

Flowering period, thermogenesis, and pattern of visiting insects in *Arisaema triphyllum* (Araceae) in Quebec

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Abstract: Jack-in-the-Pulpit (*Arisaema triphyllum* (L.) Torr.) is a perennial forest herb of southern Canada and the eastern United States. The flowering periods of male and female inflorescences in relation to the temperature of the inflorescence and the activity pattern of visiting insects were studied in one population in western Montreal Island (Quebec, Canada). The flowering period of *A. triphyllum* was long (20 d in male and female plants), which is unusual in temperate Aroideae. This floral trait could have evolved secondarily as an adaptation to increase pollination efficiency under highly variable weather conditions at high latitude. In male and female plants, no significant temperature increase of the appendix was recorded. The warming effect of sunlight during the day could be sufficient for the emission of the attractive odour. Two Dipteran families, the Mycetophilidae and the Cecidomyiidae, were the most frequent insect visitors of *A. triphyllum*. Our observations showed that odour production is linked with the pollination activity beginning with insect visits.

Key words: appendix temperature, temperate climate, long flowering period, latitudinal gradient, Mycetophilidae, Cecidomyiidae.

Résumé : Les périodes de floraison des inflorescences mâles et femelles du petit pêcheur (*Arisaema triphyllum* (L.) Torr.) ont été étudiées dans une population située dans l'ouest de l'île de Montréal (Québec, Canada). La période de floraison d'*A. triphyllum* est longue (20 jours pour les inflorescences mâles et femelles) contrairement aux autres Aroideae tempérées. Ce trait floral pourrait avoir évolué secondairement comme une adaptation pour augmenter l'efficacité de la pollinisation sous une latitude plus nordique, là où les conditions climatiques sont très variables. Aucune augmentation significative de la température de l'appendice n'a été enregistrée chez les plants mâles et femelles. Le réchauffement solaire durant la journée pourrait être suffisant pour provoquer l'émission d'une odeur attractive. Deux familles de diptères, les Mycetophilidées et les Cecidomyiidées, représentent les principaux insectes visiteurs d'*A. triphyllum*. Nos observations démontrent que la production d'odeur commence avec le début de la période d'activité des insectes visiteurs.

Mots-clés : température appendice, climat tempéré, longue période florale, gradient latitudinal, Mycetophilidae, Cecidomyiidae.

Introduction

The genus *Arisaema* Mart., a member of the Arum lily family (subfamily Aroideae), contains about 200 species mainly distributed throughout Asia (Gusman and Gusman 2002). In North America, *Arisaema* is represented by three species: *Arisaema triphyllum* (L.) Torr., *Arisaema dracontium* (L.) Schott, and *Arisaema macrospatum* Benth., which is endemic to Mexico (Dieringer and Cabrera 2000). *Arisaema triphyllum*, the species of interest, is a perennial forest herb and typically grows in the understory of forests in southern Canada and the Eastern United States (Bierzychudek 1981).

The inflorescence of *A. triphyllum* consists of a central axis called the spadix, surrounded by the spathe (e.g., modified bract). The basal part of the spadix bears the reproductive organs. The inflorescence can be male (with male flowers only), bisexual (with both male and female flowers), or female (with female flowers only) (Treiber 1980; Bierzychudek 1981; Gusman and Gusman 2002). The upper part of the spadix is the appendix, a specialized sterile structure, which in other Araceae produces heat and releases odour (e.g., osmophore) to attract insect pollinators (Meeuse and Raskin 1988). The spathe is composed of a tubular portion overtopped by a spathe limb. Contrary to other genera with unisexual flowers (e.g., *Alocasia*, *Arum*, *Syngonium*, *Xanthosoma*), there is no constriction of the spathe to form a closed floral chamber.

The flowering period in *A. triphyllum* ranges from 15 to 35 d (Rust 1980). Such a long flowering period is rare in the subfamily Aroideae (species with unisexual flowers) and only known to occur in *Arisarum* (Herrera 1988) and *Ambrosina* (Killian 1929). Contrary to *Arisaema*, most of the genera of the Aroideae, such as *Arum*, *Alocasia*, *Amorphophallus*, *Caladium*, *Colocasia*, *Helicodiceros*, *Peltandra*, and *Theriophonum* have a short flowering period (2–5 d)

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(Yafuso 1993; Patt et al. 1995; Kite et al. 1998; Seymour et al. 2003; Ivancic et al. 2004; Sivadasan and Kavalan 2005; Maia and Schlindwein 2006). In Araceae, a long flowering period is generally characteristic of genera with bisexual flowers such as *Anaphyllopsis* (Chouteau et al. 2006), *Anthurium* (Croat 1980), or *Symplocarpus* (Wada and Uemura 2000).

During their flowering period, many inflorescences of Araceae produce heat, a phenomenon called thermogenesis, which is described as a significant increase in the temperature of plant tissues. Thermogenic tissues release heat instead of producing ATP through a mitochondrial alternative cytochrome pathway, the cyanide-insensitive respiration pathway (Vercesi et al. 2006).

The heat is produced by the upper part of the spadix, which can be fertile (e.g., stamens) as in *Philodendron* species or sterile (e.g., appendix) as in the genus *Arum*. Increases in inflorescence temperature have been studied in many genera of Aroideae with unisexual flowers, *Alocasia*, *Arum*, *Caladium*, *Colocasia*, *Dracunculus*, *Heliconia*, *Homalomena*, *Philodendron*, and in a few genera with bisexual flowers, *Anthurium* (subfamily Pothoideae), *Monstera* (subfamily Monsteroideae), and *Symplocarpus* (subfamily Orontioideae) (Yafuso 1993; Bermadinger-Stabentheiner and Stabentheiner 1995; Seymour and Schultze-Motel 1999; Barabé and Gibernau 2000; Gibernau and Barabé 2000; Barabé et al. 2002; Albre et al. 2003; Seymour et al. 2003; Angioy et al. 2004; Ivancic et al. 2004, 2005; Seymour 2004; Maia and Schlindwein 2006).

In general, in Aroids, the scent produced during the flowering period is volatilized and released during the increase in temperature of the inflorescence (Skubatz et al. 1996; Angioy et al. 2004). Scent production is generally linked with pollination and pollinator attraction in the Araceae family. It has been postulated that *Arisaema* species do not produce significant heat, even if a noticeable odour is emitted (Vogel and Martens 2000).

In the Araceae family, the length of the flowering period corresponds with a particular thermogenic pattern. From this perspective, we analyzed the flowering period of *Arisaema triphyllum* in relation to the temperature of the inflorescence. We were interested in recording the temperature of the appendix of *A. triphyllum* under natural conditions, because no study has recorded the spadix temperature in *Arisaema* species. This question deserves attention, since *A. triphyllum* is characterized by a long flowering period that distinguishes it from most other species with unisexual flowers whose thermogenesis period has been documented. To elucidate the relationship between inflorescence temperatures and period of anthesis, the activity of insect visitors in relation to the flowering period was also recorded. The main goals of this study were to characterize male and female *Arisaema triphyllum* plants in terms of (i) flowering period, (ii) pattern of appendix temperature in relation to flowering period, and (iii) insect activity in relation to anthesis.

Materials and methods

Study site

This study was conducted between May and August 2005 on one population of *A. triphyllum* situated in Angell Woods

near Beaconsfield (45°26.069'N; 073°53.518'W) in the western part of the island of Montreal (Quebec). The study area (200 m²) is an *Acer* (maple) grove consisting of more than 500 mature individuals. A specimen of the studied population was collected and deposited at the Marie-Victorin Herbarium (MT): *A. triphyllum* (Barriault 25).

Flowering period and odour production

The sequence of the flowering period and odour production were studied under natural conditions; spadix temperature and visitation pattern of insects were also recorded in the same plants ($N = 15$ plants for both gender). The flowering period began when the spathe opened and ended with its fading. For male plants, pollen release was observed from its beginning until its completion. We considered the release of pollen complete when all stamens had released their pollen. Stigma receptivity was estimated by close visual examination of stigma morphology and odour production by "smelling" the inflorescence.

Temperature measurements

Six plants (three males and three females) were studied during the entire flowering period. The temperature measurements were made on a daily basis under natural conditions, from 6 to 26 May 2005. Temperatures were recorded every 10 min with a Digi-Sense® DualogR® thermocouple thermometer (Everett, Wash.) for the plant organs and an Onset Hobo temperature logger for the ambient air. To measure spadix temperature, one probe of the thermometer was inserted about 3 mm deep at one-third of the appendix height. The probe was inserted when the spathe was still closed, and the tubular spathe was perforated to insert the probe. The other probe of the thermometer was inserted at the midpoint of the petiole height, a nonthermogenic plant tissue. Moreover, during the spring of 2005, to minimize the effect of sunlight on plant temperature, inflorescences were hidden under cardboard for the entire duration of the experiment. The differences in temperature between appendices, petioles, and ambient air were analyzed by paired t tests (Systat 8 2004).

Insect visitation pattern

Frequency of insect visits was observed daily for 159 plants (79 males and 80 females) from 6 to 27 May 2005 in Angell Woods. Each inflorescence was checked several times daily for insect presence within the spathe. It is important to note that insects were not captured in the floral chamber and could escape through the top of the spathe tube. The small hole at the base of the male inflorescence was closed with duct tape to prevent insects from escaping by this hole and to delay their departure from the tubular spathe. The insects present in the spathe tube were collected with a brush, preserved with 70% alcohol, and identified to the family level for Dipteran specimens (following McAlpine et al. 1981) and at the order level for others. All insects identified were deposited at the Collection entomologique Ouellet-Robert at the Université de Montréal. Differences in insect activity (i.e., insect abundances) were analyzed by a Mann-Whitney test taking into account the floral phase of the sampled inflorescences (Systat 8 2004).

Results

Flowering period

The inflorescence dimensions in the populations studied had an average length of 5.3 cm for the spadix, while the sterile appendix was, respectively, 3.8 cm long and 0.4 cm wide. The spathe of male and female plants opened during the morning. For male inflorescences, the release of pollen occurred within 2 d after the opening of the spathe (mean \pm SD, 1.6 ± 1.3 d; range, 0–4 d). The anthesis phase lasted on average 7 d until the complete release of pollen (6.8 ± 1.8 d; range, 5–10 d) and about 20 d before the spathe faded (19.7 ± 6.1 d; range, 11–26 d). The release of pollen almost always began in the middle of the stamen zone, and spread progressively downwards and upwards. The flowering period of female inflorescences was comparable to that of males and lasted about 20 d from spathe opening to fading (19.7 ± 5.3 d; range, 13–26 d). According to field observations, the morphology of stigmas changed after 13 d from papillose to granulose and became brownish 3 d later. At the time when the spathe faded, the stigmas were completely dried up. These observations suggest that stigma receptivity might last between 13 and 16 d.

Temperature records

We recorded the temperature of the appendix and the petiole, as control, representing a nonthermogenic tissue. Since no obvious temperature pattern was recorded, temperatures were averaged for two periods, that is, daylight (0610–1800) and night (1810–0600) corresponding approximately with light and dark periods (Fig. 1).

The temperature differences were significant between the ambient air and the mean night temperatures (1810–0600 h) recorded for all the six appendices and petioles ($5.09 < t < 11.52$; $df = 17$; $P < 10^{-3}$). But, the ambient air temperatures were always higher than the appendix and petiole temperatures, indicating no significant plant temperature increase during the night (Fig. 1).

There were no temperature differences between ambient air and mean daylight temperatures (0610–1800 h) of the appendices and petioles of one male and two female inflorescences ($-1.96 < t < -1.51$, $df = 12$; $P > 0.06$). The temperature differences between ambient air and the appendices of other plants studied (two males and one female) ranged from 0.25 to 0.57 °C and were significant ($-4.58 < t < -2.47$; $df = 12$; $P < 0.028$), although not when considering temperature differences between the appendix and the petiole ($-2.03 < t < 0.845$; $df = 12$; $P > 0.058$). Finally, temperature differences decreased (Fig. 1) on rainy days (14–16 and 21–23 May).

Odour production

Male and female inflorescences released a fragrance similar to ozone or mushrooms. The odour was not produced by all plants. It appears that odour was randomly released across male and female plants of the population of *A. triphyllum*; however, female inflorescences released a fragrance over a longer period, i.e., until the end of the flowering period. Moreover, odour production was not related to weather conditions, odour being perceptible even on rainy days (14–16 and 21–23 May). The plants started to

release an odour on 11 May. This event corresponded with the beginning of insect visits. After this, odour production was discontinuous until the spathe faded for a specific individual. However, we could smell the fragrance throughout the flowering period across the population.

Insect visitation

Only 133 insects were collected during 6983 inflorescence surveys (3472 on male and 3511 on female inflorescences). The insect visitors of *A. triphyllum* included Dipteran families such as Mycetophilidae, Sciaridae, Cecidomyiidae, Chironomidae, Empididae, and Chaoboridae; one species of Thysanoptera, *Heterothrips arisaema* Hood; and insects of orders Collembola, Hemiptera, Coleoptera, Homoptera, Psocoptera, Neuroptera, and Hymenoptera. We have represented the activity pattern of the most abundant insects: two Dipteran families (Mycetophilidae and Cecidomyiidae), the Thysanoptera, *H. arisaema*, and Coleoptera (Fig. 2). Other insects were represented by a total of nine or fewer individuals each. The four major groups of visiting insects represented 77% of the 133 insects collected in male and female inflorescences (Fig. 2).

Before the start of odour release by the inflorescences (11 May), no dipteran visitors were observed within the spathes (Fig. 2). In the population of *A. triphyllum* studied, two peaks of insect activity were recorded (Fig. 2). The first peak was represented by Mycetophilidae and occurred 11–12 May. The second peak of insect activity, 15–17 May, was mainly due to the Cecidomyiidae. May 16 corresponded with the end of pollen release (Fig. 2).

Interestingly, 67% of the collected insects were attracted during the period of pollen release, and the insect activity dropped drastically the day after the end of pollen release (Fig. 2). On average, 8.6 insects per day were collected in the inflorescences during the 8 d of pollen release, and only 3.4 insects per day were collected in the inflorescences during the following 10 d. This difference of insect activity was significant ($U = 66$, $P = 0.02$). There is no clear pattern of the influence of climate conditions, such as maximum temperature and rain, on insect activities.

Discussion

Flowering period

The flowering period of *A. triphyllum* is much longer (20 d) than that of many other Aroid genera of temperate climate zones with unisexual flowers, such as *Arum*, *Dracunculus*, *Helicodiceros*, and *Peltandra*, whose flowering periods last between 2 and 5 d (Patt et al. 1995; Seymour and Schultze-Motel 1999; Albre et al. 2003; Seymour et al. 2003). However, it is comparable with those of two closely related Mediterranean genera, *Arisarum* and *Ambrosina*, also belonging to the subfamily Aroideae (Killian 1929; Koach and Galil 1986; Herrera 1988; Barabé et al. 2004). In fact, long flowering periods such as that found in *Arisaema* are very rare in the derived Aroideae subfamily, while they appear to be common in genera belonging to the early-diverged subfamilies Orontioideae (*Lysichiton*, *Symplocarpus*) and Pothoideae (*Anthurium*). For example, flowering in *Anthurium* (Croat 1980) and *Symplocarpus* (Wada and Ue-

Fig. 1. The difference between the mean temperatures of male appendices (3) and female appendices (3) and petioles with ambient air recorded from 6 to 26 May 2005, in natural conditions at Angell Woods. The period of insect activity occurred between 10 and 27 May.

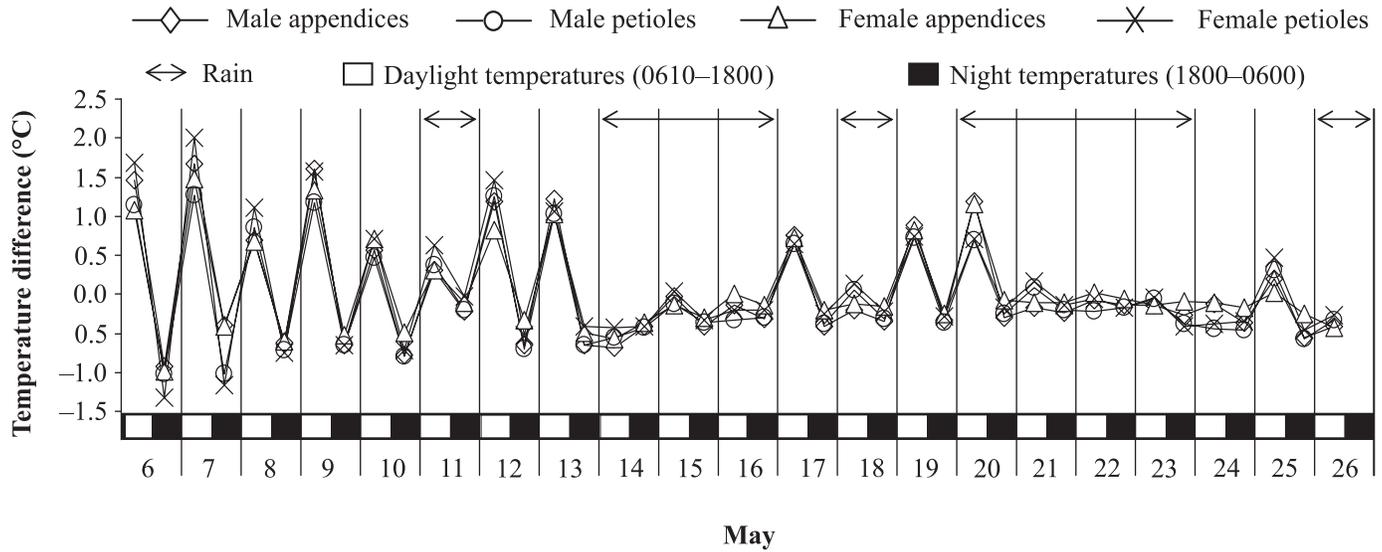
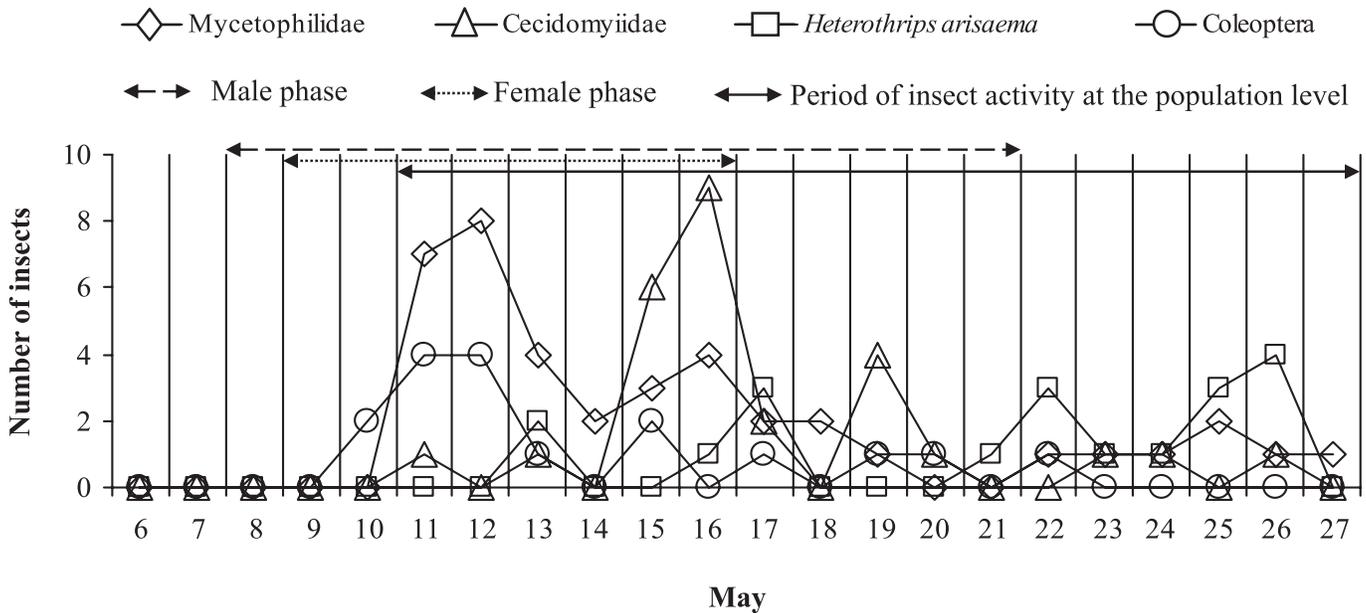


Fig. 2. Pattern of insect activities across the flowering period of the four major “groups” of visiting insects representing 77% of the 133 insects collected between 6 and 27 May 2005, in male and female inflorescences at Angell Woods.



mura 2000) lasts more than 2 weeks and around 10–14 d in *Lysichiton* (Pellmyr and Patt 1986).

The long blooming period in *Arisaema*, *Arisarum*, and *Ambrosina* may have evolved secondarily among short flowering clades and may be an adaptation to maximize pollination efficiency for taxa flowering in highly variable weather conditions while colonizing new habitats at high latitude and (or) altitude (*Arisaema*). This adaptation may also increase pollination efficiency for taxa flowering during winter (*Arisarum*, *Ambrosina*). Climate conditions can change drastically from one day to the next (e.g., frost), and consequently the activity of pollinating insects varies drastically. *Arisarum vulgare* Targ.-Tozz. and *Arisarum simorrhinum* Durand flower from October or December to

March, and their anthesis lasts, respectively, 3–4 weeks and 20–40 d (Koach and Galil 1986; Herrera 1988). Similarly, *Ambrosina bassii* L. flowers from October to January with an anthesis of 4–5 weeks (Killian 1929). The long flowering period in *Arisaema* appears to converge with that of *Symplocarpus* growing in the same region. If this hypothesis was true, we would expect to find a tendency for tropical *Arisaema* to have shorter flowering periods than temperate species. In fact, the flowering period of tropical *Arisaema* species such as *Arisaema leschenaultii* Blume, *Arisaema ciliatum* H. Li, or *Arisaema tortuosum* (Wall.) Schott lasts between 7 and 14 d (Barnes 1935; Vogel and Martens 2000). On the contrary, temperate species such as *Arisaema speciosum* (Wall.) Mart., *Arisaema consanguineum* Schott, *Ari-*

Table 1. Descriptions of *Arisaema triphyllum* populations studied in relation to the duration of individual flowering period: geographical location, source, latitude, and durations of male and female floral phases.

Site	Source	Latitude	Male phase	Female phase
Canada, Quebec	This study	45°26'69"N	20 d	20 d
US, Michigan	Cook (2004)	45°30'48"N	22–25 d	25 d
US, New York	Bierzuchudek (1981)	42°26'54"N	Shorter than female	2–3 weeks
US, Delaware	Rust (1980)	39°39'56"N	15–25 d	20–35 d
US, North Carolina	Treiber (1980)	35°54'40"N	5–11 d	8–17 d

saema erubescens (Wall.) Schott, or *Arisaema amurense* Maxim. appear to have longer flowering periods, lasting from 19 to 30 d, and are thus comparable to *A. triphyllum* (Vogel and Martens 2000).

On a regional scale, variations in the duration of the flowering period also seem to occur. In the population of *Arisaema triphyllum* studied, the duration of the flowering period was similar in male and female inflorescences (20 d, Table 1). This result differs from other published studies (Rust 1980; Treiber 1980; Bierzychudek 1981), where the flowering period of male inflorescences was shorter than that of females (Table 1). Only one study (Cook 2004) of two populations in Michigan showed results similar to ours (Table 1). We can hypothesize that the duration of the flowering period could vary according to population location (i.e., latitude) and climatic conditions. Such latitudinal variations have been documented in relation to plant size, number of male flowers, and expression of female flowers in *Arisaema dracontium* (L.) Schott (Dieringer and Cabrera 2000) and could also be true for the duration of flowering. Interestingly, the same phenomenon also occurs in *Lysichiton americanus* Hultén & H. St. John, another North American aroid, as the duration of the flowering period for male and female phases for a population studied in Alaska was longer than that of a population studied in Seattle (Pellmyr and Patt 1986; Willson and Hennon 1997).

Temperature records

No significant difference in temperature was recorded from six inflorescences (three males and three females) of *A. triphyllum*. Recording a thermogenic activity under natural conditions can be biased by variations because of the warming effect of sunlight. Consequently, shading and controlling spadix temperature differences with a nonthermogenic organ such as the petiole becomes primordial. It is important to note, that no temperature difference does not imply absence of heat production, since evaporative heat losses can be sufficient to nullify any temperature increase (Seymour and Schultze-Motel 1999). The absence of heat production by the spadix of *A. triphyllum* could be explained by the fact that the appendix tissue includes only few starchless cell layers, suggesting insufficient energy resources for thermogenesis (Vogel and Martens 2000). To date, very few studies of thermogenic activity in North American Araceae have been published. *Symplocarpus foetidus* (L.) Nutt. appears to be the only other North American Araceae exhibiting a thermogenic activity (Seymour 2004). The inflorescences of *Peltandra virginica* (L.) Kunth do not produce any significant temperature increase (Thompson 1995), and no data are available on thermogenesis in *L. americanus* and *Calla palustris* L.

Odour and activity pattern of insects

The odour produced by the population of *A. triphyllum* at Angell Woods is similar to that described by Vogel and Martens (2000) and reminiscent of ozone. According to Vogel and Martens (2000), the odour release follows no pattern and occurs during anthesis. Moreover, fragrance release begins after spathes unfold and varies according to the species (Vogel and Martens 2000). Our observations showed that odour production is linked with the pollination activity initiating insect visits. Fragrance was not continuous throughout the flowering period but occurred occasionally until the end of the flowering period. It is possible that fragrance volatilization requires little additional heat or that solar radiation may be sufficient to initiate the process.

Dipteran insects were the major group of insect visitors in the studied population of *A. triphyllum*, and in particular two families, the Mycetophilidae (fungus gnats) and the Cecidomyiidae (gall gnats). Mycetophilidae have been cited as pollinators of *A. triphyllum* (Treiber 1980; Bierzychudek 1981), and pollination by fungus gnats could be an adaptation to moist, cool, shaded habitats where the flowering period occurs during late winter and spring (Goldblatt et al. 2004). Further study will be necessary to determine the pollination efficiency of the different insect visitors in relation to the reproductive success of *Arisaema triphyllum* in Quebec.

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