Thermochimica Acta, 187 (1991) 33–40
Elsevier Science Publishers B.V., Amsterdam

SOME LIKE IT HOT
CALORIMETRIC INVESTIGATIONS OF VOODOO LILIES

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ABSTRACT

An isoperibolic calorimeter of approximately 3 liters volume and a sensitivity of 52.8 mV/W is described, specially designed for studies on whole plants. It was used to monitor thermogenesis during anthesis (flowering up) of the voodoo lily, *Sauromatum guttatum*, a member of the family of Araceae. Simultaneous measurements of oxygen consumption indicate a high ratio of heat production to oxygen consumption and a strong uncoupling of oxydative phosphorylation during anthesis. Thermographic registration and temperature determinations along the whole plant show an elevation of the appendix temperature of 7 °C above the surrounding.

INTRODUCTION

Plants are poikilothermic organisms which exhibit only small temperature differences to the surroundings due to a low rate of metabolism - as compared with animals or microorganisms - and a large surface. Moreover, evaporation of water with its high amount of endothermic heat plays an important role in plant life for transpiration and water transport. These findings explain the fact that only a few calorimetric experiments on plants are found in the literature. They mainly concern germination of seeds and development of early leaf stages [1-5].

During anthesis some plant families - among them Araceae, Palmae and Nymphaeaceae - show a strongly increased turnover rate of carbohydrate metabolism and a very intensive heat production due to uncoupling of oxydative phosphorylation by use of an "alternative pathway" [6]. The strong thermal effect was first described by Lamarck in 1778 [7] and lateron - often in a more anecdotical way and without exact measurements - by several authors. It could be shown that the heat produced in the flowers is not of interest per se but used for volatizing odor substances to attract insects as possible pollinators [6,8]. Most modern investigations of such plants were performed thermometrically and biochemically [9,10], a few with indirect calorimetry (determination of oxygen consumption and carbon dioxid production) [11,12], some very recent ones by direct calorimetry [13,14] and one on

0040-6031/91/$03.50

a variety of Araceae by thermography [15]. Table 1 compiles some quantitative results for heat production and temperature of Araceae found in literature.

Figure 1. Picture of a flowering voodoo lily (*Sauromatum guttatum*). The various parts of the plant are described in the sketch used with Fig.4.

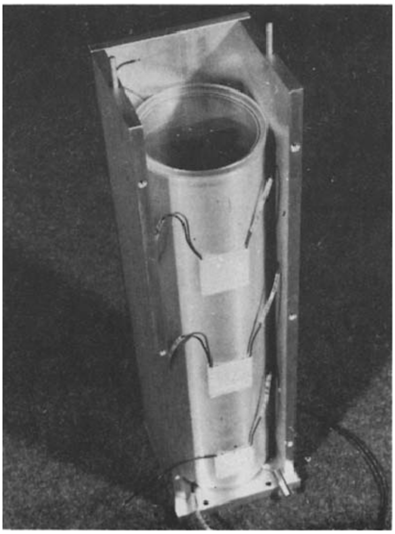

Figure 2. View of the dismantled calorimeter without styropor insulation and thermostat. 3 of the 12 Peltier-elements are seen on the circumference of the inner cylinder.

A very attractive object for such investigations is the voodoo lily (*Sauromatum guttatum*) which is indigenous to India and several islands of the Indonesic archipel. The flower develops without earth and water from a corm within 2 to 3 weeks and dies away in a few days after anthesis. The plant with its various parts is shown in Fig. 1 for the day of flowering. On this day it produces a very strong unpleasant smell like rotting flesh or decaying urine, mainly carried by amines, skatols and indols. Flowering up occurs early in the morning and lasts till to the afternoon, a much weaker second heating period might be observed on the following day. This plant was intensively investigated by several authors [11,16], but no calorimetric data are published until now.

MATERIAL AND METHODS

Plants

50 voodoo lilies were purchased in late autumn in a Berlin garden center and kept in the dark at 6 °C. The plants were succesively brought to the laboratory and grown at 25 °C under a light regime of 12 h light : 12 h dark at an illumination intensity

of 1.2 mW/cm^2. Every morning the plants were weighed and the length of the spadix (see Fig. 4) determined. During development and specially on the day before and the day of anthesis they were placed in the calorimeter for several hours to determine the rates of heat production and oxygen consumption.

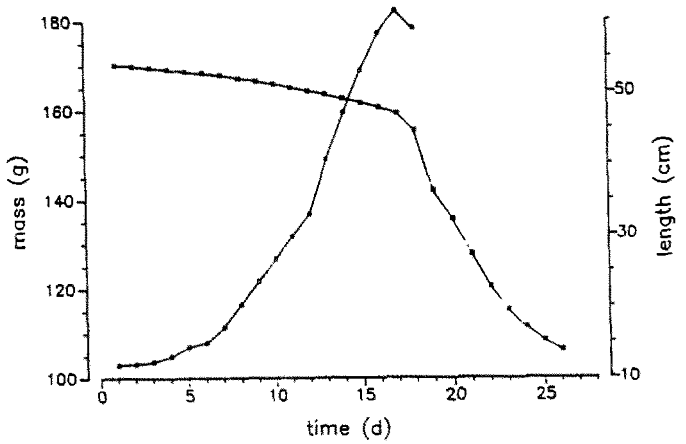

Figure 3. Time course of mass (x) and length (o) of a voodoo lily during growth and flowering. The spathe opened in the night between day 17 and 18.

Calorimetry

Fig. 2 shows the opened calorimeter constructed for the plants: a cylindrical tube with an inner diameter of 9.5 cm and a height of 39.5 cm is placed in a quadratic prisma of 50 cm total height. The walls and the bottom of the cylinder are covered with 12 Peltier-elements in series of 4.0 x 4.0 cm^2 serving as heat flow meter. The calorimeter is inserted upright into a styropor box with 4.0 cm walls, on the outside covered with aluminium foil for a more homogeneous temperature distribution. The whole setup is housed in the air thermostat of an LKB 10700 calorimeter expanded by a wooden cover for the necessary height. The inner cylinder is constructed air-tight enabling determinations of oxygen consumption, carbon dioxid production and water evaporation. The upper cover is made from plexiglass so that illuminations by light guide optics is possible.

Calibration of the calorimeter was performed in a triple manner: by electric heating in the usual way, by burning of known amounts of alcohol [17,18] (for simultaneous tests of oxygen consumption and carbon dioxid production) and by ignition of flesh-light bulbs of known energy content. They served to check the time response of the instrument to quick reactions. The three methods rendered a mean sensitivity of 52.8 mV/W, the time constant was determined to 13.2 min. Usual recorder settings were from 10 mV for non-flowering plants to 200 mV on the day of anthesis. All calorimetric experiments were run at 25 °C.

Polarography

An oxygen electrode of the Clark type was incorporated into the top cover of the cylinder. It was connected to an oxygen monitor (type Oxymeter, Draeger/Lübeck) showing the partial oxygen pressure in the chamber. The change of oxygen concentration due to metabolism was monitored simultaneously with the calorimeter signal on a two channel recorder (type BD 41, Kipp&Zonen/Delft).

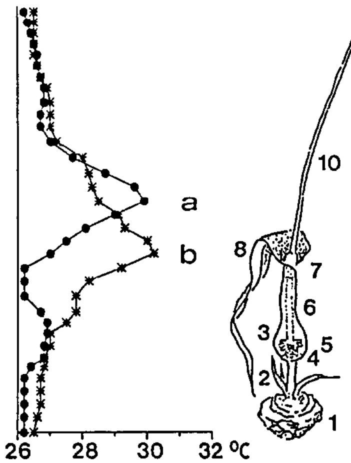

Figure 4. Temperature profile of a voodoo lily at a: 8.30 a.m. and b: 11.15 a.m. on the day of anthesis. Ambient temperature ≈ 26 °C.
The following parts of the plant are described in the text: 1: corm; 2: stem; 3: floral chamber with 4: female flowers, 5: club-shaped organs and 6: lower spadix; 7: male flowers; 8: spathe; 9: appendix (upper spadix); 10: zone of highest indol concentration. (Sketch adapted from [20])

Temperature Determination

Maximum temperatures and temperature profiles along the plant were investigated in a triple manner:
(i) A small Pt100-thermoprobe (Metratast P1; Metrawatt/Nürnberg) was used to monitor the temperature distribution in 1-cm-steps along the plant with an accuracy of ±0.2 °C. (ii) A flexible liquid crystal thermography sheet (Röhm-Pharma/Weiterstadt) with six colours in a temperature range of 26 to 32 °C was placed onto the appendix of the voodoo lily. The different colours of the sheet indicate the local temperature found in this part of the plant. Care was taken to ensure a tight contact between the thermofoil and the specimen. (iii) The problems encountered with a flat sheet on a curved plant were overcome by means of an infrared camera system (Ikotherm SK; Zeiss/Oberkochen) connected to a colour video monitor (Trinitron PVM-1443MD; Sony/Hamburg) and a colour plotter (4692; Tektronix/Köln). Ambient temperature was set to 20 °C in the thermographic cabinet and could not be changed to 25 °C for our experiments.

RESULTS AND DISCUSSION

The voodoo lily develops within two to three weeks from the corm with a mass of 170 g and 8 cm diameter to the plant shown in Fig.1 with a maximum length of 60 cm. In spite of the dramatic increase of spadix length the total weight of the plant decreases slowly with a rate of 0.4 % per day (Fig.3) due to water loss and catabolic activities. In the night before anthesis (day 17 to 18 in Fig.3) the spadix starts to shrink and a rapid decrease in plant mass with a maximum rate of 15.2 g/d (9.5 % of weight per day) begins. This weight loss is due to the "respiratory explosion" [6] used for heat production. Fig.3 shows this steep decline which was called "a dramatic example of rapid and massive senescence" [19]. In these hours an "alternative pathway" of starch catabolism is activated uncoupling the oxydative phosphorylation and dissipating all stored chemical energy as heat. It is used to volatize floral odors and to attract insects as possible pollinators [16].

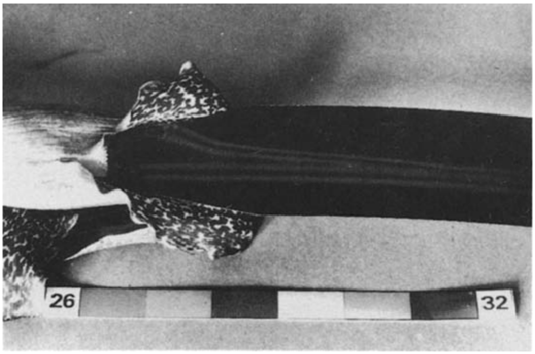

Figure 5. Temperature profile of a voodoo lily obtained with a liquid crystal thermographic sheet at an ambient temperature of 24 °C. The scale indicates the temperature region 26 to 32 °C. At the left hand side the upper part of the male flowers is seen in the opened spathe.

This strong heat production is concentrated in a few parts of the plant, mainly in the appendix. Fig. 4 exhibits the temperature profile along a voodoo lily at two times during anthesis. In the morning the thermal centre is approximately 20 cm above the male flowers in the zone of highest indol concentration and thus odor volatization.

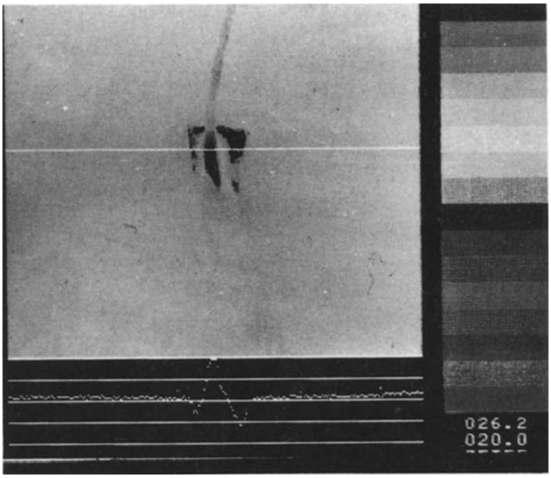

Figure 6. Infrared portrait of a voodoo lily together with the temperature scale at the right and the temperature profile along the white line (below). For further information see text.

Later on it moves downwards to the region of the male flowers. In this special case, modest temperature differences around 4 °C against ambient are observed. Two hours later the whole plant is again on the ambient temperature level.

In Fig. 5 a thermographic sheet is used to demonstrate the temperature distribution in the appendix. The scale below the sheet shows the temperature range from 26 to 32 °C which is very appropriate for these experiments. Directly right of the male flowers (left part of the picture) the appendix temperature exceeds this range so that 34 °C may be estimated, approximately 9 °C above ambient. A second area of strongly increased metabolic activity with temperatures slightly below that of the first maximum is seen 20 cm to the right in the zone of highest indol concentration.

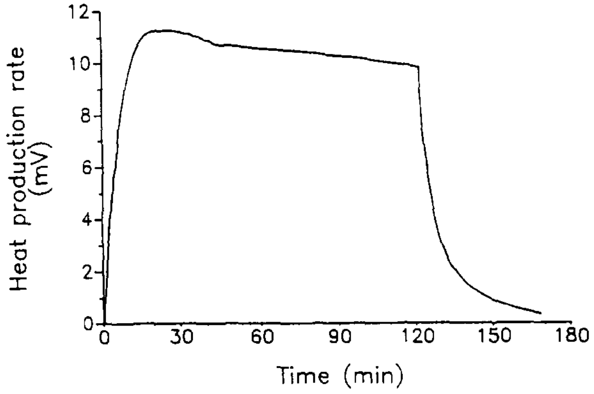

Figure 7. Power-time-curve of a non-flowering voodoo lily (163 g) at 25 °C.

Finally Fig.6 exhibits the infrared portrait of an other voodoo lily together with the 16-steps temperature scale at the right and the temperature profile of the white line below the portrait. At a maximum temperature of 26.2 °C and a scale of 10 °C, the

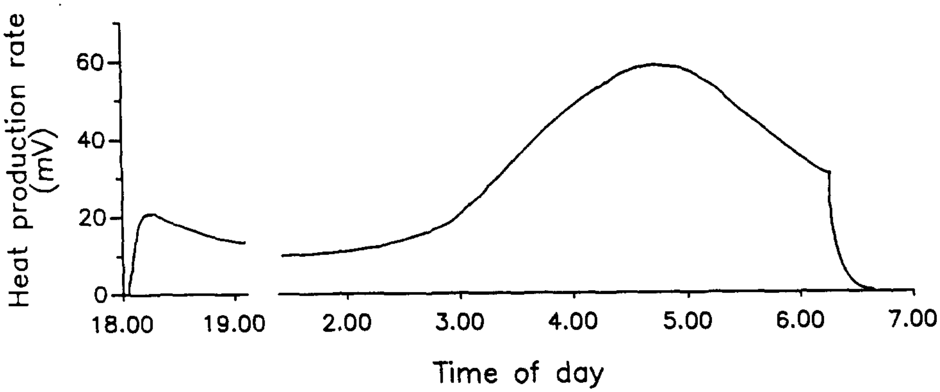

Figure 8. Anthesis of a voodoo lily (155 g) during the night in the calorimeter.

distance between two lines at the bottom indicates 2 °C. Thus one estimates a maximum difference of approximately 7 °C against the surroundings. A difference, 2 to 4 °C higher, is observed against the spathe which is cooler than the environment due to evaporative heat loss. The lower parts of the plant are seen as faint structures, while the appendix is clearly distinguishable against the background.

Calorimetric experiments are presented in the Figures 7 and 8. Fig. 7 exhibits the heat production rate of a complete, non-flowering voodoo lily (163 g w.w.). The maximum flow amounts to 200 mW or approximately 1 mW/g w.w. Simultaneous determinations of oxygen consumption underline that all heat is produced by respiratory metabolism.

Fig. 8 shows the flowering-up of a voodoo lily. The plant was placed in the calorimeter at 6.00 p.m. and remained on a low metabolic rate of approximately 175 mW or 1.2 mW/g till to the early morning hours. Between 2.00 and 3.00 a.m. the rate started to increase up to a maximum of 1020 mW or 6.8 mW/g for the whole plant. If this heat production rate is attributed correctly only to the appendix (see above) it amounts to 100 mW/g. Such mass specific rate equals those of flying insects or of hummingbirds. The following drop in heat dissipation is an artifact since oxygen is running short in the calorimeter. At the end of the experiment it dropped to 7 % of the initial value. Ventilation of the calorimeter and repeated caloric and respirometric measurements render similar slopes with a maximum heat flow of 1080 mW and a drop later on (not shown). The calorimetric signal amounts to 11.6 kJ during 4.5 h, the oxygen consumption calculates to 11.4 kJ. Again it becomes clear that the "metabolic explosion" is carried by a strongly increased respiration rate.

Table 1.
Heat Production and Temperature in Some Araceae

Maximum temperature: T_{max}; Temperature difference against ambient: ΔT; Length of the maximum flare-up: MFU; Length of the flare-up period: FUP; Number of consecutive flare-ups: NFU; Weight specific heat production rate: p (dry weight: d.w.)

Name	botanical	T_{max}	ΔT	MFU	FUP	NFU	p	Author
		°C	°C	h	d		mW/g	
Philo-dendron	*Philodendron selloum*	46	24 (39)	0,5	2	1	64 160	[21]
Philo-dendron	*Philodendron bipinnatifidum*	39	17		3	3		[21]
Skunk cabbage	*Symplocarpus foetidus*	22	35		14	1	160	[9]
Voodoo lily	*Sauromatum guttatum*	<37	15	7	<1	2	95 d.w.	[22]
Cuckoo-pint	*Arum maculatum*		15	<5		1	385	[6]
Jack in the pulpit	*Arum italicum*		15	<5	<2	1		[22]
	Amorphophallus oncophyllus	10		<4	1	2		[23]

ACKNOWLEDGMENT

We are deeply indebted to Mr.G.Bjeske for constructing the calorimeter and for invaluable help during the experiments, to Prof.Dr.U.Flesch and Mrs.H. Lehmann/Universitätsklinikum Rudolf Virchow for the possibility to take thermographic pictures and to Dr.A.O.Johnsen of Röhm Pharma/Weiterstadt for the thermosheets and helpful discussions on their application.

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PS After completion of this manuscript, the following thermographic paper on voodoo lilies has been published:
H. Skubatz, T.A. Nelson, B.J.D. Meeuse and A.J. Bendich, Plant Physiol. 95 (1991) 1084