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THE BEAUTIES OF CALORIMETRY
An overview

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This paper gives a short overview of direct and indirect calorimetric experiments to determine the heat production or at least the metabolic turnover of whole plants or their blossoms. A special emphasis is placed on thermogenic plants because of their high specific heat production rates equal to those of mammals or birds and sometimes even surpassing them.

Keywords: *direct and indirect calorimetry, heat production, metabolism, thermogenic plants*

Introduction

Investigations on plants or parts of them are rare in the calorimetric literature. The physico-chemical aspects of seed germination were studied more than fifty years ago [1, 2]. Recent research is more oriented towards a biochemical understanding of plant tissue metabolism, typically using samples of less than 1 g down to a few milligrams in isothermal (and sometimes also scanning) calorimeters. Such experiments are discussed in several review papers or monographs [3–6] and will be neglected here.

Typical modern calorimeters tend to have small sample volumes so that most blossoms are automatically excluded. A few customer made (direct) calorimeters offer volumes of 1 to 3 L and diameters of around 20 cm, large enough to house smaller plants or blossoms. As calorimetry is more or less an indoor discipline, a possibility for field studies is to use indirect heat flow monitoring via oxygen consumption or carbon dioxide production directly in the location of the plant and to transform the metabolic rates into heat production. These different approaches will be discussed here with respect to three figures incorporated in the text.

Plant metabolism is assumed to be low in comparison with that of animals, especially of some insects, mammals and birds. One interesting exception are the so-called thermogenic plants that heat up their blossoms during inflorescence to (*i*) protect sensitive young tissues in their centre, (*ii*) to give a warm shelter during the night for pollinating insects and (*iii*) to have a better dissipation of scents and thereby attract their specific pollinators [6–9]. These plants will be discussed in more detail in connection with their measurement protocols.

Retrospective view

The most exciting example of plant calorimetry is seen in Fig. 1a: an Iris blossom in a modified Berthelot calorimeter (Gascon Bonnier, before 1890 [10]). The heat produced by the blossom first warms the surrounding air and then the heat sink of water. Its temperature is read every min to three digits after the decimal point. Bonnier measured several other blossoms in the same way and found that the temperature curves looked identical. Therefore he gave only that for *Richardia* (today *Zantedeschia*) *aethiopica* which was drawn here using his temperature values (Fig. 1b). A constant temperature level is followed by a steep increase after the insertion of the blossom (first arrow), which flattens in a second period, and again a constant level after the removal of the blossom (second arrow). A specific heat production rate of 1.1 mW g^{-1} can be estimated from the first steep increase (in agreement with his 1.3 mW g^{-1} from indirect calorimetry [10]).

Voodoo lily calorimeter

One of the well-known and easy-to-breed thermogenic plants for the window shelf is *Sauromatum guttatum*, the voodoo lily, sometimes sold as *Arum cornutum*. It grows within two weeks from a corm to a height of more than 50 cm. On the first day during the female period of the inflorescence it opens an attractively spotted spathe, exposes a dark-purple appendix and dissipates an ugly stench resembling rotten meat or feces (indols, scatols). For several hours the appendix climbs to more than 10 K above the ambient air. The

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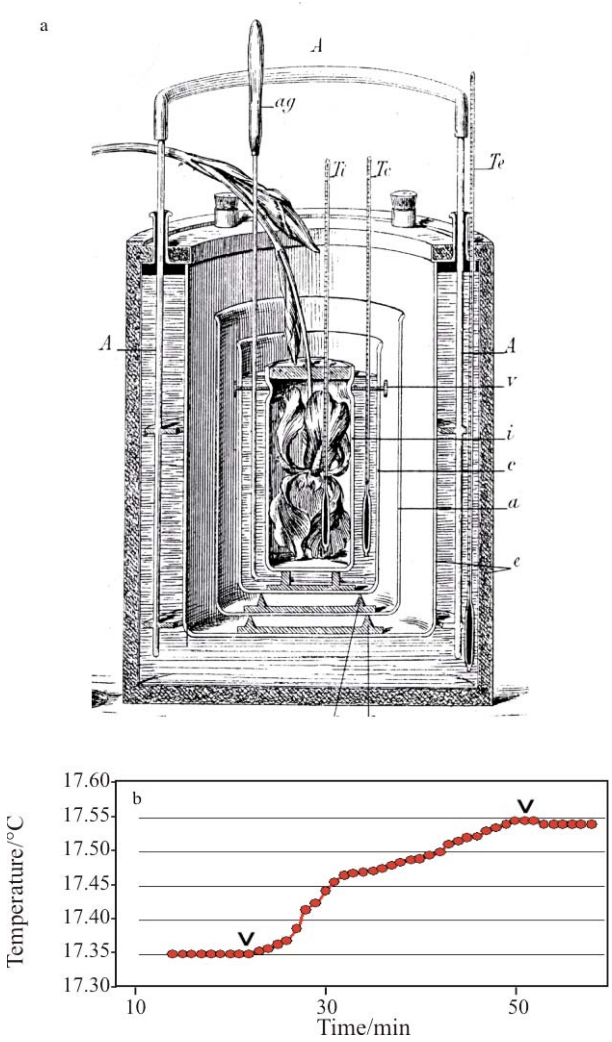

Fig. 1 a – Berthelot calorimeter with an inserted Iris blossom. The various thermometers (T_i, T_c, T_e) and the 2 stirrers (A, ag) are clearly indicated as well as the 3 containers inside the large water bath,. b – temperature increase after the insertion of the blossom (left arrow) and new plateau after removing it (right arrow) (modified from [10])

pollinators, attracted by the stench, are caught and kept in the floral chamber until the next day when the lily enters the male state and the pollinators are released, now covered with pollen for the next female flower. During these few hours of metabolic explosion the shoot plus the corm loose about 30% of their mass.

A special slim calorimeter was constructed for this plant (Fig. 2a) [11]. It consists of a 40 cm high aluminium cylinder of 3 L volume. This was connected via 4×3 Peltier elements to a cubic heat sink covered with a Styrofoam shield and placed in a modified LKB 10700 air thermostat. The sensitivity of about 50 mV W^{-1} was high enough to monitor heat flows of 200 mW (1.2 mW g^{-1}) of non-flowering voodoo lilies. This flow peaked at 7 mW g^{-1} during the 'metabolic explosion' of the blossom (Fig. 2b).

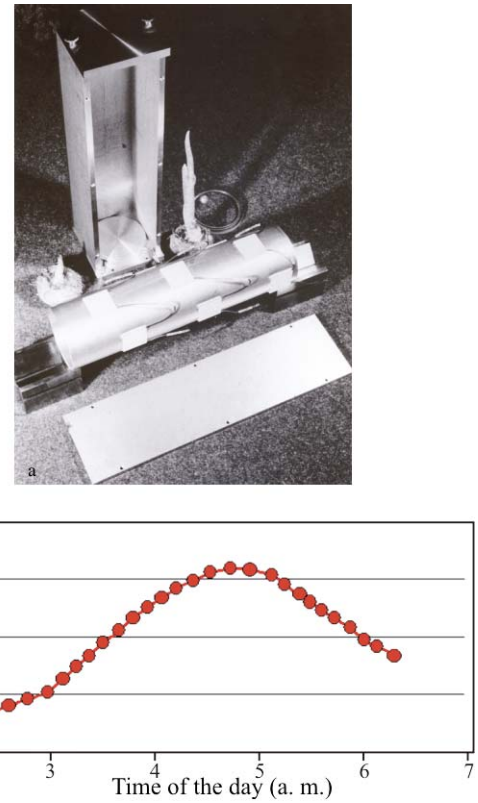

Fig. 2 a – Essential parts of the voodoolily calorimeter together with 2 corms in an early state, b – calorimetric curve of the metabolic explosion of a voodoo lily (155 g wet mass). The climax occurs around 5 am. The maximum corresponds to 1020 mW or 6.8 mW g^{-1} for the whole plant, but to 100 mW g^{-1} for the metabolically active appendix (modified from [11])

The given values are for the whole plant. Calculated for the appendix as the main heat and scent producing organ, the maximum turnover amounted to an impressive 100 mW g^{-1}. Such values are correct for an appendix still connected with the plant [11] and increase significantly when milligram pieces of tissue are investigated using conventional twin calorimeters. In these samples the oxygen diffusion rates are no longer limiting [12]. The highest values of 9097.1 mW g^{-1} were reported for a 0.1 mg piece [12].

Lotus calorimeter

A further low budget, low mass direct/indirect calorimetric system was constructed by R. S. Seymour from Adelaide and his colleagues for investigations of the thermogenic Sacred Lotus *Nelumbo nucifera*, which flowers 50 to 100 cm above the water surface [13, 14] and belongs for sure to the most beautiful and celebrated flowers in botany. The calorimeter was based on two household double-walled wine coolers which were individually placed in cubic Styrofoam boxes and mounted side by side as a twin calorimeter. Each

cooler contained a 730 mL tin box as the calorimeter vessel proper connected to the inner cooler bottom via a Peltier element as heat flowmeter. Thermostatted water serving as a heat sink was circulated through the space between the cooler walls.

This system worked perfectly well in one of the most exotic places for a calorimeter – 1 m above the water surface of the Lotus Pond in the Adelaide Botanical Gardens. It was placed upside down on long supports over the ripe lotus blossoms, with the water thermostat and the measuring units for heat flow, respiration, evaporation and various temperatures being hidden 6 m away in the reeds around the pond. All experiments were performed continuously during the whole thermogenic lotus period of 4 days [13, 14]. They showed a strong thermoregulating behaviour with maximum heat flows of about 510 mW or 60 mW g^{-1} active tissue. Cut lotus blossoms were measured in parallel in the laboratory [13] by means of a gradient-layer calorimeter [15].

Victoria calorimeter

The third picture represents the larger group of indirect calorimetric determinations of plant metabolism, here shown schematically for the highly attractive water lily *Victoria cruziana* in a greenhouse pond of the Berlin Botanical Garden (Fig. 3a). A 25 cm diameter floating container having a volume of several litres was placed upside down over the blossom to serve as a headspace [16]. An electrolytic oxygen sensor on top transferred the diminishing oxygen concentration into mV signals that were stored on a datalogger. As it is known from an RQ value of 1.00 that the Victoria blossom 'burns' carbohydrates during the inflorescence, the rate of oxygen consumption could be easily changed into mW. Figure 3b shows such an oxygen curve: a flat decrease as long as the bud is still closed, followed by a sudden steep decrease during the first hour of inflorescence. This transition occurred around 6:30 pm local time and followed an endogenous rhythm of the blossom independent of the ambient light (weather) or time of the season. After midnight the consumption rate decreased so that the diffusion of oxygen from the water into the headspace became dominant and the curve increased slowly. The heat production rate of a typical blossom amounts to 1 W, that of the thermogenic tissue to 60 mW g^{-1} [16].

This above set-up was slightly changed from a closed to an open system floating 1 cm above the water level. Air was sucked along the blossom at a rate of several hundred mL min^{-1} through a scent absorber tube at the top. A later molecular determination by means of a gas chromatograph/mass spectrometer

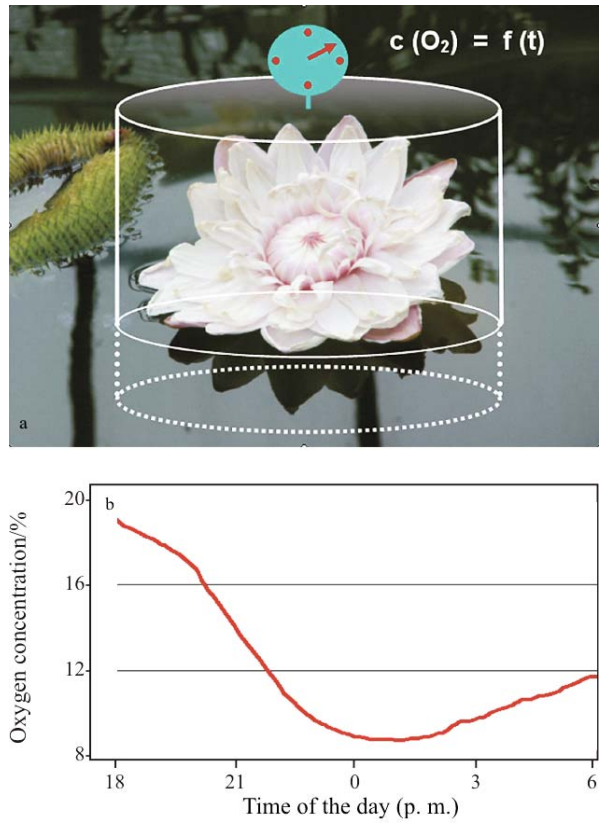

Fig. 3 a – Scheme of the indirect Victoria calorimeter with the floating hood, the oxygen sensor and the blossom short time before the metabolic explosion, b – oxygen concentration inside the hood with the sharp transition between 6 and 9 pm and the slow-down of respiration after midnight

combination allowed an analysis of the odour of the flower at different stages of inflorescence [6, 16]. Such a method was applied as indirect calorimetry by Seymour and his colleagues earlier with a number of thermogenic plants, among them the aroids *Arum italicum*, *A. creticum*, *A. cincinnatum*, *Dracunculus vulgaris*, the Sacred Lotus *Nelumbo nucifera*, *Philodendron selloum* and the skunk cabbage *Symplocarpus foetidus* (see e.g. [7, 8, 13, 14, 17]. Four essential metabolic parameters were determined in situ in these investigations: temperature, oxygen consumption, carbon dioxide production and water evaporation. Plastic water bottles without bottoms were placed as hoods over the blossoms and closed at their lower end by plastic wrap leaving just a small entrance slit for the air. The simultaneous determination of oxygen and carbon dioxide concentrations gave information about the metabolised substrates so that the two rates could be easily transferred into energy units. Table 1 compiles some of the data obtained with direct and indirect calorimetry for a selection of thermogenic plants. Just to compare: the resting metabolism of adult humans amounts to about 1 mW g^{-1} and may grow by a factor of 3 to 5.

Table 1 Compilation of some thermal data of thermogenic plants. ΔT_{max}: maximum observed temperature during inflorescence. Mass is given as wet mass

Botanical name	Popular name	Active mass/ g	ΔT_{max}/ °C	Total heat/ mW	Specific heat/ mW g^{-1}	Reference
Arum concinnatum		13.75	10.9	1071	77.9	*
Arum creticum	Cretan arum	0.57	3.4	7.3	12.9	*
Arum idaeum	Ida-mountain arum	0.20	4.7	4.2	21.0	*
Arum italicum	Jack in the pulpit				724	*
Arum maculatum	Cuckoo-pint				416	[18]
Dracunculus vulgaris	Dragon lily	1.89	8.4	99.7	52.7	[17]
Helicodiceros muscivorus	Dead horse arum lily	0.65	15.0	257	383	[19]
Nelumbo nucifera	Sacred lotus	8.50	14.0	510	60	[14]
Philodendron selloum	Philodendron	33.50	15.1	2941	87.8	[23]
Sauromatum guttatum	Voodoo lily	10.20	9.0	1020	100	[11]
Symplocarpus foetidus	Skunk cabbage	2.05	22.0	260	126	[20]
Victoria amazonica	Victoria (regia)	11.90	9.5	1182	99.3	[24]
Victoria cruziana	Victoria	~15	10.0	840	~56	[16]

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Conclusions

In our high-tech time of stream-lined instruments with black-box character, we experience automatic inputs, outputs, and computer calculations that do not allow getting to the roots of the thermal data. Some of the calorimeters shown here required fantasy, but no large budgets, and are customised to special tasks and often to working under odd conditions. They are easily constructed and transported, changed if necessary and are largely weather-proof in the field. They belong to the family of PMCs (Poor Man's Calorimeters), which were invented by the author 30 years ago and are now working in many places [21, 22].

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