Heat production by an Ecuadorian palm

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When asked to think about heat production in the natural world, our thoughts first turn to mammals, birds, and other warm-blooded animals. As mammals ourselves, we are often thankful for our ability to produce heat internally to raise body temperature above ambient temperature, through a process called endothermy. This phenomenon has fascinated naturalists and biologists for centuries (Heinrich 1999) and still has the capacity to surprise modern scientists, with new discoveries concerning the occurrence and evolution of endothermy in the animal world. Last year, for example, saw the discovery of the first entirely warm-blooded fish (Wegner *et al.* 2015). The endothermy of this fish is a remarkable adaptation for swimming in cold waters. Endothermy also occurs in some plants. Since the first description of heat production in arum flowers by Lamarck (1778), many other flowering and seed-bearing species have been shown to produce heat. The reasons for the evolution and ecological importance of endothermy in temperate and tropical plants are still a matter of debate, and any new field observations of plant endothermy constitute potentially interesting pieces in this eco-evolutionary jigsaw.

A few years ago, local botanists reported that the flowers of the ivory palm (*Phytelephas aequatorialis*; Arecaceae) produce heat. This palm, also known as the tagua (pronounced "tawha"), is endemic to Ecuador, on the western side of the Andes Mountains. It is economically important as its leaves are used for ceilings, and its seeds are used in the button industry and in handicrafts (Montúfar *et al.* 2013). Most of our knowledge of the ecology of this palm was obtained from local farmers. In particular, farmers were well aware of the heat produced by male flowers because they could feel it with their hands. Heat production has mostly been described in plants bearing the male and female organs together in the same flower (Seymour 2010), but the ivory palm is different in that it has separate male and female individuals. This piqued our curiosity, particularly given the considerable differences between the male and female flowers.

Male inflorescences – which contain hundreds of flowers – are more than 1 m long (Figure 1) and mature during a single night. The female organ is much smaller, with a length of no more than 30 cm. Until now, researchers did not know whether female flowers produced heat. In both male and female organs, the flowering sequence starts with the development of two modified leaves: the bud (orange part), which grows from the profilo (woody brown part). All flowers are exposed when the bud opens laterally. The bud integuments and the profilo remain at the base of the inflorescence throughout the life of the flowers.

We wanted to know whether heat is produced by the flowers and/or by the bud. Heat-producing plants usually warm up at the flowering stage (Seymour and Schultze-Motel 1997), so in February and June 2015, we travelled to the Otonga Reserve, in Ecuador, with the aim of recording heat production in male and female organs with infrared cameras and several dataloggers small enough to be inserted into the buds and flowers for continuous temperature measurements. The first challenge was finding the flowers, which tend to be hidden at the crown of the palm, sometimes as much as 10 m above the ground. Furthermore, the elongated flowers are ephemeral. Male flowers decay after 24 hours, and female flowers last for several days. Individual palm trees bloom several times per year, but flowering trees are randomly distributed in the forested landscape. The local farmers helped us by identifying good candidates.

Figure 1. *The male inflorescence of endemic ivory palm (*Phytelephas aequatorialis*). The orange material at the top of the image is the remnants of the bud integument.*

We were initially disappointed by the infrared images, because the flowers were not particularly warm. However, upon closer inspection, we soon noticed the presence of a bright red spot at the base of the organs, corresponding to the bud integuments and the profilo (Figure 2). Both the male and female buds produced heat. This was particularly apparent in the infrared images of the female organs, in which bud surfaces were warm while the flowers remained close to ambient air temperature (Figure 2). The male and female buds are about 60 cm and 15 cm long, respectively, just before they open. Heat production was clearly most intense in mature buds, which were 10–20°C above ambient air temperature a few days prior to opening. This heat excess is comparable to maintaining body temperature in most mammals and birds. The

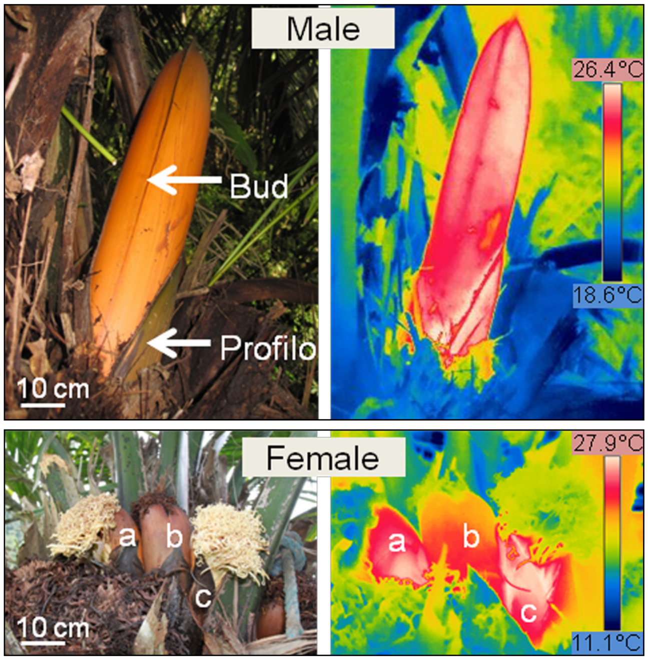

Figure 2. *Photographs (left) and thermographic images (right) of a male flower bud (top) and female flowers with the bud integument remaining at the base of the flower (bottom) taken on 9 Feb 2015 (at 18:30) and 11 Feb 2015 (at 12:10), respectively. Air temperature was 23.4°C for the male bud and 22.5°C for the female inflorescence. Three female inflorescences at different phenological stages are shown: (a) late stage, (b) senescent, and (c) recently opened.*

greatest surprise was the temporal pattern of bud temperature, which remained relatively constant despite large fluctuations in ambient air temperature. We measured internal temperatures of 37°C ± 2°C in male buds at 5-minute intervals on 3 consecutive days, whereas air temperatures fluctuated daily between 17°C and 28°C, similar to the body temperature of humans. This observation suggests that temperature is tightly regulated in the bud tissues, but this temperature regulation is lost once the bud opens. Later, once the flowers decay, the bud integument stops producing heat entirely.

It is a mystery as to why the ivory palm's bud produces heat while its flowers don't. What biological function does endothermy serve in this palm? The heat generated by the bud could be an added consequence of a high metabolic activity as the flowers are forming inside the bud tissues (Seymour and Schultze-Motel 1997). Alternatively, high temperatures may promote the rapid growth of flowers (Ervik and Barfod 1999). Yet these two hypotheses are unlikely. Female buds, which grow slowly (~5 cm per day) and develop small flowers, reach internal temperatures that are similar to those in male buds, which grow quite rapidly (~20 cm per day) and produce large inflorescences. Heat may be produced to attract pollinators, either as a direct thermal cue (Ervik and Barfod 1999) or as a thermal reward (Seymour *et al.* 2003), or to maximize the release of attractive volatile chemicals (Terry *et al.* 2007). Heat can even be produced by microorganisms colonizing the flowers or buds (Herrera and Pozo 2010).

The farmers told us that many insects could be seen flying around the tagua flowers. This was promising, given our interest in the potential links between heat production and pollination. Nevertheless, the production of heat at the bud stage, when pollen and nectar are not yet available for insects, is puzzling. Large numbers of individuals from diverse Coleopteran and Dipteran species feed on male flowers during the day, well after the bud has opened and after the temperature of the flower has already dropped. However, after many hours of flower watching in the field, we observed a single species, a stingless bee (*Trigona* sp), visiting both male and female buds during the few days before they opened. The bee flew around the buds and walked on the groove at the top of buds. We now need to determine if the bee is waiting for the buds to open or revisits the plant once it blooms. This would be interesting because the bee might first get pollen from the male flowers (which decay relatively quickly) and then nectar from the female flowers (which last longer).

Endothermy in plants may have evolved in response to an unfavorable climate (Knutson 1974) or to the selection pressures imposed by pollination (Seymour and Schultze-Motel 1997). We report here the mysterious observation of endothermy at the bud stage rather than during flowering, as commonly observed in other endothermic plants (Seymour and Schultze-Motel 1997; Seymour 2010). This raises questions about the regulation of bud temperature in both male and female palms. Are the selection pressures for endothermy the same in male and female flowers, especially since they grow at different rates? Why do buds produce heat for several days before they open? What happens if female and male buds reach different temperatures? How is the heat produced? Ivory palms bear the largest known heat-generating flower in the world. Male buds weigh several kilograms, whereas the previous record for a heat-producing flower was 600 g (Seymour 2010). It therefore constitutes an ideal model system for studying gigantism in plant endothermy.

Supporting Information

References and additional web-only material may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/fee.1442/suppinfo

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WebPanel 1. Acknowledgements and References

Acknowledgements

Financial support of this research was provided by the Pontificia Universidad Católica del Ecuador and the French Institute for Research and Development. We thank G Onore, the residents of the Otonga Reserve, and the landowners who made this fieldwork possible. We also thank J Casas and H A Woods for their comments on a previous version of the article.

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