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Pollination ecology of *Arum italicum* (Araceae)

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The pollination ecology of *Arum italicum* was studied in south-western France. This plant attracts olfactory dung-breeding flies through deceit. These insects are principally represented by Diptera, all belonging to saprophyte families. The volatilization of the odouriferous compounds, responsible for their attraction, is achieved through the production of heat by the appendix. The insects are trapped for 24 h in order to participate in both sexual phases of the protogynous inflorescence. The male flowers produce three heat events during flowering. These peaks of heat seem to be involved in the spathe movements, since they occur during the opening of the inflorescence and the liberation of the insects. The last male heat event may be linked with the liberation of pollen and its dispersion by stimulating trapped flies. According to their frequency and pollen-load, two *Psychoda* species appear to be the most efficient pollinators (*P. crassipenis* and *P. pusilla*). Nevertheless, each of the other attracted species could play a significant role under different spatio-temporal conditions. Experiments on self-pollination have shown that obligate cross-pollination is necessary for *A. italicum* to set seeds. Moreover, hand- and natural-pollinated plants showed similarly high abortion frequencies suggesting that seed set may be more constrained by resources rather than by pollination limitation.

ADDITIONAL KEYWORDS: fructification – inflorescence – pollinator – *Psychoda* – seed set – thermogenesis.

INTRODUCTION

In order to increase encounters between pollinators and flowers, e.g. pollination efficiency, entomophilous plants have developed several attractants, such as colours and odours (Proctor, Yéo & Lack, 1996). Some plant families are specialized in attracting insects that have the same ecological habit. For example, various flowers mimic the brood site (appearance, odour) of their pollinators, but do not give any reward in return. This pollination system by deception is called 'sapromyiophily' when it involves insects (mainly Diptera) associated with decaying organic matter (Proctor *et al.,* 1996). One of the first examples studied was *Arum nigrum* (Araceae), which attracts dung flies and carrion beetles (Knoll, 1926; Dormer, 1960). Today, sapromyiophily is known in Araceae, Aristolochiaceae, Asclepiadaceae and Orchidaceae species (Proctor *et al.*, 1996). Moreover, these species, except orchids, trap the attracted insects in their flowers or inflorescences for several hours or days. The flowers or inflorescences being protogynous, the insects thus participate in both the male and female phases of the same flower. Insects are attracted during the female phase (ovule fertilization) and released hours or days later during the male phase (pollen release). *Arum* species (Araceae) trap their pollinators because of their particular morphology and organization of their inflorescences. Fertile male and female flowers are enclosed in a floral chamber at the base of the spathe. This chamber is closed in its upper part by horizontal hairs (e.g. modified sterile male flowers). Attracted insects fall into the floral chamber when only the female flowers are receptive, but cannot escape because of the hairs. The next day, after the emission of pollen, these hairs wither, allowing the insects loaded with pollen to escape. Pollination in the genus *Arum* has mainly been studied for species from south-eastern Europe and the Middle East, such as *A. concinnatum*, *A. creticum*, *A. dioscoridis*, *A. elongatum*, *A. hygrophilum*, *A. nigrum*, *A. orientale*

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*Corresponding author. E-mail: gibernau@cict.fr and *A. purpureospathum* (Knoll, 1926; Kullenberg, 1953; Braverman & Koach, 1982; Koach & Galil, 1986; Drummond & Hammond, 1991, 1993). For western Europe, the pollination ecology of only one species has been intensively studied: *A. maculatum* (Prime, 1960; Lack & Diaz, 1991; Ollerton & Diaz, 1999). It appears from these studies that *A. maculatum* is pollinated only by *Psychoda phalaenoides* females (Diptera, Psychodidae). The flies are attracted during the female phase by a warm and odouriferous inflorescence, which mimics their brood site odour, in particular by emitting compounds such as *p*-cresol or 2-heptanone (Bermadinger-Stabentheiner & Stabentheiner, 1995; Kite, 1995; Kite *et al*., 1998).

The aim of this paper is to document the pollination ecology of *Arum italicum* in southern France. Though many studies have been conducted on the reproductive system of *A. italicum* (Mendez & Obeso, 1992, 1993; Mendez, 1997, 1998, 1999, 2001; Mendez & Diaz, 2001), very little is known about its pollination. During the 19th century, Arcangeli (1883) found that, in southern Europe, a wide range of midges and gnats were attracted to *A. italicum* ssp. *italicum*. But the most abundant visitors were *Psychoda nervosa*, a dung-breeder, and *Sciara nitidicollis*, a fungus-gnat. In the same way, *A. italicum* ssp. *neglectum* from continental Europe attracted mainly *P. nervosa*, but also diverse Diptera species (*Sciara nitidicollis*, *Ceratopogon pictellum*, *Chironomus byssinus*, *Drosophila funebris*, *Limosina pygmaea*; Prime, 1960). More recently, Mendez & Obeso (1992) found that the pollinators of *A. italicum* were principally undetermined Nematocera (Diptera), of which 87% were Psychodidae and 5.6% Ceratopogonidae.

It appears from these studies that inflorescences of *A. italicum* are visited by various flies whereas *A. maculatum* seems to be specifically pollinated by females of *Psychoda phalaenoides*. In this paper, we will first compare our data to previous studies on *A. italicum* in order to confirm if this species has a 'generalist' pollination system. Then we will compare the pollination system of *A. italicum* with that of *A. maculatum*, a closely related and specialized species. Finally, a hypothesis on specialization in the pollination systems of western European *Arum* species (*A. italicum* and *A. maculatum*) will be discussed.

MATERIAL AND METHODS

In the spring of 2001, a natural population of *Arum italicum* Miller was studied in a wood on the campus of the Paul Sabatier University of Toulouse (south-western France). Another population located 20 km away, in Montgiscard, was also sampled to collect inflorescence visitors. This population was situated along a small country road. Statistical analyses were performed using Statistix 4.1 (1985) and GLIM (1986) software.

We recorded the number of female flowers per inflorescence ($N = 64$) and ovules per female flower ($N = 32$). The number of fruits per infructescence and seeds per fruit were counted on 57 infructescences. The number of female flowers, fruits and seeds were also recorded on 11 inflorescences and 11 infructescences of *Arum maculatum* L., sampled in the Pyrénées (Lourdes, France). In order to determine the reproductive system of *A. italicum*, two experiments were performed. Firstly, we tested spontaneous selfing by bagging 20 inflorescences with organdie bags before their opening. Secondly, we hand-pollinated, using a small paint-brush, 13 receptive inflorescences with fresh pollen harvested from male phase inflorescences located several metres away from the pollinated plants. Fruit and seed sets were calculated for these two treatments as well as for open-pollinated inflorescences ($N = 155$).

The insects trapped in inflorescences on the University campus ($N = 142$) and in Montgiscard ($N = 32$) were collected between 23 March and 21 May, 2001. Visiting insects were preserved in 70% alcohol and identified. For each inflorescence, *Psychoda* were sexed in order to estimate their sex-ratio (female/(female + male)). To determine the efficiency of each species as pollinators, pollen loads were quantified. Several flies representing the different taxa of insect visitors were caught live and killed through freezing ($N = 51$). The number of pollen grains carried were estimated according to the body zone (head, thorax, abdomen, wings, and legs), using four classes of abundance: (0) 0 Pollen Grains (PG), (1) 1–5 PG, (2) 6–20 PG, (3) > 20 PG. Afterwards, these pollen-load estimations were compared between species and body zone, using a Poisson error (category data; GLIM, 1986).

The thermogenesis of *A. italicum* was studied by measuring the temperatures of six inflorescences belonging to different plants. Temperatures of the three different zones of the spadix (appendix, male and female flowers) and the ambient air were recorded every 10 min with four probes connected to two Digi-Sense® DualLogR® thermocouple thermometers. The two probes of one thermometer were inserted less than 5 mm deep into the fertile male and female zones. One probe of the second thermometer was inserted into the middle of the appendix, whereas the second one was used to record the ambient air temperature near the studied inflorescence. The probes were placed when the inflorescences were still closed, when possible 1 day before the spathe unfolded. On the final inflorescence, the temperature of the floral chamber was recorded by inserting one probe through the spathe at the level of the female flowers, the second probe measuring the air temperature.

RESULTS

REPRODUCTIVE SYSTEM

An inflorescence of *A. italicum* contained on average 61 female flowers, and 25 for *A. maculatum* (Table 1). As *A. italicum* female flowers contained 5.4 ± 2 ovules (range: 2–10), an inflorescence was estimated to produce 330.6 ± 227 potential seeds (47–835). In fact, *A. italicum* developed about 41 fruits and 83 seeds per infructescence vs. 16 fruits and 18 seeds for *A. maculatum* (Table 1). Moreover, the percentage fruit sets of *A. italicum* and *A. maculatum* were similar (67.8% and 62.5%, respectively).

In natural conditions, very few inflorescences of *A. italicum* (16.1%) produced infructescences (Table 2), with an average of 41 mature fruits (range: 3–94). Each fruit or berry contained an average of 1.8 developed seeds, which represented a mean of about 83 seeds per infructescence (Table 2). Thus, natural pollination of a single inflorescence results in the maturation of about two-thirds of the female flowers and only 25% of the potential seeds (34% when excluding aborted fruits).

Though three of the 20 bagged inflorescences seemed to develop two or three fruits, all the infructescences aborted quickly, one week after their opening. This result indicates that spontaneous selfing must be rare in *A. italicum*. On the other hand, 15.4% of the hand-pollinated inflorescences set fruits. The two mature infructescences contained an average of 43 fruits and 80.5 seeds (Table 2). These results do not seem to be different from those of naturally pollinated inflorescences (Table 2), but the sample size is limited.

Table 1. Mean number of female flowers per inflorescence, and mean number of fruits and seeds per mature infructescence for *A. italicum* and *A. maculatum*

	A. italicum		*A. maculatum*	
	N	Mean ± SD (range)	N	Mean ± SD (range)
Female flowers	64	60.8 ± 19 (20–109)	11	25.3 ± 7.1 (14–36)
Fruits	32	41.2 ± 19.1 (3–94)	11	15.8 ± 9.6 (4–34)
Seeds	57	82.8 ± 62 (5–335)	11	18.0 ± 10.6 (4–35)

INSECT VISITORS

The inflorescences of *Arum italicum* at both the University campus and in Montgiscard were visited by the same insect species (Table 3). Flies were the most abundant visitors, representing about 87% of the insects attracted to inflorescences of *A. italicum* in each population. Psychodidae flies, some Sciaridae, Chironomidae and Sphaeroceridae were the main trapped Diptera. The trapped psychodid flies belonged mainly to three species of *Psychoda*: *P. crassipenis*, *P. pusilla* and *P. surcoufi* (Table 3). Almost all the inflorescences of *A. italicum* inflorescences trapped insects, only three inflorescences out of 174 containing no flies. In fact, an inflorescence trapped an average of 3.5 (± 2.9) flies at the University campus and 7 (± 14.4) in

Table 3. Total numbers and percentages of the different insect taxa visiting *Arum italicum* inflorescences at two sites in southern France. For Montgiscard, one particularly crowded inflorescence is presented separately from the others

	Toulouse ($N = 142$)		Montgiscard ($N = 31$)		Montgiscard ($N = 1$)
Psychodidae*					
Psychoda crassipenis	92	19.1%	61	40.9%	68
P. pusilla	135	30.1%	10	6.7%	1
P. surcoufi	23	6.4%	14	8.7%	0
Sciaridae	70	14.9%	5	3.3%	0
Chironomidae	48	11.2%	24	16.1%	4
Sphaeroceridae	21	6.1%	15	10.1%	7
Staphylinidae	22	3.5%	8	5.3%	0
Other	44	8.7%	13	8.7%	0

*Some other *Psychoda* species have been collected on rare occasions: *P. parthenogenetica* ($N = 3$), *P.* sp. ($N = 2$) and *P. alternata* ($N = 1$).

Table 2. Percentage of infructescences (N_2) produced from the initial inflorescences (N_1) of *Arum italicum*. For mature infructescences, mean number (± SD) of developed fruits (berries) per infructescence, seeds per fruit and seeds per infructescence

	N_1	Infructescence set	N_2	No. of fruits per infructescence	No. of seeds per fruit	No. of seeds per infructescence
Self-pollination	20	0%	0	no fruit	no seed	no seed
Hand-pollination	13	15.4%	2	43.0 ± 28.3	1.8 ± 0.1	80.5 ± 56
Natural conditions	155	16.1%	25	41.2 ± 19.1	1.8 ± 0.6	82.8 ± 62

Montgiscard (4.6 ± 5.1 excluding one particularly crowded inflorescence; see Table 3).

The relative insect abundance varied significantly between the two *Arum italicum* populations for *Psychoda crassipenis* ($F_{[1,171]} = 11.95$, $P = 7 \times 10^{-4}$) and *P. pusilla* ($F_{[1,171]} = 10.77$, $P = 0.0013$). In fact, the Montgiscard population trapped mainly *P. crassipenis* (40.9%) and a few *P. pusilla* (8.4%) whereas the opposite was true for the University campus population (6.7% vs. 30.1%, respectively). The majority of inflorescences contained at least one *Psychoda* individual (78.2% at the University campus, 84.4% in Montgiscard). An average of 1.76 (±1.72) individuals of *Psychoda* were trapped per inflorescence at the University campus and 4.8 (±11.4) in Montgiscard (2.6 ± 3.1 when excluding the crowded inflorescence). The number of *P. pusilla* trapped in the inflorescences around Toulouse significantly decreases during the season ($N = 20$, $r^2 = 0.255$, $P = 0.023$), whereas no temporal variations were observed for *P. crassipenis*.

The sex-ratio of the attracted *Psychoda* was strongly female-biased (99.75%), since only one male of *Psychoda* was recorded out of the 405 captured psychodids. There was no significant variation of the pollen-load on the different body zones among the species ($\chi^2_{20} = 23.4$, $P = 0.27$). But some body zones were more loaded than others ($\chi^2_4 = 42.6$, $P < 10^{-5}$; Table 4), and some species carried significantly more pollen grains than others ($\chi^2_5 = 31.6$, $P = 1 \times 10^{-5}$; Table 4). In fact, the thorax and abdomen were more loaded with pollen than the head and legs, the wings being almost devoid of pollen (Fig. 1A). *Psychoda crassipenis* and the sphaerocerid flies appeared to be more loaded than *Psychoda pusilla* and the sciarid flies, whereas *P. surcoufi* and the chironomid flies carried only few pollen grains (Fig. 1B).

Table 4. Pollen load for the different fly taxa on different body zones. Pollen load classes: (0) 0 pollen grains; (1) 1–5 pollen grains; (2) 6–20 pollen grains; (3) >20 pollen grains

			Pollen-load classes (mean)				
	N	Insects with no pollen	Head	Thorax	Abdomen	Wings	Legs
Psychoda crassipenis	9	3	1.50	2.0	2.83	1.0	0.67
P. pusilla	15	6	0.67	1.67	2.11	0.11	0.22
P. surcoufi	4	2	0.0	0.50	0.0	0.0	0.50
Sphaerocerid flies	7	1	1.67	2.17	2.17	0.50	1.50
Sciarid flies	10	5	1.20	1.60	1.60	0.60	1.0
Chironomid flies	6	2	0.50	1.25	0.50	0.0	0.75

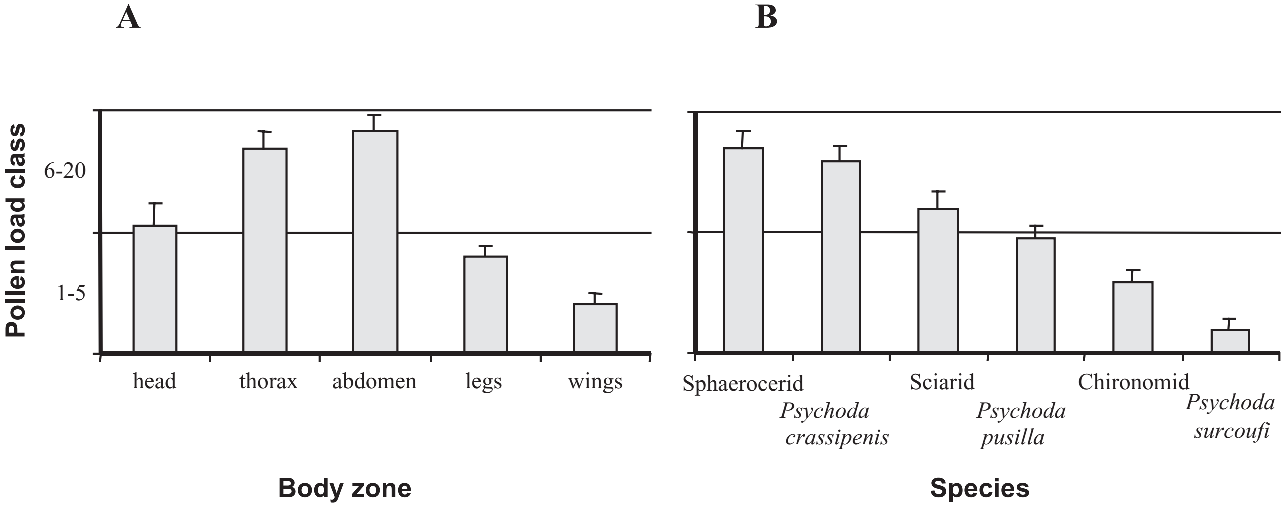

Figure 1. Pollen-load estimations according to (A) the body zone, and (B) the insect species. Pollen load classes: (0) 0 pollen grains; (1) 1–5 pollen grains; (2) 6–20 pollen grains; (3) >20 pollen grains.

THERMOGENETIC PATTERN

Despite some amplitude variations, the thermogenetic patterns appeared to be similar for the different inflorescences studied. The male flowers and the appendix produce, respectively, three and one heat peaks. The heating pattern of *A. italicum* can thus be considered as 'tetraphasic' (Fig. 2A,B). The first temperature peak (P.1), produced by the male flowers, occurred one day before the opening of the spathe, between 0900 and

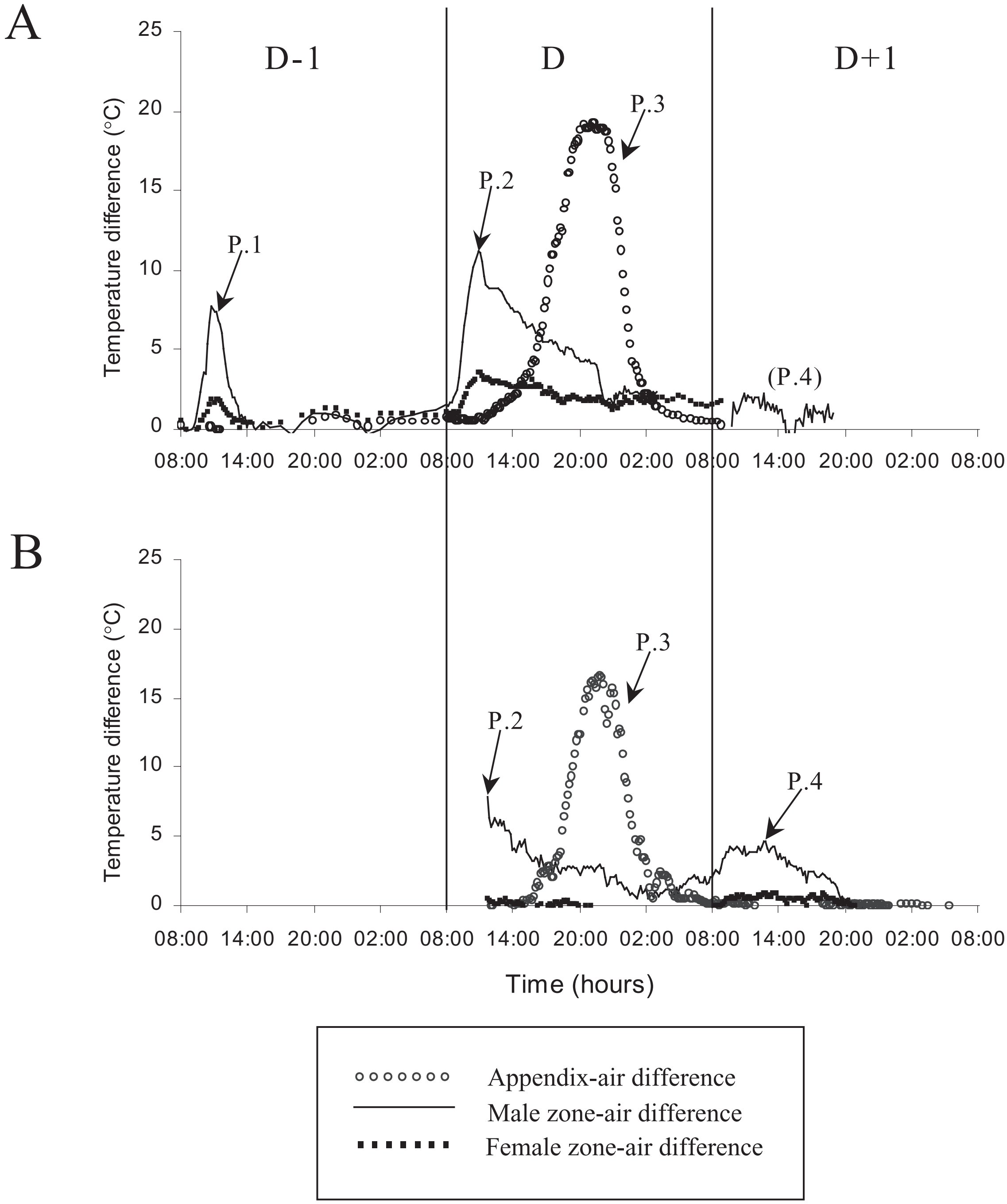

Figure 2. Temperature differences between the ambient air and the appendix (circles), the male flower zone (solid line), and the female flower zone (dotted line), recorded from two inflorescences (A and B). Temperature was recorded over three days: the day prior to the spathe unfolding (D-1), the female phase day (D), and the male phase day (D+1). The four temperature peaks are indicated by arrows (P.1-4). The fourth heat peak (P.4) is not shown on (A) because the male flower zone was eaten by a slug.

1400 hours, and peaked at 7.5°C above ambient temperature (1100 hours). The second temperature peak (P.2) was also produced by the male flowers, and happened during the opening of the spathe, between 0900 and 2200 hours, with a peak of 11.1°C above ambient temperature at 1100 hours. The third temperature peak (P.3) was the highest and occurred while the spathe was open, between 1400 and 0200 hours. It was produced by the appendix, reaching a maximum of 19.3°C above ambient temperature at 2130 hours. Finally, the male flowers became heated one last time the day after pollination (P.4), between 0900 and 1500 hours. The amplitude of this peak was about 4.6°C above ambient temperature at 1250 hours (Fig. 2B) and 6.6°C for another inflorescence (thermogenetic pattern not shown). The absence of a fourth temperature peak in Figure 2(A), with only 2.3°C of difference, is probably explained by the fact that the male flower zone was eaten by a slug.

The floral chamber also showed a thermogenetic pattern, with three heat peaks, corresponding to those of the male flowers (namely, P.1, P.2, P.4; Fig. 3). Moreover, the first one was lower (1.2°C) than the others (>2°C). On the other hand, the conduction of the heat produced by the appendix to the floral chamber was limited, probably because of the external position of the appendix. Nevertheless, the floral chamber temperature remained around 1°C higher than the ambient air temperature for 24 h (Fig. 3). After the fourth temperature peak, no significant difference in temperature between the floral chamber and the ambient air was recorded.

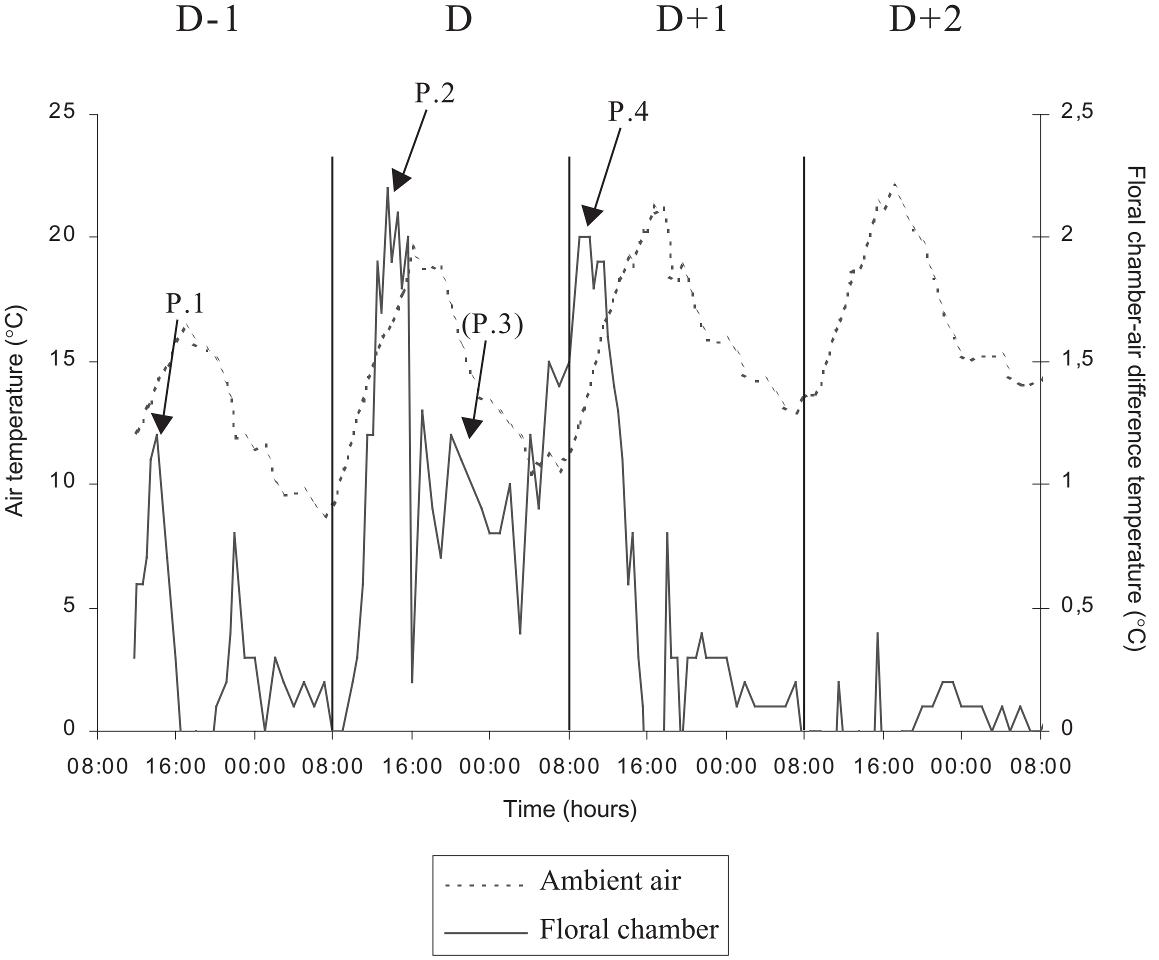

Figure 3. Temperature differences between the ambient air and the floral chamber (solid line; right Y-axis) compared with ambient air variations (dotted line; left Y-axis). Temperature records began on the day prior to the spathe unfolding (D-1), through the two days of pollination (D, D+1) until the next day (D+2). The four arrows (P.1-4) indicate the four heating events of the spadix.

DISCUSSION

All the bagged inflorescences of *A. italicum* aborted without setting any fruit, whereas 18.5% of the control inflorescences set fruits in natural conditions. As for the closely related *A. maculatum* and many other Araceae (Lack & Diaz, 1991; Patt *et al*., 1995; Mayo, Bogner & Boyce, 1997), we concluded that spontaneous self-pollination is not a common pollination mechanism in *A. italicum*. Female flower receptivity generally begins and ends before the release of pollen, protogyny thus preventing self-pollination. Nevertheless, some examples of self-compatible species are known. *Arisarum vulgare* becomes self-compatible after insect visitations, which cause the mechanical abrogation of self-incompatibility (Koach & Galil, 1986). In *Arum cylindraceum*, plants from small populations appear to be self-fertile whereas individuals cannot spontaneously self in larger populations (Fridlender, 1999). Self-pollination is common in *Montrichardia arborescens* but may be regulated by major fruit abortion (Gibernau *et al*., 2003).

Heat production in Araceae results from an increase in mitochondrial respiration uncoupled from the production of energy: the cyanide insensitive respiration (Meeuse, 1978). The increased flow of respiratory electrons is not used to produce energy but to dissipate heat (Meeuse, 1978). In fact, the heat is known to be involved in different mechanisms according to the source organ (Seymour & Schultze-Motel, 1999; Gibernau & Barabé, 2002). The thermogenetic pattern of *A. italicum* consists of a succession of four temperature peaks. This thermogenetic pattern has also been observed in the inflorescences of *A. maculatum*, a closely related species, but the observation of the first temperature peak of the male flower (D-1, Fig. 2A) was incomplete (Bermadinger-Stabentheiner & Stabentheiner, 1995). Heat production on day D-1 (P.1, Fig. 2A) corresponds to an unfolding of the spathe by several millimetres. Moreover, the heat produced by the male flowers on the opening day D (P.2, Fig. 2) and the unfolding of the spathe occur at the same time, confirming previous observations using infrared thermography (Skubatz *et al*., 1990). So, the two first temperature peaks of male flower may be involved with spathe unfolding movements. Temperature increases are also known to induce leaf movements in *Mimosa pudica* (Mohr & Schopfer, 1995). At dusk, once the spathe is open and while female flowers are receptive, the appendix warms and releases different volatile compounds (Kite *et al*., 1998), mimicking the laying-site odour of the pollinating insects, e.g. decomposing matter, urine. The insects are attracted and trapped in the inflorescence, and carry out pollination during the process. The next morning, about 8 h later, the male flowers warm one more time (P.4, Fig. 2). This heating episode is not linked with pollinator attraction or spathe unfolding, but might be related with the male function of the inflorescence, e.g. pollen dispersal. It may contribute to the release of pollen through the desiccation of the anthers (Bermadinger-Stabentheiner & Stabentheiner, 1995; Gibernau & Barabé, 2000; Gibernau, Barabé & Labat, 2000), the maturation of the pollen by an unknown physiological process as proposed by Seymour & Schultze-Motel (1999), the warming of the floral chamber, or the volatilization of a specific fragrance. Finally, it appears that the heat production by the male flowers increases the floral chamber temperature, while the heat production by the appendix has a limited effect (Fig. 3). The fact that the floral chamber remains relatively warm could play a role in the behaviour or survival of the trapped insects. In fact, they are more likely to be active within a warm floral chamber, increasing the probability of pollination (Seymour & Schultze-Motel, 1999; Gibernau & Barabé, 2002). This may also help to keep the small flies alive during cool nights (about 10°C) until the next day when the pollen is released.

The floral fragrance the appendix emits during the female phase attracts different insect taxa of which four families (Psychodidae, Sciaridae, Chironomidae and Sphaeroceridae) represent 88% of the visitors. The three psychodid fly taxa are *Psychoda* species (*P. crassipenis*, *P. pusilla* and *P. surcoufi*), and represent 56.6% of the attracted insects. *Psychoda* are often found in *Arum* inflorescences, such as *A. hygrophilum*, *A. maculatum*, *A. concinnatum* and *A. purpureospathum* (Koach & Galil, 1986; Lack & Diaz, 1991; Drummond & Hammond, 1993). Whereas *Psychoda phalaenoides* is considered as being the only specific pollinator of *A. maculatum*, *A. italicum* appears to be more generalist, attracting a more diverse entomofauna.

Most of the attracted *Psychoda* caught by the *A. italicum* inflorescences are female (99.8%). This phenomenon is well known for *A. maculatum*, which also attract only female *P. phalaenoides* (Prime, 1960; Lack & Diaz, 1991; Kite *et al*., 1998). This species and the sex attraction specificity can be linked to the floral fragrance emitted by the inflorescence at the beginning of the flowering female phase. Odour analyses of *A. maculatum* and cow-dung (the breeding site of the main pollinator) reveal that both contain some components known as being semiochemicals for several insects, such as 2-heptanone and *p*-cresol (Kite, 1995). These two main compounds may thus be implicated in the attraction of *P. phalaenoides* females. However, a study of *A. italicum* odour (Kite *et al*., 1998) reveals a simpler composition (13 vs. 20 components). Moreover, the main compounds found in *A. maculatum* are not represented in large quantities in the fragrance of *A. italicum*, which appears to be dominated by ethanol, dimethyloctadiene and methyl butyrate. This result could explain the less specific attraction observed in *A. italicum* but the blend still has sex-specific properties attracting only females. Contrasting odours between the appendix (pungent) and the floral chamber (sweet) have been found in eight species of *Arum*, including *A. italicum* and *A. maculatum*, in *Sauromatum* and *Biarum* (Mayo, 1980; Meeuse *et al*., 1984; Borg-Karlson, Englund & Unelius, 1994; Kite, 1995; Kite *et al*., 1998). It has been suggested that the sweet odour in the floral chamber provides feeding and mating stimuli to pollinators until anthesis (Meeuse *et al*., 1984). The males of the psychodid fly *Lutzomyia longipalpis* produce 9-methyl germacrene B, a sexual pheromone which attracts conspecific females (Hamilton, Dawson & Pickett, 1996; Uribe, 1999). High proportions of germacrene B were found in the floral chamber of several species of *Arum* (mainly pollinated by psychodid flies), of which three characteristically attract females (Prime, 1960; Drummond & Hammond, 1993; Kite *et al*., 1998). So, the inflorescences of *Arum* could produce germacrene B, and thus deceive specifically, the females of *Psychoda*.

At least three main non-exclusive hypotheses could explain such a biased sex-ratio for the attracted insects. First, male *Psychoda* may be indifferent or repelled by the fragrance emitted by the *Arum* inflorescence whereas females may be strongly attracted. Second, as copulations occur just after the emergence of the imago (Vaillant, pers. comm.), only females are attracted to laying sites, and thus to the inflorescences. Third, the attraction of parthenogenetic species could partially explain this biased sex-ratio, since only a few species of *Psychoda* have such a reproductive system (Vaillant, pers. comm.).

According to pollen-load counts, *Psychoda crassipenis* and the sphaerocerid flies appear to be the most effective potential pollinators (Fig. 1). Sphaerocerid flies are often found in the inflorescences of *A. dioscoridis*, *A. concinnatum*, *A. purpureospathum* and *A. maculatum* (Drummond & Hammond, 1991; Rohacek, Beck-Haug & Dobat, 1991; Drummond & Hammond, 1993). They appear to be the main pollinators of *A. purpureospathum*, since they represent 72.2% of the attracted species (Drummond & Hammond, 1993). However, since they occur only in small numbers (6.5% of the visitors) and in few inflorescences (12.2%) of *A. italicum*, they appear to be an unreliable and occasional pollinator of the latter species. On the other hand, *Psychoda crassipenis* and *P. pusilla* are both more frequent and far more abundant. Furthermore, *P. crassipenis* appears to carry more pollen than *P. pusilla* and may be the most efficient pollen vector. These results do not mean however, that *Psychoda crassipenis* is the most effective pollinator as its abundance can vary from one population to another. In the population located at the University campus, *Psychoda crassipenis* represented only 6.7% of the visitors. Even if *P. pusilla* carries on average less pollen, it is the most abundant insect (30%) and may be at this location the more important pollinator.

The frequency of infructescence abortion in *A. italicum* is very high (82.5%), and this phenomenon appears to be common in Araceae. Fifty percent of the inflorescences of *Dieffenbachia longispatha* abort, 87% for *Symplocarpus renifolius* and between 22.3 and 92.2% for *Arum maculatum* (Young, 1986; Uemura *et al*., 1993; Ollerton & Diaz, 1999). Flowering and pollinator availability could explain the high frequency of abortion. Flowering in *Arum* is known to be strongly influenced by climatic conditions (Dafni, 1984; Ollerton & Diaz, 1999). So, the poor conditions encountered during the study year (cold and rain) may have influenced the synchronicity of the flowering period of *A. italicum*. Consequently, few inflorescences were open at the same time, decreasing the probability for pollinators to go from a male phase inflorescence to a female one.

The pollinated inflorescences developed 66.4 ± 25.0% of their female flowers. Such percentages have been documented in other Araceae such as *Spathyphillum friedrichsthalii* (78.2%; Montalvo & Ackerman, 1986) or *Dieffenbachia longispatha* (48%; Young, 1986). Lack & Diaz (1991) have shown that one individual of *P. phalaenoides* is able to pollinate all the female flowers of one *A. maculatum* inflorescence. But as the inflorescences of *A. italicum* bear 2.4 times more flowers than inflorescences of *A. maculatum* and produce about 4.6 times more seeds (Table 1; Lack & Diaz, 1991), one *Psychoda* individual may not be sufficient for pollinating all the flowers of A. *italicum*. Further experiments are necessary to verify this point. Moreover, mature fruits develop only 35% of their potential seeds and no inflorescence develops all its ovules even if numerous *Psychoda* are trapped. Hence pollination may not be the only limiting factor. In fact, as infructescence development depends on the energy stored in the corm the previous year, resource limitation can also occur (Mendez & Obeso, 1992). Moreover, selective seed abortion can favour the development of the highest quality seeds, as for *Cynoglossum officinale* (Boraginaceae; Mesler & Klinkhamer, 2001). This process could also explain the overall frequency of infructescence abortion observed. If too many seeds initiate their development relative to the energy stored in the corm, the plant might abort either the whole infructescence, or some seeds. Another reason could be that fruit cannot contain more than a certain number of developing seeds otherwise the fruit wall may rip (J. Albre, pers. obs.). Hence spatial competition between seeds in the same fruit may also provoke seed abortions.

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