RESEARCH PAPER

A torch in the rain forest: thermogenesis of the Titan arum (*Amorphophallus titanum*)

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ABSTRACT

An outstanding flagship species in the plant kingdom is the Titan arum (*Amorphophallus titanum*), which produces a fountain-like bloom up to 3 m high. The unique appearance of three simultaneous inflorescences in May 2006 was a chance to analyse the flowering behaviour and thermogenesis of this giant. For the first time, the heating of the central column (spadix) could be documented using a high-performance thermographic camera. Time series analyses of the infrared image sequences revealed that the 3-m high spadix surface heats up in pulses emanating from the base of the inflorescence. The surface temperature reaches over 36 °C, compared to the ambient temperature of 27 °C. Waves of the carrion-like odour are synchronised with these heat pulses. The combination of heat pulses, the fountain-like shape plus the enormous size lead to a unique type of 'convection flower'. On the basis of our observations, we assume that *Amorphophallus titanum* is able to overcome thermodynamic decoupling by a self-produced convective process.

INTRODUCTION

The rain forests of Sumatra harbour the two largest flowers in the world. *Rafflesia arnoldii* R.Br., with a diameter up to 1, 50 m is the largest solitary flower; however, more than twice as large is the fountain-like inflorescence of *Amorphophallus titanum* (Becc.) Becc. ex Arcang. (Titan arum) in the Araceae (Fig. 1). The extremely reduced single flowers (about 500 male and some 450 female) of the latter are located at the base of the extension of the inflorescence axis (spadix), which is enveloped in the large spathe. The whole inflorescence of the Titan arum is functionally a flower. To illustrate this, we refer to it as a 'flower' in the following text.

Since its discovery by the Italian botanist Odoardo Beccari in 1878, the Titan arum has been an enigmatic plant that is still rare in cultivation. An extensive monographic survey of the species, dealing with its morphology and anatomy, was published some years ago (Barthlott & Lobin 1998). The rare flowering events in cultivation, as well as in its natural habitat, are reasons why so little is still known about the flowering behaviour and ecology of *Amorphophallus titanum*. The Titan arum is a deception flower that mimics decaying meat or carrion through the dark purple colour of the spathe and the smell of rotting flesh, thus attracting carrion beetles and blowflies that are the putative pollinators (Hetterscheid 1998). The main chemical components of the smell are dimethyl oligosulphides (Kite & Hetterscheid 1997). Araceae species that mimic carrion and carcasses are abundant (Dafni 1984) and it has been hypothesised that heat production is an important part of the deceit (Meeuse & Raskin 1988). It has, indeed, been demonstrated in the case of the Dead horse arum (*Helicodiceros muscivorus*, Araceae) that plants producing heat and odour are those more frequently visited by pollinators than plants producing odour alone (Stensmyr *et al.* 2002; Angioy *et al.* 2004).

Thermogenesis in Araceae has been studied in several species (Nagy *et al.* 1972; Skubatz *et al.* 1990, 1991;

Fig. 1. A world record flower: the fountain-like inflorescence of a Titan arum with a height of 3.06 m in the Botanical Gardens Bonn in May 2003. This very plant produced three simultaneous inflorescences in May 2006 (see Fig. 2).

Uemura *et al.* 1993; Seymour 1999; Seymour & Blaylock 1999; Seymour & Schultze-Motel 1999; Gibernau & Barabe 2000; Barabe *et al.* 2002; Ivancic *et al.* 2004, 2005). The function of floral heat may differ in different plant lineages (Thien *et al.* 2000). There are two main hypotheses regarding the ecological importance of heat production in Araceae: heat production serves as a volatiliser for the odour (Meeuse & Raskin 1988), or it may also be a direct reward for pollinators by helping insects to increase their body temperature and metabolic rate. The latter may be especially true for beetles (Seymour *et al.* 2003).

There is only weak evidence that thermogenesis in *Amorphophallus titanum* (Baumann *et al.* 1998) plays a role in pollination of the plant. Until now this could not be analysed in detail; however, the occurrence of three simultaneous inflorescences in the Bonn Botanical Gardens in May 2006 provided a unique opportunity to study flowering behaviour and thermogenesis of *A. titanum* in detail.

MATERIAL AND METHODS

Amorphophallus titanum was cultivated in the greenhouses of the Botanical Gardens of the University of Bonn. A synopsis of the cultivation of this species and its putative life cycle has been published recently (Lobin *et al.* 2007). The flowers usually open in the late afternoon, are in full bloom during the night, and, depending on lighting conditions, begin to close at noon on the next day. The plant examined had flowered three times: in 2000, 2003 and in May 2006, when it produced three inflorescences from one solitary tuber weighing 117 kg. The large inflorescences in this latest flowering were 2.6 m and 2.3 m high and the one small inflorescence was 1.6 m high. The two large inflorescences opened in the late afternoon of 13 May 2006, the small inflorescence opened 3 days later, on the afternoon of 16 May 2006. Initial thermographic measurements were made while the two large inflorescences were open; the actual thermographic analysis was performed on the small inflorescence.

To study the thermogenesis of *Amorphophallus titanum*, we used a high-performance thermographic camera (VarioCAM®, JENOPTIK, Germany). Based on a state-of-the-art uncooled microbolometer FPA detector, the camera captures radiation in the infrared range of the electromagnetic spectrum (roughly 8–13 μm) without requiring cryogenic cooling, as was necessary with older bolometers. The amount of radiation emitted by an object increases with temperature. Thus, infrared thermography represents a highly accurate measurement tool for the detection of variations in temperature.

Thermographic images of the appendix were taken on average every 2 min from 17:00 to 02:00 h, and the temperature values were later read off from the images using IRBIS 2.2. To document the non-uniform warming of the spadix, three zones on the spadix surface were chosen for extraction of the temperature values. To determine possible heating of male flowers, we took thermographic images of the zone of the male and female flowers from the top of the open spathe. It is not possible to open the spathe of *A. titanum* to obtain direct access to the flowers without causing damage to the plant.

We were unable to quantify the odour intensity, so observations of odour intensity described here are based on independent subjective impressions of the authors and about ten students.

RESULTS

The two large inflorescences opened at the same time in the late afternoon and were both thermogenic, reaching a peak surface temperature at the top of the spadix of 36 °C, compared with the ambient greenhouse temperature of 27 °C (Fig. 2). Only the appendix was thermogenic, no warming of the spathe or of the flowers was observed. The spathe began to close in the early afternoon of the next day and no warming could be documented on the second day or during the second night. The spathe
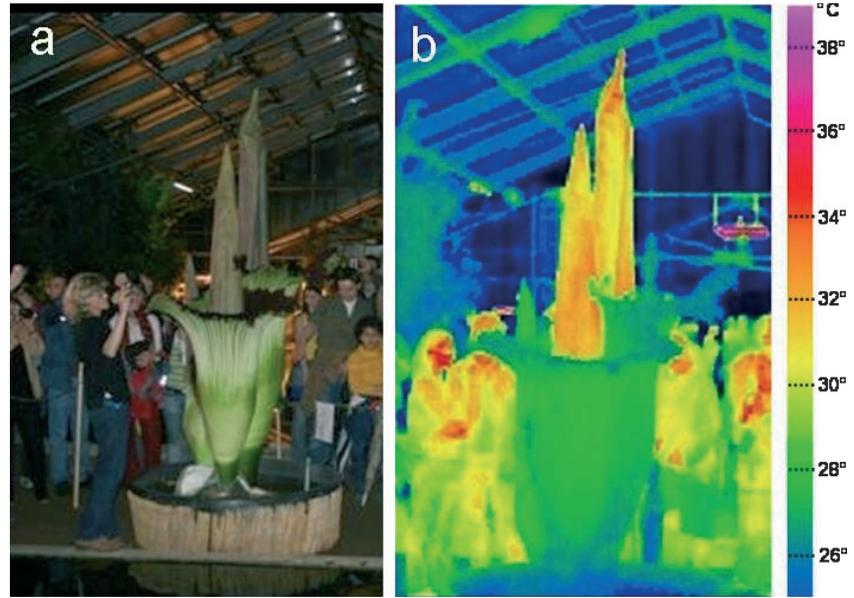
Fig. 2. Images of the three inflorescences of *Amorphophallus titanum* in the Botanical Gardens Bonn on 14 May 2006, at 23:10 h. The two large inflorescences (right) are fully expanded, the small inflorescence (left) is still closed. a: Flash photograph, b: Thermographic image, the heated spadices ('torches') are most prominent against the cooler background and reach human body temperature. Scale indicating the temperature range.
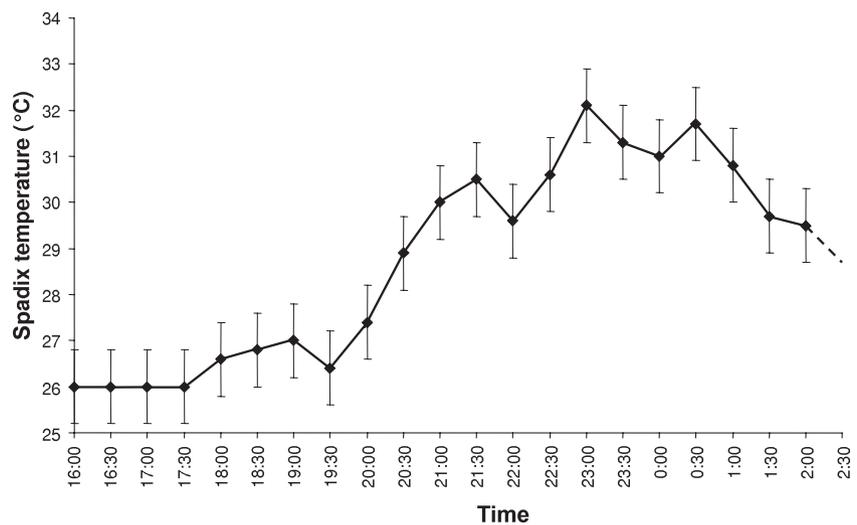
Fig. 3. Thermogenic phase of the small inflorescence of *Amorphophallus titanum* during a 12-h period after opening of the spathe on 16 May 2006. Temperature values are mean values (SD = 0.8 °C) of the spadix surface temperature at the three spatial zones calculated from the corresponding thermographic images (compare Figs 4 and 5). Temperature decline after 02:00 is illustrated with a dashed line.

of the third inflorescence opened in the afternoon 2 days later. Detailed measurements of the small inflorescence revealed a thermogenic phase that was restricted to 5–6 h in the early afternoon and to about 2 h after midnight (Fig. 3). The spadix warmed to a maximum temperature of 33 °C (7 °C above ambient greenhouse temperature of 26 °C). After 02:00, the surface temperature of the spadix cooled and thermogenesis was no longer recordable with the thermographic camera.

The thermographic images in Fig. 4 illustrate each of the warming phases. The intensive heat production began between 20:00 and 21:00 h (Fig. 4a–d), with the first temperature maxima at about 21:15 (Fig. 4e) and a following cooling until 22:00 h (Fig. 4f–h). The second warming phase started at about 22:30 (Fig. 4i), with a temperature maxima at 23:00 to 23:30 h (Fig. 4j–k), and was followed

by cooling beginning shortly after midnight (Fig. 4l). The third temperature peak, at about 00:30 h (Fig. 4m) was followed by a final cooling phase (Fig. 4n–p). As evident from Fig. 4, the warming of the spadix was non-uniform throughout different spatial zones. The detailed temperature measurements of the spadix (Fig. 5) surface show that the hottest part was the tip, with the highest measured temperature being 33.8 °C. The heating was not constant; a clear oscillation of heat pulses emitted from the base of the inflorescences could be measured and three phases of warming and following cooling were observed. The heat pulses were irregular and the estimated heat wave lasted 1–5 min. The emission of the typical carrion-like odour of the plant was also not constant. Our impression was that the odour is released at intervals of 5–10 min. Each pronounced hot phase of the plant
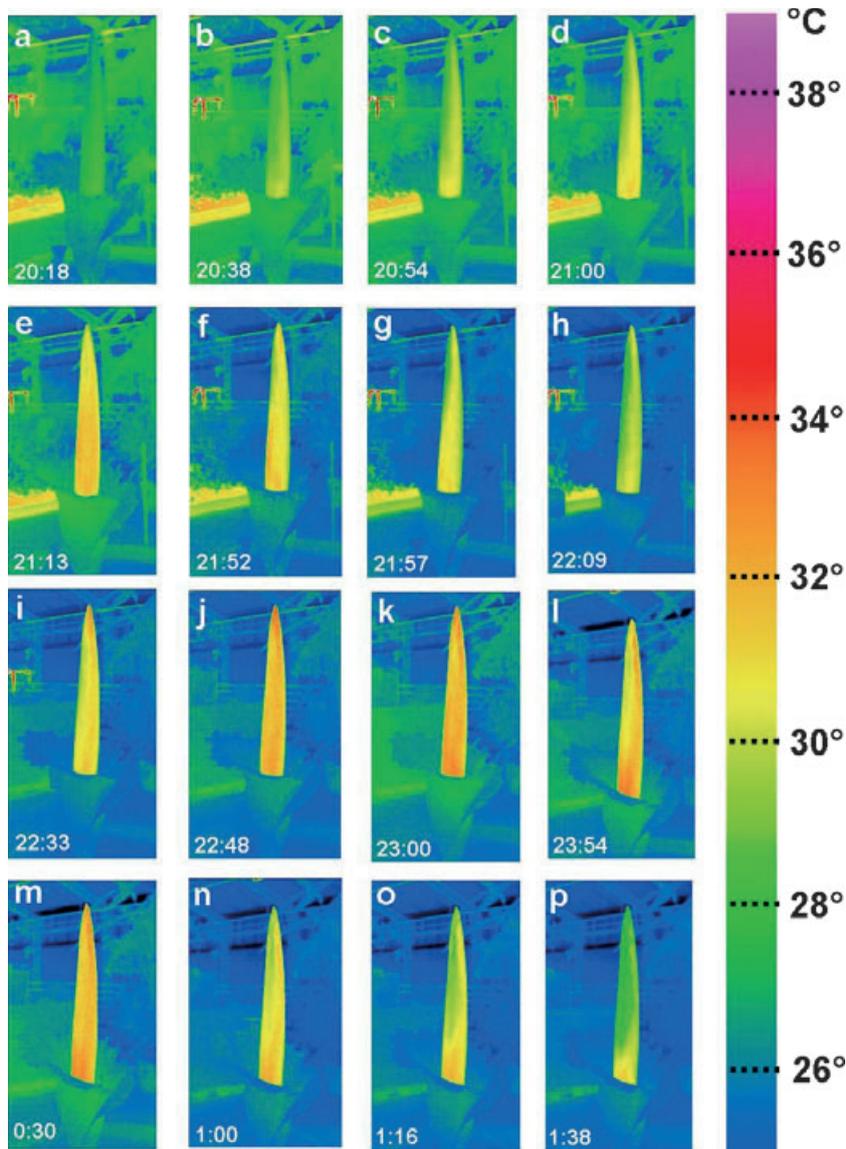
Fig. 4. A selection of 16 thermographic images of the fully expanded inflorescence of *Amorphophallus titanum* documenting the heat pulses. Temperature scale (right column) is the same for all images. a: Spadix is not heated, b: Beginning of heat production, c–d: First warming phase, e: First temperature maxima. f–h: cooling, i: Beginning of the second warming phase, j–k: second temperature maxima, l: Second cooling beginning shortly after midnight, m: third temperature maxima, which was followed by a final cooling phase (n–p).

was connected with odour production. The most intensive odour was observed in connection with the hottest spadix temperature between 22:00 and 00:30 h.

In connection with the heat pulses generated in the humid atmosphere of the greenhouse, vapour ascending along the spathe to the top of appendix could be observed (see supplementary video). The observation of the vapour was made by chance because of spotlights that were positioned at angles behind the plant for a TV camera (against-the-light photography). Vapour production was clearly correlated with odour release, and vapour was observed only during the period of the most intense heat and odour production.

DISCUSSION

Our results provide evidence that *Amorphophallus titanum* has remarkable thermogenesis, in which the huge spadix warms up to over 36 °C. The thermogenic period, as well as odour production, is restricted to a few hours during the first night after the opening of the spathe. Comparisons with thermogenic periods of other Araceae reveal similar patterns. Appendices of *Arum maculatum* (Bermadinger-Stabentheiner & Stabentheiner 1995) and *Arum italicum* (Albre *et al.* 2003) have a thermogenic phase that is restricted to several hours in the late afternoon or evening. During this period, the appendices produce one temperature peak. The main difference observed in *A. titanum* was the three successive heating and cooling phases during the thermogenic period. We found no evidence for heat production of the male flowers, as documented from other Araceae (e.g. by Skubatz *et al.* 1990, 1991; Bermadinger-Stabentheiner & Stabentheiner 1995; Lamprecht *et al.* 2002; Albre *et al.* 2003). However, heating of male flowers has been shown to occur prior to the heating of the appendix and it is still possible that the
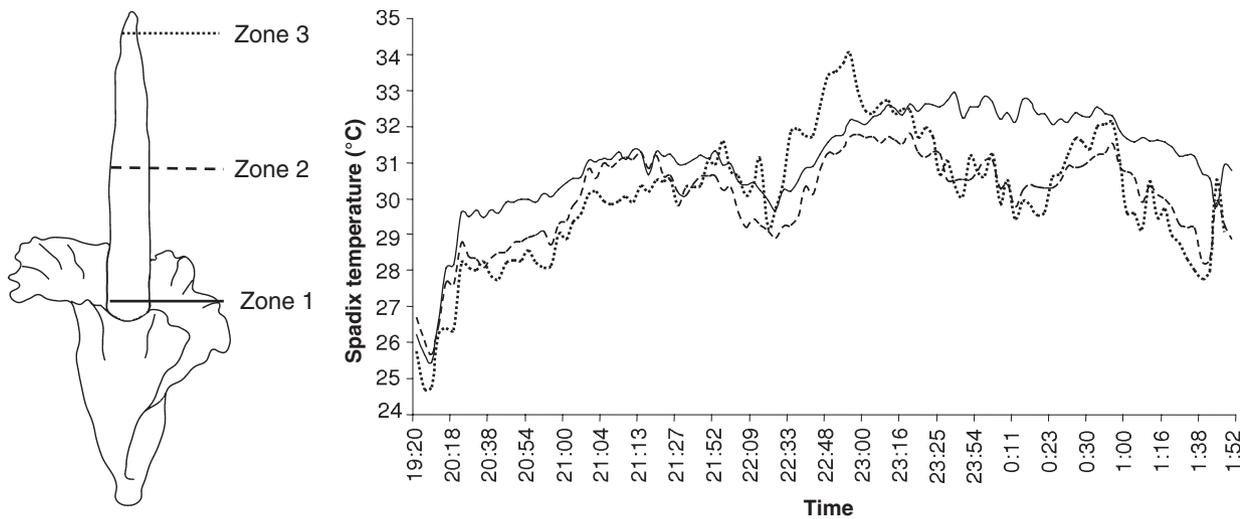
Fig. 5. Temperature trend in three spatial zones of the spadix of the small *Amorphophallus titanum* inflorescence, documenting the uneven warming of the spadix.
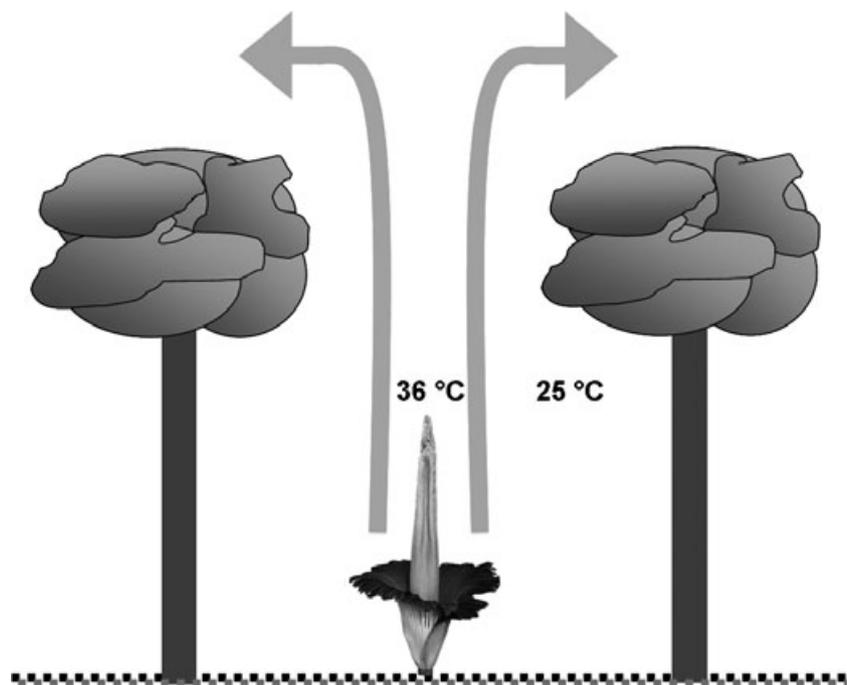
Fig. 6. Scheme of a nighttime profile in a tropical rain forest with an open flower of the Titan arum. The heated spadix (36 °C) creates a micro-convection in the cooler air (25 °C) that enhances the transport of the scent (arrows).

A. titanum male flowers also warm up several hours before spadix heating.

A first hypothesis for the occurrence of heat production of an *A. titanum* appendix was made based on studies of respiratory activity of a Titan arum inflorescence (Baumann *et al.* 1998). Based only on measurements of CO_2 exchange, these authors calculated a CO_2 exchange of 0.52–0.62 mg s^{-1} and estimated heat development of 2.5–3.0 W and an increase in temperature of 5.6–6.8 °C above ambient air temperature for an appendix surface of 0.22 m^2 and a coefficient of heat transmission of 2.0 W m^{-2} K^{-1}. The authors estimated metabolic activity of the *A. titanum* appendix to be 7.0 W (kg dry weight)$^{-1}$.

The functional explanation for thermogenesis in *Amorphophallus titanum* and its flower shape may differ from that of other Araceae species. In combination with the well-known fact that the flower is a highly mimetic system that copies carrion and attracts beetles and flies, a functional explanation for the enormous size and shape of the *A. titanum* flower can be given. Our results offer good evidence that scent molecules of thermogenic

Araceae are transported by turbulent updrafts resulting from thermal convection induced by spadix heating, as previously assumed by Lamprecht *et al.* (2002).

The above conclusion is of particular ecological interest as *Amorphophallus titanum* flowers attract pollinators at night. During this time, however, the forest canopy usually exhibits significant thermodynamic decoupling from the overlying atmospheric layer due to substantial radiative cooling, causing stable density stratification, which, in turn, reduces or even prevents turbulent mixing (Shuttleworth 1989; Fitzjarrald & Moore 1990; Szarzynski & Anhuf 2001). On the basis of our observations, we assume that *A. titanum* is able to overcome the thermodynamic decoupling by a self-produced convective process. In combination with its typical occurrence as a gap plant within its natural rain forest habitat (Hetterscheid 1998), convection creates an adequate and highly adapted vertical transport mechanism for the channelled distribution of exhalation through the open space of the overlying canopy (Fig. 6). It has already been shown that convective heat transport adequately describes the heat transfer mode in thermogenic tropical Araceae (Gibernau *et al.* 2005). This heat transport mechanism is obviously most elaborated in *A. titanum* and probably cannot be generated in such an effective way by smaller Araceae flowers. The large size of the Titan arum and the especially large spadix allows the inflorescence to create a chimney-like effect that enables highly effective transport of scent. Since population densities of *A. titanum* are low, the plant must ensure effective odour dispersal for location of the plant by its pollinators. The combination of heat pulses, the fountain-like shape of the Titan arum, plus its enormous size leads to a unique ecological type of flower that we suggest could be referred to as a 'convection flower'.

ACKNOWLEDGEMENTS

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Video Clip S1. Against-the-light video of *Amorphophallus titanum* captured on 16 May 16, at 23:20 h, showing vapour ascending toward the appendix.

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