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Crossing distance effects on prezygotic performance in plants: an argument for female choice

Nickolas M. Waser and Mary V. Price

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Seed set in the perennial larkspur *Delphinium nelsonii* is greater in crosses between plants growing an intermediate distance apart than in shorter and longer crosses. Since crossing distance is an attribute of a specific combination of parents, its effect on seed set represents an interaction of these parents, and since genetic similarity declines with physical distance in *D. nelsonii* populations, the interaction reflects parental genetic similarity. Understanding processes responsible for the effect is simplified if seed set differences result from prezygotic events, because in this case no inbreeding or outbreeding depression are involved. In 1990 we observed pollen tubes after performing crosses between plants separated by 1 m, 10 m, or 100 m, and found that the intermediate, 10 m crosses delivered the most tubes to the ovary. A combined analysis of the 1990 experiment and three earlier experiments showed that this prezygotic difference in performance is significant and of the same magnitude as seed set differences. Disproportionate failure of pollen tubes in 1 and 100 m crosses seems likely to reflect a trait of the maternal parent rather than of pollen, because the kinship of haploid pollen to a zygote it has fertilized always exceeds maternal kinship to that zygote. Thus the conditions for “pollen suicide” to evolve by natural selection are more restrictive than those for “female choice” to evolve, and the latter is more likely to control the outcome of the parental interaction.

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Over a decade ago, we reported that the proximity of mated plants affects fecundity in the self-compatible montane larkspur *Delphinium nelsonii* (Price and Waser 1979). Mean seed sets per flower in pollinations between plants separated by an intermediate distance exceeded seed sets from shorter or longer crosses. Subsequent results have confirmed this finding. In eight of ten experiments reported by Waser and Price (1991), crosses over 10 m yielded higher mean seed sets than self or 1 m crosses on the one hand, and 100 m or 1000 m crosses on the other, and this overall pattern was significant statistically.

Crossing distance is an attribute of a specific combination of parents, rather than of either parent alone. The attribute that clearly correlates with crossing dis-

tance is the genetic similarity of parents. Similarity is expected to decline with crossing distance when gene dispersal is restricted, as a result of genetic drift, a combination of drift and weak directional selection, or selection that varies through space (Wright 1943, Endler 1977, Turner et al. 1982, Campbell and Waser 1987, Van Dijk 1987, Epperson 1989). Primary seed dispersal averages less than 1 m, and pollen dispersal less than 10 m, in populations of *D. nelsonii* (Waser and Price 1983, Waser 1988). Thus one expects neighboring plants to be kin, and electrophoresis confirmed that plants growing within 2 m of each other are related on average at about the level of first cousins ($f \approx 0.06$, Waser 1987, C. F. Williams and N. M. Waser unpublished data). Conversely, plants growing more than a few meters

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Table 1. Means of maternal means for numbers of tubes delivered to the ovary by different crossing distance treatments in four experiments. Standard deviations, followed by sample sizes (number of maternal parents), are given in parentheses. The largest mean value for each experiment is shown in *italics*.

Experiment	Tube numbers at ovary		
	1 m	10 m	100 m
1985	9.8 (7.73, 47)	<i>14.3</i> (10.63, 47)	8.1 (6.46, 47)
1986	<i>14.8</i> (13.93, 199)	12.6 (12.38, 199)	13.0 (13.43, 199)
1987	10.3 (11.43, 153)	<i>13.6</i> (13.12, 153)	11.7 (12.21, 153)
1990	9.1 (11.68, 151)	<i>11.7</i> (12.89, 151)	9.9 (11.75, 151)
Overall	11.0	<i>13.1</i>	10.7

apart shared no detectable kinship. At the same time, biotic and abiotic conditions in meadows supporting *D. nelsonii* diverge monotonically through space over several tens of meters, and reciprocal transplantation studies demonstrated genetic adaptation to these local environmental conditions (Waser and Price 1985). Thus a range in crossing distance from 1 m to 100 m reflects a range that begins with inbreeding and extends through substantial dissimilarity at gene loci that confer adaptation to local conditions.

A crossing distance effect on seed set therefore implies that maternal and paternal parents interact, and that the outcome depends on their genetic similarity (see also Waser et al. 1987, Lyons et al. 1989). How might we identify the relative contributions of each parent, and of other factors, to the probability a mature seed is produced? The task is simplified when the production or non-production of a seed depends on events that occur prezygotically, i.e. before the formation of offspring whose diploid gene expression might affect the outcome. Postzygotic embryo abortion is more difficult to interpret, because it may reflect early-acting inbreeding depression (Mitchell-Olds and Waller 1985) or "outbreeding depression" (sensu Price and Waser 1979, Templeton 1986, Lynch 1991) in the fitness of offspring from short and long crosses, respectively. Distinguishing inbreeding and outbreeding depression from maternal control over embryo provisioning is difficult (Stephenson and Winsor 1986, Briggs et al. 1987, Casper 1988, Bertin and Peters 1992).

In three of the 10 experiments with *D. nelsonii* mentioned above, we explored whether differences in seed set among crossing distance treatments were mediated prezygotically. Using fluorescence microscopy, we discovered in two of these experiments that more pollen tubes grew to the base of the style following 10 m crosses than following shorter- or longer-distance crosses (Waser and Price 1991), which unambiguously is

a prezygotic difference. Here we show that an additional experiment conducted in 1990 yields the same result, and that the advantage of the 10 m treatment is significant statistically in a combined analysis of all experiments. We also develop an inclusive fitness argument suggesting that control over pollen tube performance, i.e., over the outcome of parental interaction, is most likely to reside with the maternal parent. Our argument considers the conditions under which natural selection will favor the evolution of "maternal control", (i.e., maternal characters that control pollen growth) vs "pollen suicide" (i.e., characters of pollen that cause it to forego an attempt at fertilization).

Methods

Our experimental methods followed those of Waser and Price (1991), who present further details. In June 1990, we potted 50 *D. nelsonii* plants in bud stage near the Rocky Mountain Biological Laboratory in Colorado, USA, moved them into a greenhouse, and emasculated their buds. When a flower became receptive, one of its (usually three) separate carpels received a 1 m pollination, i.e., hand-pollination with fresh pollen from a single donor plant growing 1 m in a haphazardly-chosen direction from the original site of the plant. Another carpel received a 10 m pollination, and the third carpel received a 100 m pollination. The three pollination (= crossing distance) treatments were applied "blind" and at random within each flower. Styles were excised at the base 26 h later and were fixed, cleared, and stained in aniline blue. Preparations were scored "blind" at 100X for number of pollen grains on the stigma (hereafter "pollen load") and number of pollen tubes reaching the base of the style (= entrance to the ovary). Ovaries remained attached to plants and seeds were counted when mature.

The 1990 experiment allowed us to explore effects of crossing distance on delivery of pollen tubes to the ovary, an unambiguously prezygotic stage of reproduction. Using data pooled across treatments, we fit a negative exponential regression with SAS procedure NLIN (SAS Institute 1990) to the relationship between stigma pollen load and tube number at the ovary (see Waser and Price 1991 for details). We analyzed residuals from the resulting pollen load-pollen tube relationship with SAS procedure GLM, using Type III sums of squares. Effects included in the model were plant, flower within plant, distance, and the plant by distance interaction. Distance (a fixed effect) was tested over the plant by distance interaction (Brownlee 1965), and was partitioned further with planned orthogonal contrasts of 10 m vs the other two treatments, and of the 1 m vs the 100 m treatment. This approach is a sequential analysis of covariance, in which the contribution of stigma pollen load was removed before performing ANOVA.

Table 2. Mean residuals for each crossing distance treatment from negative exponential regressions pooling all data for a given experiment, and P values from orthogonal contrasts of treatments. Values in the row beginning with “Overall” are respectively grand means of residuals, and values of the chi-squared statistic and of P from Fisher’s method for combining probabilities across experiments (df = 8). Sample sizes (number of maternal parents in each experiment) are given in Table 1. Other conventions follow Table 1.

Experiment	Mean residuals			P values, planned contrasts	
	1 m	10 m	100 m	10 m = 1 m, 100 m	1 m = 100 m
1985	−0.82	1.92	−0.91	0.02	0.63
1986	0.26	0.58	0.43	0.53	0.33
1987	−0.29	0.60	0.07	0.32	0.65
1990	−0.11	0.54	0.20	0.11	0.58
Overall	−0.24	0.91	−0.05	$\chi^2 = 15.8, P < 0.05$	$\chi^2 = 5.1, P > 0.5$

Along with the 1990 results, analyses were available from the three previous experiments in which we observed pollen tubes. As Fisher (1970: 99–100) pointed out, a combined probability of Type I error across independent experiments may be obtained from the fact that

$$-2 \sum_{i=1}^n \ln P_i$$

is approximately chi-square distributed with 2n degrees of freedom. Here n is the number of experiments and P_i is the α value from experiment i. With the small number of experiments at hand in this case, Fisher’s approach is preferable to more recent forms of meta-analysis (e.g., Gurevitch et al. 1992). A single analysis of all experiments with ANOVA was impossible because designs differed among experiments (Table 1 of Waser and Price 1991).

Results

In 1990 a 10 m crossing distance yielded the highest mean seed set per carpel. When combined with previous results (Waser and Price 1991), 10 m pollinations performed best in nine of eleven experiments carried out since 1976. Using Fisher’s method and ignoring one 1977 experiment that lacked 1 m and 100 m treatments, 10 m significantly outperformed both 100 m ($\chi^2 = 4.6$, df = 20, $P < 0.002$) and 1 m ($\chi^2 = 49.7$, df = 20, $P < 0.001$). Across all experiments, mean seed sets from the 10 m treatment averaged 123% of those from either the 1 m or 100 m treatments.

Seed set differences corresponded to differences in prezygotic pollen tube performance. The 10 m treatment delivered the most tubes to the ovary in three of four experiments (Table 1), and performed best in all four experiments when we controlled for treatment differences in stigma pollen load by analyzing residuals from pollen load-pollen tube regressions (Table 2). Overall analysis of residuals showed that the advantage

of the 10 m treatment was statistically significant ($P < 0.05$; Table 2), whereas 1 m and 100 m treatments did not differ ($P > 0.5$).

Discussion

The 1990 experiment adds to the evidence of an intermediate optimal crossing distance for *D. nelsonii* seed set, and it increases confidence that prezygotic events are responsible for differences in seed set. Across experiments from four years, the 10 m treatment enjoyed a mean advantage of 19% relative to the 1 m treatment in absolute numbers of pollen tubes delivered to the ovary ($13.1 \div 11.0 = 1.19$; Table 1), and a mean advantage of 22% relative to the 100 m treatment ($13.1 \div 10.7 = 1.22$; Table 1); these values agree well with the mean seed set advantage of 23% observed in the larger, partially-overlapping set of experiments (see Results). The probability of Type I statistical error in contrasting 10 m with longer and shorter distance treatments across all experiments was slightly below 5%, which is “significant” by standard convention. Furthermore, our test was conservative because it employed two-tailed α values from each experiment. Because we are interested in explaining seed set differences, for which we have a prior directional expectation that the 10 m treatment performs best (Price and Waser 1979), the use of one-tailed α values would have been justified, in which case the overall probability of Type I error is less than 1%. In summary, prezygotic performance differences appear to explain crossing distance effects on seed set.

A standard self-incompatibility model alone is insufficient to explain the observed variation in pollen tube performance among crosses representing different average parental genetic similarities. Whereas a single-locus gametophytic self-incompatibility model could account for a quantitative decline in pollen tube performance with increasing parental kinship, because kinship exactly equals the expected proportion of pollen grains

Table 3. Inclusive fitness values of alternative fertilizations, from the perspectives of a focal haploid pollen grain and the diploid maternal tissue. There are four entries in each row, representing four levels of kinship between maternal parent and parent of the focal pollen grain. Each entry in the “Pollen” row (or “Maternal” row) consists of three numbers. The first is kinship of the focal grain (or maternal parent) to an embryo the focal grain fertilizes (i.e., the probability of an allele the focal grain or maternal parent being identical to an allele chosen at random from the embryo). The second (following a slash) is kinship of the focal grain (or maternal parent) to an embryo that is fertilized by a pollen grain unrelated to the focal grain. Both kinship values are rounded to two significant digits. The third number is the quotient of the first two; i.e., the relative value to the focal grain (or maternal parent) of the focal grain fertilizing vs an unrelated grain fertilizing.

Perspective	Kinship of parental plants			
	Unrelated	First-cousins	Full sibs	Self
Pollen	0.50/0.0 = ∞	0.53/0.03 = 17	0.63/0.13 = 5	0.75/0.25 = 3
Maternal	0.25/0.25 = 1	0.28/0.25 = 1.1	0.38/0.25 = 1.5	0.50/0.25 = 2

carrying an allele shared by the maternal plant, a decline in performance at long crossing distances is not predicted. Furthermore, *D. nelsonii* fails to qualify as self-incompatible by a usual definition (Bawa 1974). It routinely produces seeds when selfed (Table 2 of Waser and Price 1991), whereas self-incompatibility should yield strong (in principal, absolute) rejection.

As noted in the Introduction, it is difficult to distinguish postzygotic maternal control of embryo maturation from early-acting inbreeding and outbreeding depression in embryos (e.g., Bertin et al. 1989). In the case of a prezygotic response, on the other hand, a relatively straightforward argument for maternal control is possible. Treatment differences in pollen tube number at the ovary may represent differences in tube growth rates or numbers of tubes ceasing growth altogether, but the outcome in either case derives from an interaction of haploid pollen (male microgametophyte) and diploid maternal tissue. Which of these two entities is expected to control the outcome of this interaction?

When pollen and maternal parent are unrelated, it is in the best interest of pollen to fertilize regardless of the fitness of resulting offspring, since pollen has no access to an alternative mating. But it is in the best interest of maternal tissue to block such a fertilization if other options would yield greater fitness returns (Charnov 1979). These options logically include fertilizations by other pollen tubes growing in the same pistil, fertilizations available to other flowers on the same plant, or reallocation of resources to other fitness-related ends such as increased growth and future reproduction (Waser 1993).

An analysis of inclusive fitness similar to analyses for seed provisioning (see Westoby and Rice 1982, Queller 1983) confirms that there is a conflict of interest between unrelated pollen and maternal tissue. Furthermore, the conflict of interest persists when parents are related, indeed even when they are the same individual (i.e., a self mating), because the kinship of haploid pollen to an embryo it fertilizes always exceeds the kinship of the diploid maternal parent to that embryo (Table 3). Consider the relative fitness value to a “focal” pollen grain of fertilizing an ovule vs ceasing

growth so that an unrelated pollen grain fertilizes in its place, and the analogous quotient of fitness values from the perspective of the maternal parent (Table 3). These quotients show that the value to pollen of an embryo it fertilizes, relative to an embryo fertilized by unrelated pollen, always exceeds the value to the maternal parent. Thus maternal tissue always is expected to be more discriminating of fertilization by the focal pollen grain than the focal grain is itself. Once again this assumes that other options are available to the maternal parent that will yield a higher fitness return (see also Bertin and Peters 1992).

To see the argument more precisely it helps to recognize that the quotients in Table 3 also indicate “thresholds” of relative offspring fitness above which it is in the best interest of the focal pollen grain to forego fertilization and of the maternal parent to block the focal grain (Waser 1993). Consider two examples that approximately reflect the kinship represented in our 1 m and 100 m crosses, respectively (see Introduction). First, when the parent producing the focal grain is related to the maternal parent as a first cousin, the offspring produced by a pollen grain unrelated to the focal grain must be 17 times more fit than an offspring of the focal grain for natural selection to favor “suicide” of the focal grain, whereas it must only be about 1.1 times more fit for selection to favor maternal blockage of the focal grain (Table 3). Second, when the focal grain is unrelated to the maternal parent, the offspring produced by a grain unrelated to either must be infinitely more fit than an offspring of the focal grain to favor “suicide”, which agrees with Charnov’s (1979) conclusion that the focal grain in this case will always attempt fertilization. In contrast, an alternative offspring must be only marginally more fit than that of the focal grain for selection to favor maternal control (Table 3).

Demographic studies reported elsewhere (Waser and Price 1993) provide estimates of the fitness value of alternative fertilizations that we may compare to the threshold values just discussed. Long-term survival and fecundity of F₁ offspring produced by 1 m and 30 m crosses fell below the values achieved by offspring of 10 m crosses. As a result, overall fitness estimates for

10 m offspring were approximately 2-fold those of 1 m offspring. Thus even if the fittest alternative to a 1 m fertilization is available, the 2-fold fitness differential is well below the 17-fold value necessary for "suicide" to be in the best interest of the 1 m pollen, but well above the 1.1-fold value for blockage of this pollen to be in the maternal best interest. At the other extreme, fitness estimates for 10 m offspring were 6- to 8-fold those of 30 m offspring. We will assume (see Introduction) that parents separated by 30 m are unrelated, as are those separated by 100 m, and that relative fitness of 30 m offspring equals or exceeds that of 100 m offspring. In this case, there is no possible fitness return from an alternative fertilization that would justify "suicide" of a 100 m grain, but the advantage of an alternative, which might be as large as 8-fold, is easily sufficient to favor maternal blockage of 100 m pollen. This analysis provides quantitative support for the conclusion that the reduced success of 1 or 100 m pollen relative to 10 m pollen is in the best interest of the maternal parent but not the pollen, and thus by inference that failure of pollen during the pollen-pistil interaction is under maternal control.

Ultrastructural and biochemical details of pollen-pistil interactions in other species generally suggest that maternal tissue has substantial physiological control over pollen performance (e.g., Dickinson and Lewis 1973, Malti and Shivanna 1985, Ganeshaiah et al. 1986, Zavada and Taylor 1986, Murdy and Carter 1988, Saunders and Lord 1989, for review see Waser 1993). To be sure, most of the available evidence involves partial or complete self-incompatibility rather than the differential rejection of classes of non-self pollen that occurs in *D. nelsonii*. However, this might simply reflect the focus on self-incompatibility in almost all studies of post-pollination events.

We consider maternal control over the prezygotic pollen-pistil interaction to be one form of "female mate choice" in plants. Because it involves specific parental combinations, rather than consistently favoring certain individuals, such choice does not imply sexual selection (Waser et al. 1987, Lyons et al. 1989). Furthermore, our use here of the term "choice" resembles that of Halliday (1983, p. 4), who wrote for animal systems that "Mate choice may be operationally defined as any pattern of behaviour, shown by members of one sex, that leads to their being more likely to mate with certain members of the opposite sex than with others." Such an "operational definition" stresses an *outcome* of interaction between parents and which parent *controls* the outcome, rather than a specific physiological *mechanism*, and therefore goes beyond a definition that requires neurophysiology, consciousness, or even aesthetics on the part of the chooser. No such requirement is necessary for a definition of choice to be workable and useful, although there hardly can be doubt that sophisticated physiology other than neurophysiology mediates pollen-pistil interactions.

We are well aware of the argument that results such as ours should be described simply as parental interaction, rather than mate choice, because of the difficulty in disentangling parental roles (e.g., Lyons et al. 1989). Surely, however, the situation with plants is analogous to that with animals, where investigating the roles played by males and females during a mating interaction has greatly improved our understanding of behavioral, morphological, and physiological traits! Indeed, we perceive an odd asymmetry in the attention paid in plant systems to male vs female roles. Whereas male influences over reproduction are discussed frequently (e.g., male-male conflict in the form of "pollen competition", Mulcahy 1979, Lee 1984, Snow 1990), female influences have received less attention (with the exception, perhaps, of self-incompatibility reactions). We see no logical reason for this asymmetry and suspect that relative neglect of the female role has helped to obscure many fascinating phenomena.

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