Reports

Temperature Regulation by the Inflorescence of Philodendron

Abstract. *The inflorescence of* Philodendron selloum *temporarily maintains a core temperature of 38° to 46°C, despite air temperatures ranging from 4° to 39°C, by means of a variable metabolic rate. The heat is produced primarily by small, sterile male flowers that are capable of consuming oxygen at rates approaching those of flying hummingbirds and sphinx moths.*

The inflorescences of several species of plants belonging to the arum lily family (Araceae) become much warmer than their surroundings during part of the 2- to 4-day flowering sequence (*1*). Typically, the inflorescence (spadix) warms rapidly, and then remains at its maximum temperature for 0.3 to 4.0 hours before cooling. Heating occurs at a specific time of the day and is apparently stimulated by an unidentified hormone (*2*) released in response to variations in light intensity (*3*). The heat, produced by the rapid oxidation of starch (*4*), results in the volatilization of chemicals that attract insect pollinators (*5*). The similarities between spadix temperature maintenance and endothermy in birds and mammals prompted us to investigate the thermal relations and energetics of these plant structures.

Continuous recording (*6*) of core temperatures (T_b) of the spadices of common garden philodendrons (*Philodendron selloum*) growing outdoors on the Los Angeles campus of the University of California revealed that the maximum temperatures of the spadices were maintained about 20°C higher than air temperatures (T_a). To examine the responses of spadices to a wider range of T_a than occurred outdoors, warming spadices were cut from the parent plant 1 to 2 hours before the peak T_b was due to be reached (about 19:30 P.S.T.) and placed in open 4-liter jars in a bacteriological incubator (Aminco); their T_b were monitored continuously at T_a ranging from 4° to 39°C (*7*). Most T_b were already about 35°C at the time the spadices were cut. In some, the green bract (spathe) partly enclosing the spadix was left intact.

To evaluate the effect of cutting inflorescences from the parent plant, the T_b of several spadices which had been severed from plants but left outside in situ were compared with T_b recorded from uncut spadices.

Maximum spadix temperatures were maintained within a relatively narrow range (means from 38.6° to 45.8°C), even when T_a was near freezing (Fig. 1). The least-squares regression line for these data has a small positive slope ($y = 0.179x + 38.2$; correlation coefficient $r = .77$), and the slope is significantly different (probability $P < .005$) from zero (*8*), an indication that T_b is partly dependent on T_a. Neither the removal of the spathes nor the cutting of the spadices from the parent plant had any detectable effect on T_b responses.

To determine the relationship between energy metabolism and T_b maintenance, we simultaneously measured rates of O_2 consumption and T_b at various T_a. We determined the amount of O_2 consumed by sealing the jars containing the spadices for 5 or 10 minutes and measuring the decrease in O_2 with a paramagnetic oxygen analyzer (Beckman model E2). Metabolic rates during peak temperature maintenance were inversely proportional to T_a (Fig. 1). At low T_a, the rates of O_2 consumption of spadices are comparable to those of resting hummingbirds (*9*) and small shrews (*10*).

To provide an independent check on O_2 consumption results, we measured the cooling rates of the same spadices used for metabolic rate measurements. After the spadices had been killed by freezing, they were heated to 50°C and then cooled under the same conditions obtaining during O_2 consumption measurements. Cooling rates in degrees Cel-

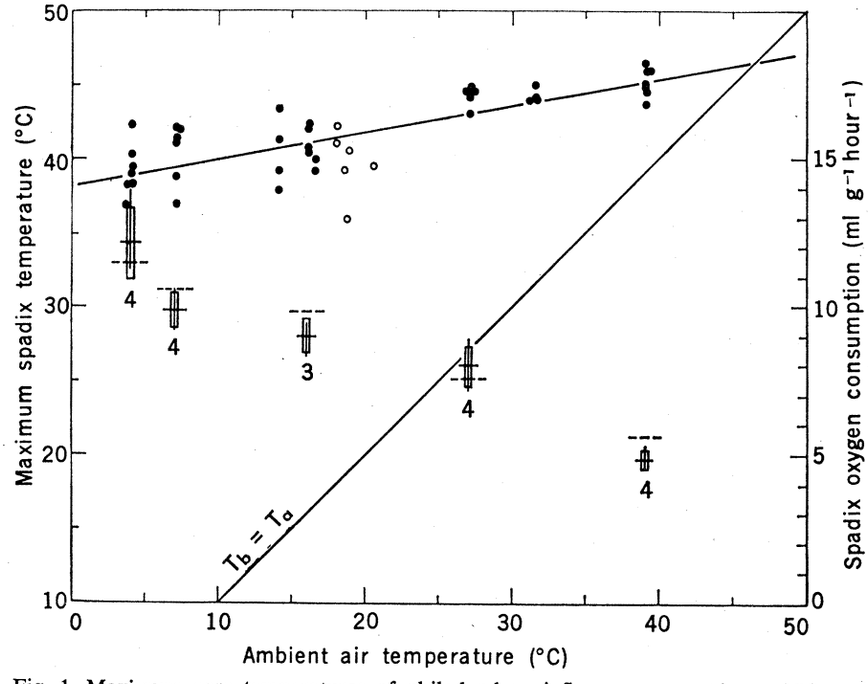


Fig. 1. Maximum core temperatures of philodendron inflorescences outdoors (○) and in incubators set at various temperatures (●). Solid horizontal lines indicate the mean spadix O_2 consumption rates; vertical lines show the ranges; rectangles are ± standard deviations. Dashed horizontal lines indicate the mean metabolic rates predicted from the cooling rates of killed spadices. Numbers below the rectangles are sample sizes for O_2 consumption and cooling rate measurements.

Fig. 2. Structure of an inflorescence (spadix) of *Philodendron selloum*. This spadix was cut longitudinally to show the insertion and structure of the three types of flowers on the stalk (magnified in the circle). The spadix is contained within a large green bract (spathe) which opens at the onset of the flowering sequence.

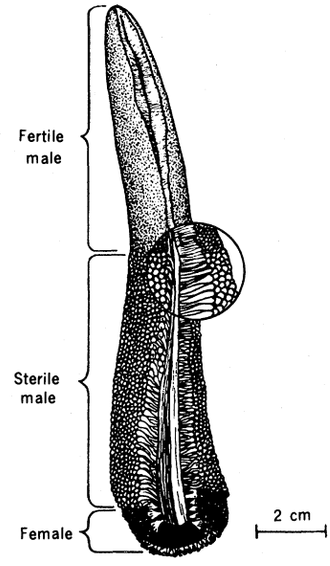
sius per minute ranged from 1.54° ± 0.14° (standard error) when T_a=4°C to 0.77° ± 0.09° when T_a = 39°C. We used these rates to estimate the metabolic rates necessary to maintain T_b at a given value by using the equation (*11*)

$$M = K\,(dT/dt)$$

where M is the metabolic rate, K is the specific heat capacity [0.595 cal g^{-1} $°C^{-1}$ for spadices, determined by the method of mixtures (*12*)], and dT/dt is the instantaneous rate of cooling when T_b of the cooling body equals T_b during temperature maintenance. The metabolic rates predicted from this equation are in good agreement with the measured rates (Fig. 1).

Thus philodendron inflorescences maintain constant, relatively high temperatures for brief periods of time by regulating their rate of oxidative metabolism. The ecological significance of this phenomenon is not clear; possibly the vaporization characteristics of the insect-attracting chemicals produced by philodendron are important in this regard. In another arum (*Sauromatum guttatum*), the volatilization rate of at least one chemical is increased twofold as a result of spadix heating (*5*).

In an effort to examine in further detail the control of respiration in philodendron, we measured the O_2 consumption rates of separate parts of the spadix. There are three flower types attached to the outside of the spadix stalk (Fig. 2). In a typical 125-g spadix female, flowers (weighing about 11 g when removed from stalk) occupy the base, sterile male flowers (about 36 g) occur in the middle section, and the distal end contains fertile male flowers (about 29 g). Preliminary measurements revealed that sterile male flowers possessed the highest weight-specific O_2 consumption rate, fertile male flowers consumed O_2 at about half that rate, whereas female flowers and stalk tissue consumed very little O_2. To test the effects of temperature, we removed 2 to 4 g of sterile male flowers from the stalk and spread them on the bottom of 0.5-liter jars placed in incubators set at various temperatures. With the use



of this procedure any metabolic heat produced was rapidly dissipated, and the temperature of the flowers remained near T_a.

Under these conditions, rates of O_2 consumption increased with temperature to a peak at 37°C and then decreased at higher temperatures (Fig. 3), in the same manner as in isolated mammalian and avian tissues and most isolated enzyme preparations. The highest metabolic rate, when T_a = 37°C, was almost 30 ml of O_2 per gram per hour; this approaches the metabolic rate of 40 to 50 ml of O_2 per gram per hour measured in hovering hummingbirds (*9*) and flying sphinx moths (*13*).

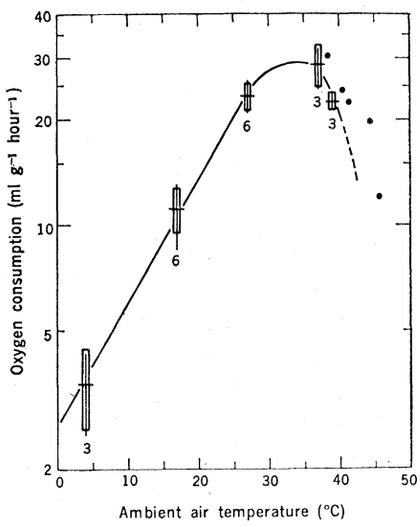


Fig. 3. Relationship between the metabolic rate of sterile male flowers removed from philodendron spadices and temperature ($T_b \cong T_a$). Solid circles represent values calculated from the O_2 consumption rates of intact spadices (*13*). Other symbols are as in Fig. 1.

We constructed a model, based on these results, that can account for the ability of spadices to regulate maximum T_b. The metabolic rates of isolated flowers drop rapidly when T_a is increased from 37° to 39°C (Fig. 3). If this trend continued to 45°C, the result would be a large change in metabolic rate over a narrow temperature range. Thus, if a spadix maintaining T_b at a given T_a somehow became warmer, O_2 consumption and metabolic heat production would decrease, causing the spadix to cool and return to the steady-state condition. The reverse would occur in a cooling spadix. The temperatures at which spadices reach the steady state should increase with T_a for the following reasons: (i) because the rate of heat loss is proportional to the temperature difference ($T_b - T_a$); (ii) because temperature maintenance requires that heat loss equals heat production; and (iii) because the model predicts that, when T_b is above 37°C, rates of heat production decrease with increasing T_b. This prediction agrees with the observed correlation between T_b and T_a (Fig. 1).

Unfortunately, the flowering season ended before we could test this model by measuring O_2 consumption of isolated flowers at temperatures above 39°C. However, we calculated estimates of these values from mean O_2 consumption rates of intact spadices (Fig. 1) by correcting for the fraction of total spadix weight that consists of sterile and fertile male flowers, and the relative metabolic rates of both flower types (*14*). When these values are plotted against the corresponding mean T_b for each group of spadices (Fig. 3), a steep inverse relationship results, thus indirectly supporting the basic assumption of the model.

It appears that the lowest T_a at which philodendron spadices can maintain a high T_b is near 4°C. In fact, two small spadices did not remain warm when placed in the 4°C incubator but rapidly cooled to 4°C. Apparently their larger ratio of surface to mass occasioned heat loss that exceeded the maximum heat production, thus providing for the cooling of metabolizing tissues and the concurrent disruption of the balance between body temperature, energy metabolism, and heat loss.

KENNETH A. NAGY
DANIEL K. ODELL
ROGER S. SEYMOUR*
Department of Biology,
University of California,
Los Angeles 90024

References and Notes

1. A. W. H. van Herk, *Rec. Trav. Bot. Neer.* **34**, 69 (1937); L. van der Pijl, *ibid.*, p. 157; B. J. D. Meeuse, *Sci. Amer.* **215**, 80 (July 1966); B. H. Brattstrom, *Bull. South. Calif. Acad. Sci.* **71**, 54 (1972).
2. R. G. Buggeln and B. J. D. Meeuse, *Can. J. Bot.* **49**, 1373 (1971).
3. B. J. D. Meeuse and R. G. Buggeln, *Acta Bot. Neer.* **18**, 159 (1969); R. G. Buggeln, B. J. D. Meeuse, J. R. Klima, *Can. J. Bot.* **49**, 1025 (1971).
4. W. O. James and H. Beevers, *New Phytol.* **49**, 353 (1950); D. P. Hackett, *J. Exp. Bot.* **8**, 157 (1957); E. W. Simon, *ibid.* **10**, 125 (1959); D. S. Bendall and W. D. Bonner, Jr., *Plant Physiol.* **47**, 236 (1971).
5. B. N. Smith and B. J. D. Meeuse, *Plant Physiol.* **41**, 343 (1966).
6. All temperatures were recorded with copper-constantan thermocouples connected to a multipoint strip-chart recorder (Honeywell Electronik 16).
7. A fan in the incubator circulated the air and kept T_a within $\pm$ 0.5°C.
8. Using the *t*-test from W. J. Dixon and F. J. Massey, Jr., *Introduction to Statistical Analysis* (McGraw-Hill, New York, ed. 3, 1969), p. 197.
9. R. C. Lasiewski, *Physiol. Zool.* **36**, 122 (1963).
10. O. P. Pearson, *Science* **108**, 44 (1948).
11. Derived from equations and assumptions presented by G. A. Bartholomew and V. A. Tucker, *Physiol. Zool.* **36**, 199 (1963).
12. R. C. Weast and S. M. Selby, Eds., *Handbook of Chemistry and Physics* (Chemical Rubber Company, Cleveland, ed. 48, 1967), p. F-87.
13. B. Heinrich, *J. Exp. Biol.* **54**, 141 (1971).
14. The equation used was: spadix O_2 consumption (in milliliters of O_2 per gram per hour) = (0.29 g of sterile male flowers per gram of spadix) multiplied by (X) + (0.23 g of fertile male flowers per gram of spadix) multiplied by $(X/2)$, where X is the O_2 consumption rate of sterile male flowers and $X/2$ is the metabolic rate of fertile male flowers.

15. We thank K. Pogany for preparing the illustration in Fig. 2. This study was supported in part by NSF grant GB-32947X to Dr. G. A. Bartholomew.

* Present address: Department of Zoology, Monash University, Clayton, Victoria 3168, Australia.

2 October 1972

Smoke of Cigarettes and Little Cigars: An Analytical Comparison

Abstract. *Chemical data are presented from a comparison study of the smoke of cigarettes and little cigars. The tobacco products and their mainstream smokes were analyzed for a number of toxic constituents in an effort to define "smoke inhalability." This issue has particular public health importance because the difference in the inhalability of cigar and cigarette smoke is generally assumed to account for the differences in the health risk to the individual smoker.*

Epidemiological studies have demonstrated that the chance of developing lung cancer is greater for cigarette smokers than for cigar smokers; however, both types of smokers face the same risk of developing cancer of the oral cavity. The difference in the rate at which cigar and cigarette smokers develop lung cancer is related to known differences in inhalation practices which are, in turn, dependent on the physicochemical properties of the different smokes (*1*).

At present, in the United States, the distinction between a cigar and a cigarette is based on the 1961 Internal Revenue Service definition, made for tax purposes, which defines a cigar as "any roll of tobacco wrapped in leaf tobacco or in any substance containing tobacco" and a cigarette as "any roll of tobacco wrapped in paper or any substance not containing tobacco" (*2*).

It is obvious that, if the distinction between cigars and cigarettes is to be meaningful in terms of the potential hazard to human health, it should be based not on the composition of the wrapper but rather on the physicochemical properties of the smoke and its resulting "inhalability." In this study we attempted to establish the specific physicochemical differences between the smoke of cigarettes, cigars, and the new, popular little cigars. It is hoped that this information will contribute to the establishment of new ways of distinguishing between cigarettes, cigars, and little cigars which are more relevant to human health.

Cigarettes without filter tips (85 mm) were obtained from the University of Kentucky (*3*); little cigars A (85 mm), from the open market in Boston, Massachusetts (December 1971); filter cigarettes (85 mm), little cigars B (85 mm), small cigars C (95 mm), and cigars D (112 mm), from the open market in New York City (December 1971–January 1972). The filter cigarettes, little cigars B, small cigars C, and cigars D chosen were the largest-selling brands in their respective categories (*4*).

The tobacco products (*5*) were humidified in a chamber maintained at a relative humidity of 60 percent and 22°C and subsequently smoked under standard conditions as established for cigarettes (*6*). Standard smoking conditions are as follows: a single puff of 2 seconds duration once a minute; a puff volume of 35 ml; a butt length of 23 mm except for the filter cigarette and little cigar A which have butt lengths of 27 mm. Subsequently, we determined the burning rate as an indicator of combustibility (*6*); total particulate matter (TPM) and nicotine as

Table 1. Analysis of cigarettes and little cigars and some of their smoke constituents.

Parameter	Nonfilter cigarette	Filter cigarette	Little cigar A	Little cigar B	Small cigar C
Filter length (mm)		21	21	18	15
Weight (mg)	1100	1010	956	1078	1522
Weight without filter (mg)		845	775	934	1355
Reducing sugars (% of tobacco weight)	9.3	7.9	1.5	2.9	2.7
Draw resistance* (mm)	6.6	13.4	13.2	13.0	8.9
Burning rate (mg of tobacco per minute)	51.3	61.7	72.7	61.0	90.1
Average number of puffs	11.0	10.0	7.7	9.8	11.6
Nicotine (mg)	2.65	1.4	0.6	1.8	3.1
TPM† (mg)	36.1	20.3	17.4	31.8	40.6
Average *p*H, 3rd puff	6.19	6.15	6.44	6.55	6.55
Average *p*H, 5th puff	6.14	6.12	6.57	6.46	6.59
Average *p*H, 7th puff	6.09	6.01	7.03	6.51	6.56
Average *p*H, 9th puff	6.02	5.83		6.98	6.59
Average *p*H, last puff‡	5.96 (11)	5.76 (10)	7.73 (8)	7.25 (10)	7.11 (11)

* For an air flow of 17.5 ml/sec. † Federal Trade Commission value for TPM = TPM wet minus water and minus nicotine. ‡ The number in parentheses is the number of the last puff. Average *p*H values of cigar D: 6.47 (3); 6.27 (8); 6.39 (13); 6.41 (18); 6.81 (23); 7.22 (28); 7.53 (33); 7.78 (38); 7.96 (43); [average number of puffs: (45)].