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DIFFERENTIAL SUCCESS OF POLLEN DONORS IN A SELF-COMPATIBLE LILY

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Abstract.—If pollen donors are equally effective at siring seeds, the presence of equal proportions of pollen from two pollen donors on a stigma will lead to equal proportions of seeds sired by each pollen donor. Variation in germination rates, pollen-tube growth, and embryo viability may cause one donor to sire more seed than another. We looked for differential donor success in the field by simultaneously applying equal amounts of pollen from two pollen donors. We simultaneously applied equal amounts of self and outcross pollen to receptive stigmas and simultaneously applied pollen from two donors at different physical distances from the recipient. Following simultaneous application of self and outcross pollen, significantly more of the seeds were sired by outcross pollen donors. Seed set following simultaneous application of two outcross donors was also nonrandom. Pollen donors from 100 m were more likely to sire seeds when competing with pollen from plants nearby (1 m). To determine whether pollen-tube growth rates were responsible for these patterns of paternity, we varied the timing of deposition of outcross pollen allowing self pollen tubes a head start on the stigma. Outcross pollen was applied 3 or 24 h after self pollen. In spite of this time delay, the majority of the seeds were again sired by outcross pollen. There was no significant difference in the amount of seeds sired by self pollen between the two delay treatments. This result suggests that mechanisms operating after ovule fertilization may contribute to the discordance between the proportions of the pollen present and the proportions of seeds sired.

Key words.—Cryptic self-incompatibility, *Erythronium grandiflorum,* inbreeding depression, mating system, outcrossing distance, outcrossing rate, preferential outcrossing.

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Self-compatible plants are often assumed to produce substantial proportions of selfed offspring. At least three considerations suggest caution in making this assumption. First, self-compatibility (SC) and self-incompatibility (SI) are not absolute classifications and must often be distinguished quantitatively rather than qualitatively (Fryxell 1957). Many workers adopt liberal operational criteria for SC or "partial SC" (e.g., a plant is considered SI only if selfing yields less than 20% of the seed set obtained by outcrossing; Bawa 1974; Zapata and Arroyo 1978; Bernhardt et al. 1984). Such classifications clearly leave room for considerable variation in selfing potential within classes.

Second, SC plants commonly exhibit floral traits, particularly the spatial or temporal separation of male and female organs (herkogamy, dichogamy, certain manifestations of monoecy) that usually have been assumed to have evolved to reduce inbreeding. Although other selection pressures have been invoked for these conditions (summarized by Lloyd and Webb 1986; Webb and Lloyd 1986), they often do reduce selfing, regardless of the pressures responsible for their maintenance. Thus, even highly SC plants may produce mostly outcrossed offspring simply by restricting self-pollination.

Third, even if SC plants can produce selfed seeds from pure self-pollinations, mixed pollinations (self plus outcross pollen) may produce only outcrossed seeds. Mechanisms include "cryptic self-incompatibility," based on pollen-tube growth rate differences or pollen-tube attrition, and differential viability or survivorship of self and outcross embryos caused by inbreeding depression ("preferential outcrossing" of Griffin et al. 1987). There are relatively few reported

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cases of either mechanism (Cooper and Brink 1940; Weller and Ordnuff 1977; Schou and Philipp 1984), although patterns of seed development suggesting preferential outcrossing have been reported (Pfahler 1965; Busbice 1968; Glover and Barrett 1986; Bowman 1987; Epperson and Clegg 1987; Casper 1988; reviewed in Barrett 1988). As many of these authors point out, such phenomena are inherently difficult to detect and may be much more common than supposed.

Although patterns of preferential outcrossing following simultaneous application of self and outcross pollen have been demonstrated, there is no reason to assume that the mechanisms that could create differential success of donors within an ovary could not also act on the more subtle differences between two outcross donors (Bertin 1982; Bookman 1984; Marshall and Ellstrand 1986, 1988; Marshall 1988, 1991). Fitness differences following pollination with pollen from outcross pollen donors at different physical distances from the recipient have been demonstrated in many plant species (reviewed in Waser 1992). To fully understand patterns of differentially developed seeds and fruits based on pollen-donor identity, we need to extend our comparisons beyond self and outcross pollen parents and include comparisons between different outcross donors.

The major goals of this study were to look for effects of differential donor success in *Erythronium grandiflorum* and to determine whether variation in pollen-tube growth rates could be responsible for patterns of differential donor success. We also include information on outcrossing rates for comparison with outcrossing rates obtained from our hand pollinations.

MATERIALS AND METHODS

Erythronium grandiflorum is a perennial herb growing in large populations throughout western North America. Plants produce zero to several flowers; plants without flowers are most common, with one- and two-flowered plants next in abundance. In Colorado, fruit set following hand self-pollinations on two- or three-flowered plants is reduced by approximately 20% compared to hand outcross pollinations; these selfed fruits develop approximately half as many seeds as outcrossed fruits. Of the available ovules, 26% (± 0.202) develop into seeds in a selfed fruit compared to 55% (± 0.212) in an outcross fruit (Rigney and Thomson unpubl. data).

Using a naturally occurring pollen-color dimorphism, we have shown elsewhere that (1) most insect visits deposit a mixture of self and outcross pollen on the stigma, (2) the outcross component includes pollen from at least several donors at various distances from the recipient, and (3) the fraction of self pollen grains deposited on recipients with fully dehisced anthers ranges from approximately 0.2 to 0.7 (Thomson and Stratton 1985; Harder and Thomson 1989; Thomson and Thomson 1989). We had hypothesized that the ratio of selfed to outcrossed seeds would also vary among flowers [the "mass-action assumption" of Holsinger (1991)].

We worked at three sites in Gunnison County, Colorado; site I at the head of Washington Gulch near Painter Boy Mine (3200 m), site II in the East River Valley near the Rocky Mountain Biological Laboratory (3000 m), and site III at Kebler Pass (3280 m).

Before anthesis, we removed approximately 1 cm^2 of leaf tip from haphazardly chosen plants and used starch-gel electrophoresis to determine the genotype at a locus of malate dehydrogenase (*MDH*). This locus has two alleles at nearly equal frequencies in both populations, yielding good numbers of both homozygotes.

We opened the flower buds shortly before natural anthesis and prevented contamination of the stigma by covering the pistil with a 2-cm-long excluder cap, either a very narrow plastic drinking straw or a grass stem, held on by a friction fit at the ovary. In contrast to bagging, this technique obviates the need for emasculation and avoids some of the physical disturbance of bagging. Self pollen remains available in the anthers.

Simultaneous Application of Pollen Mixtures

Having previously determined that *Erythronium grandiflorum* pollen loses viability rapidly after anther dehiscence (Thomson and Thomson unpubl. data), we took pains to use only the freshest pollen. *Erythronium grandiflorum* anthers, which range from 10 to 25 mm long, dehisce gradually from tip to base. We used partly dehisced anthers only, and took the most recently exposed pollen from the cleft where the thecal suture was opening. To produce approximately 50:50 mixtures of pollen, we collected pollen from one donor on each point of a pair of fine watchmaker's forceps. We compared the sizes of the two point-loads of pollen with a hand lens, then removed grains from the larger load until the loads appeared equal. To pollinate, we brought the points together and softly dabbed the stigma, attempting to apply grains evenly over the surface and to avoid clumping (see Thomson 1989). We informally tested this procedure's ability to deliver equal numbers of two donors by counting stigmatic loads comprising one red-pollen and one yellow-pollen donor (see Thomson and Stratton 1985); the mixtures were close to 50:50, and the distribution and intermingling were sufficiently even, comparable to the "spread" pollen applications used by Thomson (1989). More precise methods of controlling the pollen mixtures (e.g., Griffin et al. 1987) were rejected as too time-consuming, given the short-lived nature of the pollen.

To minimize any effect of flower age, we pollinated only recipients that had more than three dehisced anthers and did not pollinate more than 1 day after all six anthers had dehisced. After one flower on a recipient plant had been pollinated, we replaced the excluder cap and excised the remaining (nonpollinated) flower, leaving only one flower per plant. This procedure was performed to increase the probability of fruit set in the pollinated flower.

Equal amounts of self and outcross pollen were applied to the first flower of 67 two-flowered plants at site I in 1988. The pollen loads applied were more than enough to insure full seed set. Outcross pollen was used from 47 pollen donors growing 0.3 m to 250 m from the recipient. In 1989, pollen from two outcross donors was simultaneously and similarly applied to 54 two-flowered plants at site II. All three possible pairwise combinations of donors from 1 m, 10 m, and 100 m were applied to receptive stigmas. A total of 41 pollen donors was used. Pollen donors were opposite homozygotes; recipients had the same MDH genotype as one donor. Donor genotypes were independent with respect to distance from the recipient; distant and near donors were equally likely to have opposite genotypes as the recipients.

Delayed Application of Self and Outcross Pollen

This experiment was conducted at site I in 1988 and followed the protocol outlined above, except that outcross pollen was applied either 3 or 24 h after the application of self pollen. A delay of 24 h allows many of the ovules to be fertilized by the first pollen donor before the pollen tubes of the second donor arrive at the ovary (Cruzan 1989). Forty two-flowered plants were pollinated using pollen applicators made from heavy nylon fishing line instead of forceps points (Cruzan 1989).

Determination of Seed Paternity

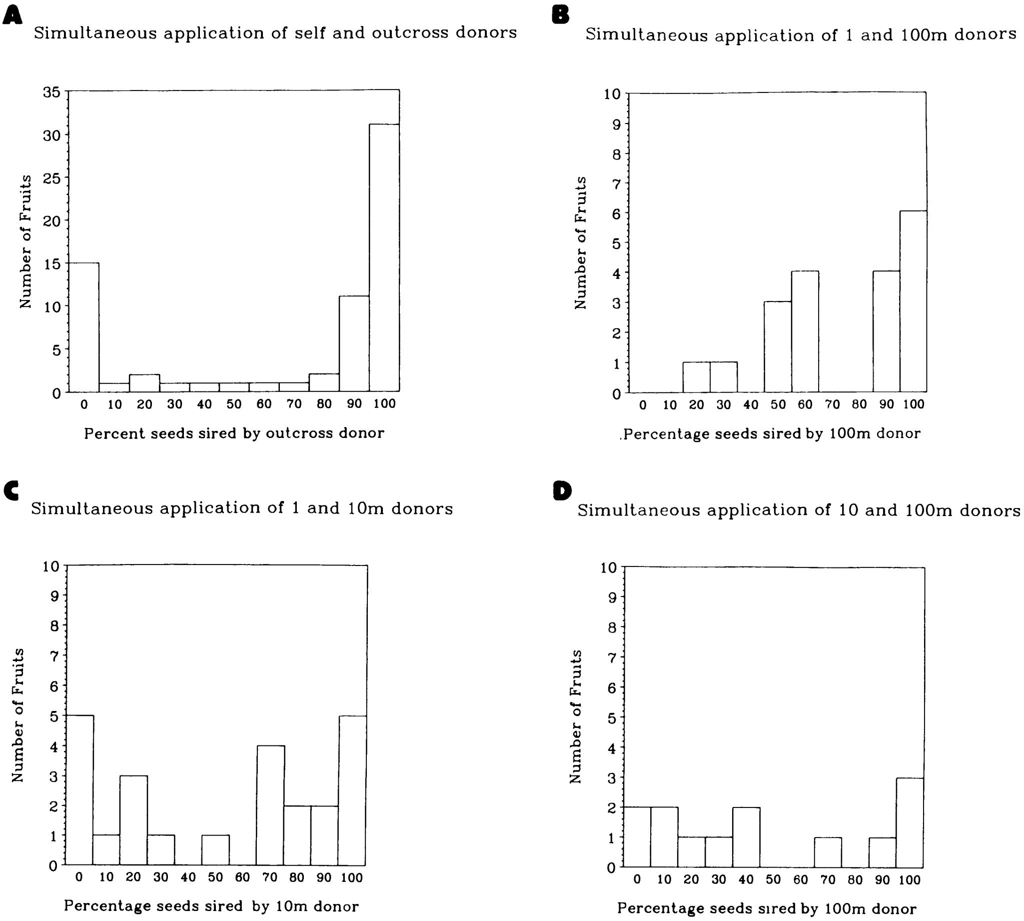
We harvested fruits shortly before dehiscence in late July. Sixty-seven fruits were collected from the self-outcross experiment, 54 from the two-outcross-donor experiment and 19 from the delayed-application experiment. All seeds from each fruit were weighed after drying for approximately 7 days at room temperature. We soaked a random sample of 15 seeds (or all the seeds present, if fewer than 15) in distilled water for 1 to 2 weeks, ground them in a buffer of polyvinyl pyrrolidone (PVP-40T), ran them on starch gels (gel buffer Tris-HCl pH 7.75), and scored them for MDH.

Paternity data were analyzed using heterogeneity G-tests (Sokal and Rohlf 1981). These tests assumed that each plant was a replicate of a certain type of mixed pollination. The resulting progenies were tested against the null hypothesis that the application of equal amounts of pollen from two donors would result in equal paternity of seeds within fruits. If pollen donors perform equally at all stages of reproduction, then the proportion of seeds sired within a fruit should be equal to the proportion of pollen applied on the stigma.

The additive nature of these tests allows for the determination of the exact nature of deviations of the data from the expected ratio, in this case, 50:50. The test for G_{pooled} treats all progenies as if they are one large population and tests against the null hypothesis that all progenies are not showing a bias toward one donor class (self, outcross, 1 m, 10 m or 100 m). This test is analogous to a single classification ANOVA. The test for $G_{\text{heterogeneity}}$ is analogous to the interaction formula in a two-way orthogonal ANOVA. It tests against the null hypothesis that the ratio of paternity of seeds within individual fruits is the same for all fruits.

Estimation of Outcrossing Rate

In July 1987, small portions of leaves were collected from 40 maternal plants at sites I and III and then freeze-dried. At fruit maturation, the dried leaf tissue and eight seeds from each of these maternal plants were electrophoresed to determine maternal plant and offspring genotype at three loci: malate dehydrogenase, 6 phos-



A Simultaneous application of self and outcross donors

B Simultaneous application of 1 and 100m donors

C Simultaneous application of 1 and 10m donors

D Simultaneous application of 10 and 100m donors

FIG. 1. Frequency distribution of the percentage of seeds sired by one class of donor following mixed pollinations. A. Percentage of seeds sired by outcross donors following simultaneous application of self and outcross pollen [0.68 ± 0.05 (mean ± SE), $N = 67$]. B. Percentage of seeds sired by 100-m donor following simultaneous deposition of pollen from donors 1 m and 100 m from the recipient (0.73 ± 0.06, $N = 19$). C. Percentage of seeds sired by 10-m donor following simultaneous deposition of pollen from donors 1 m and 10 m from the recipient (0.53 ± 0.08, $N = 24$). D. Percentage of seeds sired by 100-m donor following simultaneous deposition of pollen from donors 10 m and 100 m from the recipient (0.48 ± 0.11, $N = 13$).

phogluconate dehydrogenase-1 (*6PGD-1*) and 6 phosphogluconate dehydrogenase-2 (*6PGD-2*). Population outcrossing rates were estimated from these three loci using a multilocus maximum-likelihood procedure (Ritland and Jain 1981).

RESULTS

Simultaneous Application of Pollen Mixtures

The distribution of the percentage of outcrossed seeds following simultaneous self- and outcross pollinations appears distinctly bimodal, not with a peak at 50% as might be expected from the ratio of pollen applied (fig. 1A), nor with only a single peak near 100% as expected if there is simple cryptic self-incompatibility. The data as a whole do not conform to our null hypothesis of 50:50 parentage of seeds. Of 67 plants, 63 deviated significantly from 50:50 ($G_{\text{total}} = 2459$, df = 66, $P < 0.001$). The overall trend is toward an excess of outcross seeds sired per fruit ($G_{\text{pooled}} = 314$, df = 1, $P < 0.001$), but all plants do not deviate from this ratio in the same manner ($G_{\text{heterogeneity}} = 2144$, df = 66, $P < 0.001$) (Sokal and Rohlf 1981). Thirty-two fruits (47%) contained only outcrossed seeds, and 15 fruits (22%) contained only selfed seeds. The remaining fruits (31%) contained various proportions of both types of seeds.

Simultaneous deposition of pollen from donors at 1 m and 100 m also resulted in differential success: half of the fruits contained more than 90% seeds sired by donors 100 m distant. Ten of 17 plants differed significantly from the 50:50 expectation (G_{total} = 130, df = 17, $P < 0.001$). The overall trend was for a greater proportion of the seeds to be sired by the donor at 100 m (G_{pooled} = 40, df = 1, $P < 0.001$); only two plants deviated from the 50:50 ratio in the opposite direction. This trend was not always of the same magnitude ($G_{\text{heterogeneity}}$ = 90, df = 16, $P < 0.001$); the percentage of seeds sired by donors at 100 m varied from 20% to 100% (fig. 1B).

A similar, though weaker pattern, was seen following simultaneous deposition of pollen from donors at 1 m and 10 m. There was a strong deviation from the 50:50 ratio of seed paternity within fruits (G_{total} = 233, df = 24, $P < 0.001$), and these deviations varied significantly in magnitude ($G_{\text{heterogeneity}}$ = 228, df = 23, $P < 0.001$). Donors at 10 m showed a significant advantage over donors at 1 m (G_{pooled} = 5, df = 1, $P < 0.025$). In this case, 13 fruits contained a greater proportion of seeds sired by donors from 10 m, and 10 fruits contained a greater proportion of seeds sired by donors from 1 m (fig. 1C).

In contrast to this pattern of biased seed development toward the farther donor, patterns of seed set following simultaneous application of pollen from donors at 10 and 100 m did not show consistent advantage to either the nearer or farther donor (G_{pooled} = 0.025, df = 1, $P < 0.9$). An equal number of fruits contained only seeds sired by donors from 10 m or only seeds sired by donors from 100 m. These fruits did not contain an equal proportion of seeds sired by each donor; the ratio of seeds sired by each donor in each fruit was significantly different from the expected ratio of 50:50 (G_{total} = 122, df = 13, $P < 0.001$). All fruits did not vary from 50:50 with the same magnitude ($G_{\text{heterogeneity}}$ = 122, df = 12, $P < 0.001$) (fig. 1D).

Delayed Application of Self and Outcross Pollen

Outcross pollen continued to sire most of the seeds even when self pollen was given a 3- or 24-h head start on a stigma. There was no significant difference in the percentage of seeds sired (per fruit) by outcross donors between the two treatments (Mann-Whitney *U*-test, N_1 = 13, N_2 = 11, U_s = 97.5, $P > 0.05$) (fig. 2). Sixteen of the 19 fruits contained only outcrossed seeds, mirroring exactly our results from the simultaneous deposition experiment.

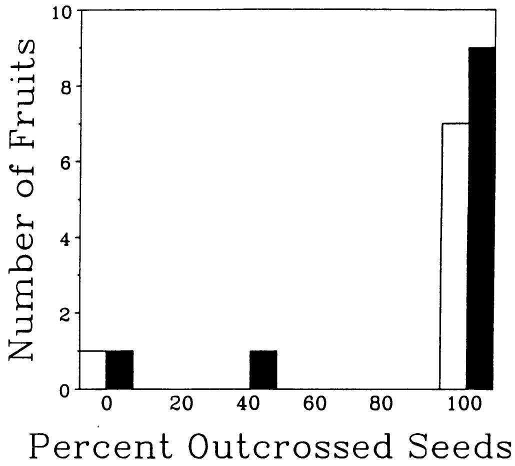


FIG. 2. Percentage of seeds sired by outcross pollen following application of outcross pollen 3 h (white bars) and 24 h (black bars) after application of self pollen.

Estimation of Outcrossing Rate

The multilocus outcrossing rate is 0.831 ± 0.057 at site I and 0.808 ± 0.053 at site II.

DISCUSSION

Following simultaneous deposition of equal amounts of self and outcross pollen, self pollen does not sire an equal proportion of seeds within most fruits. Because pollen loads deposited naturally on stigmas usually contain a mixture of self and outcross pollen (Thomson and Stratton 1985; Thomson and Thomson 1989; Harder and Thomson 1989), the opportunity for self pollen to sire any seeds in nature must be low, given the observed differential in pollen-donor success. Our estimates of outcrossing rates confirm that extensive outcrossing is occurring in these populations. However, self pollen is capable of fertilizing and developing seeds and fruit when alone on the stigma (Rigney and Thomson unpubl. data). Clearly, the designation of self-compatibility, as determined from self-pollinations, does not indicate that seeds will be sired by self pollen in this species.

Seed paternity did not reflect the proportion of pollen on the stigma when two types of outcross pollen were applied. On most but not all plants, distant pollen donors sired more seeds than donors from within 1 m of the recipient when both types of donors were present on the stigma. Following simultaneous application of pollen, donors at 10 m and 100 m were equally likely to sire most of the seeds within a fruit; neither distance class sired most of the seeds in most of the fruits.

Differential donor success can have profound influences on the genetic structure of the population. A possible consequence of the superior siring ability of distant donors over nearer ones (and over self pollen) is an eventual reduction in genetic structuring. Differential success of more distant donors should eventually swamp any small scale adaptation to local conditions, because theoretical studies have shown that only a small amount of long-distance gene flow is needed to prevent population differentiation (Wright 1946; Slatkin and Maruyama 1975; Slatkin 1976).

In direct opposition to this decay of genetic structure caused by long-range gene flow, differential donor success could also result in the buildup of family structure. If one pollen donor is siring most of the seeds within one fruit, as found in *Erythronium grandiflorum,* the offspring will be more closely related than if fruits are multiply sired. If seed dispersal is also restricted (Thomson and Weibland, unpubl. data), then plants that are nearer to each other may also be more related. Matings between near neighbors could involve some degree of inbreeding and may result in inbreeding depression. Perhaps differential success of distant donors over nearer ones is a reflection of inbreeding depression suffered after mating with near relatives. When pollen from donors at distances of 10 m and 100 m is present on the stigma, either type of donor is equally likely to sire all the seeds within a fruit. This suggests that although plants within 1 m of each other may be related enough to suffer inbreeding depression after mating, this pattern of relatedness decays at or before 10 m. The consequences of these two opposing forces on genetic structure are not known.

Differential donor success can occur at any stage in the reproductive cycle (Stephenson and Bertin 1983; reviewed in Seavey and Bawa 1986). Differences in pollen viability or germination could cause certain donors to sire more seeds than others (Heslop-Harrison 1975). However, reduced pollen viability must exist independent of the distance from the recipient plant. There is no reason to assume that donors in one distance class, for example, donors 1 m from the recipient, will produce greater quantities of inviable pollen than donors in another class. Because donors within 1 m of the recipient failed to set any seed when paired with donors at 100 m, it is difficult to imagine that the differences in donor success that we report here could be caused by inviable pollen. The mechanism of differential donor success even in *E. grandiflorum* must be one that can explain the failure of an entire class of donors.

The Paradox of Bimodal Selfing Rates

Following simultaneous application of self and outcross pollen, most fruits contained only outcrossed seeds. However, 15 fruits (22%) contained only seeds sired by self pollen. Variation in the amount of inbreeding depression resulting from particular crosses may have caused this result (Wright 1977; Price and Waser 1979; Schemske 1983; Schoen 1983; Waser and Price 1983; Dudash 1990; Morgan and Barrett 1990; Fenster 1991). Alternatively, inviable outcross pollen may have been used in these crosses. However, every care was taken to use fresh pollen.

Another possible cause is some form of "mentoring" effect. Mentoring occurs when self pollen sires more seeds when applied with outcross pollen than when alone (Visser 1983; Bertin 1990), and indeed self pollen tubes suffer less attrition when growing in the same style as outcross pollen in *E. grandiflorum* (Cruzan 1990a). After simultaneous pollinations, however, most fruits contained either all outcrossed or all selfed seeds. The proportion of seeds sired by the less favored donor does not increase incrementally as one would expect if mentoring were occurring (Stettler 1968; Pandey 1977; Sastri 1980; Visser 1983).

Historical explanations for differential success of donors have concentrated on interactions between the pollen and the stigma and style in regulating pollen-tube growth as a mechanism for determining compatibility (Bateman 1956; Pfahler 1965; Nettancourt 1977; Weller and Ornduff 1977; Schou and Philipp 1984). Control of seed paternity has also been suggested to operate in the ovary as a direct consequence of differential viability of selfed and outcrossed offspring because of inbreeding depression (Busbice 1968; Bertin 1982, 1990; Griffin et al. 1987; Casper 1988; Weller and Ornduff 1991) or as a result of competition among embryos for limited maternal resources (Westoby and Rice 1982; Queller 1983; Stephenson and Bertin 1983; Willson and Burley 1983; Briggs et al. 1987). "Late-acting self-incompatibility" (Seavey and Bawa 1986) may constitute a third postfertilization possibility, although the principal mechanism proposed for late-acting self-incompatibility by Seavey and Bawa involves an interaction between differential viability and competition. We consider these proposals in turn.

Differential Pollen-Tube Growth Hypothesis

If the regulation of fertilization success depends largely on the differences of pollen-tube growth rates, we would expect the number of selfed seeds to increase with increasing delays between the application of self and outcross pollen. However, we did not detect any increase in the amount of selfed seeds when self pollen was given either a 3- or a 24-h head start on the stigma. In these experiments, we did not measure self and outcross pollen-tube growth-rate differences directly, but previous work shows that 24 h is sufficient for self (or outcross) pollen tubes to reach the ovary under field conditions in these populations of *E. grandiflorum* (Cruzan 1989). Alternatively, if the effect of differential donor success is mainly due to greater amounts of attrition of self pollen tubes, we may not see any effect of a time delay in application of self and outcross pollen (Waser and Price 1991); self pollen would sire as many seeds when applied before outcross pollen as it would when both types of pollen were applied simultaneously. However, many fruits from the simultaneous-deposition experiment contained only seeds sired by self pollen, a pattern inconsistent with the explanation of pollen-tube attrition as the only factor important in differential donor success.

In a previous study of mixed pollination in *E. grandiflorum* (Cruzan 1990a), pollen tubes from outcross donors near the maternal plant (within 3 m) were more likely to grow to the base of the style than tubes from donors farther from the maternal plant. This pattern is seemingly at odds with the pattern of differential success of donors 100 m from the maternal plant seen here. Together, these experiments on pollen-tube growth suggest that, although style-mediated incompatibility may be important in regulating the fertilization success of certain pollen genotypes, success in reaching the base of the style is not always correlated with success at siring seeds. Mechanisms operating after pollen tubes reach the ovary may also play a role (Cruzan 1990b).

Inbreeding Depression

Variation in viability or survivorship of developing embryos can be caused by inbreeding depression or by competition among embryo genotypes for limited maternal resources. For a species in which most of the pollen is deposited on stigmas within 1.5 m to 2.0 m from the pollen donor (Thomson and Thomson 1989), it is reasonable to assume that near neighbors may often be closely related. Breeding between related individuals is a form of inbreeding (Uyenoyama 1986) and may result in inbreeding depression.

For inbreeding depression to be the sole determinant of the pattern of differential donor success, it must be strong, and it must follow matings with plants within 1 m. Inbreeding depression studies begun in 1987 indicate that even though selfing does result in reduced fecundity, selfed fruits and seeds are produced (Rigney and Thomson unpubl. data). According to the "20% rule" (Bawa 1974; Zapata and Arroyo 1978; Bernhardt et al. 1984), *E. grandiflorum* is a self-compatible plant, producing 47% as many seeds from selfing as from outcrossing (Rigney and Thomson unpubl. data). Inbreeding depression is not large enough to fully account for the frequent and complete failure of self pollen to sire *any* seeds when outcross pollen is also present on the stigma.

Although some inbreeding depression is present after selfing, seeds sired by pollen from 1 m suffer no viability or survivorship deficits compared to seeds sired by pollen from donors at 10 m or 100 m. There are no significant differences in the percentage of ovules fertilized, the percentage of ovules aborted, the percentage of seeds set, or in any measures of growth as seedlings following any of these outcross pollinations (Rigney and Thomson unpubl. data). Therefore, inbreeding depression alone cannot account for the almost complete failure of 1-m pollen to sire seeds.

Embryo Competition

Competition for limited maternal resources can reduce seed and fruit set; seed abortion is frequent in *E. grandiflorum,* and larger plants with more flowers are more likely to develop fruits following pure self-pollinations (Rigney unpubl. data). However, competition among embryos for resources per se (without any interaction with embryo genotypes or position within fruit) would not be selective. Resource limitation alone could not produce the observed patterns of differential donor success where one pollen donor is almost completely excluded from siring any seeds.

Embryo Competition and Inbreeding Depression

Although embryo competition and inbreeding depression alone may be insufficient to account for the effects we observed, competition among embryos within the ovary may intensify the viability differences initially caused by various degrees of inbreeding or pollen-donor identity (Marshall and Ellstrand 1988). Westoby and Rice (1982) proposed that when maternal resources are limited, less vigorous offspring are sealed off from resources by a thickening of the integument tissues between embryo and mother. Seavey and Bawa (1986) carried this hypothesis one step further and suggested that the cutoff threshold is genetically determined and that selfed (or inbred) offspring will always fall below this threshold in plants where late-acting self-incompatibility is operating. An interaction between the embryo genotype and the amount of available maternal resources could explain observed patterns of differential donor success, but the interaction is difficult to distinguish empirically. A crucial component of this hypothesis—whether embryos sired by certain pollen donors are being differentially aborted—is under investigation. The appearance of partially developed ovules within the ovary suggests that these ovules were indeed fertilized and then ceased development.

In summary, our investigation of mating patterns in *Erythronium grandiflorum* provides evidence for differential donor success between self and outcross pollen donors and between different outcross pollen donors. Outcross pollen donors usually sire most of the seeds within a fruit when in competition with self pollen, and more distant donors sire most of the seeds when paired with pollen from near donors. A mechanism involving competition among ovules, magnifying initial growth differences caused by inbreeding, can account for all of our findings except for the unexpectedly high number of fruits with all selfed seeds. The latter may be attributable to variation in the amount of inbreeding depression resulting from different crosses or to a pollen-mentor effect in combination with inviable outcross pollen.

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