

Flowering and thermogenetic cycles in two species of *Monstera* [Araceae]

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ABSTRACT

The authors report the measurement of temperature from the spadixes of two *Monstera* species: *Monstera adansonii* Schott and *Monstera deliciosa* Liebm. The temperature of the spadixes was recorded during the entire flowering cycle parallel to the description of the flowering biology (movement of the spathe, odour production, gum and pollen release) on plants growing in the greenhouses of the Montreal Botanical Garden. The flowering and thermogenesis cycles were a 96-h process spread out over five days and identical for both species. When the flowering cycle begins (first day, female phase), the temperature of the spadix increases slightly to a few degrees above that of the ambient air and maintains this difference until the beginning of the male phase. In the early morning of the fifth day, as ambient temperature is at its lowest, the temperature of the spadix begins to rise and peaks in synchronization with pollen release. The type of flowering and thermogenetic patterns suggest that *M. adansonii* and *M. deliciosa* may be pollinated by insects (potentially beetles) arriving before the spathe unfolds and departing on the day of pollen release. However, field studies are needed to confirm this hypothesis.

Key words: inflorescence, heat, temperature, flower, pollination.

Floraison et cycles thermogénétiques chez deux espèces de *Monstera* [Araceae]

RÉSUMÉ

Les auteurs ont mesuré l'augmentation de température dans les spadices de deux espèces de *Monstera* : *Monstera adansonii* Schott et *Monstera deliciosa* Liebm. La température des spadices a été enregistrée parallèlement à la description du cycle floral (mouvement de la spathe, production d'odeur, libération de pollen et de résine) sur des plantes cultivées au Jardin botanique de Montréal. Les cycles floraux et thermogénétiques, qui sont identiques pour les deux espèces, durent 96 heures et s'étendent sur près de cinq jours. Quand la floraison débute (premier jour, phase femelle), la température du spadice augmente légèrement au dessus de la température ambiante jusqu'au début de la phase mâle. Le matin du cinquième jour, quand la température ambiante est à son plus bas, la température du spadice commence à augmenter et atteint un maximum en même temps que le pollen est libéré. Le type de cycles floraux et thermogénétiques indique que *M. adansonii* et *M. deliciosa* pourraient être pollinisés par des insectes (probablement des coléoptères) arrivant avant que la spathe soit complètement déroulée et repartant au moment de la libération du pollen.

Mots-clés : inflorescence, chaleur, température, fleur, pollinisation.

Introduction

Thermogenesis in reproductive organs is common in the Araceae family but also exists in several other plant families: Annonaceae, Arecaceae, Magnoliaceae, Nymphaeaceae and Zamiaceae (see review in : GIBERNAU ET AL. 2005; ROEMER ET AL. 2005; THIEN ET AL. 2009). Heat production by floral structures is generally associated with the emission of fragrances, the arrival of pollinators and the liberation of pollen, and it has been well documented in the subfamily *Aroideae* (see

review in : GIBERNAU ET AL. 2005; IVANCIC ET AL. 2005; MAIA ET SCHLINDWEIN 2006; CHOUTEAU ET AL. 2007a; BARTHLOTT ET AL. 2008, SEYMOUR & GIBERNAU 2008). In this subfamily (MAYO ET AL. 1997), the spadix bears unisexual flowers arranged in sexual regions (female flowers in the lower zone, male flowers in the upper zone, and in some genus a sterile zone is present in the middle) and the heat is generally produced by either the fertile and sterile male flowers or by a specialized sterile zone, the appendix located above the male flowers (see review in GIBERNAU ET AL. 2005).

On the other hand, data on thermogenesis and pollination in the Araceae subfamilies bearing bisexual flower inflorescences (i.e. Pothoideae, Monsteroideae, Lasioideae and Calloideae) are scarce. Pollination observations concern only a few genera (see review in : GIBERNAU 2003; BOOS 1997; ZHU & CROAT 2004; GONÇALVES 2005; CHOUTEAU ET AL. 2007b; FRANZ 2007). Data on thermogenesis are still rarer and pertain to only two genera, *Symplocarpus* and *Monstera* (LEICK 1915; UEMERA ET AL. 1993; SEYMOUR 2004; CHOUTEAU ET AL. 2007b). Until now, the thermogenesis and flowering cycle in the genus *Monstera*, which comprises over 40 species (MAYO ET AL. 1997), had only been studied in *Monstera deliciosa* (LEICK 1915, SKUBATZ ET AL. 1990) and *Monstera obliqua* (CHOUTEAU ET AL. 2007b). LEICK (1915) reported the presence of a thermogenetic cycle of three days in *M. deliciosa*, and SKUBATZ ET AL. (1990) a cycle of two days. However, in *Monstera obliqua*, CHOUTEAU ET AL. (2007b) reported that the flowering and thermogenetic cycle was a 48-h process spread out over three days.

The inflorescences of the genus *Monstera* bear small bisexual flowers consisting of a whorl of stamens surrounding a pistil without a perianth (MAYO ET AL. 1997) enclosed within the spathe. Two distinct zones are present in the spadix of *Monstera*; most of the spadix consists of fertile flowers while in a small zone at its base some sterile flowers are present (RAMIREZ & GOMEZ 1978; MAYO ET AL. 1997). In *Monstera deliciosa*, the sterile flowers produce gums believed to attract pollinators (*Trigona* bees), who collect it for the construction of their nest and also inadvertently collect pollen onto their bodies (RAMIREZ & GOMEZ 1978). However, one study of the pollination ecology of *Monstera obliqua* has shown that these characteristics are not present in all *Monstera* species. *M. obliqua* has been observed to be pollinated by small beetles (*Colopterus amputatus*) in the absence of gum production (CHOUTEAU ET AL. 2007b). The pollination mechanisms for this species are surprisingly complex compared to other studied Neotropical genera bearing unisexual flowers (RAMIREZ & GOMEZ 1978; CROAT 1980; MONTALVO & ACKERMAN 1986; BEATH 1998; SCHWERDTFEGER ET AL. 2002; FRANZ 2007). Nevertheless, the pollination mechanisms in the genus *Monstera* have been studied insufficiently.

Therefore, analysis of the thermogenic and flowering cycle of additional species will enable us to formulate a hypothesis regarding the pollination mechanisms in this genus. This study will also contribute to a better understanding of the thermogenetic patterns in the subfamily Monsteroideae. We report here on the measurement of temperatures from the spadices of two *Monstera* species: *Monstera adansonii* Schott and *Monstera deliciosa* Liebm. The temperature of the spadices was recorded during the entire flowering cycle parallel to the description of the flowering behavior (movement of the spathe, odour production and gum and pollen release) on plants growing in the greenhouses of the Montreal Botanical Garden.

The specific goals of this study are: 1) to determine the relationships between the flowering cycle and the thermogenetic pattern in two species of *Monstera* (*M. adansonii* and *M. deliciosa*); 2) to compare their thermogenetic patterns and that of *M. obliqua*; and 3) to integrate the thermogenetic pattern of *Monstera* into the general framework of thermogenesis in Araceae.

Material and methods

This study was conducted during the summer of 2004 at the Montreal Botanical Garden. For both species of *Monstera*, twelve inflorescences belonging to three different individual plants were monitored regularly during the entire flowering cycle. The receptivity of the stigmas, the movement of the spathe, and the resin and pollen release were monitored by removing a 3 x 3 cm square from the spathe before the initialization of the flowering cycle. Odour production was also recorded by one of the authors (M. Chouteau) "smelling" the inflorescences.

The temperature of four inflorescences, chosen on three different plants, was measured for both *M. adansonii* and *M. deliciosa*. Temperatures of the spadix and ambient air were recorded every 20 minutes using two Digi-Sense® DualLogR® thermocouple thermometers. One of the thermometer's probes was inserted approximately 5 mm into the middle of the spadix and the second probe was used to record the ambient air temperature. Thermometers were inserted into the spadix until five days before the expected beginning of the flowering cycle. Voucher specimens were deposited at the Marie-Victorin Herbarium (MT): *M. adansonii* (Chouteau & Lavallée 5), *M. deliciosa* (Barabé 249).

Results

In both species of *Monstera* analyzed, flowering appears to be asynchronous with inflorescences opening successively on the same individual. Both the flowering and thermogenesis cycles were a 96-h process spread out over five days and identical for both species.

Before flowering begins, the spathe is tightly folded around the spadix, preventing access to the flowers (Fig. 1A). The first day, the flowering cycle begins in early morning around 6h00 (female phase, Fig. 3). At this time, stigmas are already receptive, a fragrance is produced and the spathe unfolds slightly (Fig. 1B). The spathe unfolds in such a way that direct access to the flowers is not possible and a floral chamber is created between the spadix and the spathe, which are now separated by a 4 mm gap for *M. adansonii* and a 2 mm gap for *M. deliciosa* (Fig. 1B). The inflorescences remain in this position until the morning of the fourth day. At the start of the photoperiod of the fourth day (6h00), the swollen spathe (Fig. 1B) unfolds slowly until its complete opening. During the unfolding of the spathe, first access to the flowers occurs around 12h00 and at approximately the same time, small amounts of pollen are released by the flowers of the lower zone (Figs. 2A, 2B). Also at around noon, the stigmas quickly dry and become unreceptive. At night (19h00), the basal zone flowers release a sticky resin that remains on the stigmas (Fig. 2B). During the morning (6h00 to 8h00) of the fifth day, the flowers of the inflorescences' upper zone release a large quantity of pollen (Figs 2C, 2D) which accumulates in the bowl formed by the base of the spathe and a strong, sweet fragrance is produced.

Before the initiation of the flowering cycle, the temperature of the spadix closely follows that of the ambient air (data not shown) for both species. When the flowering cycle begins (first day, female phase), the temperature of the spadix increases slightly to a few degrees above that of the ambi-

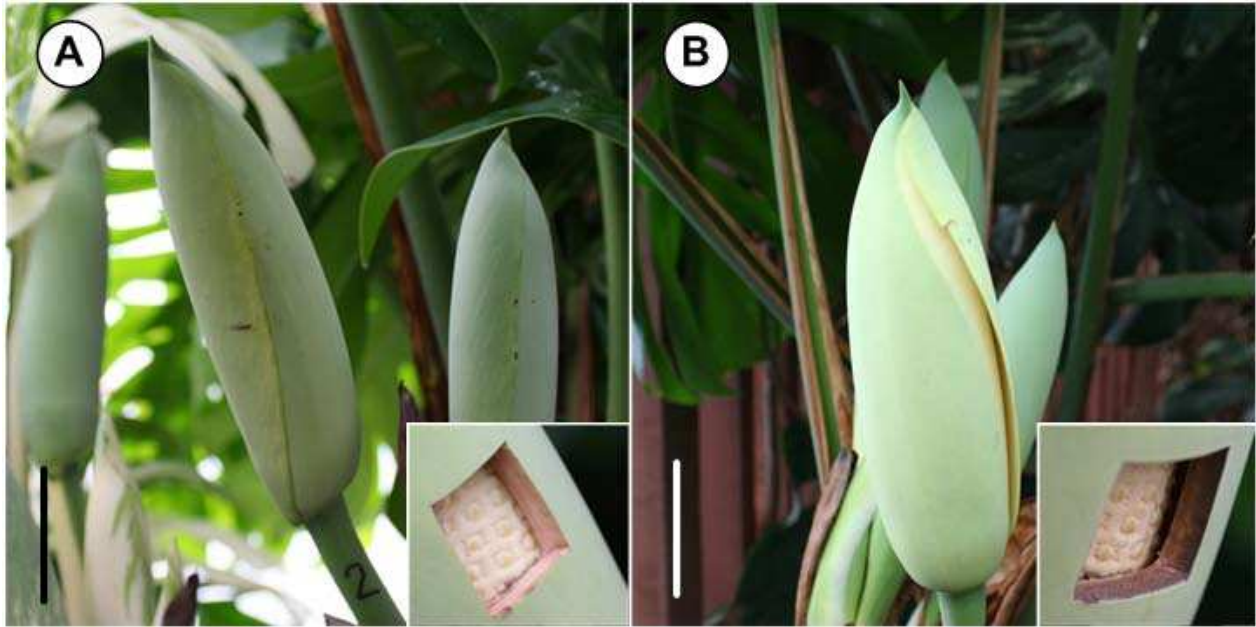


Fig. 1 : Inflorescence of *Monstera deliciosa*.

A) before flowering (note at the bottom right the lack of a floral chamber) and B) during the female phase (note at the bottom right the presence of a floral chamber). Bar = 4 cm.

ent air and maintains this difference until the beginning of the male phase (Fig. 3). The difference between spadix and ambient air temperature is cyclic during the female phase and varies with changes in ambient air temperature (Fig. 3). As a general rule, the difference is at its minimum during the morning hours (around 0°C) when ambient air temperatures increase quickly and reaches its maximum at mid-day. In the afternoon, when the ambient temperature stabilizes at its maximum, the temperature of the spadix continues to increase until it reaches $1.6^{\circ}\text{C} \pm 0.4^{\circ}\text{C}$ (spadix temperature $26.1^{\circ}\text{C} \pm 1.5^{\circ}\text{C}$) for *M. adansonii* and $2.1^{\circ}\text{C} \pm 0.8^{\circ}\text{C}$ (spadix temperature $27.4^{\circ}\text{C} \pm 1.3^{\circ}\text{C}$) for *M. deliciosa* above ambient air temperatures. In the evening, as ambient temperatures decrease, the spadix maintains its temperature a few degrees above that of ambient temperatures until sunrise. At this time, the spadix temperature of *M. adansonii* is $23.5^{\circ}\text{C} \pm 0.9^{\circ}\text{C}$ ($2.3^{\circ}\text{C} \pm 0.4^{\circ}\text{C}$ above air temperature) and for *M. deliciosa* $23.5^{\circ}\text{C} \pm 1.0^{\circ}\text{C}$ ($2.1^{\circ}\text{C} \pm 0.6^{\circ}\text{C}$ above air temperature). In the early morning of the fifth day (male phase: Fig. 3), as ambient temperature is at its lowest, the temperature of the spadix begins to rise and peaks in synchronization with pollen release.

In *M. adansonii* (Fig. 3A), the increase in temperature begins at $03\text{h}24 \pm 00\text{h}13$ and peaks at $06\text{h}59 \pm 00\text{h}52$. When peaking, the difference between ambient air temperature ($20.6^{\circ}\text{C} \pm 2.0^{\circ}\text{C}$) and the temperature of the spadix ($25.6^{\circ}\text{C} \pm 2.7^{\circ}\text{C}$) is $5.0^{\circ}\text{C} \pm 0.8^{\circ}\text{C}$. At $11\text{h}46 \pm 00\text{h}29$, the flowering cycle is completed and the temperature of the spadix closely follows that of the ambient air temperature.

For *M. deliciosa* (Fig. 3B), the spadix temperature begins to rise at $01\text{h}38 \pm 01\text{h}42$ and peaks at $06\text{h}11 \pm 00\text{h}04$. At its peak, the temperature of the spadix is $26.6^{\circ}\text{C} \pm 1.3^{\circ}\text{C}$, $5.5^{\circ}\text{C} \pm 1.3^{\circ}\text{C}$ above that of the ambient air ($21.2^{\circ}\text{C} \pm 1.7^{\circ}\text{C}$). At $10\text{h}57 \pm 00\text{h}13$, the temperature of the spadix drops and thereafter closely follows that of the ambient air.

Discussion

The documented flowering cycle of *M. deliciosa* is slightly longer (96-h) than that reported by LEICK (1915) and SKUBATZ ET AL. (1990) for the same species (72-h and 48-h). This difference remains difficult to explain. However, in *M. adansonii* and *M. deliciosa* the thermogenetic and flowering cycles are longer than those observed in *Monstera obliqua* (CHOUTEAU ET AL. 2007b). The 96-h flowering cycle of both species is twice as long as that of the 48-h flowering cycle of *M. obliqua*. In terms of volume (cm^3), the spadix of *M. obliqua* is approximately seven times smaller than that of *M. adansonii* and *M. deliciosa*. Given that the pattern of the flowering cycle is very similar in these three species, one may hypothesize that this difference may be related to the size of the spadix. However, the flowering cycle of the last two species is much shorter than that of other taxa with bisexual flowers, such as *Anaphyllopsis* (CHOUTEAU & AL. 2006) and *Anthurium* (CROAT 1980; MONTALVO & ACKERMAN 1986; SCHWERTFEGER ET AL. 2002; FRANZ 2007).

In *M. adansonii* and *M. deliciosa*, heating occurs mainly at the time of pollen release (i. e. male phase) as in *M. obliqua*

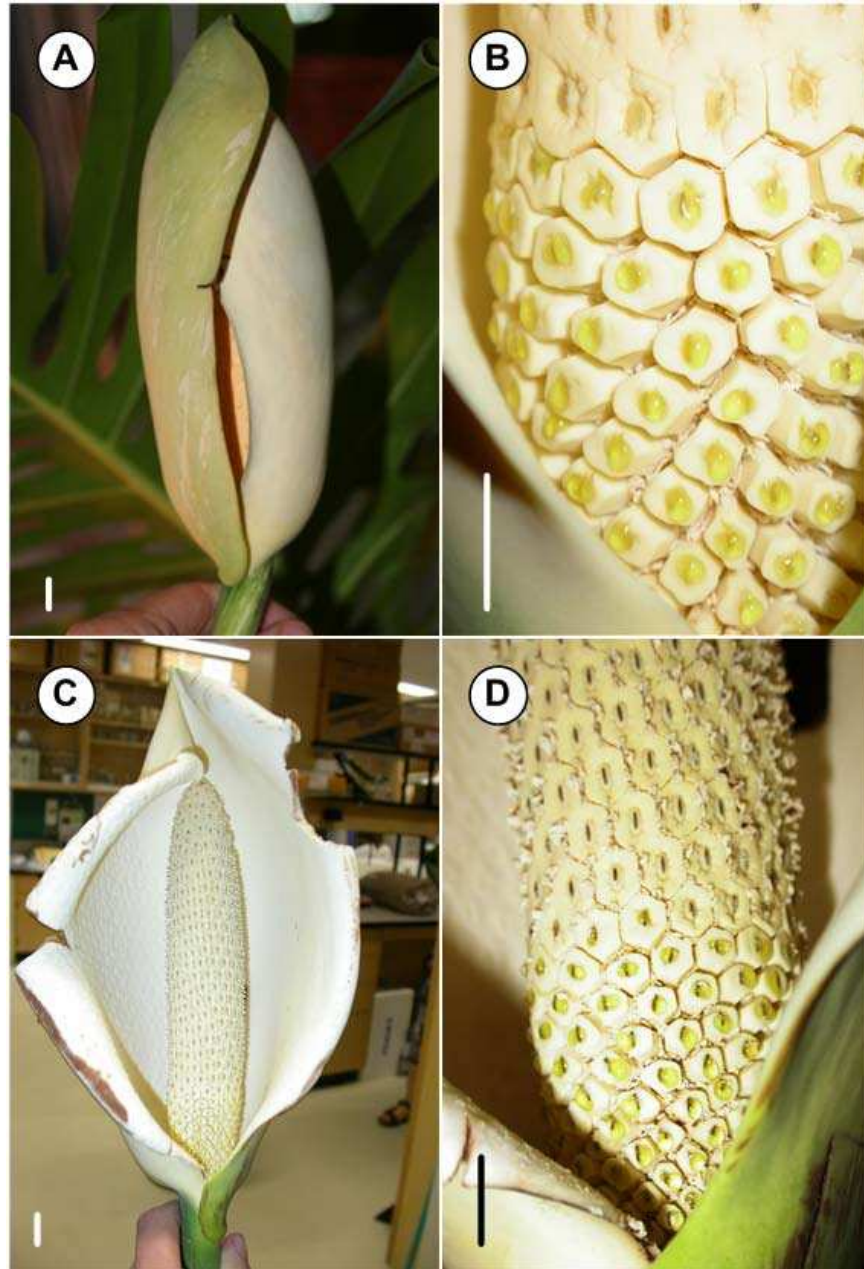


Fig. 2 : *Monstera deliciosa*.

A-B. The inflorescence at the end of the female phase displaying A) the unfolding of the spathe and B) the secretion of gums and the release of pollen by the basal flowers.

C-D. The inflorescence during the male phase displaying C) the spathe completely unfolded and D) the release of pollen by the spadix. Note the dry and unreceptive stigma. Bar = 1 cm.

(CHOUTEAU ET AL. 2007b) and in many genera with unisexual flowers such as *Philodendron* (e.g. BARABÉ ET AL. 2002; GIBERNAU & BARABÉ 2002), *Caladium* (MAIA & SCHLINDWEIN 2006), *Xanthosoma* (GARCIA-ROBLEDO ET AL. 2004), *Dieffenbachia* (YOUNG 1986), *Montrichardia* (GIBERNAU ET AL. 2003) and *Syngonium* (CHOUTEAU ET AL. 2007a). In *M. obliqua* and the genera enumerated previously, the increase in temperature is believed to aid in releasing pollen from

the stamens. In *P. solimoense*, it also helps to increase the body temperature of dynastid beetles prior to flight activity (SEYMOUR ET AL. 2003).

Interestingly, although the flowering cycle is longer in *M. adansonii* and *M. deliciosa*, the spathe unfolds in a manner similar to that observed in *M. obliqua*. This suggests that these three species may be characterized by similar pollination mechanisms. In *M. obliqua*, the beetle pollina-

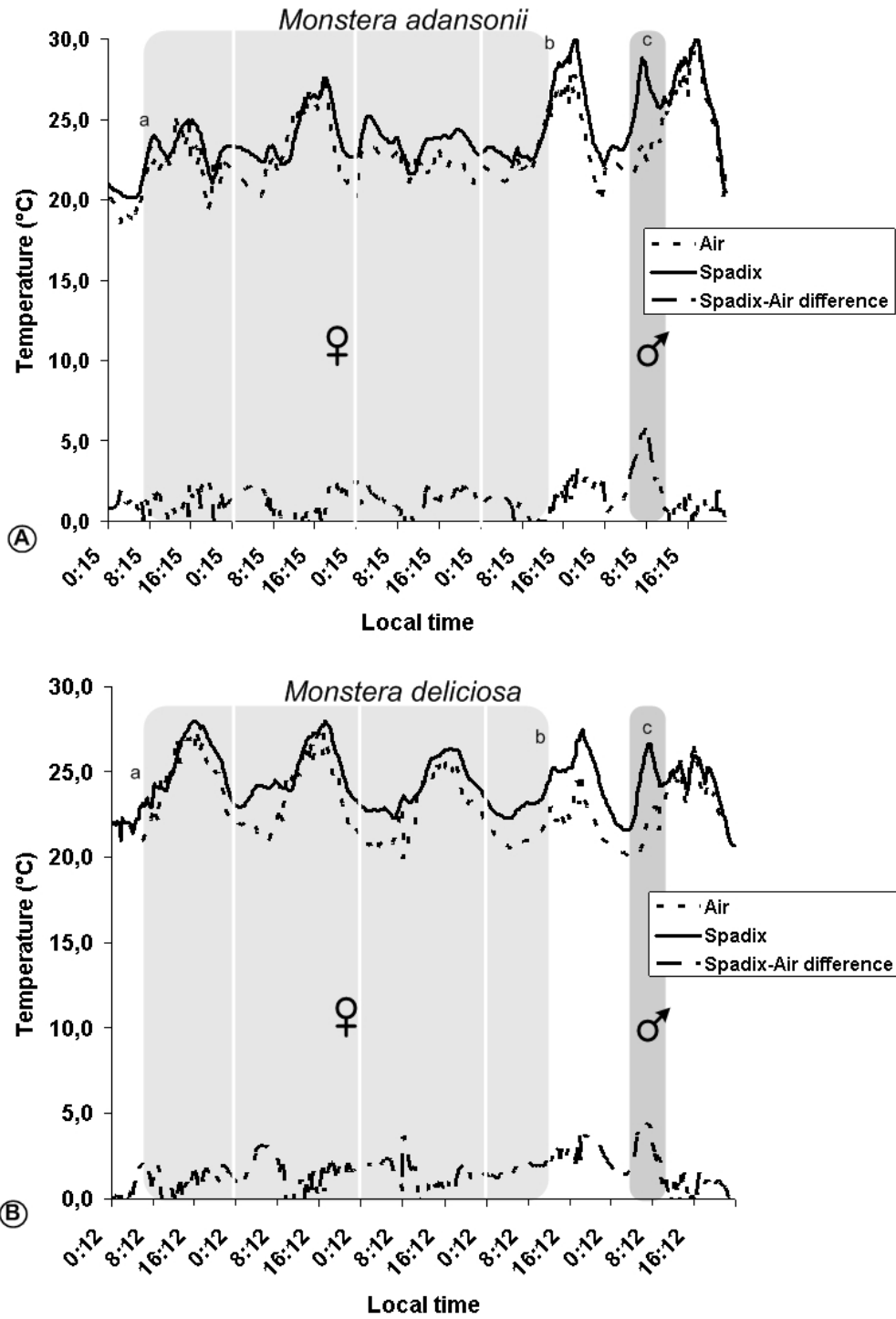


Fig. 3 : The temperature curves (°C) of the spadix, the ambient air and the difference between the spadix and the ambient air during five successive days of flowering for A) *M. adansonii* and B) *M. deliciosa*. a) The start of stigma receptivity, the spathe unfolds (floral chamber) and odour is produced. b) The spathe opens, enabling for direct access to the flowers, the stigma are unreceptive and the basal flowers produce gums and release pollen. c) The spathe is completely open and the spadix releases large amounts of pollen.

tors arrive before the spathe is completely open and use the floral chamber as a mating site and shelter. Pollinators appear to be attracted to the sweet scent produced during the 48 h of the flowering cycle, although a small increase in the spadix temperature is recorded during the female phase (CHOUTEAU ET AL. 2007b). In the same way, thermogenesis in *M. adansonii* and *M. deliciosa* begins when the spathe appears swollen prior to opening, thus creating a small floral chamber. Also, despite a weak increase in the spadix temperature, spadices from both species emit a strong fragrance. All these correlated traits suggest that *M. adansonii* and *M. deliciosa* may be pollinated by insects (potentially beetles) arriving before the spathe unfolds and departing on the day of pollen release, contrary to bee observations (RAMIREZ & GOMEZ 1978). However, field studies are needed to confirm this hypothesis.

The presence of a thermogenetic cycle in genera with bisexual flowers has been reported also for *Symplocarpus* (see SEYMOUR 2004 for a review). In this genus, the temperature may increase 35°C above the ambient air temperature. In comparison, the difference between air and spadix temperature in *Monstera* remains very low, no more than 6°C. This difference between *Monstera* and *Symplocarpus* may be due to the habitat in which the plants grow. *Symplocarpus* blooms in April-May in cold regions, where the temperature may drop to -15°C during this period. Therefore, the production of heat by the spadix would be necessary to maintain the physiological processes linked with flowering, in particular the release of pollen. On the contrary, in the case of *Monstera*, such an increase in the spadix temperature is not necessary because the plants grow in a warm, tropical environment, where the ambient temperature does not slow down physiological activities. However, validating this interpretation will require analysis of the thermogenetic cycle of other tropical genera with bisexual flowers.

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