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Flower ovens: thermal investigations on heat producing plants☆

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Abstract

Three thermogenic plants, the elephant foot yam *Amorphophallus paeoniifolius*, the voodoo lily *Sauromatum guttatum* and the tropical water lily *Victoria cruziana*, were investigated during their metabolic flare-up with different kinds of thermometry and infrared false-colour thermography. Excess temperatures of up to 10 K appeared during anthesis together with intensive odours. Areas of male flowers, appendices and floral chambers turned out to be the most active parts in the three inflorescences. The rapid temperature increases of up to 14.2 K h^{-1} justify the description as ''metabolic explosions''.

The results are discussed on the background of thermogenic effects in other aroid lilies and in flowers from different plant families, of odour production, adaptive value of the excess temperatures for plant development, and alternative biochemical pathways that provide the necessary energy for the metabolic flare-up.

Keywords: *Amorphophallus paeoniifolius*; IR thermography; Liquid crystal thermofoils; Odour; *Sauromatum guttatum*; Thermometry; *Victoria cruziana*

1. Introduction

In metabolic investigations heat production is often considered as a disturbing, unavoidable by-product of biochemical reactions. Larger organisms of spherical or cylindrical form had to develop special means to get rid of heat and to avoid overheating and too high internal temperatures. Only in the metabolism of newborn mammals including human babies [1] or of hibernating animals, uncoupling of respiration from storage of chemical energy is applied to direct all energy into heat. In this way new-borns can compete with an unfavourable new environment and hibernators come to a quick and efficient temperature increase after a strongly reduced metabolism during winter.

A group of plants applies a comparable mechanism of heat gain, but for quite different purposes. These *thermogenic* plants increase their metabolic turnover rate for a few hours, some days or even weeks, to produce strong odours and to attract pollinators over longer distances. Excess temperatures vary from a few degrees up to more than 30 K and their incline is so rapid that one often talks about a *metabolic explosion*. Moreover, plant metabolism may reach mass specific rates that are otherwise only found in small mammals or birds of similar weight. When Lamarck (1794) wrote in his Flore françoise as the first known note of thermo-

☆ Dedicated to Dr. Günther Höhne on the occasion of his 65th birthday in long friendship and even longer admiration.

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genic plants about *Arum maculatum* ''Lorsque le chaton fleuri est dans un certain état de perfection ou de développement, il est chaud au point de paroitre brûlant, & n'est point du tout à la température des autres corps; . . .'' [2], the chosen title of a flower oven is not over-exaggerated. Moreover, a special organ of many inflorescences, the floral chamber, is the most thermogenic part of the blossom, protecting sensitive structures against cold and offering rendezvous sites and mating places for the pollinators, also protecting them against predators.

In recent years many new thermogenic plants were detected, especially in the family of *Annonaceae* (custard-apples) in the neotropics [3,4] and the authors suppose that many more will be found in this family. The unexpected detection of the wholly parasitic *Rhizanthes lowii* (*Rafflesiaceae*) not only as a thermogenic but also thermoregulating plant of Pacific areas [5] stimulates a screening in new directions.

First contacts with thermogenic plants were by touching and feeling the elevated temperatures. And even today it is impressive and astonishing to sense the heat production in the floral chamber of the tropical water plant *Victoria* or the appendix of an arum lily. But soon thermometry followed, mainly in the family of *Araceae* and also in that of *Nymphaeaceae*. More and more thermogenic plants were detected, some of them not only thermogenic but also thermoregulating like homoeothermic animals [6–12]. The early question of THAT, HOW MUCH and WHERE of the strongly increased temperature changed to WHY, HOW and the biochemical backgrounds. Nowadays, many modern biophysical techniques are applied in this appealing field: all kinds of thermometry, infrared (IR) photography, electron microscopy, combination of gas chromatography and mass spectrometry for odour characterisation, elementary analysis to determine the energy content of the active tissues as well as direct and indirect calorimetry to monitor the energetic turnover. Surveys on this interesting field are found in the literature and for some aspects also in Internet [6,10,13,14].

In this paper we present three thermogenic plants, two famous ones—the tropical water lily *Victoria cruziana* and the voodoo lily *Sauromatum guttatum*—as well as the less known elephant foot yam *Amorphophallus paeoniifolius*. Since direct and indirect calorimetric experiments were published elsewhere [15,16], we concentrate here on different kinds of thermometry and on IR thermography and discuss them in connection with biochemical, biophysical or thermal results or odour characterisation from the literature.

The tropical water lily *V. cruziana* (*Nymphaeaceae*) is the smaller and less spiny, but equally attractive sister of *V. amazonica* [16–19]. *V. cruziana* grows in cooler regions of South America, mainly in Argentina and Paraguay and is called ''water platter'' (yrupe) there [20]. Its leaves are impressive with their upright rims that render stability against destruction by wind. The flower develops from an underwater bud, blooms with a diameter of about 25 cm for less than 2 days and changes its colour from an initially pure white to an intensive pink in the second day. The floral chamber is the main place of thermogenicity. *V. cruziana* is protogynous, i.e. that the female florets are fertile earlier than the male ones. The blossom returns to the water surface after the flare-up and submerses slowly with the course of time. Seeds are developed in the water and carried away for further spreading of *Victoria*, or collected by local Indian women as a healthy and nutritious food [16,17,21–23].

In contrast to the water lily that had to be investigated in a pond of the Botanical Garden, the voodoo lily *S. guttatum* (*Araceae*) is easy to breed, may be studied in the laboratory and is therefore the most intensively investigated plant (see, e.g. [24–27]). Within 2 weeks it develops without water and soil from a corm of usually 100–300 g to an inflorescence of 50–80 cm height. It flowers for one and a half days and dries off later on. Replanted to soil it produces one large leaf.

In the past, *S. guttatum* was mainly investigated by thermometric and biochemical methods [27–31], and also with direct and indirect calorimetry [15,30,32], IR thermography [15,29,30], electron microscopy for structural and a combination of gas chromatography and mass spectrometry for odour analyses [31]. It was with the voodoo lily that the triggering substance ''calorigen'' was detected that is responsible for the metabolic flare-up of many arum lilies and that turned out to be salicylic acid (see below) [27].

The third investigated thermogenic species was the ''elephant foot yam'' *A. paeoniifolius* that belongs to the *Araceae* like *Sauromatum* and *Philodendron*. As these plants are rather unknown, a shorter introduction shall be given. More than 150 species of *Amorphophallus* are found in the tropics between Polynesia and Africa [33,34]. Common to them is a strong smell of

the inflorescence that is not at all pleasant. The most famous among these seasonal herbs is the gargantuan *A. titanum* because of the huge size of its inflorescence. The appendix of the inverted cone-like flower grows up to more than a man's height and the upper diameter of the cone measures more than a meter [35]. It develops from an underground corm and produces only one leaf per year and/or one inflorescence [34].

Flowering of larger *Amorphophallus* species are rare moments in European Botanical Gardens as their typical rhythm of one leaf or flower per year is not always obeyed. It might be that several years pass by between two successive flowerings. Thus, observation and investigation of *Amorphophallus* demand patience and luck without the chance for a significant number of repetitions. By chance, two *A. paeoniifolius* could be followed in the greenhouses of the Botanical Gardens. They were of medium size with corms of a few kilograms while a specimen with a 24 kg corm can be admired in the Internet [36]. In the first hours of blooming (fertile female stage), *A. paeoniifolius* distributes an unpleasant odour, a mixture of gaseous and rotting meat components in which dimethyl disulphide and trisulphide prevail in equal amounts [34].

2. Experimental

2.1. Materials

2.1.1. Plants

The two specimens of *A. paeoniifolius* (Dennst.) Nicholson were investigated in a show- and a greenhouse of the Botanical Gardens of the Free University of Berlin in June and July 2001. The first one had a tuber of 25 cm diameter and a mass of 4300 g fresh weight, routinely determined by the garden staff some months before, the second one of 12 cm and 500 g, respectively. On the day of anthesis, the larger plant had an inflorescence of 33 cm height and 29 cm diameter, the smaller one of 10.5 and 7.0 cm, respectively. Because of the interested visitors, the inflorescence was cut only 2 weeks after the end of the flare-up in a half-dry state and subsequently dried to a final weight of 30.2 g. By comparison with other tissues, it could be recalculated to a fresh weight of about 300 g. The second blossom was much smaller with 1.53 g dry or about 15 g fresh weight.

All experiments in the show-house were performed in the morning hours at mean air temperatures of $21.1 \pm 1.8\ ^{\circ}C$, a relative humidity around 70% and illumination levels between 500 and 2000 lx.

Fifty *S. guttatum* (''voodoo lily'') corms were purchased in a commercial garden centre in the early winter. Their diameter was limited to less than 9 cm to fit into a specially constructed heat flow calorimeter [15]. The weight varied between 140 and 200 g. The corms were stored at 6 °C in the dark till to the experiments. They were grown in the laboratory without soil and water at 25 °C, 45% relative humidity and a light/dark regime of 12 h/12 h. Weight of the corm and length of the developing spadix were determined daily to 1 g or 1 cm, respectively. The energy metabolism of whole plants and of different, mainly thermogenic tissues was monitored at the day of anthesis, during blooming and at the following day by direct calorimetry and respirometry. Temperature distribution along the inflorescence was evaluated by contact thermometry, liquid crystal foils and IR thermography (for details, see [15,29]). After the experiments, the remaining corms were stored at 6 °C till to the early summer and then planted outside for further growth and new experiments in the following season.

Two plants of the tropical water lily *V. cruziana* Orb. (''Santa Cruz Water Platter'') were grown in a greenhouse pond in the Botanical Gardens of the Free University Berlin. They flowered from June to November with 1–2 blossoms per day. About 60 flowers and an equal number of leaves were investigated during the season 2000 by means of indirect calorimetry, contact and IR thermometry and IR thermography. Due to the show character of the greenhouse, all experiments had to be performed in the house to preserve the beautiful flowers for the public. All essential measurements took place directly in the pond and only few flowers were cut for further laboratory tests at the end of their flare-up when they already started to actively submerse. Water temperatures were kept constant at $30 \pm 1\ ^{\circ}C$, the air temperature at $24.5 \pm 1.5\ ^{\circ}C$ with stronger variations due to intensive sun illumination. More details about the origin, the history and the floral structure of this impressive water lily as well as about the *Victoria* experiments are presented in two recent papers [16,19] or found in the literature [20–23].

2.2. Methods

2.2.1. Thermometry

2.2.1.1. Contact thermometry. Contact thermometry was performed by means of commercial mercury thermometers with a grading of 0.1 K or with thermistors inserted into the bud or the flower from the top and the side. The thermistors were connected with small and light (20 g) data loggers (HOBO Temp, Series 01 and HOBO RH, Temp, Light, External, Series 08; Onset Computer Corporation, Pocasset, MA) that could be placed directly on *Victoria* leaves or better on small Styrofoam^{TM} "boats" floating aside the blossoms. With their help, the full sequence of the metabolic flare-up could be followed continuously in all details.

For surface temperature distributions, especially of the huge *Victoria* leaves and also of the fully opened blossoms contact thermometry was supported by non-contact IR thermometry. A handheld 260 g light thermometer (THI 300, Tasco, Japan) with a spectral band from 6 to 12 μm was applied in these investigations.

2.2.1.2. Thermofoils. Elastic cholesteric liquid crystal sheets are used in different medical fields and in various household applications. The applied foils exhibited a colour sequence: colourless (that means black because of the black background), reddish-brown, yellow, green, blue, bluish-violet and black again with increasing temperatures. For higher and longer stability, the liquid crystals are micro-encapsulated within the foil. Thermofoils are specially suited for more or less flat surfaces but they may also be adapted to curved ones.

In laboratory investigations of *S. guttatum*, a flexible liquid crystal thermography sheet (Röhm-Pharma, Weiterstadt, Germany) with a temperature scale of six colours was placed in tight contact with the appendix and the male flowers. The scale of 26–32 °C was well suited at ambient temperatures of 23–25 °C and expected temperature differences of 7 K. Their distribution along the appendix is clearly visible (Fig. 3), lower temperatures near to 26 °C and higher ones near 32 °C can be estimated. The foil was also used to monitor the temporal development of heat production in the plant and the surface temperatures in other less thermogenic parts of it.

2.2.1.3. Thermography. Thermographic investigations on flowers of *S. guttatum* were performed by a stationary IR camera system in the Rudolf-Virchow Hospital of the Free University Berlin. The applied system consisted of an IR camera (Ikotherm SK; Zeiss, Oberkochem, Germany), a colour video monitor (Trinitron PVM-1443 MD, Sony, Hamburg, Germany), a Gama Data Video Interface and a colour plotter (Type 4692; Tektronix, Köln, Germany). The spatial temperature distribution is shown in false colours on the monitor in a 16-step scale that is indicated on the right side of the screen together with the maximum temperature (top) and the temperature span (bottom). Below the main picture, this span is presented divided into five equidistant steps and showing the temperature distribution along the white horizontal search line in the picture above.

The flowering (and awfully smelling) plant was transported to the hospital in the early morning and investigated there at a fixed room temperature of 20 °C in the thermographic cabinet. Other ambient conditions could not be established due to hospital routine.

To obtain a full picture of the temperature distribution along the surface of *Victoria* blossoms and leaves and to locate "hot spots" of special metabolic activity, a handheld IR camera (AGEMA 570 PRO, Darmstadt, Germany) was applied. It uses an uncooled microbolometer with 320×240 pixels and presents an accuracy of 2 K. The handy weight of only 2.3 kg enables one to use the camera even in this strange situation: standing near the flower in the 50 cm deep water of the pond. The taken IR pictures were processed and analysed later on with the software Irwin 5.0 working under Microsoft Windows 95 [16,19].

2.2.2. Indirect calorimetry

The metabolic flare-up of *Victoria* blossoms was monitored as oxygen consumption rate by means of a 10 l floating hood that was placed over the bud or the flower in the greenhouse pond. The hood carried an electrolytic oxygen sensor (FIGARO GS Oxygen Sensor KE Series, UNITRONIC, Düsseldorf, Germany) connected to a long time data logger (UNIDAN^{PLUS}, ESYS, Berlin, Germany) with a resolution of 0.1 mV. The oxygen consumption rate (in ml $O_2\,s^{-1}$) was transformed into an energy rate ($J\,s^{-1} = W$) by the oxycaloric factor 21.1 J $(ml\ O_2)^{-1}$ assuming a pure carbohydrate metabolism.

A similar, land-bound device was applied in the investigations of *A. paeoniifolius*. In this case, the lower edge of the hood was covered with a tube of soft rubber as used for thermal insulation purposes. It guaranteed a sufficiently tight connection to the soil around the plant so that diffusion of oxygen into the hood became negligible.

3. Results

3.1. A. paeoniifolius

At the cool and dull day of anthesis of the larger of the two lilies, an unpleasant smell was detectable around the plant. Due to the low air temperature in the early morning (17.2 °C directly beside the inflorescence), it was not as overwhelming as reported in the literature. Contact thermometry showed that the region of the not yet fertile male florets was most thermogenic with 26.3 °C inside the tissue (+9.1 K excess temperature) and slightly lower at the surface (due to evaporation effects). The fertile female florets below the male ones had a rather low excess temperature of only 2.7 K, the aerenchyma inside the appendix of 2.6 K or 19.8 °C. Spathe (17.5–17.9 °C), corm (17.3 °C) and soil (17.2 °C) were close to the air temperature. All values are shown in Fig. 1 overlaid to a photograph of the larger *A. paeoniifolius* specimen. Slightly different surface temperatures determined by IR thermometry are added in brackets when they deviate from the other ones.

During the development of the inflorescence, the oxygen consumption rate of the flower increased from 32.2 ml oxygen h^{-1} (190 mW) six days before anthesis to 75.8 ml h^{-1} (440 mW) one day before and to 129.5 ml h^{-1} (760 mW) at the metabolic flare-up and drops back to 70.3 ml h^{-1} (410 mW) at the following day. Although it is stated in the literature that *A. paeoniifolius* flowers in the morning [37], it might be that the true climax was during the night and the peak intensities of respiration passed by already. The obtained rate transforms to 25 mW per g dry weight fitting to literature values of other members of *Araceae* [19].

In the following day, the male flowers became fertile and showed long yellow chains of pollen. At that time all inflorescence temperatures had returned to that of the air or were even slightly below it due to evaporation from the surface.

3.2. S. guttatum

S. guttatum is shown in Fig. 2 with the corm, the lower spadix, the floral chamber in the middle that houses the female flowers, the club-shaped organs and the male flowers at its open end and finally the long slim appendix as upper part of the spadix. In this figure, the interestingly decorated spathe still covers parts of the appendix, but later on opens completely. *S. guttatum* starts its ''metabolic explosion'' in the late night with a steep increase of heat production at a doubling rate of only 40 min. The temperature rises by 5–10 K to more than 30 °C depending upon the ambient conditions [15,29]. This higher temperature is easily detected when touching the appendix by hand. Fig. 3 presents the upper part of a lying spadix beginning at the left side with the open end of the floral chamber, the spotted spathe and the male flowers. The appendix following to the right is covered by the thermofoil that shows black colour and thus temperatures out of the measuring range (26–32 °C). They may be estimated to about 34 °C or 9 K above room temperature. A second somewhat lower maximum is detected more to the right in a part of the appendix where the indole concentration is highest and the odour production most pronounced.

These two maxima are also visible in Fig. 4, the false-colour picture of an IR thermography camera taken at a room temperature of 20 °C. Above the dark green corm at the lower edge of the frame, the faint image of the spadix is seen which is cooler than the corm because of evaporation. The thermogenic region of the floral chamber starts above the lower spadix with some heating at the club-shaped organs (yellow), maximum excess temperature in the (not yet fertile) male florets (red) and very low values (lilac and black) of the open spathe around the spadix. It follows a small green ring of lower metabolic rates and the already mentioned second maximum, the centre of the odour production. Above this stripe, the appendix is again cooler (green). The fertile female florets at the bottom of the floral chamber are not thermogenic and thus not seen in this picture. The horizontal temperature distribution along the white line is indicated in the scale below beginning at the top with the maximum value

(26.2 °C) and five sectors of 2 K each (in total 10.0 K) below. The trace indicates a background temperature slightly below 20 °C, the maximum of 26.2 °C in the male florets and the cool edges of the spathe at least 10 K below the maximum.

At the time of blooming shown in Figs. 3 and 4, the inflorescence awfully smelt like rotting meat, urine and faeces with a dominating component of indole evaporating from the upper part of the appendix (for further details, see Section 4).

3.3. V. cruziana

Although a slight temperature increase is already detectable half a day before anthesis [38], the main flare-up starts in the morning of the first day with a still closed bud that opens during the day to the early evening state shown in Fig. 5. At that time the flower is some centimetres above the water surface, the sepals are bent downward and the outer petals in a horizontal position. The "metabolic explosion" starts around 7 PM and produces maximum excess temperatures in the floral chamber of up to 10 K and a pleasant sweet fragrance. The heat dissipation declines in the morning to a much lower value and gains a second maximum in the afternoon (sometimes already in the later morning) of the second day. Meanwhile, the initially white flower changed to pink with an intensively coloured ring around the central "tunnel" [16]. During the following night, the temperature drops to ambient values, the flower closes partially and starts to submerse. Anthesis is over.

Fig. 5 presents the situation in the first evening in the false-colour picture of an IR thermography camera. At an air temperature around 24 °C and a water temperature near 30 °C, the different parts of the half-opened flower show temperatures between those two thresholds. Only the central plate above the floral chamber, the main place of heat production, warms up to about 33.5 °C or 9.5 K above air temperature. The inner petals standing upright or being slightly bent to the outside are also thermogenic with excess values between 3.0 and 5.5 K. The white area at the upper left corner signalises temperatures out of the range (37.8 °C) belonging to the experimenter's glove, a protection against the spiny flower stalk.

Victoria leaves are in close contact with the water surface and exhibit in most parts the temperature of the

Fig. 1. *A. paeoniifolius* ("elephant foot yam") on the day of anthesis. Behind "19.8" the amorph appendix is seen covered with a film of sticky liquid supposedly responsible for the obnoxious smell. The appendix contains the thermogenic aerenchyma (tissue). Below it the still sterile male ("26.3") and the fertile female florets ("19.9"). "17.9" indicates the wide open spathe (diameter 29 cm), "17.5" the lower part of it near to the stem, and "17.3" the corm that is additionally indicated by a dashed line (diameter at the surface 19 cm).

Fig. 2. True colour photograph of the inflorescence of the voodoo lily *S. guttatum* at the morning of anthesis. The spotted spathe is still closed at its upper end, but showing the lower part of the appendix with the main region of heat and stench production. It follows the floral chamber, the lower part of the spadix and the corm. The floral chamber houses the not yet fertile male florets, the club-shaped organs and the fertile female florets.

Fig. 3. Temperature distribution along a voodoo lily (*S. guttatum*) appendix indicated by a thermofoil. At the left side, the opened spathe is located with a part of the yellow male florets while the main part is covered by the foil (visible as broadening of the colour profile). The scale in the front shows the temperature range from 26 to 32 °C.

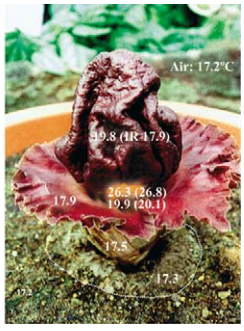
Fig. 4. Infrared false-colour thermographic picture of a voodoo lily at ambient 20 °C. The graph below the picture presents the temperature distribution along the horizontal search line through the male florets. The scale on the right spans 10 K from 16.2 °C (lilac) to 26.2 °C (red) as the maximum temperature of the thermogram.

Fig. 5. IR false-colour image of an evening blossom of *V. cruziana* just above the water surface. The white area in the upper left corner is the experimenter's glove. The red colour in the centre of the flower corresponds to 33.0 °C as the highest floral temperature, the lilac parts on the petals to a region from 27.3 to 27.9 °C as lowest values. Air temperature was 24.0 °C, water temperature determined to 30.1 °C by usual mercury thermometers (emissivity: 0.95; for further details, see text).

Fig. 6. IR false-colour image of several full size leaves of *V. cruziana* (diameter about 160 cm), a half-opened flower in the centre and a bud left of it. The picture shows the radial structure of the spin-web-like supporting ribs under the leaf (leaf in the middle) and the cooler elevations of the leaves (left and right lower corners). The higher temperatures in the IR mirror images of the rims are easily seen (for further details, see text and Fig. 7).

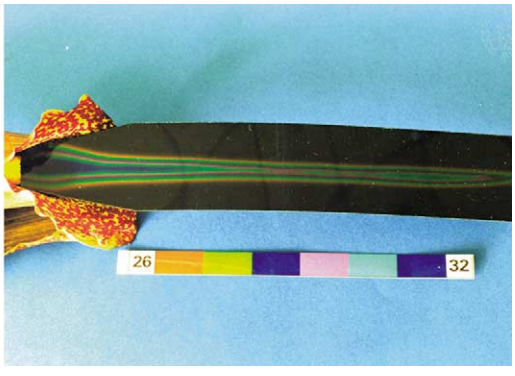
Fig. 7. IR false-colour image of a half-opened flower, a flower bud (left behind), a leaf bud (further right) and a grown out leaf of *V. cruziana*. The mirror images of all four objects are clearly detectable on the water surface. Temperature differences amount to about +3.5 K (for further details, see text).

(1)

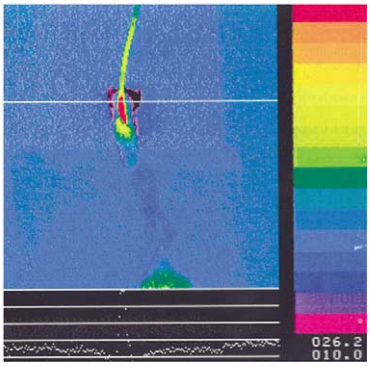

Air: 17.2°C
19.8 (IR:17.9)
17.9
26.3 (26.8)
19.9 (20.1)
17.5
17.3

(2)

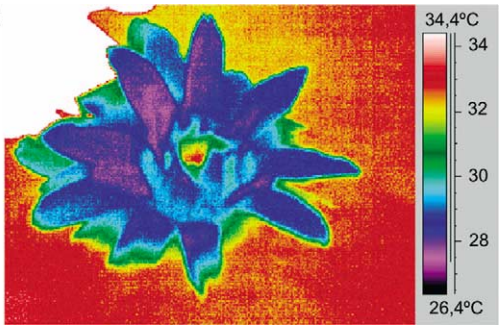
(3)


26
32

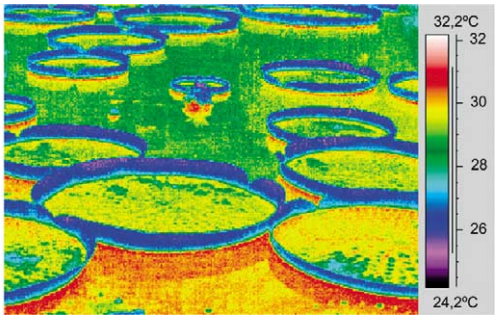
(4)


026.2
010.0

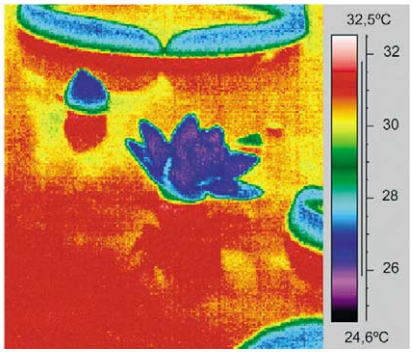
(5)


34,4°C
34
32
30
28
26,4°C

(6)


32,2°C
32
30
28
26
24,2°C

(7)


32,5°C
32
30
28
26
24,6°C

latter. But air is trapped between the spin-web-like ribs on the underside of the leaf and provides some insulation. These cooler parts of the leaf become visible as green colour in the lower left and right corners or as yellow/green in the central leaf and demonstrate the interesting morphological structure of the ''huge floating tea trays'' or ''water platters'' which renders the astonishing buoyancy of the leaves [16,19]. Fig. 6 shows the huge leaves with the upright rims and diameters around 180 cm, their temperature distribution and the thermal reflections in the water surface. They will be discussed later.

4. Discussion

Since the first calorimetric paper of the present authors on thermogenic plants ''Some like it hot—calorimetric investigations of voodoo lilies'' [15], many new members of the thermogenic family were detected; among them several *Magnolia* [39], a number of *Annonaceae* (custard-apples) [3,4,42,43] and a wholly parasitic *Rafflesiaceae* from Pacific areas [5]. Gottsberger and co-workers [3,4,42] made an intensive screening of Brazilian *Annonaceae* and found that 50–55 of the known species are likely to show floral heating. Among them *Annona coriacea* exhibits the highest excess temperature with 14–15 K that appears early in the night with a strong fragrance that attracts dynastid scarab beetles.

Only recently some *Magnolia* trees were detected to be thermogenic [39]. Their flowers produce a strong fruity fragrance mainly composed of geranyl methylether when they heat up to 9.3 K in the receptive female state of the first evening (*Magnolia tamaulipana*). The authors measured the different odour compounds and determined production rates of 195 and 126 $\mu g\ h^{-1}$ per flower for female and male flowers, respectively.

Rather recently a further thermogenic plant was detected in the Pacific tropics: *R. lowii* (*Rafflesiaceae*) [5]. It emits a strong ''cadaverous'' smell and higher concentrations of carbon dioxide that attract carrion flies and stimulate their oviposition usually happening in carrion. Already several weeks before anthesis, buds of *Rhizanthes* are thermogenic with excess temperatures around +3 K. The stalk reaches +9.6 K in three consecutive maxima and demonstrates a high degree of thermoregulation while the other inflorescence structures follow the ambient rhythm with smaller excess temperatures [5].

Dieringer et al. [39] pointed out that all known thermogenic plants belong to the same clade in only two classes and that thermogenicity is not found in any other group or clade of early angiosperms. Thus it might be that the members in the mentioned clade have a common gene or group of genes that function as a preadaptation to the development of thermogenesis. And indeed, the biochemical background of the metabolic flare-up is alike in this family of plants (see below).

The floral chambers formed by many thermogenic flowers are the main places of heat production and excess temperatures. They or the enclosing spathe may serve different purposes: they offer a ''rendezvous site'' to beetles as opportunity to mate, shelter night-active pollinators from cold, daylight and predators, provide food, keep the imprisoned animals at their working temperature and enable their early start in the cool morning without an energy consuming warm-up [40]. But they may also protect sensitive plant structures during cold nights [3,6,10,41]. From a physical point of view, floral chambers are more suited than flat leaves to keep higher temperatures due to their small surface to volume ratio and the lower possibility to evaporate water. The reduction in odour dissipation might not be essential since both, the plants' smell production and the pollinators' sensitivity for it, are high. Moreover, the fragrance inside the floral chamber can be quite different from the outside one, e.g. with *S. guttatum* [31], and may stimulate the beetles' mating activity.

The metabolic flare-up of thermogenic blossoms is sometimes called a ''metabolic explosion'' because of its sudden appearance and its strong temperature increase. Table 1 compiles some characteristic data from such flowers estimated after figures and/or values given in the literature. Heating rates of up to 14.2 $K\ h^{-1}$ are found (*A. cornifolia*) leading to the maximum temperature (8.5 K above ambient) in less than 1 h [42,43]. Other cited species are much slower depending presumably on their metabolic power and of course on the shape and structure of their inflorescence. Both, *Dieffenbachia* and *Philodendron*, with long open appendices show low rates of temperature increase, they lose more heat by convection and

Table 1
Characteristic values of some thermogenic plants taken from the literature

Name	Time[a]	Organ/stage	Rate (K h^{-1})[b]	ΔT (K)[c]	T_{max} (°C)[d]	Reference
Annonaceae						
A. coriacea	e	Female	5.3	14.6	34.5	[3]
	e	Male	9.3	12.6	34.0	[3]
A. cornifolia	e	Female	14.2	8.5	30.0	[41]
Aracaceae/palms						
Attalea microcarpa	a	Male	2.2	12.0		[4]
Oenocarpus bacaba	a	Male	2.4	12		[4]
Araceae						
A. maculatum	a	Male flowers	2.5–5.5	4.1–8.0	28.9–30.8	[61]
Dieffenbachia longispatha	e	Female stage	1.2, 1.45	3.3, 4.1		[41]
Philodendron selloum	a	Central spadix	1.4	14.9	39.6	[7]
S. guttatum	m	Appendix	<5.5	9.5	37.1	[24]
Cycadaceae/palm-like						
Encephalortes ferox	a	Male cone	7.1	13	36	[62]
E. hildebrandii	a	Male cone	2.5	6.2	27.5	[62]
Macrozamia moorei	a	Male cone	3.7, 2.8	6.0, 9.3	27.1, 29.6	[63]
Nymphaeaceae/water lilies						
V. cruziana	m	Floral chamber	4.3	9.0	34.1	[19]

[a] Time of the day when the flare-up happens (a: afternoon, e: evening, m: morning).
[b] Rate of temperature increase during the flare-up.
[c] Maximum excess temperature against ambient.
[d] Maximum obtained flower temperature.

evaporation than plants with closed floral chambers. Nevertheless, *P. selloum* gains the highest excess temperatures in this list (14.9 K). But the specific ability of this species is its long phase of thermoregulation, not a short time burst of heat production. If one plots the rates of temperature increase as function of excess temperatures from Table 1, a linear regression ($r = 0.82$) results with a slope of 0.54 h^{-1}. This means that all thermogenic flowers would attain their final maximum excess temperature within the same time of 1.85 h or 110 min if they heated at full power. Flare-up is thus a quick process as stated above. Only *Aracaceae* with their extreme excess temperatures and the low rates of increase (Table 1) do not fit into this slope.

Odour dissipation is tightly coupled with thermogenesis although it is not the only reason for the metabolic flare-up [44,45]. But its importance as a cue to a fertile flower—specially in the evening or night when optical signals are sparse—is clearly demonstrated by the observation that potential pollinators are flying against the wind and in a zigzag course till to the next surrounding of the baiting blossom [3,41,42]. Then other cues like a bright colour, an open spathe or a specific form may be more important. They never land on inflorescences that are not ''in heat'' and thus not smelling [41]. For long distances with optical obstacles, in the dark or for flowers hidden between leaves or branches stenches are indispensable. There are only few colours in the visible range and the near UV or IR, but hundreds of chemical compounds available to establish a fragrance bouquet typical for one plant species and its pollinators. Odour production is synchronised with the activity regime of the wanted pollinators. Many flowers waiting for night-active beetles or flies start to produce their odours with the beginning dusk. Others are more productive in the early morning so that a broad spectrum of insects is engaged in the business of fertilisation.

Odours of thermogenic plants may be ordered in two different categories, a large one of malodorous compounds described as ''not at all pleasant till nauseating'' (carrion-like, disagreeable, dung-like,

horrifically putrid, like rotting fish or meat, likened to a cadaver, long-dead half-dried fish or fermenting human faeces, pungent) and a smaller one that cajoles the human nose (agreeable, fruity and fresh, like anise, banana, cyanide, nuts or tropical fruits) [46,47]. The two most beautiful plants among the thermogenics fall into the latter class. The queen of the water lilies *Victoria* tempts with a sweet aroma like fruit salad, and the sacred lotus *Nelumbo nucifera*, ''admired since 3000 years in the Orient and connected with everything beautiful, elegant and charming'' [48] convinces with a ''sweet pleasant smell with overtones of an aromatic organic solvent'' [49].

It is known from several thermogenic plants that they posses a weak agreeable smell as long as their flowers are not fertile and that they change to an intensive ugly stench when they are ripe. The idea may arise that both odours exist simultaneously before but that the second rises above the first one during the heating up. Data from the literature [50,51] and estimations from the Clausius–Clapeyron equation indicate that all analysed odour compounds increase their vapour pressure—nearly independent of their boiling point—by 60% for a temperature change of 10 K (mean value: 1.60 ± 0.13; range: 1.32–1.78; $n = 18$). This indicates that during the metabolic flare-up new biochemical pathways are encountered that produce the changed stenches. Moreover, one has to keep in mind that the detection thresholds are very different for important fragrance compounds: the pleasant ''white-flower'' component phenyl ethanol has a threshold of 750 ppb for the human nose, while the ''carrion-like'' dimethylsulphide needs only 12 ppb to disturb us [46,47].

The appendix of the voodoo lily *S. guttatum* was intensively studied as an osmophore evaporating more than 100 different substances, 70% of them terpenes and sesquiterpenes [31]. They are responsible for the sweet fragrance within the floral chamber that keeps the pollinating beetles active till to the next day and stimulate their mating behaviour. But the N- and S-compounds with a much lower detection threshold overtone them with the pungent note of indole and the foul one of dimethyldisulphide. This is understandable because many of the 30 different insect species bailed by *S. guttatum* are engaged in dung deterioration [31].

The slim appendices of many arum lilies lose a considerable amount of heat by convection and warm up the air in their immediate environment. This creates a microclimate around them with an upward circulation of air. In this way odour compounds ascend out of the thicket of leaves to the free space above them from where they will be transported away by the wind. Thus, airways of odours are established for insects to or between plants in heat that wait for their pollinators.

All life processes are intimately bound to consumption of free energy that is provided via metabolism. As real processes are far away from 100% efficiency, the major part of this energy is dissipated as heat and only a smaller part stored as chemical energy in form of ATP. These necessary energy units are provided by respiration that proceeds via the mitochondrial electron transport and the cytochrome pathway. In special moments of animal life, e.g. at the arousal from hibernation or in the first days of new-borns, respiration can be uncoupled from oxidative phosphorylation. Under such conditions, no ATP is formed and all energy is used for heating up the body. Thermogenin (the ''uncoupling protein'') is responsible for this process in brown fat tissue (see, e.g. [1,52,53]).

Higher plants posses an additional ''alternative'' pathway that is cyanide-insensitive in contrast to the other one mentioned above. Only 1 mol of ATP is formed per mole of NADH on this alternative route instead of the usual 3 mol. Thus, more energy is available for the intended temperature increase. van Herk [54] showed already in 1937 that a messenger substance called calorigen was sent from the sterile male flowers to the appendix of *S. guttatum* a short time before the flare-up proper [24,26]. It turned out that this molecule is salicylic acid [27] and that it is present in different thermogenic species, but not in all. It was determined later that in *S. guttatum* the concentration of this substance is 100-fold higher during the respiratory climacteric than in the days before and after [55]. The cytochrome chain is shut down considerably so that the electrons are forced to flow through the alternative pathway with less ATP and increased heat production [56–58].

An interesting phenomenon became visible in the IR images of *V. cruziana* that puzzled the authors for a while. In many IR pictures, reflections of buds, flowers and leaf rims on the water surface appeared. In all cases, the reflections showed higher temperatures than the emitting objects and thus an upward shift in the scale on the right of the presentation. But temperatures

are ''intensive'' quantities, which one is not allowed to add. The values observed in Fig. 6 amounted to 26.7 °C for the leaf rim and to 30.2 °C for its mirror image, a shift by +3.5 K. Fig. 7 presents some very distinct examples of IR reflections: the leaf at the top with +4.5 K, the bud in front of it with +2.6 K, the flower in the centre with +3.9 K and the leaf bud right of it with +4.5 K. In contrast to such an observation with false colours, one is used in the optical range to see the same colours in the mirror image of an object as in the object itself. The solution of the problem is that usual photography monitors the wavelength distribution of an object, while the IR camera collects all radiance that enters the diaphragm [19,59,60]. In this way the radiation from the water surface sums up with that of the reflection to a higher total radiance that is then interpreted as an increased temperature. Emissivity of an object and reflectivity add up to 1 so that objects with strong emissivities have small reflectivities and vice versa. Water with an emissivity of more than 95% keeps the degree of reflection low. Thus, the temperature increases seen in Fig. 7 are small but easily detected in the narrow chosen band of less than 10 K [19].

5. Conclusions

In this paper, different own investigations on thermogenic plants are compared with data from the literature. Weighing the results one has to discriminate between experiments with dissected flowers, special organs and tissues and experiments with whole flowers still connected with the plants. And moreover between those in the laboratory with all necessary facilities and those in the natural environment. The latter have to be simpler and more robust under changing outside conditions. But they are of course nearer to the biologic reality and truth than the more sophisticated ones.

Thermometry offers the easiest approach for whole flowers, and when IR thermometers or even IR thermography cameras are used the plant is not disturbed at all. But it is difficult to calculate quantitative metabolic data from excess temperatures since energy is lost via evaporation, conduction and convection. Energy turnover rates are best determined by indirect calorimetry, i.e. from rates of oxygen consumption and carbon dioxide production. Knowing these two values, one can estimate the substrate and then calculate the corresponding heat production rate via the oxycaloric equivalent. Direct calorimetry is by far more difficult to perform as it needs a stable reference temperature and as it integrates over all simultaneous heat consuming and heat producing processes.

Summing up, all kinds of thermometry and indirect calorimetry with electrolytic sensors will continue to be the most successful means to investigate intact thermogenic plants in their natural environment.

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