Flowering dynamics in *Arum italicum* (Araceae): relative role of inflorescence traits, flowering synchrony, and pollination context on fruit initiation[1]

Marcos Méndez[2,4] and Anita Díaz[3]

[2]Departamento de Biología de Organismos y Sistemas (Unidad de Ecología), Universidad de Oviedo, E-33071 Oviedo, Spain; and
[3]Bournemouth University, School for Conservation Sciences, Dorset House, Talbot Campus, Fern Barrow, Poole, BH12 5BB UK

We studied the relative role of inflorescence traits, flowering synchrony, and pollination context for infructescence and fruit initiation in two Spanish populations of *Arum italicum,* a species in which inflorescences are the pollination unit. In this species, a specialized inflorescence organ, the appendix, is important for pollinator attraction. However, the short floral longevity and the production of mostly one inflorescence per plant make its pollination potentially dependent on strong flowering synchrony and on external factors not controlled by the plant (the pollination context). The flowering period in both sites lasted >3 mo. Day-to-day variation in simultaneous antheses was high, and 11–50% of antheses occurred on days during which no pollen donor was present. Inflorescence traits, flowering synchrony, and between-plant distance all influenced infructescence and fruit initiation, but their relative importance differed between sites. In one large population, infructescence initiation was positively related to inflorescence traits; in a smaller population infructescence initiation increased with the number of donor inflorescences. In both sites, percentage of fruits initiated per infructescence was dependent on a combination of inflorescence traits, flowering synchrony, and between-plant distance. Plants producing 2–4 inflorescences had higher probability of infructescence initiation and overlapped their antheses with more plants than single-inflorescence ones.

Key words: Araceae; *Arum italicum*; between-plant distance; floral display; flowering dynamics; flowering synchrony; inflorescence number; pollination context.

Pollen limitation commonly constrains reproductive success in flowering plants (Burd, 1994). Floral biology studies usually test the assumption that floral traits have some adaptive value to pollination and reproductive success (Waser, 1983). Shape or size of floral structures (Campbell et al., 1991), nectar rewards (Mitchell, 1993), and floral display size (combining both size and number of flowers) (Andersson, 1991) are known to influence rates of pollinator visitation and subsequent pollen export and/or receipt.

The hypothesis that floral traits play a significant role in pollination and reproductive success assumes either implicitly or explicitly that additional confounding factors are not present or can be safely neglected. However, reproductive success of particular individuals in one population can be more related to the context in which those individuals reproduce than to their intrinsic properties. For example, several species require disassortative mating between members of two groups (e.g., pin–thrum, male–female). In such species, relative abundance of plants in every group (Wyatt and Hellwig, 1979; House, 1992) or the quality of the neighbors as pollen donors (e.g., their flower number; House, 1993) can affect reproductive success. In addition, negative effects of small population size and plant isolation on fecundity have been documented for species with diverse breeding systems (Widén and Widén, 1990; House, 1992; Kearns, Inouye, and Waser, 1998). Weather can also be an important determinant of fitness. Low temperature decreased pollinator activity and seed set in two subarctic species (Bergman, Molau, and Holmgrem, 1996). We will refer to all the abovementioned factors as the flowering context. Despite their disparity they share two characteristics: they potentially influence the pollination and reproductive success and they are not factors on which natural selection can act (as opposed to intrinsic properties such as floral morphology or display).

Within-season timing of events can also influence the fitness of particular individuals in a population. Variation in pollination success can be a result of weak flowering synchrony in hermaphrodites (Augspurger, 1981; Guitián and Sánchez, 1992), as well as variation in floral sex ratio in monoecious (Le Corff, Ågren, and Schemske, 1998) or gynodioecious (Williams, Kuchenreuter, and Drew, 2000) species. The pollination context, such as pollinator visitation rate (Totland, 1994) or weather (Totland, 1994; Bergman, Molau, and Holmgrem, 1996), may also vary over short time scales. Vagaries of the pollination context and its temporal variation can have strong consequences for reproductive performance of species producing one or few flowers. Long floral longevity (Primack, 1985) or high flowering synchrony (Rathcke and Lacey, 1985) of single- or few-flowered species can be considered as adaptations to reduce the effect of the pollination context in reproductive success.

Previous studies have shown that external factors can override the effects of floral traits on fitness (Herrera, 1993; Mitchell, 1994; O'Connell and Johnston, 1998), although pollination context has been an understudied topic. *Arum italicum* Miller (Araceae) is a good system to study how interactions among floral traits, flowering synchrony, and pollination context af-
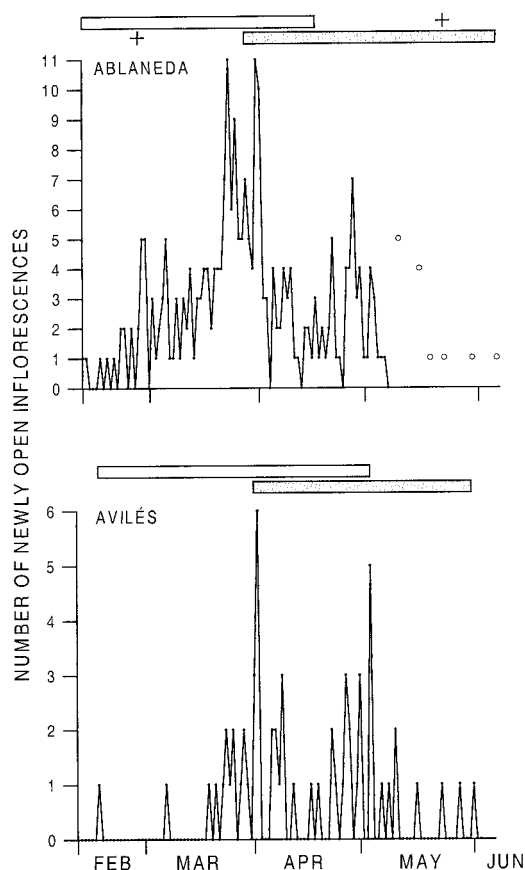
Fig. 1. Daily number of newly open (female phase) inflorescences along the flowering period in two populations of *Arum italicum* in 1994 ($N = 256$ inflorescences in Ablaneda; $N = 60$ inflorescences in Avilés). Open dots in Ablaneda indicate number of inflorescences opened after 9 May (not checked daily). Horizontal bars above each plot indicate the period of anthesis of first or single inflorescences (open) and of second to fourth inflorescences (shaded). Crosses refer to two "outlier" inflorescences that opened more than a month after or before the others in their respective groups. Notice the different *y*-axis scale among plots.

fect pollination success. The inflorescence of *A. italicum* is a spadix bearing separated whorls of female and male flowers in its lower portion. The upper half of the spadix consists of a club-shaped sterile appendix. A large green bract surrounds the spadix. At blooming this bract unfolds, showing the appendix but still forming a chamber around the fertile flowers (see Fig. 1 in Méndez, 1998). This inflorescence is the pollination unit (Faegri and van der Pijl, 1979). Most reproductive plants produce a single inflorescence in the axil of the third or fourth leaf (M. Méndez, unpublished data), but up to five inflorescences can be produced, in subsequent leaf axils, by large individuals. *Arum italicum* is pollinated by deception (Dafni, 1984) of small nematoceran flies. Anthesis occurs over two consecutive days. The species is temporally dioecious sensu Cruden and Hermann-Parker (1977). In the evening of the first day, the inflorescence opens and female flowers are functional (female phase of anthesis). Pollinators are attracted to the foul and urinous odor produced by the appendix. Heat production by thermogenic respiration in the appendix (Meeuse, 1975) volatilizes the attractive substances. Insects are trapped in the lower chamber. In the afternoon of the following day, heat production has stopped, stigmas wither, anthers on

male flowers dehisce (male phase of anthesis), and escaping insects are covered with pollen. For further details on *Arum* pollination, see Faegri and van der Pijl (1979). Pollination by deception in *A. italicum* implies that selective pressures on inflorescence traits can be strong, because of the need for attracting pollinators in a short temporal period. In addition, the low number of inflorescences produced by reproductive plants and the very short functional period makes successful pollination potentially dependent on a strong flowering synchrony with other conspecifics (Fridlender, 1999; Ollerton and Díaz, 1999). On the other hand, functional dioecy in *A. italicum* makes pollination potentially susceptible to the relative abundance of, and distance between, male and female phase plants. In addition, pollen availability for the blooming plant depends on the number of insects trapped by previous inflorescences, which is a function of their appendix length (Méndez and Obeso, 1992).

In this paper, we describe the flowering dynamics of *A. italicum* and study the role of inflorescence traits on infructescence and fruit initiation. Some studies on pollination in Araceae have reported thermogenesis by inflorescences (Young, 1986; Uemura et al., 1993; Yafuso, 1993). But, as far as we know, no previous study has related intraspecific differences in heat production to individual differences in pollination or fruit initiation. In addition, we address the relative role of flowering synchrony and pollination context on infructescence and fruit initiation. Specific questions addressed are: (1) are inflorescences attractive structures related to fruit initiation?, (2) do flowering synchrony and pollination context influence fruit initiation?, (3) what is the relative importance of pollination context on fruit initiation as compared with inflorescence traits or flowering synchrony?, (4) does production of several vs. one inflorescence increase successful fruit initiation by buffering against a changing pollination context?

MATERIALS AND METHODS

Study sites—In the study area (province of Asturias, northern Spain), *A. italicum* is common in riparian forests, hedgerows, roadsides, and other shaded, disturbed, lowland sites. Population size in this clonal species ranges from a single spot of a few ramets to big, dense populations with hundreds of ramets. In 1994, we studied flowering of *A. italicum* ramets in two sites. Ablaneda (43°30′ N, 5°54′ W) was chosen as representative of a large population (~500 ramets). There, *A. italicum* was growing along a roadside jointly with other ruderal forbs and grasses, *Rubus* sp., and *Salix atrocinerea*. As a representative of a middle size population, we used an experimental population located in Avilés (43°31′ N, 5°54′ W). It consisted of 67 plants planted as tubers originally collected in a riparian forest in Arlós (43°29′ N, 5°54′ W; for further details see Méndez, 1997). Plants occurred within a rectangular plot, spaced ~30 cm apart. The greatest distance between two plants within this plot was ~4.5 m. A small group of plants was naturally growing 10 m apart from the plot; the only inflorescence in this group overlapping anthesis with the plants in the experimental population was included in our data set. Aside from that small group, this population was at least 1 km from any suitable habitat for *A. italicum* populations. The isolation of this experimental population allowed us to accurately measure the donor and competitor number (see below) while keeping density and flowering dynamics similar to the one in natural populations.

Variables measured—Both sites were visited daily during the flowering period, February through June. Daily observations in Ablaneda were made until 9 May; subsequent antheses were scarce (<15 inflorescences) (Fig. 1) and widely spaced in time.

We noted rain in a qualitative way (rainy vs. not rainy) for each sampling

TABLE 1. Summary statistics for the inflorescence traits, flowering synchrony, and pollination context variables and for infructescence and fruit initiation variables in two populations of *Arum italicum*. Range numbers beginning with −1 or −3 indicate that "donors" were present 1 or 3 d previous to anthesis, respectively.

Variable	Mean ± 1 SD	Range	N
Ablaneda			
Appendix length (mm)	47 ± 13	23–100	106
Number of "donors"	3[a]	−1–11	106
Number of "competitors"	2[a]	0–10	106
Appendix length of nearest "donor" (mm)	45 ± 13	20–100	106
Distance to nearest "donor" (m)	3.20 ± 3.58	0.06–20.10	106
Fruits initiated per infructescence (%)	51.7 ± 31.1	0.9–100	55
Avilés			
Appendix length (mm)	53 ± 12	10–83	58
Temperature excess (°C)	12.5 ± 3.3	4.0–18.2	27
Number of "donors"	1[a]	−3–5	58
Number of "competitors"	0[a]	0–6	58
Appendix length of nearest "donor" (mm)	54 ± 9	32–67	58
Distance to nearest "donor" (m)	1.42 ± 1.29	0.30–10.00	58
Fruits initiated per infructescence (%)	53.5 ± 37.7	1.4–100	37

[a] Mode, i.e., the most frequently occurring measurement in a data set (Zar, 1999), is given. For ordinal variables mode is biologically more meaningful than mean when data distribution is asymmetrical.

day. We also counted the number of inflorescences in female (*f*) and male (*m*) phases. From these counts we obtained the daily variation in the number of newly open (female phase) inflorescences and daily variation in the number of "donors" (i.e., *m*) and putative "competitors" (i.e., *f* − 1) that each newly open inflorescence faced. In Ablaneda, the large population size made it impractical to examine all the plants. Instead, we monitored all the plants within a 25 × 1.5 m plot (>200 plants, ~40–50% of the plants at this site). *Arum italicum* is fully self-compatible (A. Díaz, personal observation), which makes all pollen donors suitable as mates independent of genetic relatedness to the focal inflorescence.

For each newly open inflorescence we measured the following variables: (a) appendix length, from its tip to the joint with the stipe, to the nearest millimeter; (b) appendix length of its nearest "donor" (an estimate of neighbor quality as pollen donor); (c) distance to nearest "donor," to the nearest centimeter. In Ablaneda, we searched for the nearest "donor" both within and outside the plot monitored. When inflorescences opened on days when no "donors" were in bloom, we noted the time elapsed from the most recent day in which "donors" had bloomed. The data on variables (b) and (c) above for these cases refer to the most recent day in which "donors" were present (usually the previous day; Table 1). Final sample size (inflorescence number) is shown in Table 1 and corresponds to 82 plants in Ablaneda (a subsample of all the flowering plants within the plot monitored) and 43 in Avilés (all the flowering plants).

For a subsample of 27 inflorescences in Avilés, we estimated the heat production by the appendix using two digital thermometers. One of them, fixed with plastic tape to the appendix, measured the appendix temperature. The other, situated on one leaf, measured the ambient temperature. Temperatures to the nearest 0.1°C were recorded every hour from the beginning of anthesis in the evening until next morning, when heat production stopped. We calculated the difference between appendix and ambient temperatures and used the highest difference recorded (temperature excess hereafter) as an estimate of heat production by the appendix.

After anthesis, we estimated pollination success as infructescence and fruit initiation (sensu Stephenson, 1981), i.e., whether, and how many, flowers in the inflorescence initiated their fruit development. Thirty days after anthesis, we scored any inflorescence appearing dry and shriveled as unsuccessful and any inflorescence showing fruit development as an infructescence. We scored inflorescence status after 30 d because bagged inflorescences (i.e., unpollinated) dried and abscised by that time in a previous assay; despite being self-compatible, we never observed self-pollination in *A. italicum*. We excluded inflorescences from analyses if abscission occurred <21 d after anthesis. This early abscission, related to the presence of an unidentified pathogen, made it not possible to discern whether growth of fruits or ovules had occurred. For

every infructescence, we analyzed fruits and recorded whether they developed (contained seeds or expanded ovules) or not (dry, brown fruits with undeveloped ovules).

Statistical analyses—We considered two successive components of female fecundity: (1) the probability of infructescence initiation and (2) the percentage of fruit initiation within an infructescence, i.e., number of fruits initiated per flower, expressed as a percentage. First, the relative influence of variables measured on the probability of infructescence initiation was identified by means of logistic regression (Hosmer and Lemeshow, 1989). We tested the significance of variables using the likelihood-ratio test (Trexler and Travis, 1993).

Second, we identified variables that influenced the percentage of fruit initiation within an infructescence using multiple linear regression. We treated two discrete variables (number of "donors" and number of "competitors") as continuous for these analyses (Sokal and Rohlf, 1981), and we modeled "rain" as a dummy variable (Zar, 1999). No transformation was applied to these or any other variable, because the analysis of residuals did not show significant departures from the assumptions of the regression. No strong colinearity was found between independent variables, according to the variance inflation factor (all values below 10) or condition index (all values below 30) (Philippi, 1993).

Disagreements exist on the best method (enter, forward, backward, or stepwise) of selecting variables in multiple regression. We ran logistic and linear regressions using both enter and stepwise methods, as performed by the statistical package SPSS-PC 4.0 (Norušis, 1990). For logistic regression, we got identical results by using either enter or stepwise methods; for linear regression, the stepwise method gave more conservative (i.e., less significant variables) results than the enter method. In the following, we will give results using the enter method, signaling differences with stepwise method when necessary.

Throughout the text, values are given as means ± 1 SD.

RESULTS

Flowering dynamics—The duration of the flowering period in both populations was similar (Fig. 1). Flowering lasted 119 d (10 February–8 June) in Ablaneda and 107 d in Avilés (16 February–2 June). In both sites, high variation in the number of newly open inflorescences was observed between successive days (Fig. 1). Rain coincided with the anthesis of 29.2% (*N* = 106) of inflorescences in Ablaneda and of 32.8% (*N* = 58) in Avilés.

TABLE 2. Results of logistic regression analysis for the probability of infructescence initiation by *A. italicum* as a function of inflorescence traits, flowering synchrony, and pollination context variables measured in two populations. The coefficient B (± 1 SE), the partial correlation coefficient (R), a measure of the influence on the dependent variable (e^B), change in model fit when removed (ΔG), and level of significance are given.

Population and variable	$B \pm 1$ SE	R	e^B	ΔG	P
Ablaneda ($N = 106$ inflorescences)					
Constant	-1.61 ± 1.52				
Appendix length	0.07 ± 0.02	0.203	1.07	8.408	<0.005
Distance to nearest "donor"	0.12 ± 0.09	0.015	1.13	2.390	>0.1
Rain	-0.78 ± 0.51	-0.052	0.45	2.322	>0.1
Number of "donors"	-0.07 ± 0.10	0.000	0.94	0.461	>0.25
Number of "competitors"	0.05 ± 0.12	0.000	1.05	0.220	>0.5
Appendix length of nearest "donor"	-0.01 ± 0.02	0.000	0.99	0.125	>0.5
Avilés ($N = 58$ inflorescences)					
Constant	-2.07 ± 2.63				
Number of "donors"	0.83 ± 0.26	0.325	2.30	12.581	<0.001
Rain	0.54 ± 0.76	0.000	1.71	0.512	>0.25
Distance to nearest "donor"	0.26 ± 0.45	0.000	1.29	0.448	>0.5
Appendix length	0.02 ± 0.03	0.000	1.02	0.443	>0.5
Number of "competitors"	0.10 ± 0.24	0.000	1.11	0.184	>0.5
Appendix length of nearest "donor"	-0.01 ± 0.04	0.000	0.99	0.094	>0.75

The overall percentage of infructescence initiation was 73.6% ($N = 106$) in Ablaneda and 65.5% ($N = 58$) in Avilés. These percentages were not significantly different (G test: $G_1 = 1.163$, $P = 0.281$). Other summary statistics are presented in Table 1. We found that 11% of inflorescences in Ablaneda ($N = 106$) and 50% in Avilés ($N = 58$) opened on days when no "donor" was blooming. These percentages were significantly different (G test: $G_1 = 29.169$, $P < 0.0001$). From those inflorescences, 67% ($N = 11$) initiated fruit in Ablaneda and 48% ($N = 29$) did in Avilés. These percentages did not differ significantly (G test: $G_1 = 1.174$, $P = 0.279$).

Relative influence of inflorescence traits, flowering synchrony and pollination context on infructescence and fruit initiation—At Ablaneda, the logistic regression analysis showed a positive relationship, as indicated by the sign of the partial correlation coefficient (R), between appendix length and the probability of infructescence initiation (Table 2). No other variables were significantly related to the probability of infructescence initiation in this population. In the multiple regression analysis, percentage of fruits initiated per infructescence was positively related to number of "donors," appendix length, and appendix length of nearest "donor" (Table 3). Distance to nearest "donor" was negatively related to fruit initiation (Table 3). In the more conservative regression analysis using the stepwise method, only number of "donors" and appendix length were significantly related to fruit initiation (Table 3). Sign and magnitude of coefficients of partial correlation for these two variables were similar in both models.

At Avilés, the logistic regression analysis revealed that the relationship between number of "donors" and the probability of infructescence initiation was significantly positive (Table 2). For the subsample in which temperature excess was measured ($N = 27$), the appendix length of nearest "donor" was negatively and significantly related to the probability of infructescence initiation (results not shown). Number of "donors" was only marginally significant ($P > 0.05$). None of the variables considered explained a significant amount of variance in per-

TABLE 3. Results of multiple-regression analysis for the percentage of fruit initiation within an infructescence as a function of inflorescence traits, flowering synchrony, and pollination context variables measured in two populations of *A. italicum*. ANOVA results, coefficient of determination, R^2, and partial regression coefficient, B (± 1 SE), are given for the enter method. The t value and level of significance are given for both enter and stepwise (step) methods.

Population and variable	$B \pm 1$ SE	t (enter)	P (enter)	t (step)	P (step)
Ablaneda ($F_{6, 48} = 4.436$, $P = 0.001$, $R^2 = 0.36$)					
Constant	-17.76 ± 22.34	-0.795	0.430	0.102	0.919
Appendix length	0.78 ± 0.29	2.728	0.009	2.515	0.015
Number of "donors"	4.10 ± 1.69	2.432	0.019	3.128	0.003
Distance to nearest "donor"	-2.36 ± 1.03	-2.283	0.027	-1.538	0.130
Appendix length of nearest "donor"	0.61 ± 0.29	2.121	0.039	1.515	0.136
Rain	-9.30 ± 9.15	-1.016	0.315	-1.144	0.258
Number of "competitors"	0.28 ± 1.60	0.176	0.861	0.163	0.871
Avilés[a] ($F_{7, 11} = 15.565$, $P = 0.0001$, $R^2 = 0.91$)					
Constant	-44.65 ± 38.49	-1.160	0.276	-1.523	0.147
Temperature excess	10.08 ± 1.22	8.258	<0.0001	6.040	<0.0001
Number of "competitors"	-14.16 ± 2.56	-5.538	0.0002	-5.554	<0.0001
Appendix length of nearest "donor"	-1.25 ± 0.47	-2.640	0.023	-2.112	0.052
Number of "donors"	7.12 ± 3.05	2.334	0.040	1.774	0.096
Appendix length	0.64 ± 0.42	1.519	0.157	0.137	0.892
Distance to nearest "donor"	-2.64 ± 2.04	-1.294	0.222	-0.633	0.536
Rain	10.46 ± 9.79	1.069	0.308	-0.024	0.981

[a] Analysis only includes data for the subsample in which heat production was estimated.

TABLE 4. Comparison between single and multi-inflorescence plants in two populations of *A. italicum*. (A) Mean number ± 1 SD (sample size) of plants flowering on the same day. Results of ANOVAs testing differences between groups of plants are also given. (B) Percentage of plants initiating infructescences (sample size in parentheses). Results of a binomial test for differences between groups of plants are also given. Only plants in which fruit initiation could be determined for all the inflorescences produced were included in the analyses.

Population	No. of inflorescences		P
	1	>1	
A) No. of plants flowering on the same day			
Ablaneda	4.3 ± 3.4 (27)	7.7 ± 3.9 (17)	<0.01
Avilés	1.0 ± 0.8 (18)	1.8 ± 1.2 (17)	<0.05
B) Percentage of plants initiating infructescences			
Ablaneda	66.7% (27)	94.1% (17)	0.071
Avilés	41.2% (17)	88.2% (17)	<0.001

centage of fruits initiated, using multiple regression. However, for the subsample of inflorescences in which heat production was estimated ($N = 19$ inflorescences initiating fruits), temperature excess and number of "donors" showed a positive relationship with fruit initiation (Table 3). In addition, number of "competitors" and appendix length of nearest "donor" were significantly negatively related to percentage of fruit initiation (Table 3). Again, stepwise multiple regression was more conservative and showed only a significant relationship between temperature excess and number of competitors and fruit initiation (Table 3), although both sign and partial correlation coefficients were similar in both models.

Consequences for single- vs. multi-inflorescence plants— Percentage of multi-inflorescence plants (range: 2–4 inflorescences) was 63.9% ($N = 122$) in Ablaneda and 51.1% ($N = 43$) in Avilés. In multi-inflorescence plants, inflorescences were produced sequentially and their antheses were separated by 33.7 ± 8.3 d (range: 7–56 d, $N = 43$) in Ablaneda and 31.6 ± 8.3 d (range: 18–52 d, $N = 25$) in Avilés. Production of several inflorescences by the same plant extended the flowering period both at the plant and the population level (Fig. 1). At the population level, a second peak of flowering was apparent.

At both sites, multi-inflorescence plants overlapped their flowering with significantly more plants than single-inflorescence ones (Table 4A). In addition, probability of infructescence initiation was significantly higher for multi-inflorescence plants in Avilés (Table 4B) and close to significantly higher in Ablaneda (Table 4B).

DISCUSSION

Specialized inflorescence structures, as appendices or nutritious staminodia, play a role in pollination of many Araceae (e.g., Knoll, 1926; Bown, 1988; Vogel, 1990; Young, 1990; Gottsberger and Silberbauer-Gottsberger, 1991; Gibernau et al., 1999). Most previous studies on the importance of such structures for pollinator attraction have been qualitative (e.g., Lack and Díaz, 1991), but there is some quantitative evidence of the positive influence of size or number of those structures on pollinator attraction (Young, 1990; Gibernau et al., 1999). In the present study, appendix length was positively related to both the probability and amount of fruit initiation. In addition, fruit initiation increased with temperature excess, a component

of floral display understudied until now in Araceae. A previous paper also showed a positive relationship between appendix length and pollinator visits in this species (Méndez and Obeso, 1992).

Some evidence exists regarding the influence of pollination context, such as between-plant distance or weather, in pollen transfer or reproductive success in Araceae. Fruit set decreased as distance to male inflorescences increased in *Arisaema triphyllum* (Rust, 1980; but see Bierzychudek, 1982) and *Amorphophallus johnsonii* (Beath, 1996). Also, cool weather made midges pollinating *Arum maculatum* torpid (Kite, 1995). In *A. italicum,* fruit initiation decreased with increasing between-plant distance in Ablaneda, although this result was not consistent between regression models. On the other hand, any daily variations in pollinator abundance or activity due to rain seemed to have little effect on infructescence initiation. Temperature could be a more important factor, but it was not measured in this study. Everything else being the same, we expected that infructescence or fruit initiation would increase for inflorescences having "donors" with long appendices, because these should attract more pollinators (Méndez and Obeso, 1992) and, consequently, be better sources of pollinators for newly opened inflorescences. This was the result for Ablaneda, but the opposite effect occurred in Avilés. In all cases, the effect of appendix length of nearest "donor" was weak and its significance changed among regression models. Further observations should be made in order to test the importance of this aspect of "donor quality" for fruit initiation.

Flowering synchrony affected reproductive success in *Arum maculatum* (Ollerton and Díaz, 1999). In the same way, in the present study number of "donors" was positively related to either infructescence or fruit initiation at both sites studied. This was not surprising, because of the high daily variation in number of "donors." However, some ability of buffering against this variability seemed to be present in *A. italicum* because infructescence initiation also occurred on days in which no "donors" were in bloom. This fact is opposed to findings of Beath (1996) for *Amorphophallus johnsonii*. In the latter species, no successful fertilization occurred unless pollen was transferred on the same day of anthesis. Results in *A. italicum* inflorescences could be due either to carryover of viable pollen on pollinators for 1 or 2 d or to pollen arrival from other populations. Unfortunately, data on pollen longevity in this species are lacking to test this.

The relative effect of inflorescence traits, flowering synchrony, and pollination context was population specific. The present study was correlative; thus, it is difficult to disentangle which population characteristics were responsible for such differences. One tentative explanation is offered here that should be tested by means of future experimental manipulation. In Ablaneda, a large population, probability of overlapping antheses was higher than in Avilés (89 vs. 50%, see RESULTS), and this could mean both a lower uncertainty in the Ablaneda pollination context and a lower influence of number of "donors" on infructescence initiation. This, combined with a lower average appendix length, could give better opportunities for the effect of inflorescence traits to become apparent.

A higher flowering synchrony would apparently be advantageous in *A. italicum* (Méndez, 1998). A similar result was obtained by Ollerton and Díaz (1999) for *A. maculatum*. However, flowering synchrony was not high in *A. italicum* (maximum of 11 simultaneous antheses in Ablaneda, a population in which 256 antheses were recorded; see Fig. 1) or other

Araceae studied (*Dieffenbachia longispatha*—Young, 1988, 1990; *Philodendron solimoesense*—Gibernau et al., 1999). At present it is not known which proximate cues or ultimate mechanisms can be responsible for that asynchrony. Benefits of an increased flowering synchrony in *A. italicum* could be overridden by an increase in competition for pollen, as indicated by the negative effect of number of "competitors" on fruit initiation found in Avilés.

Another way to cope with environmental uncertainty is to produce several inflorescences (Burd, 1995). But despite its benefits for multi-inflorescence plants, this is a limited possibility, because inflorescence number in *A. italicum* is size dependent (Méndez and Obeso, 1993). Production of additional inflorescences could potentially be dependent on the pollination success of the first inflorescence but this possibility could not be explored with the data available. On the other hand, an increased inflorescence longevity could also buffer against a variable pollination context. Although many Araceae inflorescences exhibit a short functional period (Gibernau et al., 1999; Ollerton and Díaz, 1999), extended flowering also exists (Wada and Uemura, 2000). To what extent phylogenetic constraints (Ollerton and Díaz, 1999) or a high maintenance cost (Primack, 1985) of an energetically expensive floral display affect inflorescence longevity in Araceae should be addressed by future studies.

Finally, although we have mainly discussed the evidence concerning Araceae, the interaction among floral characters, flowering synchrony, and pollination context can be important for fitness in many other species producing one or a few flowers (Totland, 1994) or requiring disassortative mating between members of two groups (Wyatt and Hellwig, 1979; House, 1992). The pollination context could potentially affect selective pressures on flowering synchrony or floral characters (Schemske and Horvitz, 1989) differently in populations of varying densities or sex ratios, as well as influence genetic neighborhoods (Young, 1988). This will be a fruitful topic for future studies.

LITERATURE CITED

ANDERSSON, S. 1991. Floral display and pollination success in *Achillea ptarmica* (Asteraceae). *Holarctic Ecology* 14: 186–191.

AUGSPURGER, C. K. 1981. Reproductive synchrony of a tropical shrub: experimental studies on effects of pollinators and seed predators on *Hybanthus prunifolius* (Violaceae). *Ecology* 62: 775–788.

BEATH, D. D. N. 1996. Pollination of *Amorphophallus johnsonii* (Araceae) by carrion beetles (*Phaeochrous amplus*) in a Ghanaian rain forest. *Journal of Tropical Ecology* 12: 409–418.

BERGMAN, P., U. MOLAU, AND B. HOLMGREN. 1996. Micrometeorological impacts on insect activity and plant reproductive success in an alpine environment, Swedish Lapland. *Arctic and Alpine Research* 28: 196–202.

BIERZYCHUDEK, P. 1982. The demography of jack-in-the-pulpit, a forest perennial that changes sex. *Ecological Monographs* 52: 335–351.

BOWN, D. 1988. Aroids. Plants of the *Arum* family. Timber Press, Portland, Oregon, USA.

BURD, M. 1994. Bateman's principle and plant reproduction: the role of pollen limitation in fruit and seed set. *Botanical Review* 60: 83–139.

BURD, M. 1995. Ovule packaging in stochastic pollination and fertilization environments. *Evolution* 49: 100–109.

CAMPBELL, D. R., N. M. WASER, M. V. PRICE, E. A. LYNCH, AND R. J. MITCHELL. 1991. Components of phenotypic selection: pollen export and flower corolla width in *Ipomopsis aggregata*. *Evolution* 45: 1458–1467.

CRUDEN, R. W., AND S. M. HERMANN-PARKER. 1977. Temporal dioecism: an alternative to dioecism? *Evolution* 31: 863–866.

DAFNI, A. 1984. Mimicry and deception in pollination. *Annual Review of Ecology and Systematics* 15: 259–278.

FÆGRI, K., AND L. VAN DER PIJL. 1979. The principles of pollination ecology, 3rd ed. Pergamon Press, Oxford, UK.

FRIDLENDER, A. 1999. Observations sur la biologie de l'*Arum cylindraceum* Gasp. (Araceae) en Corse. *Acta Botanica Gallica* 146: 297–309.

GIBERNAU, M., D. BARABÉ, P. CERDAN, AND A. DEJEAN. 1999. Beetle pollination of *Philodendron solimoesense* (Araceae) in French Guiana. *International Journal of Plant Sciences* 160: 1135–1143.

GOTTSBERGER, G., AND I. SILBERBAUER-GOTTSBERGER. 1991. Olfactory and visual attraction of *Eriocelis emarginata* (Cyclocephalini, Dynastinae) to the inflorescences of *Philodendron selloum* (Araceae). *Biotropica* 23: 23–28.

GUITIÁN, J., AND J. M. SÁNCHEZ. 1992. Flowering phenology and fruit set of *Petrocoptis grandiflora* (Caryophyllaceae). *International Journal of Plant Sciences* 153: 409–412.

HERRERA, C. M. 1993. Selection on floral morphology and environmental determinants of fecundity in a hawk moth-pollinated violet. *Ecological Monographs* 63: 251–275.

HOSMER, D. W., AND S. LEMESHOW. 1989. Applied logistic regression. Wiley, New York, New York, USA.

HOUSE, S. M. 1992. Population density and fruit set in three dioecious tree species in Australian tropical rain forest. *Journal of Ecology* 80: 57–69.

HOUSE, S. M. 1993. Pollination success in a population of dioecious rain forest trees. *Oecologia* 96: 555–561.

KEARNS, C. A., D. W. INOUYE, AND N. M. WASER. 1998. Endangered mutualisms: the conservation of plant–pollinator interactions. *Annual Review of Ecology and Systematics* 29: 83–112.

KITE, G. C. 1995. The floral odour of *Arum maculatum*. *Biochemical Systematics and Ecology* 23: 343–354.

KNOLL, F. 1926. Insekten und Blumen. Experimentelle Arbeiten zur vertiefung unserer kenntnisse über die Wechselbeziehungen Zwischen Pflanzen und Tieren. IV. Die *Arum*-blütenstände und ihre Besucher. *Abhandlungen der zoologisch-botanischen Gesellschaft in Wien* 12: 379–481.

LACK, A. J., AND A. DÍAZ. 1991. The pollination of *Arum maculatum* L.—a historical review and new observations. *Watsonia* 18: 333–342.

LE CORFF, J., J. ÅGREN, AND D. W. SCHEMSKE. 1998. Floral display, pollinator discrimination, and female reproductive success in two monoecious *Begonia* species. *Ecology* 79: 1610–1619.

MEEUSE, B. J. D. 1975. Thermogenic respiration in aroids. *Annual Review of Plant Physiology* 26: 117–126.

MÉNDEZ, M. 1997. Sources of variation in seed mass in *Arum italicum*. *International Journal of Plant Sciences* 158: 298–305.

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

MÉNDEZ, M., AND J. R. OBESO. 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., AND J. R. OBESO. 1993. Size-dependent vegetative and reproductive allocation in *Arum italicum* (Araceae). *Canadian Journal of Botany* 71: 309–314.

MITCHELL, R. J. 1993. Adaptive significance of *Ipomopsis aggregata* nectar production: observation and experiment in the field. *Evolution* 47: 25–35.

MITCHELL, R. J. 1994. Effects of floral traits, pollinator visitation, and plant size on *Ipomopsis aggregata* fruit production. *American Naturalist* 143: 870–889.

NORUŠIS, M. 1990. SPSS introductory statistics student guide. SPSS Inc., Chicago, Illinois, USA.

O'CONNELL, L. M., AND M. O. JOHNSTON. 1998. Male and female pollination success in a deceptive orchid, a selection study. *Ecology* 79: 1246–1260.

OLLERTON, J., AND A. DÍAZ. 1999. Evidence for stabilising selection acting on flowering time in *Arum maculatum* (Araceae): the influence of phylogeny on adaptation. *Oecologia* 119: 340–348.

PHILIPPI, T. E. 1993. Multiple regression: herbivory. *In* S. M. Scheiner and J. Gurevitch [eds.], Design and analysis of ecological experiments, 183–210. Chapman and Hall, New York, New York, USA.

PRIMACK, R. B. 1985. Longevity of individual flowers. *Annual Review of Ecology and Systematics* 16: 15–37.

RATHCKE, B., AND E. P. LACEY. 1985. Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematics* 16: 179–214.

RUST, R. W. 1980. Pollen movement and reproduction in *Arisaema triphyllum*. *Bulletin of the Torrey Botanical Club* 107: 539–542.

SCHEMSKE, D. W., AND C. C. HORVITZ. 1989. Temporal variation in selection on a floral character. *Evolution* 43: 461–465.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry, 2nd ed. W. H. Freeman, New York, New York, USA.

STEPHENSON, A. G. 1981. Flower and fruit abortion: proximate causes and ultimate functions. *Annual Review of Ecology and Systematics* 12: 253–279.

TOTLAND, Ø. 1994. Intraseasonal variation in pollination intensity and seed set in an alpine population of *Ranunculus acris* in southwestern Norway. *Ecography* 17: 159–165.

TREXLER, J. C., AND J. TRAVIS. 1993. Nontraditional regression analyses. *Ecology* 74: 1629–1637.

UEMURA, S., K. OHKAWARA, G. KUDO, N. WADA, AND S. HIGASHI. 1993. Heat-production and cross-pollination of the Asian skunk cabbage *Symplocarpus renifolius* (Araceae). *American Journal of Botany* 80: 635–640.

VOGEL, S. 1990. The role of scent glands in pollination: on the structure and function of osmophores. Amerind, New Delhi, India.

WADA, N., AND S. UEMURA. 2000. Size-dependent flowering behavior and heat production of a sequential hermaphrodite, *Symplocarpus renifolius* (Araceae). *American Journal of Botany* 87: 1489–1494.

WASER, N. M. 1983. The adaptive nature of floral traits: ideas and evidence. *In* L. Real [ed.], Pollination biology, 242–285. Academic Press, London, UK.

WIDÉN, B., AND M. WIDÉN. 1990. Pollen limitation and distance-dependent fecundity in females of the clonal gynodioecious herb *Glechoma hederacea* (Lamiaceae). *Oecologia* 83: 191–196.

WILLIAMS, C. F., M. A. KUCHENREUTER, AND A. DREW. 2000. Floral dimorphism, pollination, and self-fertilization in gynodioecious *Geranium richardsonii* (Geraniaceae). *American Journal of Botany* 87: 661–669.

WYATT, R., AND R. L. HELLWIG. 1979. Factors determining fruit set in heterostylous bluets, *Houstonia caerulea* (Rubiaceae). *Systematic Botany* 4: 103–114.

YAFUSO, M. 1993. Thermogenesis of *Alocasia odora* (Araceae) and the role of *Colocasiomyia* flies (Diptera: Drosophilidae) as cross-pollinators. *Environmental Entomology* 22: 601–606.

YOUNG, H. J. 1986. Beetle pollination of *Dieffenbachia longispatha* (Araceae). *American Journal of Botany* 73: 931–944.

YOUNG, H. J. 1988. Neighborhood size in a beetle pollinated tropical aroid: effects of low density and asynchronous flowering. *Oecologia* 76: 461–466.

YOUNG, H. J. 1990. Pollination and reproductive biology of an understory neotropical aroid. *In* K. S. Bawa and M. Hadley [eds.], Reproductive ecology of tropical forest plants, 151–164. UNESCO and Parthenon, Paris, France.

ZAR, J. H. 1999. Biostatistical analysis, 4th ed. Prentice-Hall, Upper Saddle River, New Jersey, USA.