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The effectiveness of some mechanisms of reproductive isolation in *Arum maculatum* and *A. italicum* (Araceae)

ANITA DIAZ[1]*, MÉLANIE AKA AMOIN[2] and MARC GIBERNAU[2]

[1]*Centre for Ecology & Conservation Biology, School of Conservation Sciences, Bournemouth University, Dorset House, Talbot Campus, Fern-Barrow, Poole, Dorset, BH12 5BB, UK*
[2]*Laboratoire d'Evolution & Diversité Biologique (UMR 5174), Université Paul Sabatier, 118 Route de Narbonne, Bât 4R3-B2, 31062 Toulouse Cedex 4, France*

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Mechanisms of reproductive isolation were studied in two species of *Arum*, *A. italicum* and *A. maculatum*, growing in England and the south of France. The study focused on three potential mechanisms for reproductive isolation: the effectiveness of dichogamy as a barrier to autogamy; the ability of self and outcrossed pollen to germinate on stigmas at different stages of anthesis and to effect pollination; and postzygotic barriers to selfing. Dichogamy was found to provide a very effective barrier to within-inflorescence selfing in these species, as no seeds were produced by spontaneous self-pollination (i.e. autogamy) in any population of either species. However, the study found that geitonogamy (cross-pollination between inflorescences of a same individual or clone) was possible, as genotypes frequently produced several inflorescences and stigmas were found to be receptive to pollen from before anthesis until their contraction at the end of the female phase of flowering. Hand pollination with self pollen from clone inflorescences produced as numerous and heavy seeds as outcross pollination. In addition, the germination and growth of geitonogamously produced seed was similar to that of outcrossed seed, suggesting that this potential postzygotic barrier is absent or weak. These findings suggest that geitonogamous seed production may be unrestricted by significant pre- or postzygotic barriers. The possible advantages of geitonogamy in *Arum* are discussed. © 2006 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2006, **150**, 323–328.

ADDITIONAL KEYWORDS: autogamy – breeding system – dichogamy – geitonogamy – herkogamy – pollination.

INTRODUCTION

Angiosperms have evolved a wide range of breeding barriers that promote allogamy by preventing autogamy (Barrett, 2002). Breeding barriers can be prezygotic or postzygotic and many species have both these types of barrier (Bertin & Newman, 1993). Common prezygotic barriers are dichogamy, i.e. a separation in time of the receptivity of stigmas and the release of pollen (Lloyd & Webb, 1986), and herkogamy, i.e. a separation in space of receptive stigmas and dehiscing anthers (Webb & Lloyd, 1986). Postzygotic barriers include selective ovule abortion, and reduced germination and fitness of selfed progeny. Prezygotic barriers can prevent autogamy but may not prevent geitonogamy (cross-pollination between inflorescences of the same individual or clone) (De Jong, Waser & Klinkhamer, 1993; Snow *et al.*, 1996; Montaner, Floris & Alvarez, 2001; Galloway, Cirigliano & Gremski, 2002). Postzygotic barriers can prevent both autogamy and geitonogamy but result in the wastage of ovules and so are, in this sense, less efficient than prezygotic barriers (Waser & Price, 1991).

Members of the Araceae produce elaborate inflorescences that attract their insect pollen vectors with a wide range of scents and inflorescence design, including trap pollination systems (Mayo, Bogner & Boyce, 1997; Gibernau, 2003). Basal taxa in this family have inflorescences composed of bisexual flowers. By contrast, more derived taxa in the subfamily Aroideae have unisexual flowers and the potential for herkogamy as they have spatially structured inflorescences

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*Corresponding author. E-mail: adiaz@bournemouth.ac.uk in which female flowers are located at the base of the inflorescence and male flowers are situated somewhere above (Mayo *et al*., 1997; Gibernau, 2003). However, such an arrangement still risks autogamy by pollen shedding down onto the stigmas unless the inflorescence also exhibits dichogamy. In fact, many species of Araceae use dichogamy as a prezygotic barrier and all species appear to be protogynous (Mayo *et al*., 1997). There is also is a potential selective pressure for postzygotic barriers to prevent geitonogamous seed set as many species produce more than one inflorescence per genotype. The potential combination of prezygotic isolating mechanisms and other breeding barriers has not been investigated within the Araceae.

Most species of the genus *Arum* produce inflorescences that lure insect pollinators into open inflorescences during the female phase of flowering and then trap them for about 24 h until the male flowers open and release pollen (Prime, 1960; Lack & Diaz, 1991; Boyce, 1993; Albre, Quilichini & Gibernau, 2003; Gibernau, Macquart & Przetak, 2004). The inflorescences of all species exhibit herkogamy (Boyce, 1993) and many species also appear to exhibit dichogamy. A single genotype may, however, produce several inflorescences, and pollinators exiting one inflorescence are often captured by another, female-phase, inflorescence of the same genotype (A. Diaz, pers. observ.). In this paper we investigate whether this potential for geitonogamy is restricted by other breeding barriers by examining whether self pollen is as effective as outcrossed pollen at fertilizing ovules and producing seed in two species of *Arum*, *A. italicum* Miller. and *A. maculatum* L.

MATERIAL AND METHODS

A comparison was made of the reproductive system of *A. italicum* ssp. *italicum* Miller, *A. italicum* ssp. *neglectum* F. Towns. and A. *maculatum* L. from several populations in England and southern France. Comparisons were made of: (i) the effectiveness of dichogamy as a barrier to autogamy, (ii) the ability of self and outcrossed pollen to germinate on stigmas at different stages of anthesis and to effect pollination, and (iii) the extent of postzygotic barriers to selfing.

Five populations of *Arum* were investigated, four in England and one in the south of France. The English samples were collected from one population of *A. italicum* ssp. *italicum* growing in a woodland in the village of Ridge, Dorset; one population of *A. italicum* ssp. *neglectum* growing in hedgerows near Langton Matravers, Dorset; and two populations of *A. maculatum,*; one growing in a wooded lane in Wareham, Dorset, and the other growing in a wood adjacent to the University of Exeter, Devon. The French samples were collected from a population of *Arum italicum* ssp. *italicum* growing in a wood on the campus of the University Paul Sabatier of Toulouse (south-west France).

The effectiveness of dichogamy as a barrier to autogamy was investigated for each population by bagging 20 inflorescences to exclude pollinators. The inflorescences were bagged prior to anthesis and remained bagged until seed ripening or abortion occurred. The relative ability of self and outcrossed pollen to effect seed set was tested in each population by hand pollinating some plants with selfed and others with outcrossed pollen. Inflorescences were bagged prior to anthesis to exclude pollinations and bagged again immediately after hand pollinations were performed until seed ripening or abortion occurred. All hand pollinations were carried out using a small paintbrush and the females flowers were accessed by inserting the paintbrush through two small holes cut in the spathe chamber wall. The self-pollen was obtained from inflorescences that had flowered the day before on the same individual. These species of *Arum* exhibit clonal growth; each tuber usually produces only one inflorescence but tubers often divide, thus producing an individual consisting of a clumped colony of clones. Such clones are readily identifiable, particularly as they often grow discretely from other individuals. Only inflorescences that were clearly part of the same clone were used as pollen donors. The largest individual clump used had a diameter of approximately 1 m and thus all donor inflorescences were located less that 1 m from the recipient inflorescence. Ten inflorescences in each English population and 20 in the Toulouse population were hand pollinated with self-pollen. Outcrossed pollen was obtained from donor plants growing at least 10 m away from recipient plants. Ten inflorescences in each English population and 26 in the French were hand pollinated with outcrossed pollen. All the inflorescences were then labelled and left to set seed. Fruit and seed sets were calculated for all the inflorescences of the three treatments. The number of fruits and the number and weight of seeds produced by geitonogamy vs. cross-pollination were compared by two-sample *t*-tests using Systat 8.0 (1998) software.

To test the extent to which geitonogamy is limited by stigma receptivity, a comparison was made of the success of pollen germination on stigmas of varying ages. This was carried out during the spring of 2004 for each taxon in the three Dorset populations: *A. italicum* ssp. *italicum* (growing in Ridge), *A. italicum* ssp. *neglectum* (growing near Langton Matravers) and *A. maculatum* (growing in Wareham). All inflorescences used were bagged prior to anthesis and re-bagged immediately after treatment. Inflorescences were assigned to treatments at random. There were three self-pollen treatments: at anthesis (i.e. as the spathe unfurls), 12 h prior to anthesis and 12 h after anthesis (i.e. just prior to the usual time for the end of the female phase of flowering in these taxa). There were also three out-crossed pollen treatments, again at anthesis, 12 h prior to anthesis and 12 h after anthesis. The sample size for each of these six treatments was ten inflorescences per treatment. Inflorescences were assigned to treatments at random and pollen was applied to at least ten stigmas per inflorescence. Pollen was collected from bagged inflorescences and applied to recipient inflorescences using a small paintbrush as described above. Fresh pollen was applied to at least ten stigmas of each of ten bagged inflorescences. The pollination treatments were carried out over several days in a random order to avoid any bias across treatments caused by environmental conditions.

Any pollen germination and growth was stopped in each treatment 3 h after the application of pollen by excising the stigmas, fixing them using 30% glacial acetic acid for a few hours and then preserving them in 70% alcohol. Any stigmas not holding pollen were discarded and then the success of pollen germination was examined on a random ten stigmas per inflorescence. Pollen germination was recorded as simply presence/absence per stigma and results were then combined to produce a percentage frequency of germination per inflorescence. A Kruskall–Wallis test (Systat 8.0, 1998) was used to establish whether there were significant differences in the mean germination success per treatment.

Postzygotic barriers to seed germination and early growth were investigated using seed produced from the hand pollinations performed to test the relative ability of self and outcrossed pollen to effect seed set. Only the Dorset population of each taxon was used in this part of the investigation. Ten seeds were collected from each population, washed to remove the surrounding pulp and then sown into individual pots of local soil in September 2001. The pots were kept free of weeds and the percentage of seeds that had grown into seedlings was recorded in April 2004. This scoring was not carried out until this point to avoid under-recording of germination success caused by the seed taking up to 2 years to germinate under natural conditions and by the fact that the first year of growth is usually entirely below ground. The success of germination and establishment of selfed and outcrossed progeny was compared using a Mann–Whitney test (Systat 8.0, 1998).

RESULTS

All the 100 inflorescences tested for spontaneous self-pollination (i.e. autogamy) aborted with no seed production in all the taxa studied (Tables 1–3). This

Table 1. *Arum italicum* ssp. *italicum* (France): Infructescence set is the percentage of maturing infructescence from the initial inflorescences (*N*). Given for mature infructescences is the mean number (± SD) of developed fruits (berries) and seeds per infructescence. No significant differences were found between inflorescences pollinated with selfed or outcrossed pollen

Population locality	Pollination experiment	*N*	Infructescence set (%)	Fruits per infructescence	Seeds per infructescence
Universit of Toulouse	Autogamy	20	0	No fruit	No seed
	Geitonogamy	20	80	32.5 ± 20.2	79.3 ± 60.5
	Cross-pollination	26	85	31.5 ± 17.6	65.8 ± 45.5

Table 2. *Arum italicum* (Dorset, UK): Infructescence set is the percentage of maturing infructescence from the initial inflorescences (*N*). Given for mature infructescences is the mean number (± SD) of developed fruits (berries) and seeds per infructescence, and seed mean weight (mg). No significant differences were found between inflorescences pollinated with selfed or outcrossed pollen in either population studied

Population locality	Pollination experiment	*N*	Infructescence set (%)	Fruits per infructescence	Seeds per infructescence	Mean weight of seeds (mg)
ssp. *italicum* Ridge	Autogamy	20	0	No fruit	No seed	No seed
	Geitonogamy	10	100	41.9 ± 3.3	99.6 ± 18.9	36 ± 1.7
	Cross-pollination	10	100	41.4 ± 5.8	99 ± 17.7	35 ± 1.8
ssp. *neglectum* Dancing Ledge	Autogamy	20	0	No fruit	No seed	No seed
	Geitonogamy	10	100	41.5 ± 5.6	101 ± 17.4	35 ± 1.3
	Cross-pollination	10	100	41.6 ± 5.2	100.3 ± 18.8	37 ± 2

Table 3. *Arum maculatum* (UK): Infructescence set is the percentage of maturing infructescence from the initial inflorescences (*N*). Given for mature infructescences is the mean number (± SD) of developed fruits (berries) and seeds per infructescence, and seed mean weight (mg). No significant differences were found between inflorescences pollinated with selfed or outcrossed pollen in either population studied

Population locality	Pollination experiment	*N*	Infructescence set (%)	Fruits per infructescence	Seeds per infructescence	Mean weight of seeds (mg)
Wareham, Dorset	Autogamy	20	0	No fruit	No seed	No seed
	Geitonogamy	10	100	35.8 ± 7.9	83 ± 39.8	32 ± 3.8
	Cross-pollination	10	100	36.8 ± 7.8	86 ± 38.5	31 ± 2
Exeter, Devon	Autogamy	20	0	No fruit	No seed	No seed
	Geitonogamy	10	100	36.3 ± 8.5	82 ± 32.6	31 ± 3.5
	Cross-pollination	10	100	38.7 ± 7	91.6 ± 31.6	30 ± 1.9

Table 4. Effect of stigma age on mean percentage (± SD) of pollen that germinated for each taxon studied. Ten stigmas were sampled from each of ten inflorescences per treatment. Stigma age had no significant effect on pollen germination for any of the taxa

	A. italicum ssp. *italicum*	*A. italicum* ssp. *neglectum*	*A. maculatum*
12 h before anthesis	76.7 ± 14.0	80.0 ± 14.5	83.3 ± 12.7
At anthesis	78.9 ± 12.3	82.2 ± 12.0	85.6 ± 8.4
12 h after anthesis	74.4 ± 13.5	83.3 ± 11.7	80.0 ± 17.3

Table 5. Mean percentage germination success (± SD) of selfed and outcrossed progeny for each taxon. Twenty seeds were sown from each of ten inflorescences per taxon. No significant differences were found between selfed or outcrossed progeny

	A. italicum ssp. *italicum*	*A. italicum* ssp. *neglectum*	*A. maculatum*
Selfed seed	45.0 ± 20.4	35.5 ± 25.4	62.0 ± 21.5
Outcrossed seed	53.0 ± 21.4	47.0 ± 17.8	66.5 ± 26.1

result indicates that dichogamy effectively prevents autogamy in *Arum italicum* (ssp. *italicum* and *neglectum*) as well as in *A. maculatum*. By contrast, pollinations between inflorescences of the same individual or clone (i.e. geitonogamy) in general produced as many fruits and seeds as outcrossed pollination. In the French population of *A. italicum* (ssp. *italicum*) from Toulouse, no significant difference was found between inflorescences pollinated with selfed or outcrossed pollen for the number of fruits ($t_{36} = 0.13$, $P = 0.89$) or seeds ($t_{36} = 0.77$, $P = 0.44$) per infructescence (Table 1). Similarly, the English populations of *A. italicum* (ssp. *italicum* and *neglectum*) showed no significant difference for fruit ($t_{18} = -0.24$, $P = 0.81$ for ssp. *italicum*; $t_{18} = -0.08$, $P = 0.92$ for ssp. *neglectum*) or seed numbers ($t_{18} = -0.18$, $P = 0.86$ for ssp. *italicum*; $t_{18} = 0.19$, $P = 0.53$ for ssp. *neglectum*) per infructescence or the average seed weight ($t_{18} = 0.37$, $P = 0.71$ for ssp. *italicum*; $t_{18} = -0.49$, $P = 0.63$ for ssp. *neglectum*) between inflorescences pollinated with selfed or outcrossed pollen (Table 2). Finally, both populations of *A. maculatum* studied also showed no significant difference between inflorescences pollinated with selfed or outcrossed pollen in the success of fruit set ($t_{18} = 0.06$, $P = 0.95$ in Wareham; $t_{18} = 0.61$, $P = 0.55$ in Exeter), seed set ($t_{18} = 0.17$, $P = 0.87$ in Wareham; $t_{18} = 0.67$, $P = 0.51$ in Exeter) or average seed weight ($t_{18} = -0.97$, $P = 0.34$ in Wareham; $t_{18} = -0.49$, $P = 0.63$ in Exeter) (Table 3).

A comparison of the success of pollen germination on stigmas of different ages showed that stigmas were as receptive to pollen 12 h either side of anthesis as they were at anthesis (Table 4) (Kruskal–Wallis tests: $H = 0.18$, $P = 0.91$ for *A. italicum* ssp. *italicum*; $H = 0.46$, $P = 0.79$ for *A. italicum* ssp. *neglectum*; $H = 0.57$, $P = 0.75$ for *A. maculatum*). Results comparing the germination and growth of outcrossed and selfed seedlings indicated that outcrossed seedlings had higher mean germination and early establishment success than selfed seedlings (Table 5) but these differences were not significant for any of the three taxa of *Arum* (Mann–Whitney tests: $U = 38.5$, $P = 0.38$ for *A. italicum* ssp. *italicum*; $U = 36$, $P = 0.29$ for *A. italicum* ssp. *neglectum*; $U = 42$, $P = 0.54$ for *A. maculatum*).

DISCUSSION

Our results provide strong evidence of (complete) dichogamy as an effective prezygotic barrier to within-inflorescence selfing in *Arum maculatum* and *A. italicum* as no seed was produced in this way. Such a result has been found in other Araceae, e.g. *Peltandra virginica*, *Philodendron solimoesense* and *Symplocarpus renifolius* (Uemera *et al*., 1993; Patt *et al*., 1995; Mayo *et al*., 1997; Gibernau *et al*., 1999). However, some examples of self-pollination or apomixis are also known or suspected in this family, e.g. *Amorphophallus bulbifer*, *Anthurium bakeri*, *Lysichiton americanum*, *Calla palustris* and *Pinellia* spp. (Prime, 1960; Pellmyr & Patt, 1986; Mayo *et al*., 1997). There are also some species with interesting intermediate strategies, as indicated by the following examples: (i) *Dieffenbachia longispatha* is self-compatible, as 21.4% of the hand-selfed inflorescences set fruit, but autogamy is in fact rare, as only 3.5% of the bagged inflorescences spontaneously produced fruits (Young, 1986); (ii) *Arisarum vulgare* becomes self-compatible only after insect visitations that cause the mechanical abrogation of self-incompatibility (Koach & Galil, 1986); (iii) *Arum cylindraceum* plants from small populations appear to be auto-fertile whereas individuals cannot spontaneously self in larger populations (Fridlender, 1999); and (iv) self-pollination is common in *Montrichardia arborescens* but may be regulated by major fruit abortion (Gibernau *et al*., 2003).

The finding that self-pollen germinated and grew as well as outcrossed pollen, irrespective of the age of the stigma, suggests that there are no ontogenetic constraints on stigma maturation that would limit autogamy if dichogamy broke down. It also suggests that the stigmas of a newly opening inflorescence would be mature and so enable geitonogamy effected by insects leaving one inflorescence of a clone and entering straight into a newly opening inflorescence of the same clone.

We found no strong postzygotic barriers, as cross-pollination between inflorescences of the same individual or clone (i.e. geitonogamy) produce as numerous and heavy seeds as outcross pollination. Good germination rates and survival of seeds issued from self-pollination were obtained in all three taxa of *Arum* examined. Other species of *Arum* also appear to have weak postzygotic barriers, as sets of viable seeds have been obtained from single isolated clones of *Arum cylindraceum*, *A. idaeum*, *A. balansanum*, *A. hygrophilum* and *A. purpureospathum* (P. Boyce, pers. comm.). The present study found that in all three taxa studied, seed establishment was not significantly depressed in selfed progeny compared with outcrossed progeny. These results indicate that there are no strong post ygotic barriers operating at the establishment stage of development. However, mean seed establishment was slightly lower for selfed progeny than outcrossed progeny, and threrefore further work is required to determine whether there are weak postzygotic barriers at the establishment stage of development and to investigate whether other postzygotic barriers are expressed at later stages of development.

Overall, our results indicate that whereas *A. italicum* ssp. *italicum*, *A. italicum* ssp. *neglectum* and *A. maculatum* rely on dichogamy to provide a strong prezygotic barrier to autogamy, these species have no real mechanism to avoid geitonogamy. From an evolutionary point of view, geitonogamy is almost never advantageous and can only be directly selected if the fitness of selfed progeny exceeds that of outcrossed progeny (Lloyd, 1992). In many cases, geitonogamy appears to be a non-adaptive accompaniment of adaptations for outcrossing and may select for the evolution for separate sexes, various morphological devices (dichogamy) and self-incompatibility (Lloyd, 1992). It bears two potential mating costs: inbreeding depression in self-compatible species (Eckert & Barrett, 1994) and pollen discounting given that pollen involved in self-pollination cannot be exported to other plants (Harder & Barrett, 1995). In contrast to autogamy, geitonogamy provides no reproductive assurance as it depends on pollinators and thus requires the same conditions as for cross-fertilization by an extrinsic pollinating agent. However, there are some cases, such as for isolated plants growing in pioneer stages of population development, where geitonogamy may be adaptive, as it provides a mechanism for extending the flowering period, and hence the probability of outcrossing. It also enables selfing from another inflorescence of the same clone in circumstances where no outcrossed pollen source is available (De Jong *et al*., 1993). In such situations, fitness costs of geitonogamy may be counterbalanced by the gains of extended time for outcrossing and/or reproductive assurance (De Jong *et al*., 1993). *Arum* populations are often pollen-limited (Ollerton & Diaz, 1999; Albre *et al*., 2003) and so such gains may mean that geitonogamy is an important adaptive trait in this genus.

In conclusion, this study has found that for *A. italicum* and *A. maculatum*, dichogamy provides the main prezygotic barrier to autogamy but that there are no strong prezygotic or postzygotic barriers that prevent geitonogamous seed set. Further studies are needed to assess whether geitonogamy in *Arum* is a trait that has a direct selective advantage or whether it is an incidental consequence of adaptations for outcrossing.

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REFERENCES

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

Barrett SCH. 2002. Sexual interference of the floral kind. *Heredity* **88:** 154–159.

Bertin RI, Newman CM. 1993. Dichogamy in angiosperms. *Botanical Review* **59:** 112–152.

Boyce P. 1993. *The genus Arum*. A Kew magazine monograph. London: HMSO.

De Jong TJ, Waser NM, Klinkhamer PGL. 1993. Geitonogamy – the neglected side of selfing. *Trends in Ecology and Evolution* **8:** 321–325.

Eckert CG, Barrett SCH. 1994. Inbreeding depression in partially self-fertilizing *Decodon verticillatus* (Lythraceae): population genetic and experimental analyses. *Evolution* **48:** 952–964.

Fridlender A. 1999. Répartition et écologie de l'*Arum cylindraceum* Gasparr. en Corse. *Candollea* **54:** 410–416.

Galloway LF, Cirigliano T, Gremski K. 2002. The contribution of display size and dichogamy to potential geitonogamy in *Campanula americana*. *International Journal of Plant Sciences* **163:** 133–139.

Gibernau M. 2003. Pollinators and visitors of aroid inflorescences. *Aroideana* **26:** 66–83.

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

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

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

Harder LD, Barrett SCH. 1995. Mating cost of large floral displays in hermaphrodite plants. *Nature* **373:** 512–515.

Koach J, Galil J. 1986. The breeding system of *Arisarum vulgare* Targ – Tozz. *Israel Journal of Botany* **35:** 79–90.

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

Lloyd DG. 1992. Self- and cross-fertilization in plants. II. The selection of self-fertilization. *International Journal of Plant Sciences* **153:** 370–380.

Lloyd DG, Webb CJ. 1986. The avoidance of interference between the presentation of pollen and stigmas in angiosperms I. Dichogamy. *New Zealand Journal of Botany* **24:** 135–162.

Mayo SJ, Bogner J, Boyce PC. 1997. *The genera of the Araceae*. London: Royal Botanic Gardens, Kew.

Montaner C, Floris E, Alvarez JM. 2001. Geitonogamy: a mechanism responsible for high selfing rates in borage (*Borago officinalis* L.). *Theoretical and Applied Genetics* **102:** 375–378.

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

Patt JM, French JC, Schal C, Lech J, Hartman TG. 1995. The pollination biology of Tuckahoe, *Peltandra virginica* (Araceae). *American Journal of Botany* **82:** 1230–1240.

Pellmyr O, Patt JM. 1986. Function of olfactory and visual stimuli in pollination of *Lysichiton americanum* (Araceae) by a staphylinid beetle. *Madroño* **33:** 47–54.

Prime CT. 1960. *Lords and ladies*. London: Collins.

Snow AA, Spira TP, Simpson R, Klips RA. 1996. The ecology of geitonogamous pollination. In: Lloyd DG, Barrett SCH, eds. *Floral biology*. New York: Chapman & Hall, 191–216.

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

Uemera S, Ohkawara 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.

Waser NM, Price MV. 1991. Reproductive costs of self-pollination in *Ipomosis aggregata* (Polemoniaceae): are ovules usurped? *American Journal of Botany* **78:** 1036–1043.

Webb CJ, Lloyd DJ. 1986. The avoidance of interference between the presentation of pollen and stigmas in angiosperms II. Herkogamy. *New Zealand Journal of Botany* **24:** 163–178.

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