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Thermologic investigations of three species of *Amorphophallus*

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Abstract Thermologic investigations were carried out on three species of *Amorphophallus*: *A. konjac*, *A. paeoniifolius* and *A. titanum*, all the three strongly thermogenic. Moreover, their breeding system is described as protogynous, the heat production occurs in the appendix and male florets, no warming is seen in the female florets and pollen is shed after the end of heat dissipation. All the three have large, impressive inflorescences developed from big corms and have considerable sizes. During their inflorescence, they have a strong scent like rotting meat with carrion smell. *Amorphophallus konjac* (K. Koch) has a large, exposed appendix that produces a disgusting scent during the day of the female phase of blooming. The appendix produces about 3 W for several hours, and the temperature elevation is about 2.9 K. The low temperature elevation is attributed to a high surface area and a high evaporative heat loss from the appendix. During the male phase of blooming, a second episode of thermogenesis occurs during the same time of day, apparently from the male florets, reaching a maximum of 1.6 W. *Amorphophallus paeoniifolius* (Dennst.) Nicolson has a spadix that varies considerably from that of *A. konjac* and *A. titanum* with an amorphous upper end of the appendix like a shrunken red pepper instead of cone-like appendices for the two others. It shows thermogenic temperature increases of up to +9.1 K in the male florets and +2.6 K for a short time in the appendix. *Amorphophallus titanum* (Becc.) Becc. ex Arcang is the largest inflorescence of the world, growing up to 300 cm high and 250 cm across. A much smaller plant was observed during its thermogenic period by means of infrared (IR) thermography, IR thermometry, and thermometric data logger. The temperature maximum showed 36.6 °C at ambient 24.0 °C, which means a temperature difference of about +12.6 K. In the morning of the next day, all temperatures are back to ambient at about 24 °C. Estimates of the heat production (about 74 W) were made from the geometric data and special assumptions with respect to the heat transfer.

Keywords Amorphophallus · Heat production rate · IR-thermometry · Thermogenic plants · Thermography

Introduction

De Lamarck described more than 200 years ago for the first time that thermogenic plants of the Arum lily family (Araceae) warm up their blossoms by more than 10 degrees above the ambient and usually distribute an unpleasant smell, to say the least. Nowadays, it is known that thermogenic plants exist among 11 families of ancient angiosperms and cycads [1]. They were intensively investigated in the past and up to recently for their degree of warming, the metabolism (including the biochemical pathways for heat generation), the repetition and period of this phenomenon, its duration, the time of the day, scent production and the interconnection with possible pollinators. Most

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experiments were performed not only in the family of Araceae, but also on the water lily *Victoria* and the sacred lotus *Nelumbo nucifera*. Many specific and astonishing results were detected, among them their ability to regulate the temperature within a small range and over hours or days.

The most astonishing members of plants in the Araceae family are found among the *Amorphophallus* which comprises about 170 species, growing in or at the edge of forests in the Tropics, from West Africa to Polynesia with the exception of the New World [2]. They possess underground tubers that are sometimes cultivated, because the corms are rich in starch, easy to harvest and a welcome addition to nutrition. One leaf with a vertical stalk and a horizontally leaf blade with finger-like leaflets develops from the tuber. As is well known from other Araceae, a spathe together with the spadix forms the inflorescence (ensemble of many small male and female florets and accessory structures). At the base of the spadix are the protogynous female florets, above them the male florets, sometimes sterile male florets and the by far larger top of the spadix, the appendix. "Protogynous" means that the female flowers are receptive at first for about 1 day, and afterwards the male florets shed pollen, so that self-pollination is excluded. Later in the year when the spathe disappears, the female florets show mostly red berries (W. Hetterscheid, International Aroid Society, http://www.aroid.org/genera/amorphophallus/amintro.html).

Within the genus *Amorphophallus* well-known species are *A. konjac*, *A. paeoniifolius* and *A. bulbifera*. But the largest inflorescences of the world are produced by *A. titanum*. They originate from tubers of many tens of kilograms, exceptionally more than a hundred, and are found exclusively in Rain Forests in Sumatra. Leaves and inflorescences alternate in temporal appearance, sometimes bring a series of years with leaves only and then a blossom appears without leaves. The leaves form "trees" of up to 6 m in height and endure for up to 24 months. During this period, they produce the metabolites for a new, even larger tuber. After some years of leaf growth, an inflorescence appears developing up to a height of 3 m and a diameter of about 1.5 m. Owing to their dark brownish colour and their more than unpleasant smell like decaying flesh or carrion, they attract pollinators, once thought to be elephants, but now recognised as dung or carrion beetles [3], which pollinate the protogynous female florets before the males produce pollen. The spectacle of inflorescence is rare and a matter for press, television and radio: only about 75 plants have been observed to flower since the Titan arum was detected in 1878 by the Italian botanist Odoardo Beccari [4]. Flowering in Sumatra has been observed by Bogner [5] and described in detail by Barthlott and Lobin [6].

Amorphophallus konjac (K. Koch)

Amorphophallus konjac is a common food-plant cultivated around the world (Fig. 1). Temperatures and respiration rate were measured between 16 and 22 September, 1995, on one specimen that was growing in the Adelaide Botanic Gardens. The plant was potted in a container about 50 cm in diameter and 50 cm deep, so it was moved to a glass house on the campus of the University of Adelaide for measurements. The source of the plant is not known.

Temperature was measured with copper–constantan thermocouples placed inside the appendix, at the top, middle and bottom. Respirometry was accomplished by the decrease in oxygen level in an air stream that flowed through a hood over the inflorescence, through a water trap and flow meter, and into a Taylor-Servomex model OA570 paramagnetic oxygen analyser. Air from an aquarium pump flowed through a calibrated Fischer and Porter rotameter at about 400–500 mL min^{-1}, which was recorded regularly. The hood was fashioned from thick plastic and gas entered the bottom, where the hood was partially sealed at the base, and was sucked out of the top to the analyser. A timer-controlled solenoid valve switched the

Fig. 1 *A. konjac* blooming in the botanical garden in Berlin. Please notice the simultaneous growth of a leaf (*left*) with the stalk and the dissected leaf on top with a large diameter. More *A. konjac* are growing in the background with larger or developing leaves

analyser to read air for 5 min every 20 min to control for analyser drift. Note that neither water vapour nor carbon dioxide was absorbed prior to analysis of oxygen. Because water vapour condensed in the trap on the way to the analyser, the water vapour pressure was assumed to be saturated at analyser temperature. Considering the error in the flow meter and the assumptions of the calculations, the error in measurement of oxygen consumption is estimated to be less than about 10% [7]. Respiration rate was converted to heat production according to the equivalence of 21 J/mL of oxygen consumed [8].

The hood was placed over the entire inflorescence on the days before opening of the spathe. After the spathe opened, the hood covered only the appendix and male florets within the floral chamber. Opportunistic observations were made during the flowering sequence, and measurements were made of the height of the inflorescence from the base of the spathe to the top of the appendix. About 24 h after the thermogenic episode of the male florets, the appendix with male florets was cut and weighed.

Measurements of the inflorescence covered the complete sequence of flowering, from 5 days before the first thermogenic episode, when the spathe was closed, through opening of the spathe and intense thermogenesis during the female phase, and the final episode of thermogenesis associated with pollen release in the male phase. Between 15 and 19 September, the inflorescence grew from 63 to 88 cm in height. On the day before opening (19 September), the spathe was observed to be loosening significantly. For more than 24 h before opening, temperatures of the appendix were not greatly elevated over hood temperature, and the level of respiration indicated that heat production was low (Fig. 2). During the night, the inflorescence produced about 0.3–0.4 W, but this increased to about 0.7 W during the day, when hood temperatures were higher. On the morning of opening day (20 September), the spathe was closed, and little scent was apparent in the outflow of the respirometer. However, there was an explosive rise in thermogenesis that occurred after 10:00, continued throughout the day and started to decline precipitously at about 17:30 (Fig. 2). This was accompanied by a horrendous odour that resembled a combination of a decaying animal and vomit. During this period, the spathe had opened, so the hood was removed at 18:45 for examination and repositioning over the appendix and male florets only. Respirometry was resumed at 19:50. During the subsequent night, heat production decreased to previously low values. However, a second thermogenic episode began on the next day (21 September) at about the same time (10:00), and with a similar duration. At 12:10, the hood was removed for sampling of exudates and odour. This time, the smell was less powerful and different, akin to an open latrine. No pollen was evident at 12:10, but it began to appear during the afternoon as a brown coating of the male florets that was confirmed to be pollen under a microscope. There were no more thermogenic episodes, and so measurements were discontinued on 22 September. On this date, the mass of the excised appendix and male florets was 213 g. The appendix was 67 cm long and 4.6–8.1 cm at the widest part of its irregularly shaped cross section. The inside of the appendix was hollow. The specific mass of the *A. konjac* inflorescence with a mean diameter of 6.4 cm amounted to 0.1 g cm^{-3}, the same value as Boecker [9] determined for *A. titanum* with a comparable appendix structure (see below).

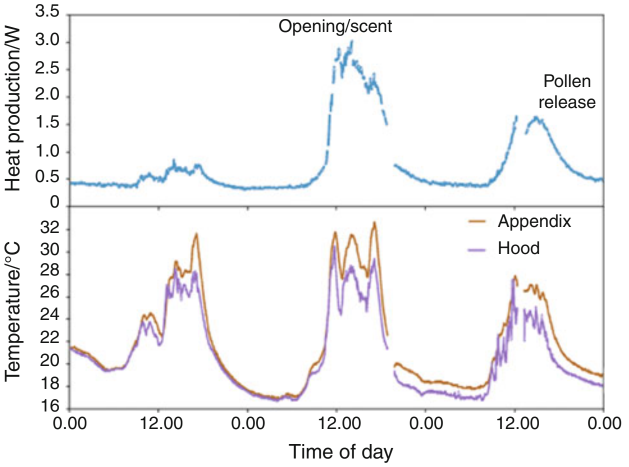

Fig. 2 Thermogenic episodes of an *A. konjac* inflorescence of 213 g. *Top*: Rate of heat production during 3 days of blooming, showing ambient temperature induced small increases on the 1st day, major thermogenesis by the appendix on the 2nd day and a lesser episode by the male florets on the 3rd day. *Bottom*: Temperatures of the appendix and respirometry hood. Gaps in the record represent disruptions for calibration and manipulation (for details see text)

The increase in heat production during the day before spathe opening was apparently caused by passive heating of the inflorescence due to higher day-time ambient temperatures. An increase from 0.35 to 0.70 W at ambient temperatures of 18 and 26 °C, respectively, would require a Q_{10} of 2.4, which demonstrates the van't Hoff/Arrhenius effect only. Unlike some other species that show a circadian lead up to the intense thermogenic episode in the female phase [10], this does not occur in *A. konjac*.

The maximum heat production during the female phase was about 3 W at 14:00 h, resulting in a 2.9 °C rise in middle appendix temperature (Fig. 2). In the male phase, heat production was about 1.6 W at 14:00, but the temperature increase in the male florets was unfortunately not measured, because at the time of the study, thermogenesis by the male florets of arum lilies was not established. It is surprising at first that, despite a 3 W rate of heat production, the temperature elevation of the appendix was quite small. By comparison, a 1 W heat generation in the lotus

Nelumbo nucifera can raise floral temperature about 20 K above the environment. There are at least two explanations for this result. First, the appendix of *A. konjac* has a high surface area and is directly exposed to the environment, so that it has little insulation for retaining heat, unlike the heat-generating receptacle of the lotus that is surrounded by petals. The larger the surface area of a heat-generating object, the lower the surface temperature will be. Second, the rate of evaporation from the appendix was undoubtedly high in *A. konjac*. Liquid water was observed running down the appendix and the interior hood walls during peak thermogenesis. In *Dracunculus vulgaris*, an aroid that has a similar, but smaller exposed appendix, the maximum appendix heat production is 1.7 W, but the evaporative heat loss is 2.2 W, so the temperature of the appendix can actually be lower than ambient [11]. This demonstrates that measurements of thermogenesis by thermometry can seriously underestimate actual heat production as measured by direct or indirect calorimetry. The purpose of thermogenesis in the appendices of *Amorphophallus* appears to be volatilisation of scented compounds that may be associated with secretion of water. Therefore, evaporation can be considerable, without a great elevation of appendix temperature.

Amorphophallus paeoniifolius (Dennst.) Nicolson

Amorphophallus paeoniifolius (Dennst.) Nicolson, called also *A. campanulatus* Blume or with the trivial name, the elephant foot-yam, is found in Madagascar, South-East Asia and Polynesia, and is cultivated in open fields or as intercrop in coconut gardens. Its corms are globose or depressed-globose with a deep dip in the centre looking like a donut. Its growth structure is similar to that of *A. titanum* with one leaf on a high stalk of 150 cm and with a blade of about 300 cm. *A. paeoniifolius* is an Ayurvedic medicinal plant and also good for other pharmaceuticals, edible and cultivated in plantations from corms or 100-g pieces of them, because it is also rich in nutrients and a delicacy as food [12]. Flowering is seldom seen in plantation, occurring, if at all, in May or June.

The plants are regularly cultivated in the Botanical Garden of Berlin, and flower sporadically. We could follow the development and inflorescence between the 27 June and 10 July 2001. The corm had a diameter of 25 cm and a mass of 4,300 g (determined half-a-year earlier); the fresh mass of the inflorescence was estimated to 300 g from the known dry mass of 30.2 g. The temperature profiles were taken by means of thermosensors inserted into different parts of the inflorescence or with IR thermometry at its surface. Its metabolism was estimated by monitoring the oxygen consumption under a headspace container of 10 L. The putrid odour of the 1st day of blooming resembles the smell of rotting meat. Dimethyl disulphide and trisulphide were the only components found in equal amounts [13, 14].

A. paeoniifolius was closely watched in its development during a fortnight, beginning with a status of just emerging from the cataphyll. All temperatures were at ambient level, fluctuating with the sunshine in the greenhouse. Six days later, the inflorescence started its thermogenic phase in the morning of a rainy day with ambient temperatures of 17.2 °C. The large open inflorescence (diameter about 30 cm, height 31 cm) made a strong and astonishing impression. The apex of the spadix was formed by a dark brownish appendix in the shape of a brain or a shrunken red pepper. Below this was a dense yellow zone of male florets above a clear constriction by a ring of looser female florets. The spotted spathe had opened and surrounded both zones like a broad curled frill bending downwards, giving access to the male and female florets. It was strongly wrinkled and creased. Thermogenesis reached a maximum around 9:00 a.m., decreased around noon and vanished at 16:00. Figure 3 shows the plant in the morning of the female period when a shiny film covered the head of the plant and gave off a distinct, but not very strong stench. Such a film is similar to that of *A. johnsonii* as described by Beath [15]. The female florets were receptive, when the ring of male florets was at peak temperature. The males topped at 26.3 °C at the surface of the ring and 26.8 °C 3 mm inside the ring, which was 8.5 and 9.0 K above ambient, respectively. The appendix also warmed up a bit, with nearly no increase above ambient on the outside, but of 2.6 K inside. A slight, but passive heat up was seen in the

Fig. 3 *A. paeoniifolius* on the day of thermogenesis. The brain- or shrunken-pepper-like structure on top is the appendix, below this is the yellow ring of the male florets, below them are the female florets and around all is the curled frill-like spathe. The cataphyll is still attached to the spathe. The corm with the deep dip in the centre is seen in the soil of the pot

female florets because of heat transfer from the neighbouring male florets. On the next day, all temperatures were back to ambient values, and the ripe male florets had long protruding yellow pollen threads.

A. campanulatus Blume is supposed to be another name for *A. paeoniifolius*. Skubatz and colleagues [16] showed by infrared thermography that *A. campanulatus* is among the strongly thermogenic inflorescences of the *Arum* family, with highest temperatures developing in the male florets, and no warming is seen in the appendix or female florets. However, temperatures of the appendix are considerably lower if the structure has a large surface area, such as *Dracunculus vulgaris* [11], but higher if it has a small surface area, such as *Arum concinnatum* [17]. At 8:45 in the morning, the male florets were 2 K warmer than air, increasing to 6 K by 11:15. Meanwhile, the appendix increased from about 1–5 K at 12:05. By 16:00, all temperatures were back at the ambient level.

The metabolism of *A. paeoniifolius* was followed by indirect calorimetry. It was performed by head-space technique with a 10-L plastic bottle without bottom, which was placed over the whole plant and sealed to the ground. An electrolytic oxygen sensor (FIGARO GS Oxygen Sensor KE-Series, UNITRONIC, Düsseldorf, Germany) on the top of the bottle monitored the decrease of the oxygen concentration, and the mV signal was registered in a data logger (UNIDAN$^{\mathrm{PLUS}}$, ESYS, Berlin, Germany). As this volume was not thermostatted, it followed the ambient temperature between 17 and 26 °C. In order to adjust for these changes, the obtained values were corrected to 22 °C with a Q_{10} value of 2.0 in both directions. Subsequently, the oxygen consumption was transformed into heat by the value 21 J/mL oxygen for carbohydrates. In the 1st days before opening, the plant had low heat production rates of approximately 140 mW which increased about sevenfold in the female phase and endured into the male phase before they declined to the first level. The values were taken as approximations as they were measured in the morning between 7:30 and 9:00 because of technical reasons. It might be that they were more pronounced at other times.

Amorphophallus titanum (Becc.) Becc. ex Arcang

Amorphophallus titanum is regularly cultivated in the Berlin Botanical Garden. In 2006, a specimen originating from the Botanical Garden in Bonn started to flower and developed an inflorescence of about 57 cm high, above a 13-cm stalk. It stopped growing when the spathe was still closed and died away. The tuber of the present plant came from the Palm Garden in Frankfurt/Main, Germany, and as wild material from near Padang, Indonesia. It had a mass of 11.95 kg when replanted in a larger pot on November 2008. The emergence of a shoot was seen in the first half of February 2009, and it became clear on the 17 April that an inflorescence was developing. In the last 10 days before the opening of the inflorescence, a linear increase of 4.8 cm day^{-1} was observed. The final height was 131 cm, and the spathe was 84.5 cm in diameter and 265 cm in circumference (Fig. 4). For comparison: A 32-kg tuber in Bonn showed a daily growth rate between 7 and 19 cm day^{-1} at 30 °C [18], another cultured inflorescence at first a rate of 11.7 cm day^{-1} and slowed down to a total rate of 8.5 cm day^{-1} over a period of 8 days [http://www.ftg.org./blooms/Amorphophallusalice01.html Fairchild Tropical Garden, Gables (Miami) FL33156 USA]. Gandiwijaja and colleagues [19] reported about an *A. titanum* on Sumatra which was potted in March, and 8 weeks later, developed a shoot. Its growth rate was 6.2 cm day^{-1} 3 weeks later, and 7.3 cm day^{-1} 1 week later. Its final height was 164 cm. All of these data compare quite well with growth rates of 8.0 cm day^{-1} for bamboo and of 15 cm day^{-1} of the radius of a leaf of the water lily *Victoria cruziana* [20].

It was the first time that *A. titanum* flowered successfully in the Botanical Garden of Berlin, which was captured by a web cam transmitted online to the internet and discussed there (Fig. 4). It started to flower in the afternoon of 28 April 2009, when the sun still touched it and the ambient

Fig. 4 Optical photography of *A. titanum* at 1:00 in the night. The cataphyll, spathe and appendix are clearly seen. The male and female florets are hidden deep in the cone of the spathe. Dataloggers are behind the appendix

temperature was at 27 °C. The timing was as described by Barthlott and co-workers [21] with the slow opening of the spathe in full daylight into the evening. While ambient temperature was declining to 24 °C, the top of the spadix reached the maximum temperature of 36.6 °C around 20:00. In the subsequent hours, the elevated temperature spread over the whole spadix and faded away in the early morning of the next day (Fig. 5). Around 7:45, it was back to the temperature of the green house. The spathe had already closed a little bit continued shrinking. The spadix collapsed at 5:21 at the 3rd day (2 May 2009) when the appendix turned vertically down (see videos of the Botanical Garden, Berlin). The blossom separated after 3 weeks from the tuber. In the middle of July, it made a new shoot; 1 month later, it had a height of 56 cm; and just 2 months later, a stalk of 170 cm developed, topped with a dissected leaf of 280 cm diameter.

Thermographic pictures were taken with an un-cooled "D-Infrared Camera PYROVIEW 380 L compact, DIAS Infrared GmbH, Dresden, SN C1000102". A sensitive 2D-array with 384 × 288 micro-bolometer elements was used. Technical data were $\lambda = 8\text{–}14\ \mu\text{m}$, $T_M = -20$ to 500 °C; $U_B = 10\text{–}36$ V DC, 20 VA. The spatial resolution amounted to 1.4 mrad, the temperature resolution 2% of the signal. The evaluation of the results was carried out by a PYROSOFT Control Software. As the borrowed camera was not handheld, but bought for laboratory experiments on optical benches, it had to be fixed on a massive tripod and could not be moved during the investigation.

The different false-colours indicate the temperature of the specimen. The camera was not calibrated when used, but was calibrated after the fact by correlating measured object temperatures with apparent thermographic temperatures according to the equation:

$$\text{Object temperature} = 1.29\,\text{Thermographic temperature} - 22.3.$$

The blooming of *A. titanum* was monitored by this fixed IR camera (Fig. 6). The picture shows the upper part of the appendix in the centre and part of the widely opened spathe. As the spathe played no role in the thermogenic episode of the plant, we concentrated on the appendix. The male florets are not visible from above, because they are deep in the floral chamber of this species, and we were prevented from damaging the plant. Similarly, Barthlott and co-workers [22] did not observe heating of the male florets. However, this was successfully done later by Korotkova and Barthlott [21] observing the second thermogenic period and the pollen shedding of the male florets on the second evening.

The heating of the appendix began around 20:00, with the hottest point initially at the top, as previously described [22]. The thermographic values amounted to 35.3 °C in the top, 31.7 °C in the upper middle, and 29.8 °C in the middle. Lower positions of the appendix were covered by the spathe and not accessible with the fixed camera. Two hours later (22:30), the values were 35.8, 32.7 and 31.5 °C, respectively. Shortly before midnight, the values changed to 35.6, 31.5 and 31.2 °C and, at 01:15 to 31.8, 27.4 and 25.5 °C, respectively. Later values were monitored by the data loggers only. Thermal images of the inflorescence sequence were taken every 15 min and showed impressively the beginning of heat evolution at the top, spreading over the full appendix until to the early morning (Fig. 7), as well as in a time-lapse video for the time between 20:00 and 01:30 the next day (Amorphophallus_Film_2.avi). The heat production proceeded from the top downwards over

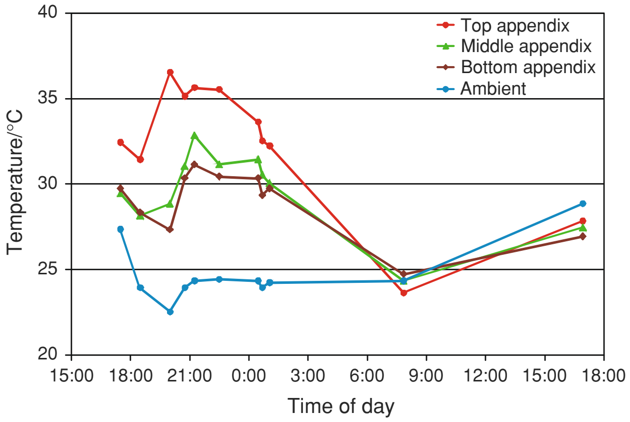

Fig. 5 Temperature development determined with an IR thermometer of the inflorescence of *A. titanum* and its environment for more than 1 day. Temperatures of the top, middle and bottom of the appendix and the ambient surface just outside of the spathe are recorded

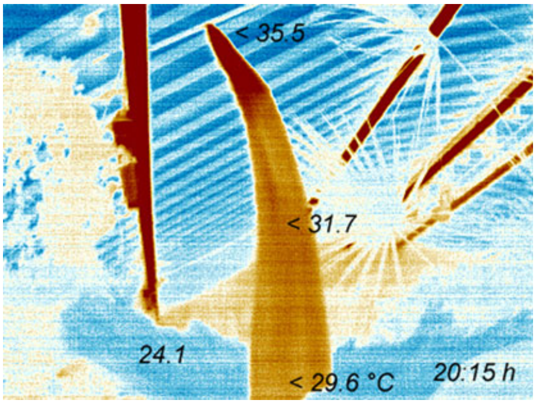

Fig. 6 IR thermography picture of the appendix of *A. titanum* at 20:15 h. Heat production is apparently highest in the tip of the appendix. As the IR camera was not calibrated, correct temperatures are shown for some points. The *dark brown lines* are heating pipes of the greenhouse; the *lighter blue ones* show the glass construction; the *bright fan-like* structures are palm-leaves in the background

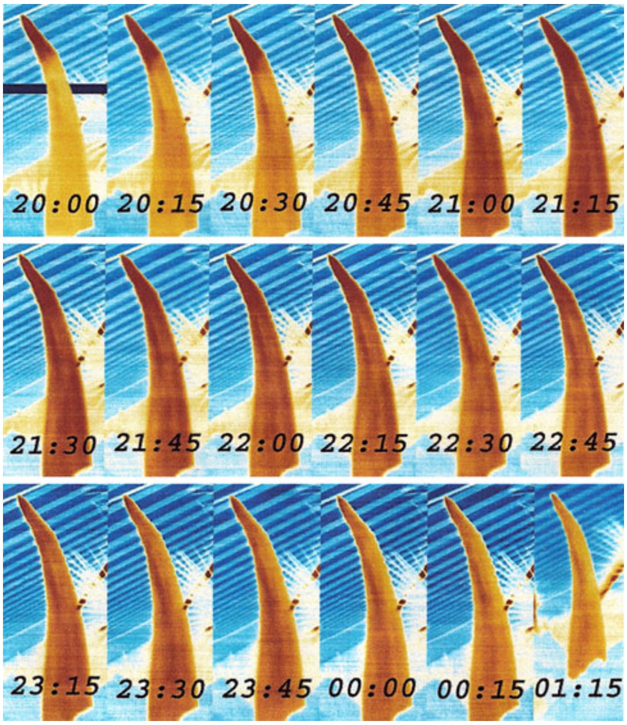

Fig. 7 Thermographically determined temperature development in *A. titanum* during the early night. The records clearly show that the heat production starts at the top, spreads downwards along the appendix and fades away nearly homogeneously with the exception of a slightly warmer top

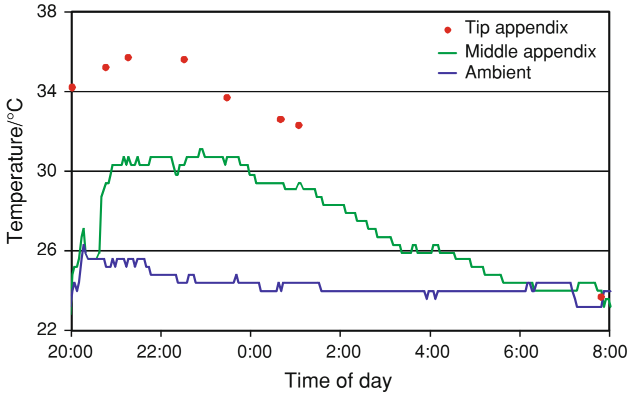

Fig. 8 Temperature development of *A. titanum* during thermogenesis. Temperatures of the ambient air (*lower continuous line*) and the middle (*upper continuous line*) and top of the appendix (*points* determined with an IR thermometer) are represented

the entire spadix. However, no periodic phenomena [22] could be observed with our Titan arum. This might be because of different sizes and ages of the plants and varying conditions in both greenhouses.

Simultaneously, four data loggers (HOBO Temp 508-563-9000) monitored the temperatures with the sensors placed through plastic drinking straws in two points of the appendix, in the air within the spathe and in the ambient air. The first logger was inserted into the middle of the spadix, the second lower down the appendix approximately 30 cm above the male florets. The top of the spadix remained without a logger not to injure the plant, a precaution that proved superfluous later on during the experiment. As the temperature at the top could not be registered because of security reasons, it is shown as point wise determinations (circles) together with the curves of logger 1 and logger 4 (Fig. 8). At 19:30 the sun no longer touched the plant so that a value around 23 °C resulted. About 20:00 the curve of the middle of the appendix began to climb to a value of 31 °C, which remained constant until midnight and returned steadily back to the initial value. Superimposed are the red points of the appendix top which culminate in the maximum of 36.6 °C and maintain this value to 01:30 before they decline to ambient values also. The temperature within the spathe in the time from 21:30 until 7:30 the next morning was nearly constant at 24.0 °C in agreement with Korotkova and Barthlott [21] who saw no warming inside the floral chamber during the blooming. The ambient temperature at the same time was 24.3 °C, about the same as in the spathe. From 22:00 until 00:00 the temperature in the middle appendix remained at 30.6 °C and that in the lower appendix area at 30.3 °C between 23:00 and 02:00 the next day. They show the slow wandering of temperature through the appendix. In any case, they were +6.6 and +6.3 K higher than the air inside the cone of the spathe.

Figure 5 shows the temperatures determined with the handheld IR thermometer during the night (Non-Contact Infrared Thermometer TH1-300, Tasco Japan Co. Ltd.). The emission was set to 0.95 as was usually done with plants (Jones 2004). In the beginning, the setting sun hit the opening plant with decreasing intensity, so that all four curves followed the ambient temperature for a short time (Fig. 5). However, while it dropped to 22.5 °C and then climbed up to 24.4 °C, the bottom of the appendix was 27.4 °C and rose to 31.0 °C due to the general warming of the inflorescence. The middle appendix increased to 29.0, 31.0 and 32.5 °C, while the tip temperature showed a small dip around 31.8 °C and a strong increase to 36.6 °C, then a plateau about 35.7 °C ($\Delta T = 11.3$ K) and a subsequent larger decrease. All curves met in the morning at around 24.3 °C (Fig. 5). The brim of the spathe remained at a value of 22.6 °C, one degree below ambient in the mean. Later in the day the appendix values fluctuated a bit and lay 1–2 K lower than the greenhouse temperature (28.9 °C), obviously due to evaporation despite more than 70% humidity.

Not even one of the Berlin scientists had nearer contact with *A. titanum* blooming before, so that the expectations were derived from the article of Barthlott et al. [22]. The expected carrion smell was very strong before and around

18:00 but not monitored by us, waiting for even more. No sign of dimethyldi- and trisulfides as the single molecules in *A. titanum* smell detected by Kite and coworkers [13, 14] could be found in the belated spectra, although these compounds were easily traceable in *Dracunculus vulgaris* with our methods (unpublished results). They went unnoticed even by the human nose which is by far more sensitive than the applied techniques.

A weak sweet smell started around 19:00 and lasted until 03:00 the next day. It was sensed by the nose, sampled two times (air flow of 340 mL min^{-1}; sampling duration 1 h) at 21:35 and 22:35 by an active charcoal absorber and analysed by a coupled gas-chromatographic/mass-spectrometric machine (Fisons GC Model 8060; Fisons MD800 quadrupol MS). Organic compounds with a sharp, pungent smell as well as pleasant ones used for perfumes were found. Benzaldehyde with an almond-like odour dominated the second odour spectrum. The odors are similar to those of the voodoo lily (*Sauromatum guttatum*) whose appendix evolves a bad smell of carrion, while the club-shaped organs in the floral chamber have a sweet odour like fruit salad, stimulating beetles to different activities, including mating [23]. In the same way, *Arum maculatum* also produces a fruit-like smell during the heating of male florets, which occurs both before and after heating of the appendix which produces a dung-like smell [24]. It remains speculative whether this pleasant smell here serves the same purpose of stimulating mating activities in beetles.

As no direct or indirect calorimetric measurements by respiration were possible due to the size of the plant, a calculation of the energy output was made from the known geometric and thermal data. The energy balance of the appendix consists of the energy taken up and dissipated by the system as well as the stored energy which must balance:

$$
\begin{aligned}
&E\,(\text{uptake and production}) - E\,(\text{dissipated})\\
&- E\,(\text{stored})\\
&= 0.
\end{aligned}
$$

The energy taken up reduces in our case to the infrared radiation which is proportional to the 4th power of the absolute temperature. The dissipated energy contains this term also, just with slightly higher temperatures, so that it outweighs the absorbed energy. In addition, heat is lost by evaporation, but in the case of a green house with more than 70% saturated humidity, is reduced. Heat dissipation is also affected by convection and conduction. The stored energy might be taken as zero when the temperature is stable.

Based on the book of Park S. Nobel [25] *Introduction to Biophysical Plant Physiology*, one may apply the energy flows at a flat leaf in the steady state with slight modifications to the appendix of *A. titanum*. The biological dimensions of the appendix are approximately the following: height from the earth surface in the container to the tip—131 cm, minus petiole below the spathe—118 cm, minus male and female florets—105 cm; maximum diameter of the appendix—15 cm; volume may be taken in a first approximation as that of a straight cone and calculated to be 6,200 cm^3, although its cross section is by far not a circle and the surface characterized by many longitudinal dents and grooves; specific mass after Boecker [9] is 0.1 g cm^{-3}, which means that the mass of the appendix becomes 620 g.

If we consider [25] that a stationary air layer of 0.13 cm exists around the appendix and a measured temperature gradient of 6.7 K between the appendix and the air in the spathe, one calculates a heat flow of 12.2 mW cm^{-2} through the cone surface of 2,480 cm^2 or a total flow of 30.3 W by conduction and convection, corresponding to 48.9 mW g^{-1} for a mass of 620 g. This specific heat production nearly doubled at the tip of the appendix.

The heat exchange with the environment via radiation is calculated as follows: There is a linear dependence between the radiation and the 4th power of the absolute temperature (Stefan–Boltzmann law). For the emitted radiation, one gets

$$E = e_{\mathrm{IR}}\,\sigma\,(T)^4$$

with e_{IR} being the emission coefficient (about 0.95; see [26]), σ the Stefan–Boltzmann constant (5.67×10^{-8} W m^{-2} K^{-4}) and T the absolute temperature. For $T = 304$ K (31 °C)—for the total appendix—one gets a radiation of 46.0 mW cm^{-2} and for the maximum $T = 309$ K (36 °C)—a radiation of 49.5 mW cm^{-2}. Taking a partition of 20% top and 80% rest of the appendix, i.e. 46.7 mW cm^{-2}, we obtain 115.8 W of emitted radiation for the total appendix of 2,480 cm^2. At the same time, the appendix takes up 104.9 W (42.3 mW cm^{-2} at $T = 297$ K (24 °C)). In the difference, it emits $115.8 - 104.9 = 10.9$ W more energy than it receives. If one takes the above calculated 30.3 W for the total appendix and a temperature difference of 6.7 K as a mean, then one obtains a total heat export of $10.9 + 30.3 = 41.2$ W, which has to be produced by the metabolism of the plant in the stationary state.

Until now, no evaporation was taken into account which appears without any doubt, even at or above 70% RH. Taking Nobel's model [25] for one side of a mesophyllic leaf and a temperature difference of 5 K, one gets a water flow of 0.29 µmol s^{-1} cm^{-2} (at 50% RH), which results in 684 µmol s^{-1} for the above given values of the appendix. With a heat of vaporization of 10.44 kcal mol^{-1} at 30 °C (Nobel 1974, App, II) corresponding to 43.7 kJ mol^{-1}, one arrives at 29.9 W at 50% RH. With our values of $\Delta T = 7$ K and 70% RH, one obtains 25.1 W responsible for evaporation. Taking all together, the heat production for the appendix of *A. titanum* sums up to 41.2 + 25.1 = 66.3 W, that is 107 mW g^{-1} for a mass of 620 g. This value is about 20 times higher than the value of 3.0 W which Baumann and colleagues [27] calculated from the CO_2 metabolism and a heat transition coefficient of 2 W cm^{-2} K^{-1}. There are hints that their value must be too small, e.g. the plumes of condensation which ascend in parallel along the appendix in a video movie by Barthlott and coworkers [22].

It was mentioned above that the appendix of *A. titanum* is not smooth, but is characterized by vertical dents and grooves. Using the cross section given by Boecker [28] and determining its periphery, it is larger by about 12% than a circle with the same area. Therefore, if the surface of the cone is larger by the same factor, that means 1.12 × 2,480 cm^2 = 2,778 cm^2. The total heat dissipation of *A. titanum* thus amounts to 1.12 × 66.3 = 74.3 W, and the specific dissipation to 120 mW g^{-1} as the mass is not influenced by the change of the circumference.

Conclusions

Three strongly thermogenic plants of the genus *Amorphophallus* are compared in this article, namely *A. konjac*, *A. paeoniifolius* and *A. titanum*. All the three have inflorescences belonging to the largest and most impressive plants in the kingdom. They consist of a spathe and an appendix, attractive for pollinators by their dark reddish to brown colour and even more by their obnoxious carrion-like odour. However, at the same time, they differ in both their spathes as well as their appendices. As long as the plants are still developing and not in the thermogenic period, the spathes lie close to the appendix which extends a bit over the spathe. At their lower end, they form a floral chamber around the female florets that are visited by the pollinators. In the beginning of the opening day when the spathes loosen the contact to the appendix, the differences in the spathes become obvious. While *A. konjac* has a slim and asymmetric spathe with male and female florets being visible from above, *A. titanum* is of similar construction but with an approximate horizontal upper end of the spathe. Both male and female florets are deep down in the spathe and not visible from outside. *A. paeoniifolius* is compact with an appendix like a shrunken red pepper and a spathe which opens wide into the horizontal and even further like a collar in the female day, exposing male as well as female florets.

All the three show the same periods of thermogenic metabolism: at first, the female florets are receptive (protogynous) with the male florets being inactive. It is the time of a considerable heat production in the appendix and the dissipation of ugly smells that attract the pollinators into the floral chamber where they unload their pollen charge to the female florets. Later on, the metabolic “explosion” of the appendix decreases, smell becomes less intensive and the female florets loose their receptivity. Heat production by the male florets continues, but without pungent scent production until 1 day later at about the same time of day, the male florets shed pollen, mainly in the form of sticky threads. This is the time when the pollinators are released from their compulsory “prison” in the floral chamber loaded with pollen to seek for the next inflorescence in the female stage.

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