thermal conductance of whole spadices and the proportion of spadix mass attributed to the sterile male florets [1], we calculate a thermal conductance for the sterile florets of 21.7 J $g^{-1}h^{-1}K^{-1}$. Multiplying this by the total temperature excess yields 5.54 J mg^{-1} of energy loss from the sterile florets, or about 57% of their initial energy content (not 24% as reported in ref. 4). This value can be used to calculate the changes in total energy, wet mass and dry mass of sterile florets from the available data as follows.

Before heating, 1 g of florets has 426 mg of dry material and 574 mg of water. With an energy density of 22.8 J mg^{-1} (dry mass), the total energy content is 9700 J. If 5540 J is lost during heat production, the florets have 4160 J remaining. A respiratory quotient of 0.82 [5] indicates that a mixture of carbohydrates and lipids is oxidised. Interpolating energy density data for carbohydrates and lipids [10], I arrive at a value of 29.4 J mg^{-1} (dry mass). Thus 5540/29.4 = 189 mg of substrate have been used, leaving 426 − 189 = 237 mg of dry matter remaining. The measured energy density of 19.32 J mg^{-1} indicates that 4585 J is present after heating, a value similar to the one calculated above. Because the water content after heating is 2.23 mg mg^{-1}, 528 mg of water remains. Therefore the original 1 g of florets has decreased to 766 mg.

Heat production and temperature regulation have been measured in only two species of arum lilies [2,4]. It would be interesting to examine other species which have inflorescences differing in mass from about a gram (*Arum maculatum*) to many kilograms (*Amorphophallus* sp.).

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