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A tropical water lily with strong thermogenic behaviour—thermometric and thermographic investigations on *Victoria cruziana*

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Abstract

The paper presents data on the thermogenic blossom of the giant tropical water lily *Victoria cruziana* investigated in a greenhouse of the Berlin Botanical Gardens. Usual mercury and handhold non-contact infrared (IR) thermometers rendered temperature increases of up to 9 K compared with the ambient air. Continuously registering data loggers evaluated the temporal thermal structure of the flower during blooming. Temperature distributions in the blossom and on the floating green leaves were determined by means of a transportable IR thermographic camera. Moreover, it showed the puzzling phenomenon of thermal reflection of flowers and leaves which is discussed in some details. © 2002 Elsevier Science B.V. All rights reserved.

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1. Introduction

The tropical water lily genus *Victoria* was discovered in 1801 by the German botanist Hänke in a tributary of the Amazon. But his observation was lost so that the impressive plant was ''rediscovered'' several times: a few years later by Aimé Bonpland who accompanied Alexander von Humboldt to South America, by d'Orbigny 1827, 1832 by E. Pöppig and 1836 by Sir Robert H. Schomburgk in British Guayana. The botanical name of this ''aquatic monster'' changed several times and was finally fixed to *Victoria regia* under which the plant is best known around the world. Nevertheless, the correct name today is *Victoria amazonica*.

The plant grows in calm waters, ox-bow lakes and flooded grasslands along the Amazon and its affluents, but also further north up to British Guayana. Although, seeds of *Victoria* were sent to Europe already a short time after detection, it was not before 1849 that the first blossom opened in an English greenhouse specially constructed for this plant. Breeding of *Victoria* became fashionable all over Europe and it was from Ghent in 1850/1851 that Planchon reported for the first time on a temperature difference of 6 K between the flower and the ambient air [1,2]. Otto observed a similar difference in Hamburg [3] and Caspary/Berlin [4] published a graphic display of the temperature evolution during inflorescence. Many other similar observations followed.

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There is a further member of the genus *Victoria*, the smaller *V. cruziana*, that got its name by d'Orbigny in honour of the Spanish general Santa Cruz who joined and helped him during his expeditions. *V. cruziana* grows in cooler and more southern areas of South America in Argentina and Paraguay where it is called ''Yrupe'' what means ''water platter''. This plant is not as spiny as *V. amazonica*, the leaves remain smaller but their stiff upright rims are more impressive. Usually, both *Victoria* species are cultivated in the Botanical Gardens of Berlin. Due to some problems with the seeds only *V. cruziana* was available in the season 2000 so that the present investigation concentrates on this plant.

But *Victoria* is even better known by its gargantuan leaves than by its beautiful flowers because it is difficult for most greenhouse visitors to come near enough to the blossoms to detect their real beauty and to smell their sweet odour, so much the more in the evening and during the night. And who of us has ever a chance to meet the queen of the water lilies in her natural habitat? The leaves were called ''huge floating tea trays'' in the first descriptions and it was reported that the Indian mothers parked their smaller children securely on the leaves when collecting the tasty and nutritious seeds of *V. amazonica* from the water. Leaves grow up to about 2 m in diameter for *V. amazonica*, a little less for *V. cruziana*. Their bottom side is covered with a spider-web of tall supporting ribs of less than 1 cm thickness and up to 7.5 cm height. They form a manifold of pockets under the leaf that trap air and thus give the leaves the astonishing buoyancy. Calculations for a typical summer leaf of *V. cruziana* of 1.50 m diameter render a total volume of about 55 l trapped air able to carry a corresponding load of 55 kg. Nevertheless, the lips at the leaf circumferences standing upright to 7 cm in *V. cruziana* and less significantly in *V. amazonica* show two diametrical notches to allow the rain to drain off and not to press the leaf under the water surface. The plant tissue between the ribs is rather thin and forms a small convex elevation of a few millimetres between the troughs above the ribs. The leaves are light (about 5 kg wet weight) and fragile, but the upright rim renders them a special stability during storms and protects against overlapping of neighbouring leaves which would reduce the active surface for photosynthesis.

The interest in *Victoria* originates not only from the beauty of its blossoms or the enormous size and the elaborated structure of its leaves but also from the fact that *Victoria* belongs to the group of thermogenic plants. This group—comprising some aroids like *Arum maculatum*, *A. italicum*, the voodoo lily *Sauromatum guttatum* and the American skunk cabbage *Symplocarpus foetidus* or the giant *Amorphophallus titanum*, then the sacred lotus *Nelumbo nucifera* or some cycads and palms—shows a strongly increased metabolic rate during blooming that is used to heat up the flowers or parts of them. In this way, special odours—nice or awful—are volatilised to attract pollinating insects or to provide them with warm shelters for cool nights even stimulating insect copulation in them [6]. Temperature increases up to 30 K in thermogenic plants may endure for only a few hours, for days or even weeks and may show a high degree of thermoregulation as in *N. nucifera*, *Philodendron selloum* or *S. foetidus* [5–11]. A frequently used, easy to breed aroid species is the voodoo lily *Sauromatum guttatum* that shows a weak thermogenic region around the male and female flowers and a strong one in the upper sterile part of the inflorescence, the appendix. This plant was investigated calorimetrically as a whole in an indirect and direct approach [12,13], in its different tissues and by infrared (IR) thermography [14]. Temperatures in the appendix increase up to 32 °C [14] and to 26 °C or 7 K above ambient [13].

Our interest in *V. cruziana* was to perform thermometric measurements with different methods, to show temperature distributions in various parts of the blossoms and to compare them with the metabolic activities of the different plant materials. Here, we will concentrate on the thermometric and thermographic aspects while calorimetric data will be published later.

2. Experimental

2.1. Plant material

V. cruziana was grown in a greenhouse water pond of the Botanical Gardens, Free University of Berlin. The size of the pond was 4 m × 16 m, the water depth 0.40 m except for a central channel of 1.5 m width and

1.40 m depth. The volume of water thus amounted to 55 m^3. The water was constantly thermostatted to nominally 30 °C. No efforts were made in the greenhouse to shade the direct sunlight so that during special times of the day parts of the pond surface were directly irradiated, others not. But in agreement with results found in the literature [15], such irradiation had nearly no influence on the flower temperature due to the high heat capacity of the blossoms. The relative humidity in the greenhouse was always near to 100% and outside the range of exact measurements for standard hygrometers. This is the reason why transpiration [16] and thus cooling of the leaf surfaces can be neglected in all these investigations. Although, the season for *V. cruziana* continues from end of May to the beginning of November, first results were obtained only on 8 August 2000.

Most space in the pond was taken by two *V. cruziana* plants inserted in the central channel. Both developed differently which was most obvious in the growth rate of the leaves following a sigmoid curve. The maximum rate was 3900 $cm^2\,day^{-1}$ for plant 2 and only 1400 $cm^2\,day^{-1}$ for plant 1. The reason for such a large difference was not known. As the deviation of temperatures between the two plants was smaller than the daily fluctuations, the results were pooled and are presented here together. During the observation period, 61 blossoms of *V. cruziana* were monitored for their development. Ten of them could be cut after blooming for further energetic investigations in the laboratory. The number of leaves under investigation was not counted, but at least two were cut per week by the gardeners to give space for the new ones. Thus, more than 50 leaves were measured during the same time. Moreover, a general rule for *Victoria* says that always one new leaf is produced per new flower.

Due to the ''show character'' of the greenhouse, plant material could only be investigated in situ but not cut for further laboratory research except for inflorescences after the flowering days. All temperature values presented under results were obtained at the side of or directly in the pond.

Buds of *Victoria* develop under water and move up to the surface within one week. Slightly above the water they follow a strict protocol in blossoming [15,17–20] which is partly triggered by light intensity but never changed by weather [15]. The active phase takes two consecutive days starting in the late afternoon of the first day when the bud slowly opens. The pure white petals appear between the dark green–brown sepals and fully open after sunset. This is the first thermogenic phase when *Victoria* disperses a fruity fragrance like pineapple, volatilised due to a significant increase in floral metabolic activity. Temperature differences of 5–10 K and sometimes even more against ambient are reported in the literature (Table 1, see also [15]). The flowers are pistillate (female) during this period and can be fertilised by visiting beetles covered with pollen from an other plant. They enter the floral chamber through a small tunnel between the paracarpels (Fig. 1) that close in the early morning of the next day when the temperature decreases. The beetles are trapped in the chamber for many hours. In the late afternoon of the second day the flower turns to male with an intensive pink colour, own pollen is shed on the beetles, the temperature increases a second time, the tunnel opens again and the pollen covered visitors are released to the next fragrant and thus female flower. In this way, self-fertilisation is avoided in favour of cross-pollination. Botanically interested readers can find a full sequence of more than 30 interesting pictures of the flowering event in the internet [21].

Table 1
Some historical data about maximum temperature increase in *Victoria* blossoms, taken from the literature

Author	Year	Location	Time	Increase (T/K)
Planchon [1,2]	1850/1851	Greenhouse, Ghent		6
Otto [3]	1852	Greenhouse, Hamburg		5
Caspary [4]	1855	Greenhouse, Berlin	20:30	10.4
Knoch [16]	1899	Greenhouse, Marburg	19:15	10.2
			6:00	9.3
Decker [18]	1936	Amazon		11–14

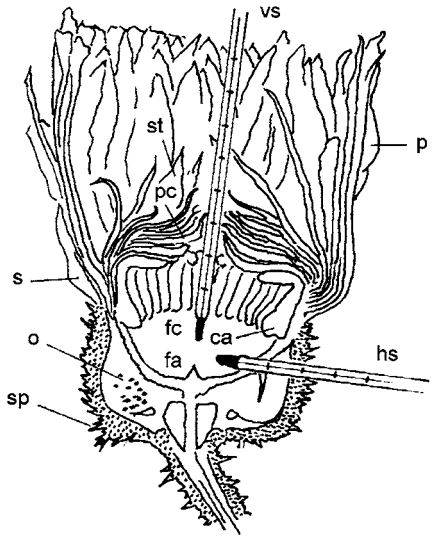

Fig. 1. Cross section of a *V. cruziana* flower at the end of blooming (ca: carpellary appendages; fa: floral apex; fc: floral chamber (stigmatic cup); hs: horizontal sensor; o: ovaries; p: petals; pc: paracarpels; s: sepals; sp: spines; st: stamens; vs: vertical sensor).

2.2. Thermometry

Thermometry was performed in a three-fold manner: (i) by usual mercury thermometers with a grading of 0.1 K for the temperature inside the bud or the blossom. These measurements were performed once or twice per day; (ii) by a non-contact hand-held IR thermometer to determine the surface temperatures of blossoms, leaves and the water; (iii) by data loggers for a continuous monitoring of ambient temperatures and those of the blossoms.

2.2.1. IR thermometry

In addition to the usual thermometric measurements, a non-contact IR sensor was applied to determine temperatures of interest at different spots. A hand-held 260 g light IR thermometer (THI-300, Tasco, Japan) with a temperature range from 0 to 300 °C and a spectral band from 6 to 12 μm was chosen for this purpose. It had an accuracy of ±1% of the full-scale, a repeatability of ±0.8 K and a field of view that was half the measuring distance. The front tube had an outer diameter of only 1.2 cm. Thus, this sensor was specially useful to look through the tunnel into the floral chamber of the half-opened blossom or to its paracarpels to monitor their temperature. Moreover, these measurements were important for the thin floral leaves (sepals, petals, stamens) where no contact thermometry was possible.

2.2.2. Data logging

Continuous temperature monitoring was performed by means of two types of small (6.4 cm × 5.9 cm× 1.8 cm, 20 g) data loggers (Onset Computer Corporation, Pocasset, MA, USA). The first one (HOBO Temp, Series 01) was a one-channel temperature logger with an internal sensor (10 kΩ NTC resistor) that can be easily prolonged outside the case for a temperature range from −20 to 70 °C with an accuracy of ±0.7 K at 20 °C. It stores up to 1800 data points (2KB). Data are read out to a PC with a special software (BoxCar 2.06) and can be imported to Microsoft Excel or any graphic programme for further treatment. The second type (HOBO RH, Temp, Light, External, Series 08) is a four-channel version for internal (or external) temperature, humidity, light intensity and an external signal, e.g. a second temperature. It is an 8KB, 8.000 data point version that was applied to monitor the ambient conditions in the greenhouse.

The one-channel HOBOs were always placed near to the flowers or buds, usually floating on a ''boat'' of styropore™, sometimes on one of the *Victoria* leaves. The first variant was preferred as larger movements of leaves and flowers happened during the day. In all experiments, two temperature sensors were inserted into the floral chamber of the blossom: one from the side and one from the top through the tunnel (see Fig. 1). They always showed slight differences due to the varying protection by the plant tissue or to the special location.

In some experiments, a reference thermal sensor inserted into a styropore™ block was floating on the same boat near the flower. Due to the short or even not existing distance between the blossom and the water surface, it was not possible to place the reference sensor in the stenge or an other part of the plant.

The four-channel versions were hidden behind the greenhouse construction in 1.5 m height (sometimes exposed to the sun) and under a bridge (0.5 m height above the water surface) without direct irradiation.

2.3. IR thermography

IR images of *V. cruziana* buds, blossoms and leaves were taken with an uncooled hand-held IR measurement camera, Type AGEMA 570 PRO, Darmstadt/Germany, with a thermal sensitivity of 0.1 K at 30 °C, a temperature range of −20–500 °C and a spectral range of 7.5–13 μm. The detector was a Focal Plane Array, uncooled microbolometer of 320 × 240 pixels. The accuracy amounted to ±2% of the range or ±2 K. Moreover, the camera offered the chance for voice annotation of the taken pictures. Under this working conditions, 700 images (14-bit) with full annotation can be stored on a 170 MB PC-card in such a format that all necessary data are available later on independent of the camera setting in the moment of taking the picture. The low camera weight of only 2.3 kg allows to take photos even under difficult and extreme conditions, e.g. standing in a 40 cm deep water pond near to the *Victoria* blossom as in the present investigations.

The camera is supported by the software package Irwin 5.0 running under Microsoft Windows 95 that offers numerous analysis functions such as point temperatures, profiles, histograms, isotherms or the determination of the maximum temperature in the image. The range of the actual temperature and the false-colours of the IR images can be chosen by will.

3. Results

3.1. Ambient temperatures

Temperatures in the greenhouse were rather stable. The water temperature amounted to a several-months mean of 29.9 ± 1.0 °C. The long term maximum was 31.2 °C, the minimum 26.2 °C. Air temperature fluctuated by far more with a mean of 24.5 ± 1.5 °C for the point measurements in the morning and the late afternoon/evening with maximum and minimum values of 28.1 and 22.3 °C, respectively. Continuous monitoring by means of HOBO data loggers showed short term fluctuations up to 50 °C.

3.2. Floral temperatures

Temperatures were taken in a two-fold manner during the development of *V. cruziana* flowers: (i) in a point-in-time fashion at special instants during the day and just for a few minutes (mercury and IR thermometers, thermography) and (ii) in a continuous mode by application of data loggers. Results are collected in Tables 2 and 3. Usually, observations were done in the morning between 7:00 and 9:00, in the late afternoon between 17:00 and 18:30 or in the evening between 19:30 and 21:00. Thus, it can not be guaranteed that the maximum values of temperature were found in these short periods. They could only be evaluated from the permanent registration of the data loggers. In the three thermometric results, there are no differences between buds, half and fully opened blossoms, but all three values are significantly above the mean air temperature of 24.1 °C. Maximum elevations of 6–8 K are seen against air while flower temperatures remain around the mean water value (30 °C).

The mercury thermometer was pushed through the still closed protecting sepals of the bud or the closed or opened tunnel down to the floral chamber (Fig. 1). Thus, it was not possible in this way to make any differentiation between the various parts of the blossom. But this could be done by means of the IR thermometer. In Table 3, the results are pooled for half or completely opened flowers, while only sepals are accessible in buds. Sepals and petals are near to air

Table 2
Temperature (°C) of *V. cruziana* flowers in three states of development, taken with different techniques[a]

Taken by means	Bud	Half opened	Fully opened
Thermometer (mercury)	28.9 ± 1.9 (51)	28.7 ± 1.3 (33)	28.4 ± 1.2 (39)
IR thermometer[b]		30.1 ± 1.4 (16)	29.8 ± 0.7 (22)
Continuous registration[c]	32.0 ± 1.7 (21)	30.4 ± 2.0 (21)	31.0 ± 1.4 (17)

[a] The mean temperature of the air during this period was 24.1 ± 1.5 °C ($n = 199$), that of water 30.0 ± 1.0 °C ($n = 198$). Mean value ± S.D. (number of determinations).

[b] The temperature at the bottom of the floral chamber was determined.

[c] The maximum temperatures during the blooming of individual flowers were pooled.

Table 3
Detailed analysis of temperatures taken with an IR thermometer[a]

Object	Temperature Θ (°C)	Minimum/ maximum Θ (°C)	n
Sepals	25.5 ± 0.9	24.1/27.3	36
Petals	25.2 ± 0.9	23.6/27.0	58
Staminodes/stamens	28.8 ± 1.2	25.8/31.0	44
Floral bottom	29.9 ± 1.1	27.5/32.7	43
Leaf[b]	28.4 ± 0.9	25.4/29.8	41
Water near the plant	29.3 ± 0.5	28.0/30.5	42

[a] Temperature ± S.D., minimum/maximum temperatures and number of determinations n. The mean temperature of air during this period was 24.1 ± 1.5 °C ($n = 199$), that of water 30.0 ± 1.0 °C ($n = 198$).

[b] The elevations in the leaf structure were taken as measuring points.

temperature and are in no case thermogenic. Small deviations from the mean in the order of about tenth of a degree can be observed along these floral leaves. The staminodes and stamens are significantly warmer than the rest of the plant and the air. Indirect calorimetric investigations proved that they have an increased metabolism compared with other floral tissues and are slightly thermogenic, while the true heat production happens in the floral chamber by the paracarpels and the carpellary appendages (results will be published elsewhere).

3.3. Continuous temperature monitoring

Continuous registration of floral temperature was possible by means of the HOBO data loggers. They were positioned in double in the flower (see Fig. 1) and at different points in the greenhouse. Fig. 2 presents a diagram of the temperature differences against ambient air in blossom 8 of plant 2, the blossom that is shown in the centre of Fig. 3. The upper grey line stems from the horizontal sensor, the lower black one from the vertical probe. Two main periods of heat production are visible, the first in the late afternoon of the first day with a maximum of 10 K at 20:40 for the horizontal sensor. This maximum is followed by a steady decrease till to the late night hours and a second increase which culminates around 11 K at 11:30 of the next day. A smaller extremum appears at 15:10 with 9 K before the floral temperature returns to ambient. The temperature difference between the two probes is always positive with a mean value of 2.1 K (S.D. ± 0.8 K). It is independent of the chosen sensors and loggers and appearingly a function of floral architecture, insulation and some air convection in the floral chamber and through the tunnel. Mean values of the maximum floral temperatures are compiled together with those from thermometers in Table 2.

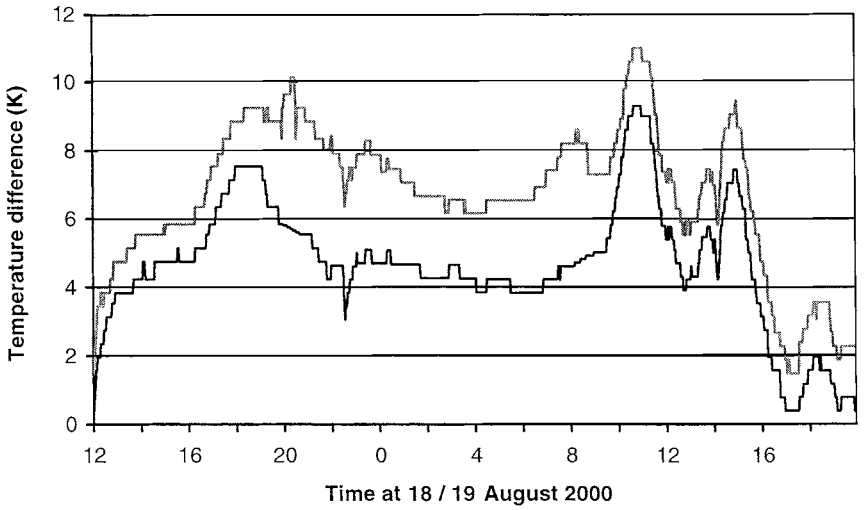

Fig. 2. Development of the temperature difference between a flower and the ambient air during the blooming of a *V. cruziana* blossom. The upper slope originates from the horizontal, the lower one from the vertical sensor in the floral chamber (see Fig. 1). Maximum values are found in the evening of the first day and the late morning of the following day (further details in text).

Fig. 3. *Victoria* pond in the greenhouse of the Berlin Botanical Gardens. In the centre of the picture is a first day, half opened flower of *V. cruziana*; left behind, is a bud with a mercury thermometer and the styrofoam ''boat'' with the data loggers. Directly in front of the boat, it is a few days old leaf bud. Leaves of different age are around the blossom (look at the leaf structures and the spines at the leaf rims).

3.4. IR thermography

Fig. 4 shows an infrared image of a *V. cruziana* blossom in the late afternoon of the first day, taken with an IR thermography camera in false colours. The usually applied colours from violet over green and yellow to red were changed in the Irwin programme to a grey scale with 26.5 °C (white) as the lowest

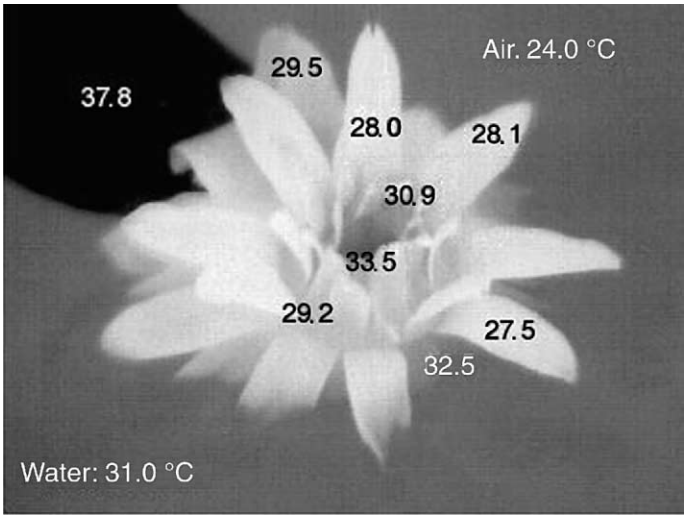

Fig. 4. IR thermographic image of a *V. cruziana* blossom in the afternoon of the first day. Temperature indication in a grey scale from 26.5 °C (white) to 36.2 °C (black). For better orientation, some essential temperatures are included in the image. Air temperature: 24 °C, water temperature: 31 °C.

temperature and 36.2 °C (black) as the highest one. The black area in the upper left corner is a gloved hand turning the flower towards the observer. Its temperature is slightly outside the range. Air temperature is 24 °C while water temperature is 31.0 °C—both given by the camera. Some specific temperatures are indicated in the picture showing a maximum value of 33.5 °C on the inner staminodes near the central tunnel (not seen) and a minimum of 27.5 °C on one of the horizontally orientated petals. The inner upright standing paracarpels are at 30.9 °C. In total, the image shows a maximum temperature difference of 9.5 K against air. Such values are in good agreement with data found in the literature and own thermometric measurements.

3.5. Thermal reflection

The IR thermography images contain a detail that may puzzle the inexperienced observer. Just as in the visible part of the spectrum, IR pictures sometimes show the mirage of an object on the surface of a reflecting medium, e.g. water. In daily life, a mirage has the same colours as the real object while in the IR image, there is a shift in the wavelength, i.e. the temperature of the reflection. This astonishing result seems to contradict the fundamental laws of classical physics. But it can be easily explained by the fact that an IR camera measures bolometrically the intensity of the incoming radiation that is a function of temperature only. Radiation intensity of the reflecting medium and of the reflection add up to a higher total intensity and render thus a changed temperature indication.

Fig. 5 is an illustration for the mentioned thermal reflection seen with the thermography camera. At a temperature of 30.3 °C for water and 24 °C for air, we observed mirages in a temperature range between 31.4 and 31.7 °C, while the real objects are at temperatures between 27.1 and 29.6 °C. That this true difference of 2.5 K is reduced to only 0.3 K is understandable since water renders the main contribution of about 95% to the thermal signal while only 5% originate from the reflected object (Appendix A).

Thermal reflections not always appeared in our IR images, but often under varying conditions. In total, we analysed 33 different objects (buds, flowers, leaf rims) and found mean object temperatures of 28.0 ± 1.8 °C and mean mirage temperatures of 31.8 ± 0.5 °C. The mean of the differences in pairs was 4.11 ± 0.8 K, that between mirage and water 1.4 ± 0.6 K. The latter difference is rather small, but with a 0.1 K thermal sensitivity of the camera, it is easily detected.

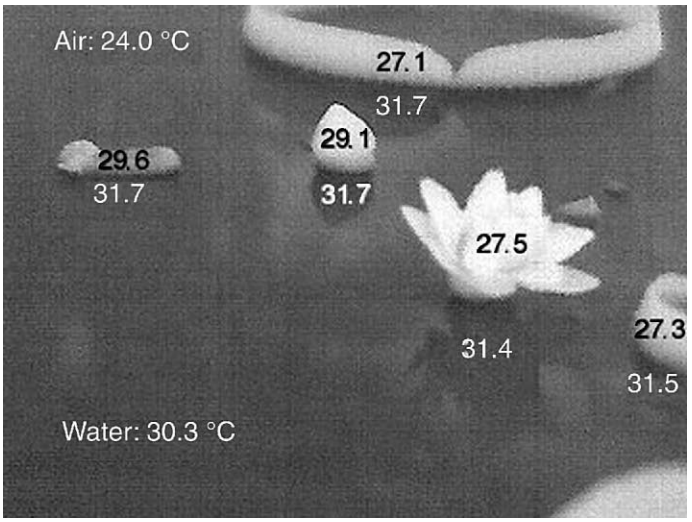

Fig. 5. Thermal reflection in an IR thermographic image of the *V. cruziana* plant that is shown in Fig. 3. Temperature in a grey scale from 24.6 (white) to 32.5 °C (black). The reflections are the hottest points in the image. For better orientation, some essential temperatures are included. In false colour representation reflections are more obvious.

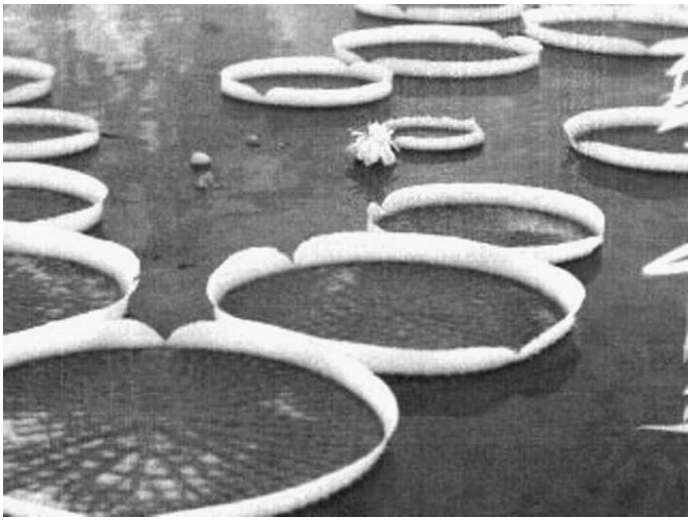

Fig. 6. IR thermographic image of *V. cruziana* leaves showing the leaf structures of troughs (dark) and elevations (light). Temperature in a grey scale from 24.2 (white) to 32.2 °C (black). Air temperature: 24 °C, water temperature 30.1 °C. The leaf rims are the coolest points with 25.2 °C. Pay attention to the black mirages of the rims.

3.6. Temperature of the leaves

As the leaves of *V. cruziana* are floating on the water surface with a further contact by the ribs and the stenge, one tends to assume that their temperature has to be similar to that of the supporting water. Such imagination is strengthened by the fact that there is no cooling effect by evaporation of water on the leaf surface. Transpiration can be neglected because of the high relative humidity near to 100% in the greenhouse. The same holds good for convection as there is no air movement in the greenhouse that is necessary for convection [16]. Nevertheless, one observes a slight temperature gradient across the leaves and a temperature structure over the surface of the leaf (Fig. 6). The small elevations between the ribs are isolated against the water by the trapped air so that their temperature is always lower than those of the troughs between them. This difference—determined with IR thermometry—amounts to about 0.5 K with a few exceptions above 1 K. IR thermography renders typical values between 1 and 2 K (see Fig. 6). The effect becomes more pronounced to the end of the season.

Moreover, the thermograhic pictures show that the upright rim of the leaves is always the coolest part with 2–3 K less than the main part.

4. Discussion

First mentioned thermogenic plants were members of the arum family: *Arum venis albis*, *A. italicum* and *A. maximum*, described by Lamarck 1778 [22] with the words ‘‘il est chauds au point de paroître brûlant’’. Their temperature elevation during blooming was high enough—and the ambient temperatures rather low—that one could sense the increased heat production just by touching. In contrast, thermogenecity of *Victoria* was first observed in greenhouses in Europe [1–4,23], 50 years after its detection (Table 1), and it took further 90 years before this fact was confirmed by Decker in the natural habitat at the Amazon [18]. Meanwhile, several descriptions of this phenomenon, under glass as well as in nature, are published [24–27]. Such investigations were not only performed on *V. amazonica*, but also on the smaller *V. cruziana* [28] that is adapted to cooler climates and thus more easy to breed. But these latter authors cut their flowers, took them to the laboratory and determined the temperature only there. It is not known how the flowers react on this treatment. It was not possible in Berlin to compare these specific observations on *V. cruziana* as we were able to measure the temperature in situ right through all phases of blooming, but not allowed to cut them before they stopped to be active.

Several authors dealt with the elaborated time regime of flowering. Their observations showed that *V. amazonica* opened the blossoms always between 17:30 and 18:30 for the first time in their natural habitat [15]. This is true for the tropical area without significant influences of season light. But in moderate European climates with distinct seasons, the time course of blooming shifts with the progressing year. In the bright summer weeks, *Victoria* starts to open already in the afternoon between 16:00 and 17:00 and obtains its full size in the evening. In autumn, blooming commences in the later afternoon or early evening. Then, the blossom has a pure white colour during midnight and remains open till to the next morning [29]. Moreover, it shows a second flowering and thermogenic period in the afternoon of the second day that is clearly indicated in Fig. 2. In any case, light plays an important role in triggering the blooming process while changes in weather remain without influence on the regime [15].

Knoch [17] showed in an early greenhouse investigation on *V. amazonica* that the thermogenic phase started already in the bud 9 h before the blossom opened and that the temperature increased steadily up to the first maximum. A corresponding behaviour can be seen for *V. cruziana* in Fig. 2. Moreover, Knoch found out by thermometry that stamens, paracarpels and carpellary appendages are the most important thermogenic organelles while petals remained relatively cool [17]. And he showed that the appendages are responsible for odour production. At the same time, appendages are the warmest tissues with 12.3 K against ambient when the flower is cut and the appendages analysed separately. Later, it could be proved by the neutral-red method of Vogel [30] that other parts of the blossoms co-operate in scent production, e.g. the petals, whereas, sepals remained inactive [15,28].

Arias and Prance chose a second day blossom with no longer increased heat production as reference point. But it was still 4.5 K above the air, presumably due to a good thermal insulation [15]. This insulation was also proved by the fact that the ambient temperature might well be above that of the flower for shorter periods, an effect that we often saw when sunlight directly touched the reference sensor and the flower simultaneously. They observed temperature elevations in the active flower of 3.5 K on the first and 5.5 K on the second day against the old blossom and 9.5 or 11.0 K against air, respectively. Such measurements were not possible in the Botanical Gardens since the old flowers were actively drawn into and under the water by the plants and thus had the nearly constant 30 °C of the water.

Although IR thermography is a well-introduced method in all fields of industry and some parts of medicine, it is rather unknown in biology and specially in botany. More recently, a few papers were published on freezing and ice nucleation in plants [31–33], on plant infections [34–36], on leave energy balances [37] and seedling quality assessment [38]. Two earlier papers dealt with water stress in sunflower leaves [39] and the characterisation of barley mutants [40].

Interesting in connection with the present experiments are the paper of Jones [37] on thermal IR measurements of leaf temperature and those papers dealing with the inflorescence of thermogenic plants. Skubatz et al. [41] investigated 12 different aroid species for their flowering behaviour, among them *Arum italicum*, *Philodendron selloum*, *Dracunculus vulgaris* and *Monstera deliciosa*. Temperature increases to around 40 °C at ambient 20–23 °C were observed on the first day for *P. selloum* and at ambient 24–26 °C for *A. dioscorides*. Other aroid species were less thermogenic with only slight temperature elevations above the environment. Moreover, the paper showed a complex temporal structure in the heating period with several maxima, but a general tendency that first the male flowers become thermogenic on the first day of inflorescence opening when no pollen is shed. Later, other parts of the inflorescence may become thermogenic also, while female flowers never heated up.

Intensive IR thermographic investigations on *Arum maculatum* L. demonstrated two centres of heat production, namely the male flowers and the appendix, and a temperature regime with three maxima [42]. As long as the spathe was closed, the temperature increases were less pronounced with only 4.1–8.0 K above ambient in the male flowers. But they rose to 5.0–14.0 K in the appendix when the spathe opened. In the second day, the values were less impressive with only 0.5–6.1 K.

5. Conclusions

Thermogenic plants are an interesting family within the broad field of botany. They produce mass specific

metabolic rates that well compete with those of homeothermic animals. This effect is generated by special biochemical pathways that transform all stored chemical energy into heat. They become active during a short period in the plant's life to attract pollinators by a typical scent at a well defined time of the day, to offer a warm shelter for cooler nights or to stimulate copulation of beetles in the floral chamber [6,11]. Thermogenic flowers are found among different groups of plants, most frequently among the aroids.

In the present paper, some results on the giant water lily *V. cruziana* are presented that were obtained in a greenhouse pond. The initial idea was to deal with the even larger *V. amazonica* and to apply the techniques that were developed in an easily accessible and secure place in Berlin to plants under field conditions at the Colombian Amazon. Due to technical problems only *V. cruziana* was available in Berlin in the year 2000, but it is expected that the greenhouse investigations will proceed in the season 2001 with *V. amazonica* and hopefully 2002 at the research station of the Universidad Nacional de Colombia/Bogota in Leticia at the Amazon. All instruments applied in Berlin were light, easy to handle, robust enough for field conditions or constructed from very simple material that is available everywhere so that they can be used under rough Amazon conditions.

Greenhouse experiments are an essential step in the investigation of tropical plants, but they are just half the truth.

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Appendix A. Thermal reflection

A dominant feature seen in the IR thermographical images [43,44] of *Victoria* is the thermal reflection of flowers, buds and leaves in the water. Although, unintended reflection of objects is always a disturbing contribution in thermography, it is rarely observed and considered in the estimation of the results. Therefore, some further information shall be given to this interesting phenomenon.

Reflections in the visible range are of the same colour as the object. Colours in the thermographic picture are false-colours indicating the different temperatures of the image. Spectral radiance emitted in the IR range is a measure of the amount of energy emitted in a chosen wavelength range by an object. Integrating Planck's law for blackbody radiation leads to a relation between the total energy emission M (in $\mathrm{W\,m^{-2}}$) of a body in all directions with temperature T (in K)

$$M = \varepsilon\sigma T^4\ \mathrm{W\,m^{-2}}.$$

ε is the total emissivity and σ the Stefan–Boltzmann constant with $\sigma = 5.67051 \times 10^{-8}\ \mathrm{W\,m^{-2}\,K^{-4}}$. Moreover, emissivity of ε and reflectivity of ρ add up to 1

$$\varepsilon + \rho = 1.$$

Objects with high emissivity have low reflectivity, in the case of a black body no reflectivity at all.

The radiance entering a thermography camera originates from three sources: (i) the observed object itself; (ii) an emission from an other object reflected at the surface of the first one and; (iii) from an atmospheric contribution. If we assume that the transmission coefficient of the atmosphere in the chosen IR window is near to unity the part can be neglected and the signal is only composed by the radiance of the two objects. This leads to the equation

$$N_{\mathrm{Cam}} = \varepsilon N_{\mathrm{Object1}} + (1 - \varepsilon) N_{\mathrm{Object2}}$$

where $(1 - \varepsilon)$ corresponds to the reflectivity. As the IR radiation is only dependent on the temperature, we can combine the two equations and calculate the total radiance received by the camera and thus the new total temperature. In the case of the reflecting water with a temperature of 30 °C (303 K) and an emissivity of 95% and the reflected leave with 27 °C (300 K), we arrive at an indicated temperature of 33.5 °C in the thermal reflection—an increase of 3.5 K against water. If we assume an emissivity of 99%, the appearing temperature increase is only 1.5 K. Both values

represent the borders in which the temperature elevation of the reflected image is found with the *Victoria* material.

But when the temperature of the reflected object is higher than that of the water surface, the mirage becomes cooler by a corresponding amount. This is clearly seen in images where the hand of the scientist (37 °C = 310 K) keeps the flower in the correct position to look into the camera (Fig. 4). Here, the resulting mirage temperature at a reflectivity of 0.95 is 307.3 K, equal to 34.3 °C. In a first approximation, one can state that the mirage temperatures are shifted in a symmetrical manner towards the temperature of the reflecting medium.

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