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On the thermogenesis of the Titan arum (*Amorphophallus titanum*)

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The Titan arum (Araceae) produces the largest bloom of all flowering plants. Its flowering period of two days is divided into a female flowering phase in the first night and a male flowering phase in the second night. Recently, we have documented thermogenesis in the spadix of the Titan arum during the female flowering phase. Here, we document a second thermogenic phase in which the male florets are heated during the male flowering phase. Obviously the two nocturnal thermogenic phases are linked with the two flowering periods. These observations now allow a more detailed understanding of the flowering behavior of the Titan arum.

Key words: *Amorphophallus titanum*, araceae, thermogenesis, infrared thermography, pollination

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The Titan arum (*Amorphophallus titanum*) is one of the most spectacular flowering plants. It has drawn the attention of botanists and naturalists since its discovery in 1878. However, the species has been rare in cultivation and flowering events in botanical gardens were even rarer. Besides, flowering events observed in the plant's natural habitat are very few.[1,2] Therefore, the knowledge on *A. titanum* that depended on exact observations and scientific experiments remained very limited. It was only in the late 90s when a monograph on the species, containing anatomical details and some first experimental hypotheses, has been published.[1]

The Botanical Gardens of the University of Bonn (Germany) have been cultivating *Amorphophallus titanum* for more that 70 years and obtained 14 flowerings between 1937 and 2009. These regular flowering events have been the prerequisite to study *A. titanum* in detail. Consequently the data and hypotheses in the monograph mentioned above were gained mainly from the *A. titanum* plants in the Botanical Gardens Bonn. As a result of three flowering events in 2006, we have recently documented for the first time, that the inflorescence undergoes thermogenesis in which the central column (spadix) heats up to 36°C. Meanwhile four additional flowering events yielded additional insights into the flowering behavior of *A. titanum*.

The inflorescence of *A. titanum* consists of a thickened unbranched inflorescence axis bearing hundreds of small female and male florets which are spatially separated (**Fig. 1A**). The inflorescence axis is extended into an appendix (spadix) and enveloped by a large bract referred to as spathe. The spathe enclosing the florets forms the floral chamber. Since the whole inflorescence functions as a single unit in pollination is often referred to as a bloom or "flower". *A. titanum* has two timely separated flowering phases: a female flowering phase during the first evening and night after opening of the spathe and a male flowering phase in the following night.

Thermogenesis plays an important role in the pollination ecology of Araceae[3,4] and therefore occurs in many genera.[4-7] Similarly in *A. titanum*, we have reported the thermogenic spadix during the female flowering phase. Based on our observations of now six inflorescences, the heat production is determined and begins around 20 h, the temperature maximum of 36–38°C being reached around midnight. The duration of heat production differs between individual plants but usually stops between 2 h and 4 h in the morning. The spathe begins to close the next day in the early morning hours or in the forenoon. The opening and closing of the spathe seems to be influenced by the hours of daylight but these might be different in European countries from the

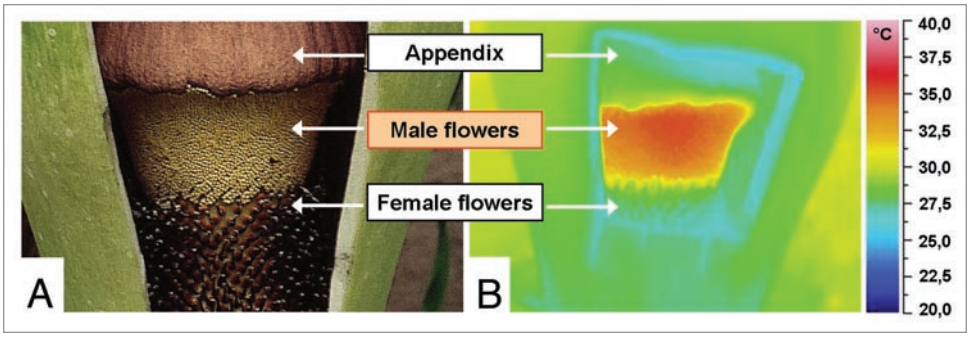

Figure 1. (A) Flash-light photograph of an *Amorphophallus titanum* flowering zones showing part of the appendix, the male florets and the female florets. (B) Thermographic image taken during the male flowering phase. The male florets are heated to the maximum temperature of 35.9°C whereas the other parts of the plant have largely ambient air temperature of 26°C.

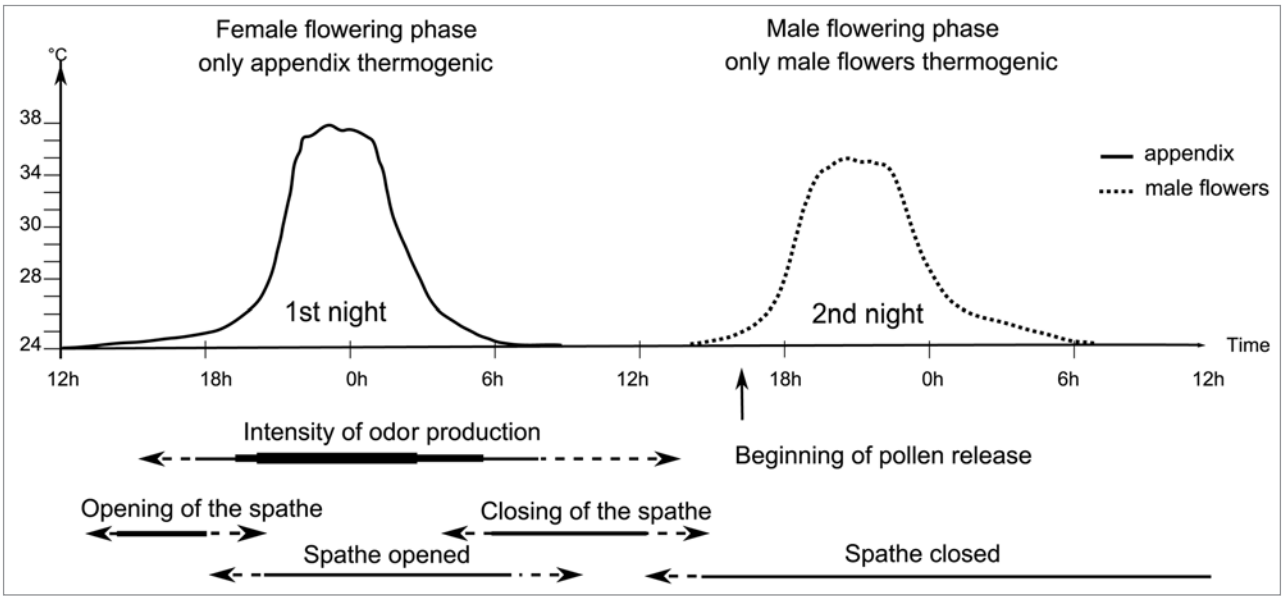

Figure 2. Scheme of the flowering behavior of *Amorphophallus titanum* over its two-days flowering period. The scheme is idealised but represents observation of seven *A. titanum* inflorescences that all behave highly similar. Deviations in the time when opening and closing of the spathe begin in individual plants are indicated with a dashed line.

plants native habitat in the tropical rainforests of Sumatra. The flowering events in Bonn usually take place in summer, the spathe opens during a daytime when it is still very bright and is fully opened when the daylight is decreasing while it is already dark then in the tropics.

Some authors have observed heating of the male florets prior to appendix heating in other Araceae species.[4,5,8,9] In *A. titanum* however, we could not find an evidence for this, as stated in our previous article. But a question that still remained open is: when exactly the male flowering phase begins and if there might be thermogenic activity during the male flowering phase. To study this, the male florets were made visible by removing a part of the spathe of two flowering *A. titanum* and observed right after opening of the spathe. The beginning of the male flowering phase is easily to determine since the pollen is shed in well visible string-like structures.

The pollen dissemination began in the evening around 17:20 h. Thereupon we filmed the male florets with a thermographic camera (Flexcam, GORATEC) taking an image every five minutes. The male florets were clearly thermogenic reaching a temperature maximum of 35.9°C between 18:40 h and 20:00 h (**Fig. 1B**). They slowly cooled down to ambient air temperature (ca. 26°C) around midnight. To test whether the temperature in the floral chamber around the male florets increases while they are heated, we recorded the temperature within the spathe of three intact inflorescences with data loggers (Tinytag, Gemini Data Loggers). However, no warming within the chamber in comparison with ambient air temperature could be measured, so the heated florets seem not to affect the temperature within the floral chamber.

The flowering behavior of *A. titanum* is summarised in **Figure 2**. The carrion-like odor and the thermogenic spadix attract pollinators in the female flowering phase,

during the first evening and night of the flowering period. Heating of the male florets occurs when no more odor is produced and hence no olfactorical attraction of the pollinators can take place. As a consequence, there must be only one attraction time period which is more or less restricted to the female flowering phase and to the nighttime where pollinators can be successfully attracted. The pollinators, although not exactly known,[10] hence must be active only in these evening hours and at night. Once attracted, the pollinators stay inside the inflorescence and most likely use it as mating site or as a place to stay during the following day. It has already been hypothesised that Araceae inflorescences forming floral chambers may offer mating sites or places to rest for insects and rather keep their pollinators inside the floral chamber instead of a second attraction phase.[11, 12] Numerous insects inside a *A. titanum* inflorescence have indeed been observed in its natural habitat,[13] although the author did not explain these observations, it provides evidence for our hypothesis that pollinators spend some time inside the inflorescence.

The male florets are heated while pollen is released. There is evidence that at least some insects are able to percept IR light and it has been hypothesised that infrared radiation itself could be an attractant for insects, most likely to locate food sources.[15] Floral heat may also be a direct reward for pollinators, helping them increasing their body temperature and thus faster reaching their activity level.[11,14] Both may also apply to *A. titanum*—the insects that have spent the day within the flower chamber may use the heated surface of the male florets to warm themselves up and by this collect pollen or feed on pollen. Still, a verification of these hypotheses could only come from field observations.

To draw a conclusion, the new observations reported here now allow us a good understanding of the flowering behavior of *A. titanum*. Its two thermogenic phases are clearly linked with the two flowering phases and the plant's complex interaction with its pollinators.

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