Botanical Journal of the Linnean Society, 2008, **156**, 43–49. With 3 figures

Reproductive biology of *Arum italicum* (Araceae) in the south of France

JEROME ALBRE and MARC GIBERNAU*

Université Paul Sabatier, Laboratoire d'Evolution et Diversité Biologique (UMR 5174), Bât. 4R3-B2, 31062 Toulouse cedex 9, France

Received 2 February 2006; accepted for publication 24 August 2007

The reproductive success of *Arum italicum* in south-western France showed a positive relationship with plant vigour at both the plant (number of inflorescences) and inflorescence (number of seeds) levels. However, the infructescence and berry numbers were not related to the number of inflorescences, and two-fold more seeds were produced by individuals flowering several times than by those flowering just once. Moreover, the reproductive success of this species appeared to be limited by the high abortion rate (50%), strong predation pressure on the inflorescences (34%), and low seed set rate of nonpredated inflorescences (36%), suggesting pollination limitation. Nevertheless, a positive relationship was found between the mean number of *Psychoda* trapped per inflorescence and the number of maturing infructescences, particularly for the most abundant species, *Psychoda crassipenis*. Therefore, pollinator availability appeared to be an important limiting factor for fructification in the studied population, by contrast with other studies in which the fruit set appeared to be related more strongly to the density of inflorescences. Such different results may have been caused by the relatively low abundance of *Psychoda* in the present study.

ADDITIONAL KEYWORDS: fructification – fruit abortion – pollinator abundance – seed set – temporal variation.

INTRODUCTION

The reproductive success of a flowering plant is not dependent only on floral traits, which are, in general, adapted to increase the pollination probability, but also on the context in which the plants reproduce, that is, ecological factors (Proctor, Yeo & Lack, 1996; Méndez & Diaz, 2001). Some parameters affecting the flowering context are the population size, the abundance and quality of pollen donors, and plant isolation. By contrast, the pollination context depends on the flowering synchrony, floral sex ratio, flower size and longevity, and pollinator activity (Ollerton & Diaz, 1999; Méndez & Diaz, 2001; Diaz & Kite, 2002). Some parameters of the pollination and flowering contexts have been shown to affect individual fitness in the genus *Arum*. The inflorescences of *A. italicum* which open on days when no other inflorescences are already open (i.e. potential pollen donors) are 45% less likely to produce fruits than are inflorescences which open on days when other inflorescences are already open (Méndez & Diaz, 2001). Similar results have also been observed for *A. maculatum* (Ollerton & Diaz, 1999). The flowering phenology is unimodal in *A. italicum* and *A. maculatum*, with anthesis lasting for 24 h and inflorescences then withering rapidly (Méndez & Obeso, 1992; Ollerton & Diaz, 1999; Méndez & Diaz, 2001; Albre, Quilichini & Gibernau, 2003).

A general ecological factor is the weather: cold weather delays the flowering of *A. maculatum* and decreases the activity and/or abundance of its pollinator *Psychoda phalaenoides* (Psychodidae), with the consequence of fewer fruits produced (Prime, 1960; Kite *et al.*, 1998; Ollerton & Diaz, 1999). There is a great variation in the number of fructifications

---

*Corresponding author. E-mail: gibernau@cict.fr

Table 1. Number of mature plants (%, $N = 79$) that produced a given number of inflorescences

One inflorescence	Two inflorescences	Three inflorescences	Four inflorescences
15 (20%)	53 (67%)	10 (12.7%)	1 (1.3%)

between different years, but the most important factors seem to be the abundance and pollen load of pollinators at the population level, even though, at the individual level, fruiting success does not appear to be related to the number of insects caught, as only one pollen-bearing insect is necessary for full fruit set (Lack & Diaz, 1991; Ollerton & Diaz, 1999). In the same way, *A. italicum* is pollinated by various types of insect (Gibernau, Macquart & Przetak, 2004), but variations in their abundance or activity (in relation to climatic conditions) have little effect on the initiation of fruits on individual plants (Méndez & Diaz, 2001).

Although clonal reproduction occurs regularly in *A. italicum*, the sexual reproduction of this monoecious and protogynous plant is achieved through obligate cross-pollination by dung flies, mainly *Psychoda* (Psychodidae; Albre *et al.* 2003). These flies are attracted by a dung-like odour produced by the appendix, that is, the distal part of the inflorescence (Kite *et al.*, 1998). They are then trapped for about 24 h with no reward except for stigmatic fluid, and so participate in both the female and male phases. This pollination system is thus based on deceit attraction by mimicking the oviposition site (Gibernau *et al.*, 2004). The aim of this study was to quantify some aspects of the reproductive biology of *A. italicum* in south-western France. Firstly, the dynamics of flowering and fructification (number of inflorescences, development/maturation time, time lag between two successive inflorescences) were studied. Secondly, the fruiting success (predation, abortion, number of seeds) was quantified. Finally, the probability of fructification in relation to intrinsic (number of inflorescences, plant vigour) and environmental (pollinator abundance) factors was studied.

MATERIAL AND METHODS

During the spring of 2001, 79 mature individuals of *A. italicum* Miller were observed every 2 days in a natural population in south-western France (Toulouse) from late March to the end of fruit development (mid-August). For each plant, the flowering dynamics, from the appearance of the inflorescence to infructescence maturity, were recorded, and events such as predation or abortion were noted. From these data, the time required for the development of each inflorescence was calculated as the time between the inflorescence emergence from the leaf sheath and its opening. The delay between the flowerings of two consecutive inflorescences of the same plant was also noted. The time for fructification was also calculated as the period between the second day of anthesis and the falling of the red berries. The numbers of leaves, inflorescences, fruits, and seeds per fruit were also counted. Plant vigour was estimated by measuring the height of the longest petiole, and the limb length and width of the leaves (at the level of the petiole). Leaves were approximated as a triangle with respect to their surface. Inflorescences were harvested in April in order to count the number of male and female flowers per inflorescence ($N = 64$) and the number of ovules per flower ($N = 32$). Infructescences were harvested in July at maturation in order to count the number of fruits ($N = 52$) and seeds ($N = 36$). The relationships between the plant height/leaf surface and inflorescence number, seed number, and time lag between two successive inflorescences were studied using linear regressions (Systat, 1998). The development times (defined as the period from the appearance of the inflorescence from the petiole sheath to its opening) of two successive inflorescences on the same individual were compared by a paired *t*-test (Systat, 1998). The number or frequency of fructifications was analysed according to the number of inflorescences or the flowering week with a Poisson error (count data, χ^2 statistic; Glim, 1986).

The determination of the most efficient pollinator was attempted between the two main *Psychoda* (Diptera) species, namely *P. crassipenis* and *P. pusilla*, visiting *A. italicum* inflorescences (Albre *et al.*, 2003), using their temporal variations from capture surveys within five to ten open inflorescences every 5 days. Linear regressions were performed to determine seasonal pollinator variations, and the relationship, for a given week, between pollinator abundance and successful infructescence number initiated in that given week (Systat, 1998).

RESULTS

MORPHOLOGY

Individual plants of *A. italicum* produced an average of 1.96 inflorescences [standard deviation (SD), 0.61; $N = 79$], with two inflorescences being most frequent (Table 1). Leaves developed in autumn, and flowering occurred in spring, from early March to late May.

Table 2. Inflorescence condition of the studied population ($N = 155$ inflorescences). All of the altered inflorescences aborted before maturity

	Unaltered inflorescences		Altered inflorescences			
			Preyed upon		Not preyed upon	
	Matured	Aborted	Appendix	Spathe	Broken	Rotten
N (%)	25 (16.1%)	77 (49.7%)	34 (22.0%)	5 (3.2%)	7 (4.5%)	7 (4.5%)

Table 3. Number and proportion of fructifications, berries (fruits), and seeds developed for plants that flowered once, twice, or thrice (mean ± SD)

Variable measured	One inflorescence ($N = 15$)	Two inflorescences ($N = 53$)	Three inflorescences ($N = 12$)	Test
Number of inflorescences matured per plant	0.27 ± 0.45	0.41 ± 0.60	0.72 ± 0.90	NS
Proportion of inflorescences matured per plant (%)	0.27 ± 0.45	0.21 ± 0.30	0.24 ± 0.30	NS
Total number of fruits per plant	41.7 ± 12.7	45.7 ± 26.8	50.5 ± 20.5	NS
Proportion of fruits per plant (%)	0.56 ± 0.17	0.62 ± 0.26	0.62 ± 0.23	NS
Total number of seeds per plant	59.3 ± 16.6	92.4 ± 69.3	89.8 ± 43.2	*

These variables show no significant difference (NS) according to the number of inflorescences, except for the total number of seeds per plant (*). Plants flowering once produced significantly fewer seeds than plants flowering two or three times ($\chi^2_1 = 35.79$; $P < 10^{-5}$).

Mature individuals were an average of 31.6 cm high (SD, 6.2 cm) and produced a variable number of leaves (mean ± SD, 6.41 ± 1.66; range, 2–8). Moreover a positive relationship was found between the leaf surface (mean ± SD, 201.6 ± 78.6 cm^2) and the number of inflorescences ($R^2 = 0.07$, $F_{1,77} = 5.7$, $P = 0.02$).

FLOWERING

Inflorescence development lasted 17.3 ± 5.0 days (mean ± SD, $N = 105$), the pollination stage lasted 2 days, and fructification maturation from pollination was much longer at 93.6 ± 18.1 days ($N = 34$). During the survey, the number of open inflorescences per day varied between one and seven (mean, 2.26; SD, 1.4; $N = 64$). The number of successful fructifications was unrelated to the number of inflorescences per individual ($\chi_2{}^2 = 2.97$, $P = 0.23$). For plants flowering twice, the development time was significantly longer for the first inflorescence than for the second ($t = 2.98$, d.f. = 14, $P = 0.01$). The time between the opening of two successive inflorescences ranged from 2 to 42 days (27.6 ± 8.7 days; $N = 55$) and was negatively correlated with the leaf surface ($R^2 = 0.22$, $F_{1,72} = 20.3$, $P < 10^{-4}$).

FRUCTIFICATION

An inflorescence produced an average of 155.6 ± 42.7 ($N = 64$) male flowers and 60.8 ± 19.2 ($N = 64$) female flowers. Half of the inflorescences aborted naturally and only 16.1% achieved development (Table 2). The other inflorescences (34.2%) were preyed upon, broken, or rotten; none of them completed their development (Table 2). Most of the altered inflorescences (74%) were consumed by herbivorous animals, which ate mainly the appendix and rarely the spathe. These infructescences always aborted even if they had initiated their development.

Mature infructescences produced 42.9 ± 20.8 fruits ($N = 52$), that is, 70% of the female flowers set berries, with an average of 2.46 ± 1.27 seeds ($N = 322$). Female flowers contained 5.4 ± 2.1 ovules ($N = 32$). An infructescence produced an average of 83.4 ± 47 seeds ($N = 36$).

There were no differences in the number of infructescences per plant or the probability for an inflorescence to mature for individuals that flowered once, twice, or three times (Table 3). The same result was found for the number and proportion of mature fruits per plant (Table 3). However, when considering only mature fruits, a positive linear regression was found between the number of fruits and the mean

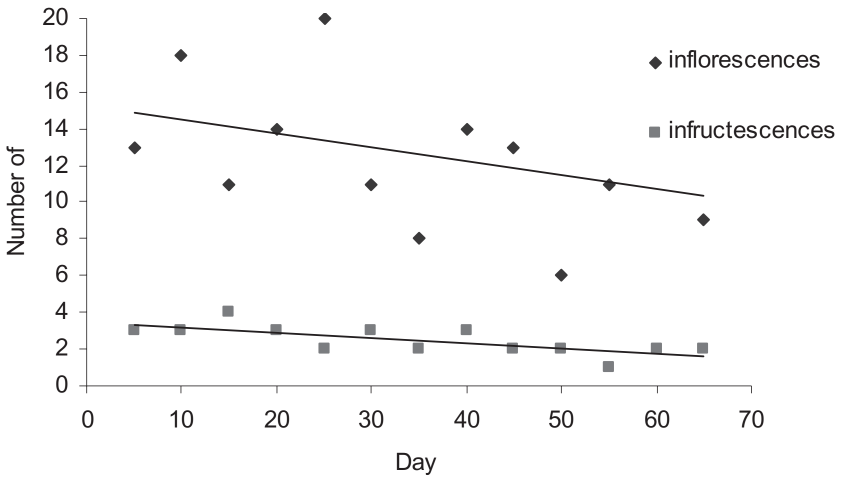

Figure 1. Variation in the number of open inflorescences and maturing infructescences at different dates in the flowering period (Day 1, 20/03/01; Day 65, 23/05/01).

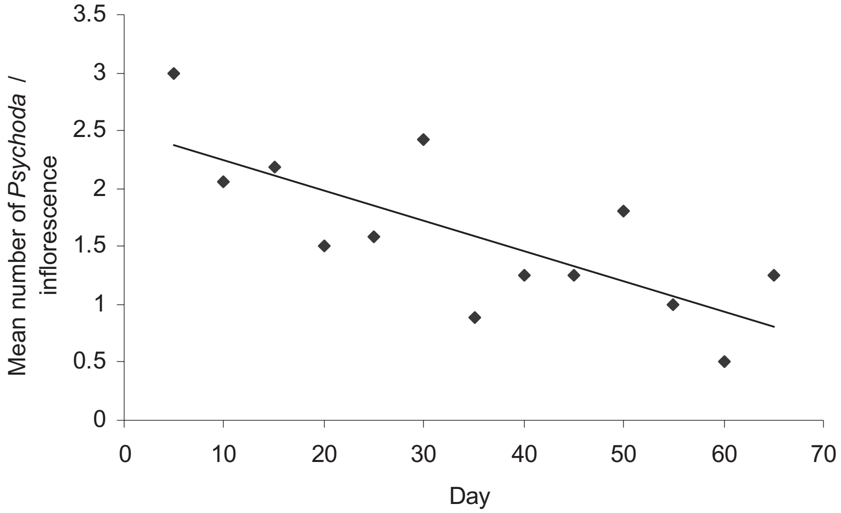

Figure 2. Variation in the mean number of *Psychoda* per inflorescence (collected from five to ten inflorescences) at different dates in the flowering period (Day 1, 20/03/01; Day 65, 23/05/01).

number of seeds per fruit ($R^2 = 0.38$, $F_{1,53} = 31.8$, $P < 10^{-4}$). The number of seeds also increased with plant vigour, measured as the leaf surface ($R^2 = 0.34$, $F_{1,23} = 12$, $P = 0.002$) or plant height ($R^2 = 0.42$, $F_{1,22} = 15.9$, $P = 6 \times 10^{-4}$). The total number of seeds per plant produced by plants flowering once was significantly lower than for individuals that flowered twice or three times (Table 3).

TEMPORAL VARIATIONS IN FRUCTIFICATION AND *PSYCHODA*

Because of the limited sample size (79 individuals), no flowering peak was observed as in other studies (Ollerton & Diaz, 1999; Méndez & Diaz, 2001). The number of maturing infructescences for a given week declined during the flowering season (Fig. 1), but, as the number of open inflorescences also declined, the frequency of maturing infructescences did not vary in time ($\chi_3^2 = 0.3$, $P = 0.96$).

The overall mean number of *Psychoda* trapped per inflorescence was 1.7 ± 0.9 ($N = 20$). The mean number of *Psychoda* trapped per inflorescence decreased during the flowering season ($R^2 = 0.55$, $F_{1,11} = 13.7$, $P = 0.0035$; Fig. 2). The same was true for both species *P. crassipenis* ($R^2 = 0.59$, $F_{1,11} = 16.1$, $P = 0.002$) and *P. pusilla* ($R^2 = 0.53$, $F_{1,11} = 12.6$, $P = 0.005$) considered separately.

For a given week, there was a positive correlation between the mean number of *Psychoda* individuals

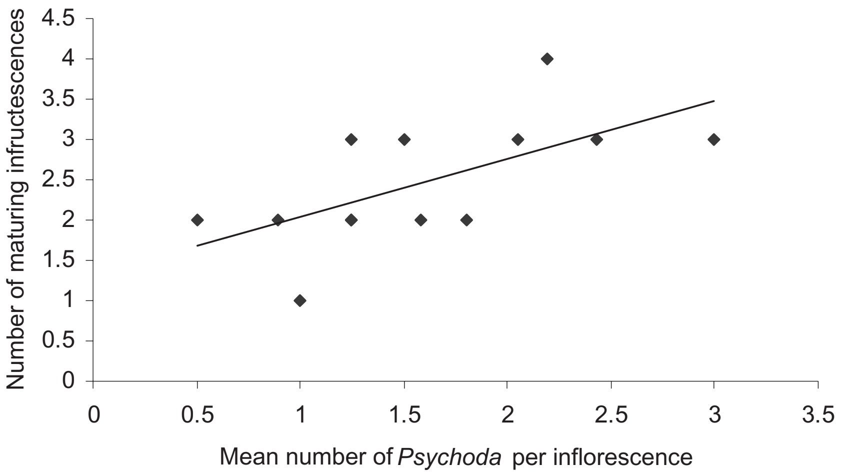

Figure 3. Linear regression, for a given week, between the mean number of *Psychoda* per inflorescence (collected from five to ten inflorescences) and the number of inflorescences which matured an infructescence.

trapped per inflorescence and the number of maturing infructescences ($R^2 = 0.40$, $F_{1,11} = 7.3$, $P = 0.02$; Fig. 3). Moreover, for a given week, a positive relationship was found between the infructescence set rate and the mean number of *P. crassipenis* trapped per inflorescence ($R^2 = 0.49$, $F_{1,11} = 10.4$, $P = 0.008$), but not *P. pusilla* ($R^2 = 0.16$, $F_{1,21} = 2.2$, $P = 0.17$). Through the flowering season, *P. crassipenis* was, on average, twice as abundant as *P. pusilla* (2 ± 1.6, $N = 20$).

DISCUSSION

MORPHOLOGY AND PLANT VIGOUR

It appears that the number of inflorescences increases with the mean plant or leaf size, that is, with plant vigour. A previous study has shown that *A. italicum* does not produce an inflorescence until the tuber mass has reached a determined weight, but, afterwards, larger *Arum* produce more inflorescences than smaller *Arum* (Méndez & Obeso, 1993). Moreover, one-third of the inflorescences of *A. italicum* do not reach the pollination stage because of accidents occurring during their development, such as rot and predation.

FLOWERING

During their flowering period, mature *A. italicum* individuals frequently produce two inflorescences. However, the consecutive inflorescences produced by the same plant never open simultaneously (mean time delay, 27.6 ± 8.7 days), as for many Araceae: *Dieffenbachia longispatha* (Young, 1988), *Philodendron solimoesense* (Gibernau *et al.*, 1999), *Arum italicum* (32–34 days; Méndez & Diaz, 2001), and *Montrichardia arborescens* (Gibernau *et al.* 2003a).

For *Arum* producing several inflorescences, the first tends to be larger than its consecutive(s) (Méndez, 1998). It was also observed that the development time of the second inflorescence was shorter than the first. Warmer climatic conditions and/or resource limitation may explain the shorter development time and smaller size for the second inflorescence. Moreover, the time lag between two successive inflorescences decreases with plant vigour, suggesting resource limitation, as larger plants may have more resource reserve or a better assimilation rate which, in both cases, may produce a quicker flowering sequence. Moreover, leaf and inflorescence development are partially supported by the energy stored in the bulb in the previous year (Chapin, Schulze & Mooney, 1990; Zimmerman & Whigham, 1992). Further studies are needed to explain the observed developmental pattern.

FRUCTIFICATION

In the studied population, only 16% of the inflorescences set fruits, producing 25–36% of the potential seeds per infructescence. Such reproduction rates seem to be frequent in the Araceae family. Indeed, 13% and 50% of inflorescences of *Symplocarpus renifolius* and *Dieffenbachia longispatha*, respectively, develop in natural conditions (Young, 1986; Uemura *et al.*, 1993). For *A. maculatum*, this rate can vary between 8 and 78% according to the population and the year (Ollerton & Diaz, 1999). Higher infructescence sets (65 and 74%, respectively) were found in two Spanish populations of *A. italicum* in 1994 (Méndez & Diaz, 2001). *Arum* species produce trinucleate pollen grains (Grayum, 1990), which quickly lose their viability after 24–48 h (Dafni, 1992;

Gibernau, Macquart & Diaz, 2003b). This factor may limit the fertilization success of female flowers, particularly when pollinators are scarce.

In addition to this natural infructescence abortion, predation pressure is responsible for the destruction of 22% of the inflorescences. Indeed, the odour released during the female phase may attract mammals (probably rodents) that mainly eat the appendix. Although some fruit initiation occurs, all the damaged infructescences abort several days later. In Spain, Méndez & Obeso (1993) noted that only 40% of the inflorescences which lost their appendix when heating also initiated fruit development. These authors suggested that the appendix was not an indispensable structure for fruit initiation. Nevertheless, cross-pollination by insects is obligatory for *A. italicum*, because of the protogyny and the particular morphology of its inflorescences. Indeed, as the insect visitors are attracted only by the volatile compounds emitted by the appendix (Knoll, 1926; Méndez & Obeso, 1992; Kite *et al*., 1998; Miyake & Yafuso, 2003), this structure appears to be important for fructification.

TEMPORAL VARIATIONS IN FRUCTIFICATION AND *PSYCHODA*

At the individual level, the fruit and seed set increase with plant vigour. This relationship may be explained by a positive correlation between the plant vigour and the amount of resources available to mature the fruits (Méndez & Obeso, 1993), and/or the increase in appendix size with plant vigour (Méndez, 1998, 2001), which may enhance pollinator attraction (Méndez & Obeso, 1992; Miyake & Yafuso, 2003) and thus pollination efficiency (Méndez & Diaz, 2001; Miyake & Yafuso, 2003; Garcia-Robledo *et al*., 2005).

It was also found that, at the population level, the numbers of fruits and seeds were dependent on the pollination efficiency, that is, the number of attracted insects. In the studied population, *P. crassipenis* and *P. pusilla* were the most efficient pollen vectors amongst the visitor species (Albre *et al*., 2003). Hence, the infructescence set increased with the mean number of *P. crassipenis* per inflorescence, but showed no relationship with the mean number of *P. pusilla*. Therefore, it can be supposed that, during the year of study, *P. crassipenis*, the most abundant species, was also the most efficient pollinator of *A. italicum*. However, it cannot be excluded that *P. pusilla* may also be an important pollen vector in different populations or years. Therefore, pollinator availability appears to be an important limiting factor for fructification.

Such relationships between fruit set and pollinator abundance were not found in another population of *A. italicum* (Méndez & Diaz, 2001), or in *A. maculatum* (Lack & Diaz, 1991; Ollerton & Diaz, 1999). In these *Arum* populations, the mean number of *Psychoda* per inflorescence averaged 6.6 in *A. maculatum* (Lack & Diaz, 1991) and almost 18 in *A. italicum* (Méndez & Obeso, 1992). Consequently, the fruit set appeared to be more strongly related to the density of the opened inflorescences (i.e. pollen donors) rather than the abundance of *Psychoda*. Such discrepancies could be explained by differences in pollinator abundances. In the present study, the mean number of *Psychoda* per inflorescence was less than two, and sufficiently scarce to be the limiting factor of fruit set. Flowering densities and pollinator abundances vary between years and populations, and thus the limiting factor for fruit set may fluctuate between these two factors (Somanathan & Borges, 2001; Sanchez-Lafuente, 2002; Field, Ayre & Whelan, 2005; Nishizawa *et al*., 2005).

ACKNOWLEDGEMENTS

The authors are grateful to François Vaillant for the psychodid identifications. The authors are also grateful to A. & A. Dejean and D. Barabé for proofreading the manuscript. The authors thank J. Ollerton, M. Méndez, and two anonymous referees for their corrections of an earlier version of the paper.

REFERENCES

Albre J, Quilichini A, Gibernau M. 2003. Pollination ecology of *Arum italicum* (Araceae). *Botanical Journal of the Linnean Society* **141:** 205–214.

Chapin FS, Schulze ED, Mooney HA. 1990. The ecology and economics of storage in plants. *Annual Review of Ecology and Systematics* **21:** 423–447.

Dafni A. 1992. *Pollination ecology, a practical approach*. Oxford: IRL Press.

Diaz A, Kite GC. 2002. A comparison of the pollination ecology of *Arum maculatum* and *A. italicum* in England. *Watsonia* **24:** 171–181.

Field DL, Ayre DJ, Whelan RJ. 2005. The effect of local plant density on pollinator behavior and the breeding system of *Persoonia bargoensis* (Proteaceae). *International Journal of Plant Sciences* **166:** 969–977.

Garcia-Robledo C, Kattan G, Murcia C, Quintero-Marin P. 2005. Equal and opposite effects of floral offer and spatial distribution on fruit production and pre-dispersal seed predation in *Xanthosoma daguense* (Araceae). *Biotropica* **37:** 373–380.

Gibernau M, Barabé D, Cerdan P, Dejean A. 1999. Beetle pollination of *Philodendron solimoesense* (Araceae) in French Guiana. *International Journal of Plant Sciences* **160:** 1135–1143.

Gibernau M, Barabé D, Labat D, Cerdan P, Dejean A. 2003a. Reproductive biology of *Montrichardia arborescens* (Araceae) in French Guiana. *Journal of Tropical Ecology* **19:** 103–107.

Gibernau M, Macquart D, Diaz A. 2003b. Pollen viability and longevity in two species of *Arum*. *Aroideana* **26:** 27–32.

Gibernau M, Macquart D, Przetak G. 2004. Pollination in the genus *Arum* – a review. *Aroideana* **27:** 148–166.

Glim. 1986. *Generalised linear interactive modelling 3.77*. London: Royal Statistical Society.

Grayum MH. 1990. Evolution and phylogeny of the Araceae. *Annals of the Missouri Botanical Garden* **77:** 628–697.

Kite GC, Hetterscheid WLA, Lewis MJ, Boyce PC, Ollerton J, Cocklin E, Diaz A, Simmonds MSJ. 1998. Inflorescence odours and pollinators of *Arum* and *Amorphophallus* (Araceae). In: Owens SJ, Rudall P, eds. *Reproductive biology*. Kew: Royal Botanic Gardens, 295–315.

Knoll F. 1926. Die Arum – Blütenstände und ihre Besucher. *Abhandlungen der Zoologisch-Botannischen Gesellschaft in Wien* **12:** 382–481.

Lack AJ, Diaz A. 1991. The pollination of *Arum maculatum* L. – a historical review and new observations. *Watsonia* **18:** 333–342.

Méndez M. 1998. Modification of phenotypic and functional gender in the monoecious *Arum italicum* (Araceae). *American Journal of Botany* **85:** 225–234.

Méndez M. 2001. Sexual mass allocation in species with inflorescences as pollination units: a comparison between *Arum italicum* and *Arisaema* (Araceae). *American Journal of Botany* **88:** 1781–1785.

Méndez M, Diaz A. 2001. Flowering dynamics in *Arum italicum* (Araceae): relative role of inflorescence traits, flowering synchrony, and pollination context on fruit initiation. *American Journal of Botany* **88:** 1774–1780.

Méndez M, Obeso JR. 1992. Influencia del osmóforo en la producción de infrutescencias en *Arum italicum* Miller (Araceae). *Anales del Jardín Botánico de Madrid* **50:** 229–237.

Méndez M, Obeso JR. 1993. Size-dependent reproductive and vegetative allocation in *Arum italicum* (Araceae). *Canadian Journal of Botany* **71:** 309–314.

Miyake T, Yafuso M. 2003. Floral scents affect reproductive success in fly-pollinated *Alocasia odora* (Araceae). *American Journal of Botany* **90:** 370–376.

Nishizawa T, Watano Y, Kinoshita E, Kawahara T, Ueda K. 2005. Pollen movement in a natural population of *Arisaema serratum* (Araceae), a plant with pitfall-trap flower pollination system. *American Journal of Botany* **92:** 1114–1123.

Ollerton J, Diaz A. 1999. Evidence for stabilising selection acting on flowering time in *Arum maculatum* (Araceae): the influence of phylogeny on adaptation. *Oecologia* **113:** 340–348.

Prime CT. 1960. *Lords and ladies*. London: Collins Clear-Type Press.

Proctor M, Yeo P, Lack A. 1996. *The natural history of pollination*. London: The Bath Press.

Sanchez-Lafuente AM. 2002. Floral variation in the generalist perennial herb *Paeonia broteroi* (Paeoniaceae): differences between regions with different pollinators and herbivores. *American Journal of Botany* **89:** 1260–1269.

Somanathan H, Borges RM. 2001. Nocturnal pollination by the carpenter bee *Xylocopa tenuiscapa* (Apidae) and the effect of floral display on fruit set of *Heterophragma quadriloculare* (Bignoniaceae) in India. *Biotropica* **33:** 78–89.

Systat. 1998. *Systat for Windows statistics*, Version 8.0 edition. Evanston, IL: Systat.

Uemura S, Ohkawara K, Kudo G, Wada N, Higashi S. 1993. Heat-production and cross-pollination of the Asian skunk cabbage *Symplocarpus renifolius* (Araceae). *American Journal of Botany* **80:** 635–640.

Young HJ. 1986. Beetle pollination of *Dieffenbachia longispatha* (Araceae). *American Journal of Botany* **73:** 931–944.

Young HJ. 1988. Differential importance of beetle species pollinating *Dieffenbachia longispatha* (Araceae). *Ecology* **69:** 832–844.

Zimmerman JK, Whigham DF. 1992. Ecological functions of carbohydrates stored in corns of *Tipularia discolor* (Orchidaceae). *Functional Ecology* **6:** 575–581.