Thermogenesis in *Syngonium* (Araceae)

Mathieu Chouteau, Denis Barabé, and Marc Gibernau

Abstract: Floral cycles and spadix temperatures were recorded for two species of *Syngonium*: *Syngonium schottianum* Wendl. ex Schott (section *Cordatum*) and *Syngonium angustatum* Schott (section *Syngonium*). Both species exhibited a 3-day flowering cycle, beginning with stigma receptivity and opening of the spathe the first day, the female phase continues over the second day, and the male phase continues over the third day. These species displayed two distinct patterns of heat production during flowering. In *S. schottianum*, the spadix warmed up twice during the beginning of the second and third nights, but in *S. angustatum*, the spadix warmed up twice the second day, once the second night, and once the third day. These different thermogenic cycles are discussed in regard to other genera that are phylogenetically close or sharing similar flowering and thermogenic cycles.

Key words: Syngonium, Araceae, flowering cycle, thermogenesis.

Résumé : Les auteurs ont etudié les cycles floraux et les températures des inflorescences chez deux espèces de *Syngonium* : *Syngonium schottianum* Wendl. ex Schott (section *Cordatum*) et *Syngonium angustatum* Schott (section *Syngonium*). Les deux espèces possèdent un cycle floral de trois jours, débutant avec la réceptivité des stigmates et l'ouverture de la spathe le premier jour, la phase femelle continue le deuxième jour, suiviede la phase mâle le troisième jour. Ces espèces exhibent deux types distincts de courbes de température des spadices. Chez le *S. schottianum*, le spadice produit deux pics distincts de chaleur au début des seconde et troisième nuits, tandis que chez le *S. angustatum*, le spadice produit des pics de chaleur deux fois au cours de la première journée, une fois la deuxième nuit, et une fois la troisième journée. Les auteurs discutent ces différences de cycles thermogèniques, en relation avec d'autres genres phylogénétiquement voisins ou qui ont des cycles similaires de floraison et de thermogenèse.

Mots-clés : Syngonium, Araceae, cycle floral, thermogenèse.

[Traduit par la Rédaction]

Introduction

Thermogenesis in reproductive organs is common in the Araceae but also exists in several other plant families: Annonaceae, Arecaceae, Magnoliaceae, Nymphaeaceae, and Zamiaceae. Heat production by floral structures is generally associated with emission of fragrances, arrival of pollinators, and liberation of pollen (Tang 1987; Gottsberger 1990; Yafuso 1993; Azuma et al. 1999; Seymour 1999; Thien et al. 2000; Lamprecht et al. 2002). Although numerous studies have focused on the production of heat by inflorescences of Araceae, few of them document the complete thermogenic cycle (Nagy et al. 1972; Seymour et al. 1983; Barabé and Gibernau 2000; Gibernau et al. 2000, 2003; Gibernau and Barabé 2000; Ivancic et al. 2004, 2005; Maía and Schlindwein 2006).

Thermogenesis and the flowering cycle have not been studied in the neotropical genus *Syngonium*, which consists of over 32 species (for unpublished observations see Beath 1998). The protogynous inflorescences of the genus *Syngonium* bear small flowers enclosed in the spathe (Fig. 1). The pistillate flowers occupy the lower portion of the spadix, whereas the male flowers are located on the upper portion. In the median portion of the spadix, there is a zone consisting of sterile male flowers (Fig. 1). The genus *Syngonium* belongs to the Caladieae tribe, which contains seven genera, including *Xanthosoma* and *Caladium* (Mayo et al. 1997; Barabé et al. 2004). Given that floral morphology, flowering cycle, thermogenic pattern, and pollinators (beetle) of *Caladium* (Maía and Schlindwein 2006) and X*anthosoma* (García-Robledo et al. 2004) are similar to those of *Philodendron*, which have been studied in detail (Gibernau et al. 1999, 2000; Gibernau and Barabé 2000, 2002; Barabé et al. 2002), one would expect to find the same pollination mechanism in *Syngonium*.

Our study measured the temperature in the different zones of the spadix for two *Syngonium* species belonging to two different sections (*i*) *Syngonium schottianum* Wendl. ex Schott (section *Cordatum*) and (*ii*) *Syngonium angustatum* Schott (section *Syngonium*). The temperature of the spadix was recorded during the entire flowering cycle, and at the same time the flowering behaviour (movement of the spathe, odour production, pollen release) was recorded on plants grown under greenhouse conditions.

The specific goals of this study are (*i*) to characterize the pattern of heat production in two different sections of the genus *Syngonium*, (*ii*) to compare the thermogenic cycle of *Syngonium* with phylogenetically related genera, and (*iii*) to analyze the thermogenic pattern of *Syngonium* in relation to the putative mechanism of pollination in this genus.

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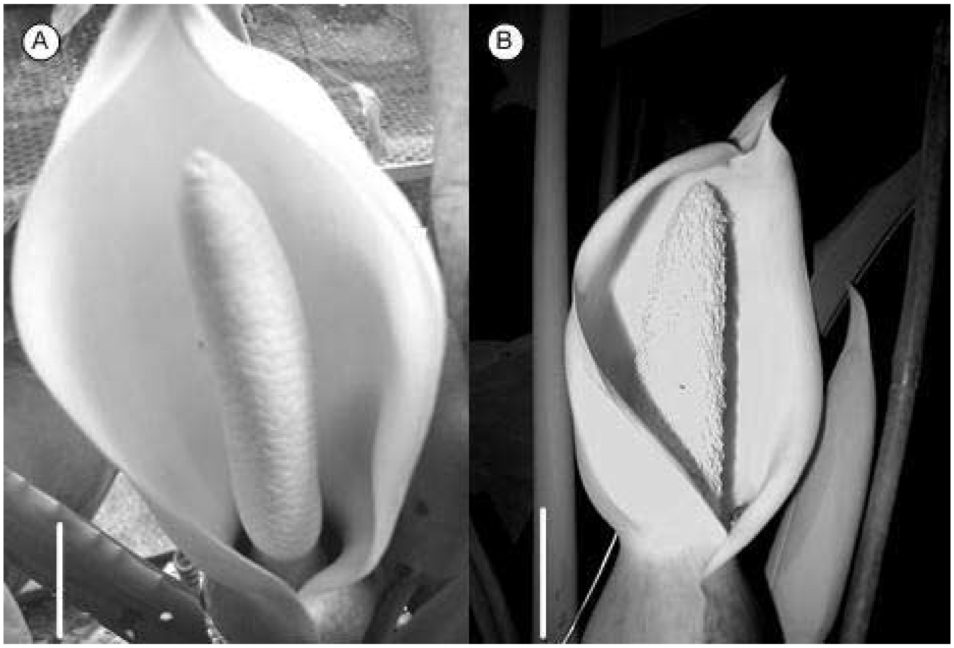
Fig. 1. (A) Inflorescence of *Syngonium schottianum* during the first day of the flowering cycle. (B) Inflorescence of *S. schottianum* during the first day of the flowering cycle. The spathe (left) has been removed from the inflorescence, and the different zones of the spadix (right) can be observed. FF, zone of female flowers; SMF, zone of sterile male flowers; MF, zone of male flowers. Scale bar = 6 cm.

Fig. 2. (A) Inflorescence of *S. schottianum* during the first day of the flowering cycle. The constricted zone of the spathe is fully open (arrow), and access to the pistillate flowers (lower zone of the spadix) is possible. (B) Inflorescence of *S. schottianum* during the third night of the flowering cycle. Filamentous pollen is released from the male zone, which falls and accumulates in the bowl formed by the constriction zone of the spathe (arrow). Scale bar = 4 cm.



Materials and methods

Syngonium schottianum Wendl. ex Schott (section *Cordatum*) is a hemiepiphyte. The four inflorescences per axil open successively at the base of the leaves. The spadix, measuring between 18.6 and 20.2 cm, is whitish and about one-third shorter than the spathe. The female flowers occupy the lower portion (2.8–3.5 cm) of the spadix, whereas the male flowers are located on its upper portion (13.8–14.2 cm). In between, there is a short intermediate zone (2–2.5 cm long) of sterile male flowers. The spathe is 22–26 cm long and green with red stripes on the tube. There is a clearly defined constriction zone at the level of the spadix between sterile and fertile male flowers (Figs. 1 and 2).

Syngonium angustatum Schott (section *Syngonium*) is a hemiepiphyte that usually grows below the tree canopy. The inflorescences, generally seven per axil, are situated in the upper part of the plant. The spadix (4–8.5 cm) is whitish and about half the length of the spathe. The female flowers occupy the lower portion (1.3–2.6 cm) of the spadix, whereas the male flowers are located on its upper portion (2.5–6.5 cm). In between, there is a short intermediate zone (0.2–0.4 cm long) of a few (8–17) closely packed sterile male flowers. The green spathe (7–14 cm long) has a constriction zone at the level of the spadix between the sterile and fertile male flowers.

This study was conducted during the fall of 2002 at the Montreal Botanical Garden and Montreal Biodôme. Individual *Syngonium* plants were monitored regularly, and the flowering cycle temperatures were recorded during the opening of the inflorescence. The temperatures of five inflorescences belonging to the same plant were measured for *S. schottianum*, as were five inflorescences of *S. angustatum* belonging to two different plants. Temperatures of the different zones of the spadix and ambient air were recorded every 20 min with two Digi-Sense® DualLogR® thermocouple thermometers. The two probes of one thermometer were inserted approximately 5 mm deep into the spadix in the middle of the fertile male and sterile male zones. The sterile male zone of *S. angustatum* was not measured because it was too thin; inserting a probe would have broken the spadix. In this species, one probe of the thermometer was inserted into the middle of the female and male zones, and the third probe was used to record ambient air temperature. Voucher specimens were deposited at the Marie-Victorin Herbarium (MT): *S. angustatum* (*Barabé* 217), *S. schottianum* (*Barabé* 212).

Results

Flowering appears to be asynchronous for the two species, with inflorescences opening successively on the same individual. The flowering cycle was a 3-day process in both species: the spathe began to open during mid-morning or early afternoon of the first day of the flowering cycle. At this time, the stigmas were already moist, and no heat production was recorded (Figs. 3 and 4). By the end of the afternoon, the upper portion of the spathe was wide open (1/2 to 2/3 of the spathe length). At this stage, the constriction zone of the spathe was broadly opened, and access to the pistillate flowers was possible (Fig. 2A). In both species, the opening of the spathe was associated with a small increase of the spadix temperature. During the second day of the flowering cycle, the spadix began to warm up and a spicy odor emanated from the inflorescence throughout the entire day. On the third day, the spathe constricted the spadix at the level of the upper sterile male flowers by slowly folding around it. By late afternoon, 1–2 h before pollen release, the lower part of the spathe was strongly constricted around the sterile zone of the spadix, and the pistillate flowers were no longer accessible, while the upper spadix part was still fully exposed (Fig. 2B). At this time, the anthers released large quantities of pollen clustered in filaments, which fell and accumulated in the bowl formed by the constriction of the spathe (Fig. 2B). The release of pollen was associated with the end of the thermogenic cycle (Figs. 3 and 4) and the production of a strong fragrance.

Because recorded data were similar between individuals belonging to the same species, only one temperature measurement is shown for each species, but the temperature values and times are means of five records per species.

In *S. schottianum,* the three zones (male, sterile male, and female) of the spadix are synchronized in regard to temperature variations (Fig. 3A). The temperatures of the fertile and sterile male flower zones peaked at 36.2 ± 0.8 °C on the evening of the second day and at 32.4 ± 3.0 °C on the evening of the third day. This second temperature increase (associated with pollen release) peaked earlier (1908 ± 0038 hours) than on the previous night (1922 ± 0015 hours). With regard to temperature differences between the inflorescence zones and ambient air (Fig. 3B), the fertile and sterile male flower zones were 16.2 ± 0.7 °C warmer than ambient air during the first peak (second night) and 12.2 ± 3.0 °C warmer during the second peak (third night). Between the two nights, the temperature of the fertile and sterile male flower zone was 5.7 ± 1.5 °C above ambient temperature. The temperature of the female flowers remained more or less constant within the floral chamber during the thermogenic cycle, following the temperature variations of fertile and sterile male zones but without any peak.

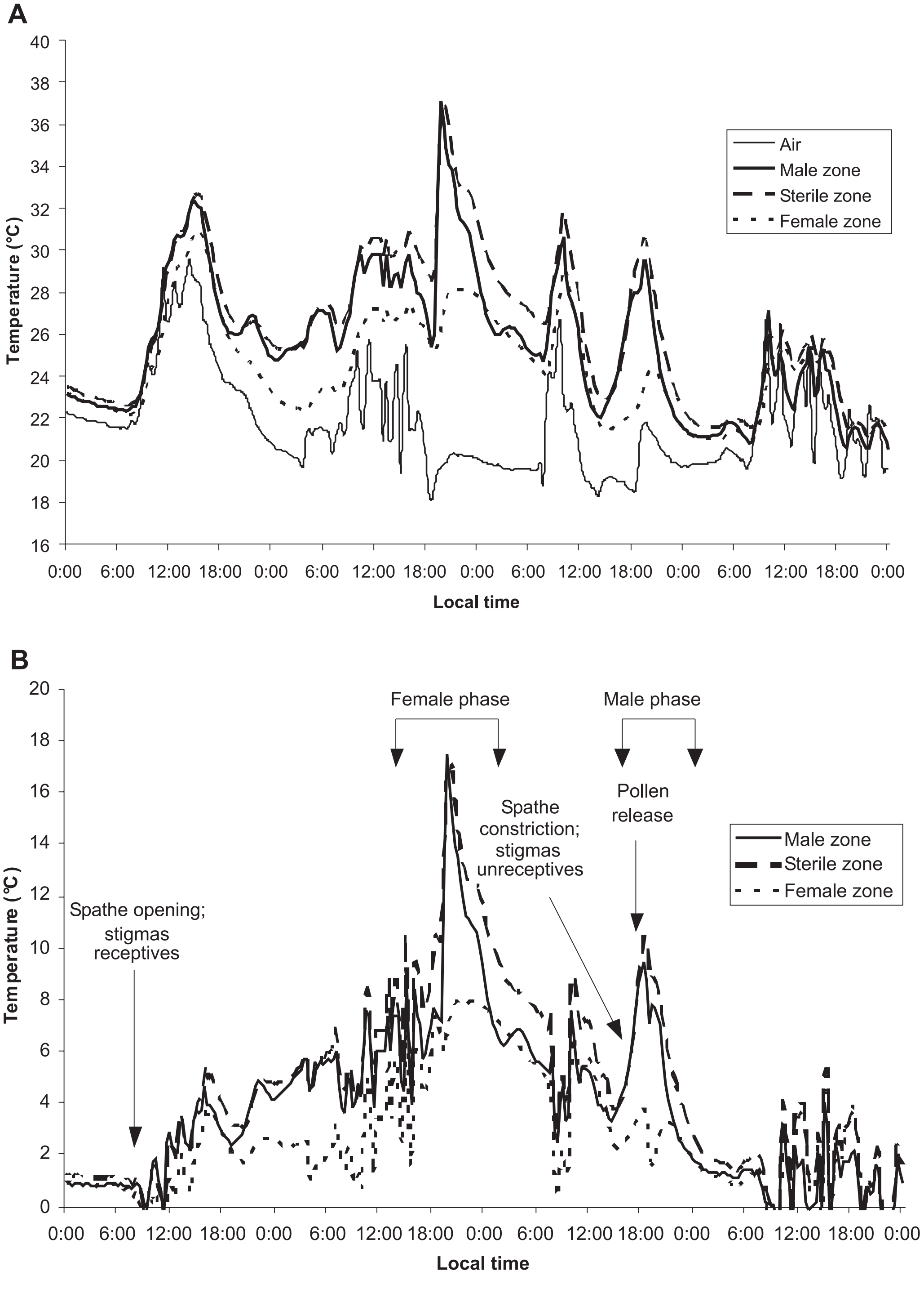
During the morning of the second day of flowering of *S. angustatum* (Fig. 4A), the temperature started to increase only in the male zone and peaked at 29.8 ± 2.7 °C (0932 ± 0056 hours). Then the male zone cooled down but remained clearly higher (2.1 ± 0.3 °C) than ambient air temperature before peaking a second time in the afternoon of the same day, at 28.4 ± 3.5 °C (1511 ± 0043 hours). Early during the night, the temperature of the male zone began to rise, peaking at 25.7 ± 0.2 °C (2158 ± 0105 hours). The male zone then cooled to 20.2 ± 0.8 °C and peaked again shortly after at 28.8 ± 0.1 °C in association with the release of pollen (0816 ± 044 hours), on the third day. The last heating peak was not very clear because of variations in ambient air temperature, which induced decreases in the spadix temperature (Figs. 4A and 4B). During the first peak, male flowers were 9.4 ± 4.7 °C warmer than ambient air and during the second peak, they were 7.6 ± 3.6 °C warmer. In the evening, the male zone rose again to 5.3 ± 0.1 °C above air temperature and still 6.2 ± 0.9 °C warmer than ambient air on the morning of the third day, when pollen was then released (Fig. 4B).

When comparing the temperature differences between the spadix and ambient air for *S. schottianum* and *S. angustatum*, two distinct patterns are revealed (Figs. 3B and 4B). For *S. schottianum* (section *Cordatum*), two clear peaks appeared early on two successive nights, and the rest of the time, spadix temperatures remained higher than ambient air (Fig. 4B). For *S. angustatum* (section *Syngonium*), inflorescence temperature peaked three times during the second day (once in the morning, again in the afternoon, and a third time before midnight) followed by a final heating peak on the morning of the third day.

Discussion

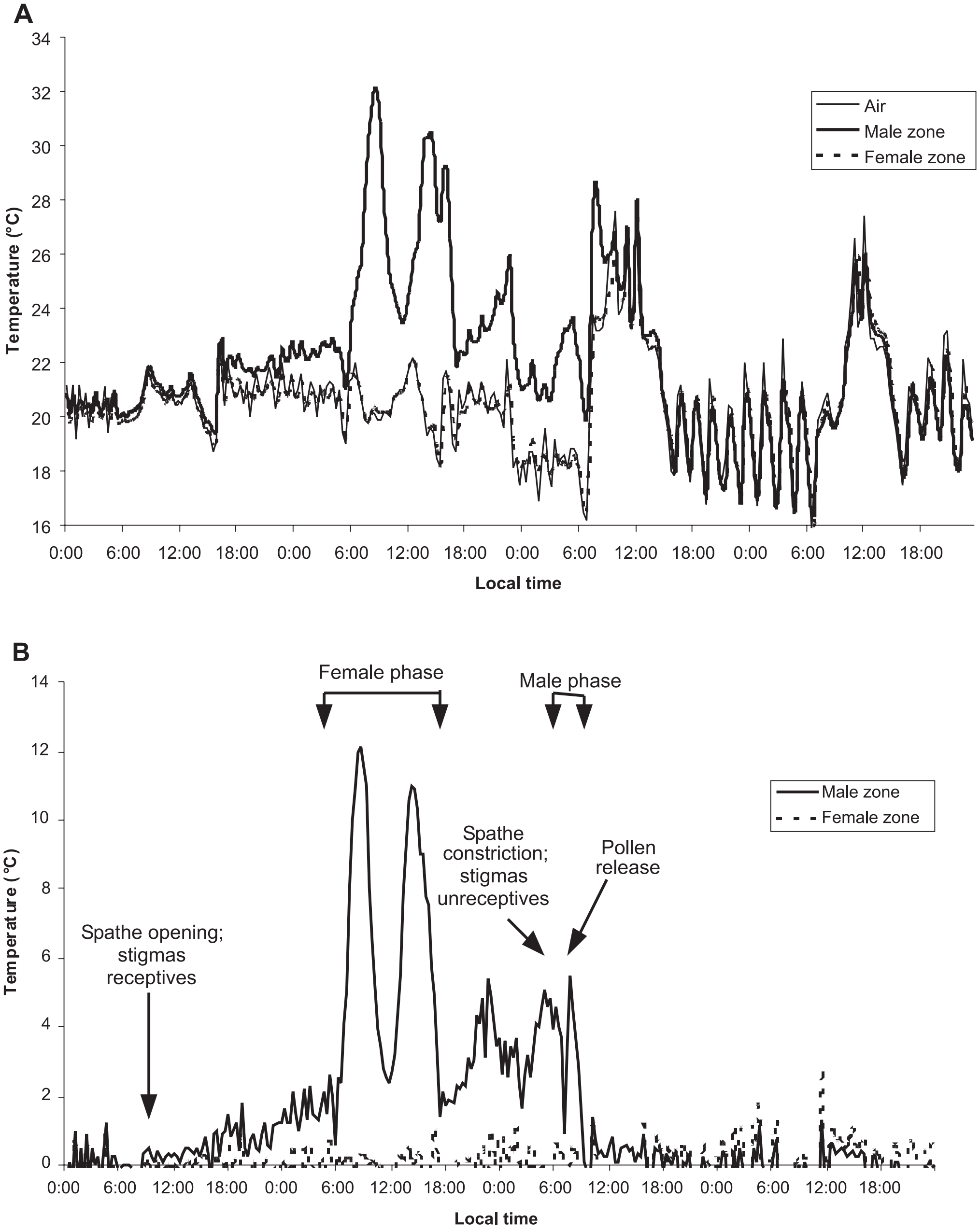
In *S. schottianum*, there is a “two peak” pattern of heat production (Fig. 3B). A peak occurs after the second sunset, followed by a “plateau” (e.g., a prolonged heating) phase,

Fig. 3. (A) Temperature curves (°C) of the male zone, the sterile male zone, the female zone, and the ambient air during 4 successive days of flowering for *S. schottianum*. (B) Curves of differences in temperature (°C) between the male zone, the sterile male zone, and the female zone, and the ambient air during 4 successive days of flowering for *S. schottianum* with information on the flowering cycle. The flowering cycle is completed during the first 3 d.



during which the temperature of the different zones (female, sterile male, and fertile male) is maintained 4–7 °C above ambient air temperature until the third night, when the second peak occurs, in association with pollen release. The "plateau" phase is not always very clear because of the rapid increase of ambient temperature before noon (Figs. 3A and 3B). The amplitude of the first peak (35–37 °C) and its occurrence under greenhouse conditions (Montréal in October–December) is in accordance with unpublished observations made by Beath (1998) on the same species at La Selva Biological Station, which is visited by beetles (supposedly *Erioscelis columbica*: Dynastinae, Scarabaeideae). At anthesis, during the second peak, Beath (1998) reported that pollinators are attracted a second time to the inflorescence to eat pollen. Observations in the field and results obtained under greenhouse conditions are thus similar.

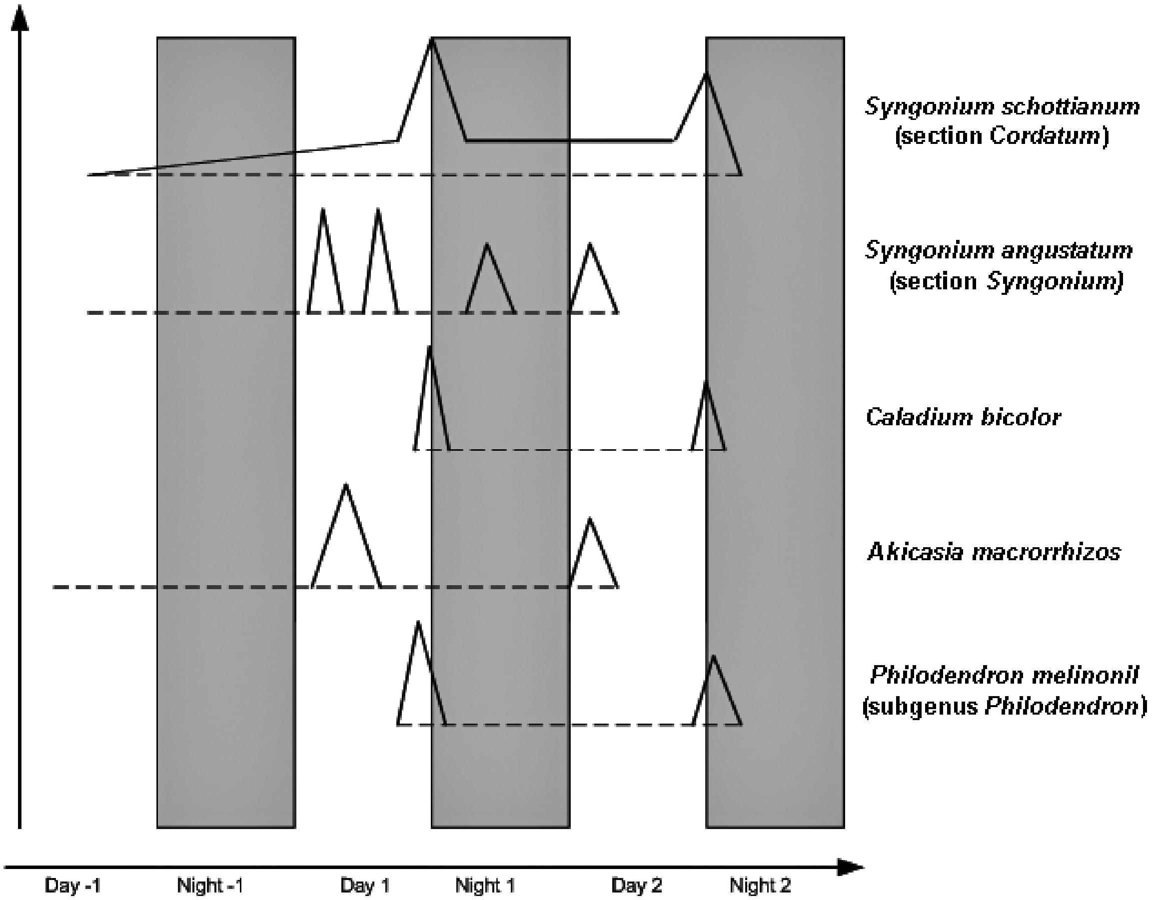
Fig. 4. (A) Temperature curves (°C) of the male zone, the female zone, and the ambient air during 4 successive days of flowering for *Syngonium angustatum*. (B) Curves of differences in temperature (°C) between the male zone, the female zone, and the ambient air during 4 successive days of flowering for *S. angustatum* with information on the flowering cycle. The flowering cycle is completed during the first 3 d.



Syngonium angustatum shows a different pattern of heat production from that of *S. schottianum*. The spadix temperature of the smaller *S. angustatum* displays a "four peak" pattern: the male zone temperature peaks three times on the second day (once in the morning, again in the afternoon, and a third time around midnight) followed by a final heating peak on the morning of the third day (Fig. 4B). As in *S. schottianum*, our results indicate that *S. angustatum* has the capacity to remain warm for a prolonged time, even if spadix size and volume are much smaller. The smaller inflorescence of *S. angustatum* releases pollen during the day when ambient air temperature is higher than at night.

In the *Syngonium* species studied, the initial heating peaks, one for *S. schottianum* and two for *S. angustatum*, may be associated with the attraction of pollinators, which arrive, potentially, carrying pollen from another plant to the female flower (Beath 1998). After this first peak, the spathe tube closes and strongly constricts the spadix above the sterile male flower zone. At this stage, only the fertile male flowers are accessible to pollinators and contrary to what has been reported for the genus *Philodendron* (Gibernau et al. 1999, 2000; Gibernau and Barabé 2002), the spathe does not loosen or open later in the flowering cycle to permit pollinators to exit the inflorescence as pollen is released. The strong constrictions of the spathe in *Syngonium* suggest that pollinators do not remain in the floral chamber throughout

Fig. 5. Schematic representation of the thermogenic cycles of *Caladium bicolor* (Maía and Schlindwein 2006), *Alocasia macrorrhizos* (Ivancic et al. 2005), *Philodendron melinonii* (Barabé et al. 2002), *Syngonium schottianum*, and *Syngonium angustatum*. Day 1 represents the time when insects arrive at the inflorescence.



the whole flowering cycle. Therefore, the *Syngonium* species studied might attract pollinators to the inflorescence a second time when pollen is released, which is consistent with the heating peak occurring in both studied species at the end of the flowering cycle. Another possibility is that pollinators leave the floral chamber before it constricts completely and stay in the bowl formed by spathe constriction until pollen is released.

The genus *Syngonium* belongs to the Caladieae tribe, which contains seven genera, including *Xanthosoma* and *Caladium* (Mayo et al. 1997; Barabé et al. 2004). When considering the floral cycle, differences appear between *Syngonium* and both *Caladium* and *Xanthosoma*. In the *Syngonium* species studied, the day before the first heating peak (in the morning) (Figs. 3B and 4B), stigmas are moist and supposedly receptive when the spathe opens. Also, at the end of the flowering cycle, the spathe constricts the spadix, preventing access to the pistillate flowers, before pollen is released (Figs. 3B and 4B). In *Caladium* and *Xanthosoma*, these two particularities of the flowering cycle are not present. The opening of the spathe and stigma receptivity in *Xanthosoma daguense* (García-Robledo et al. 2004) and *Caladium bicolor* (Maía and Schlindwein 2006) begin a few hours before or during the first heating peak, and the spathe does not constrict the spadix before pollen release as in *Syngonium*. Therefore, the flowering cycle of *Xanthosoma* and *Caladium* is different from *Syngonium* and closer to what has been found in the genus *Philodendron*, which is also pollinated by beetles (Gibernau et al. 1999, 2000; Barabé et al. 2002; Gibernau and Barabé 2002).

Surprisingly, even if they are not phylogenetically close to *Syngonium* (Barabé et al. 2004), the fly-pollinated genera *Alocasia* (Yafuso 1993; Ivancic et al. 2005) and *Colocasia* (Ivancic et al. 2004) display nearly identical flowering cycles to *Syngonium*. These genera have a flowering cycle beginning with the opening of the spathe and stigma receptivity 1 d before the first heating peak and, before pollen is released, the spathe strongly constricts the spadix thereby preventing access to the female flower zone.

The two *Syngonium* species studied are also different in their respective time of male and female attraction phases. *Syngonium schottianum* attracts pollinators (*Erioscelis columbica* according to Beath 1998) early during the second and third nights of the flowering cycle, but *S. angustatum* attracts an unknown pollinator during daylight. For both species, the two attraction phases (associated with heating peaks) on 2 successive days (during the night for *S. schottianum* and the day for *S. angustatum*) are synchronized and nearly overlap (Figs. 3 and 4), facilitating pollinator movement from male-stage inflorescences to female-stage ones.

When comparing thermogenic cycles of *Syngonium* with the genera mentioned earlier (Fig. 5), it appears that *S. schottianum* has a cycle similar to *Caladium bicolor* and the *Philodendron* subgenus *Philodendron*, which are both night-pollinated by beetles (Gibernau et al. 1999, 2000; Barabé et al. 2002; Gibernau and Barabé 2002). However, the smaller *S. angustatum* with its four heating-peaks pattern (Fig. 5) has a cycle different from that previously identified in Aroids. The female (first two peaks) and male attraction phases (last peak) occur during the morning (daylight), as in *Alocasia macrorrhizos* (Ivancic et al. 2005), *Alocasia odora* (Yafuso 1993), and *Colocasia esculenta* (Ivancic et al. 2004), which are all pollinated by flies.

We hypothesize that *S. angustatum* is pollinated by day-active insects like flies, although no neotropical aroid is known to be pollinated by flies (Gibernau 2003); or by a day-active beetle, as is the case in palms (Núñez et al. 2005). Our work suggests that *Syngonium* has two apparently different pollination syndromes. This conclusion must be verified through field studies.

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