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Pollen competition and sporophyte fitness in *Brassica campestris*: does intense pollen competition result in individuals with better pollen?

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In flowering plants, competition among pollen grains can result in positively correlated responses in sporophytic vigor. Whether this indirect selection on the sporophyte can drive the evolution of sporophytic traits depends in part upon whether the strength of pollen competition in any given (F₀) generation is positively related to both the vigor of the F₁ sporophytes and the ability of pollen from those sporophytes to sire seeds. We performed two experiments to address this question. In the first experiment we simulated three levels of pollen competition by manipulating pollen load size in the F₀ generation and examined correlated responses in the F₁ sporophytes. We found that F₁ seed germination was significantly and positively related to the strength of pollen competition, while no significant responses were observed in seed number or seed weight. In the second experiment we asked whether the strength of pollen competition under which F₁ plants were sired affected the ability of equivalently sized pollen loads from those plants to set seed. We found that the intensity of pollen competition in the F₀ generation had a significant effect on the ability of F₁ pollen to set fruit, while having no significant effect on seed number per fruit initiated, seed weight and seed germination probability. Our results demonstrate that pollen competition can result in marked differences in sporophyte fitness over two generations.

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Natural selection operates on organismal traits in a number of interesting ways. In classical Darwinian selection in its simplest form, a trait that confers a direct fitness advantage will enjoy increased representation in subsequent generations. However, selection does not always act in such a straightforward manner. Consider an organism with a two-stage life cycle in which some percentage of the genes expressed in one stage are also expressed in the other. In this case, selection acting on one stage of the life cycle can result in strong correlated responses in the other stage.

There has been considerable interest in the ways in which this form of selection may be important in the evolution of flowering plants (see Mulcahy and Mulcahy 1987 for an historical perspective). All flowering plants possess both gametophyte (pollen grains and ovules) and sporophyte (seeds, seedlings, and mature plants) life stages, and the genomes of these stages have been shown to overlap for a number of species (Tankley et al. 1981, Willing and Mascarenhas 1984, Sari-Gorla et al. 1986). Further, there is clearly the potential for competition and selection at the level of the haploid pollen grain whenever

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the number of pollen grains reaching the stigmatic surface of a plant exceeds the number of available ovules. Since the ratio of competing pollen grains to available ovules is potentially large in many flowering plants, pollen competition might result in intense selection on both gametophytic and sporophytic stages of the plant life cycle. This observation has led a number of authors (Mulcahy 1979, Crepet 1983, Wilson and Burley 1983) to suggest that this form of competition may be a potent force in the evolution of angiosperms.

For pollen competition to drive the evolution of sporophytic characters, three conditions must be met: 1) there must be genetically based variability in pollen performance; 2) these differences in pollen performance must result in differential fertilization success of pollen genotypes; and 3) a positive correlation must exist between pollen performance and sporophyte fitness. Reasonable support exists for the first two conditions. Genetically based variation in one measure of pollen performance, pollen tube growth rates, has been demonstrated in both agricultural (e.g. Bemis 1959, Sari-Gorla et al. 1975, Mulcahy 1979, Ottaviano et al. 1980) and non-agricultural species (Cruzan 1990, Snow and Spira 1991). Further, several studies (Pfahler 1965, Marshall and Ellstrand 1986, Bertin 1990, Snow and Spira 1991) have shown non-random fertilization success of different pollen genotypes. Evidence for the third condition, however, is incomplete. Most studies addressing the fitness consequences of increased pollen competition have examined only characteristics of the F1 sporophyte, such as probability of fruit maturation (Davis et al. 1987, Winsor et al. 1987), seed number (Shore and Barrett 1984, Davis et al. 1987, Winsor et al. 1987), seed weight (Davis et al. 1987), and seed germination speed and frequency (Mulcahy 1974, Mulcahy and Mulcahy 1975, Davis et al. 1987).

These correlated responses to pollen competition are necessary but not sufficient evidence for the hypothesis that pollen competition is important in the evolution of sporophytic characters. A rigorous test of this hypothesis must allow for discrimination among the F1 generation in terms of fitness. While survivorship and vigor are important components of fitness, it remains to be established whether pollen from individuals sired under different competitive regimes differs in ability to effect seed set, and/or whether correlated responses to pollen competition in the F0 generation will be manifested in the F2 sporophytes. Recent studies testing for heritability of pollen competitive ability have not detected significant heritability of this trait (Snow and Mazer 1988, Schlichting et al. 1990). Consequently, the evidence that pollen competition is an evolutionarily relevant phenomenon remains inconclusive.

In the present paper we present results from experiments designed to test whether the strength of pollen competition under which a plant is sired can affect the ability of that plant to sire seeds. Our approach consists of two experiments performed on the mustard *Brassica*

campestris L. In the first experiment, we performed outcrosses simulating three levels of pollen competition to assess correlated responses of the F1 sporophytes. In the second experiment, we asked whether the pollen of these F1 sporophytes sired under different competitive regimes differed in ability to effect fruit and/or seed set. In our first experiment we hypothesized that performance measures (fruits produced per pollination, seed number per fruit, total seed weight per fruit, seed germination probability, and seedling height) of F1 sporophytes should be positively correlated with pollen load size. In the second experiment we hypothesized that given equivalent pollen loads, F2 sporophyte characteristics (fruits produced per pollination, seed number per fruit, total seed weight per fruit, and seed germination probability) should be positively correlated with the competitive regime under which the F1 parents were sired. This experimental protocol provides a means of assessing whether pollen competition can result in consistent differential success of pollen genotypes over two generations.

Methods

Brassica campestris is an annual, hermaphroditic mustard commonly found throughout North America. A rapid-cycling strain of this species (obtained from M. Melampy, Baldwin-Wallace College) with a life cycle of approximately nine weeks was used for the present study. *Brassica campestris* is sporophytically self-incompatible (Bateman 1955), which insured pollen donor identity in our outcrosses.

The plants used in the present study were grown from seeds planted in 5 × 5 cm plastic pots filled with standard potting soil on 29 January, 1989. These pots were immediately placed in a grow room (L:D 22:2) to hasten the onset of flowering. The plants were watered daily with normal tap water and temperature was maintained at 20°C. Under these conditions, the plants began flowering asynchronously on 23 February, 1989.

Pollen competition tests

To evaluate the effects of pollen competition on sporophytic characteristics, we performed single-donor outcross pollinations with three different sizes of pollen loads, approximating conditions of low, intermediate and high pollen competition. Anthers were removed from recipient flowers to avoid contaminating stigmas with self pollen. For low and intermediate pollen loads, dehiscing anthers were removed from randomly selected donor plants using forceps and brushed across a clear glass slide until most of the pollen had been shed. The slide was then placed under a dissecting microscope and a needle was used to collect approximately 30 or 75 grains

Table 1. Results of Kruskal-Wallis ANOVA among treatments for three measures of F1 sporophyte characteristics. N = 33, 39, and 40 for light, intermediate and heavy pollen loads, respectively. Data on aborted fruits are not included.

Variable	mean	S.D.	H	P
Seed number per fruit				
Low	5.09	3.05		
Intermediate	5.97	3.62	3.02	>0.22
High	6.50	3.97		
Total seed weight per fruit (mg)				
Low	5.47	3.21		
Intermediate	5.38	4.08	2.31	>0.31
High	5.91	3.77		
Percent germination per fruit				
Low	42.0	38.0		
Intermediate	35.7	35.7	7.85	<0.02
High	59.1	32.4		

for low and intermediate applications, respectively. We transferred pollen from the needle to the apical portion of the stigma, taking care to distribute the pollen evenly without damaging the stigma. The low pollination level was sufficient for full seed set. High pollen loads were applied by removing an entire dehiscent anther from the donor plant and thoroughly coating the stigma of the emasculated recipient. Paternal pollinations were distributed randomly within and among maternal plants, and approximately half of the plants served as both pollen donors and recipients. Pollinated flowers were marked with colored thread to indicate treatment.

Examination of ten stigmas from each treatment revealed mean deposition of 29.5 (± 4.5), 76.6 (± 9.0), and 215 (± 34.6) pollen grains for low, intermediate and high pollen loads, respectively. Each plant received at least one complete set of each of the three pollination treatments. Each set was performed in sequence along the stalk, varying the order of application within each set. Flowers were pollinated when their anthers began to shed, usually the second day after the flower opened. We performed a total of 141 sets on 80 recipient plants. Plants remained in the grow room through fruit development.

Fruits were collected for 1.5 weeks beginning 4 April, 1989. Seed number per fruit was counted and total seed weight per fruit was measured to the nearest 0.001 mg on a Mettler digital balance.

To assess germination probabilities for seeds resulting from each pollination intensity treatment, each fruit was assigned a pot in which all seeds from that fruit were planted. Seeds were planted evenly across the soil at a uniform depth (1.5 cm). Seedlings began to emerge from the soil beginning three days after planting, and germination frequency was determined 12 d after planting. Seedling survivorship was high after 12 d and no further seedlings emerged beyond this time. Seedling height was

determined at 20 d after emergence for a subsample of 30 plants per treatment.

To test for differences in germination probability resulting from differences in seed weight, we selected 20 each of small, medium and large seeds from the original seed bank for use in germination trials. The seeds selected spanned the range of natural variability in seed size observed. Seeds were individually weighed and planted in 5 × 5 cm plastic pots with standard potting soil. After three days pots were checked every other day for the following two weeks and the number of seedlings emerging from each size class of seeds was recorded.

Tests for second generation effects

To evaluate second generation effects of previous pollen competition in this species, we asked whether pollen from F1 parents arising from low, intermediate and high pollen competition differed in ability to produce seeds. In this experiment, pollen load size was kept constant (equivalent to the intermediate pollen load from the previous experiment) to ensure that differences in the resulting fruits, if any, would be attributable to differences in the quality rather than the quantity of the pollen applied. Outcross pollen loads were transferred to the stigmatic surface of recipient flowers in the same manner as described for intermediate loads in the first experiment. Each plant received at least one set of the three pollen donor types, varying the sequence of treatments among plants. Donors were randomly selected within treatments. We performed 50 complete sets of pollinations on 40 recipient plants. All plants used in these outcrosses were from the F1 generation, and approximately half of the plants served as both pollen donors and pollen recipients. Recipient flowers were marked with colored thread to indicate treatment, and fruits were collected for two weeks beginning 8 July, 1989. The number of fruits set, seed number per fruit, and total seed weight per fruit were determined. Germination probabilities were determined in the same manner as described for the competition trials above.

Results

Pollen competition tests

Variation in pollen load had no significant effect on average seed number per initiated fruit or average total seed weight per initiated fruit (Table 1). The range of total seeds per fruit for all treatments was 0–15. Fruit abortion was high in all treatments (72%, 68%, and 66% for light, medium and heavy applications, respectively). No significant differences were found in the number of fruits initiated and aborted among treatments (G-Test, $P > 0.50$). No significant differences existed among

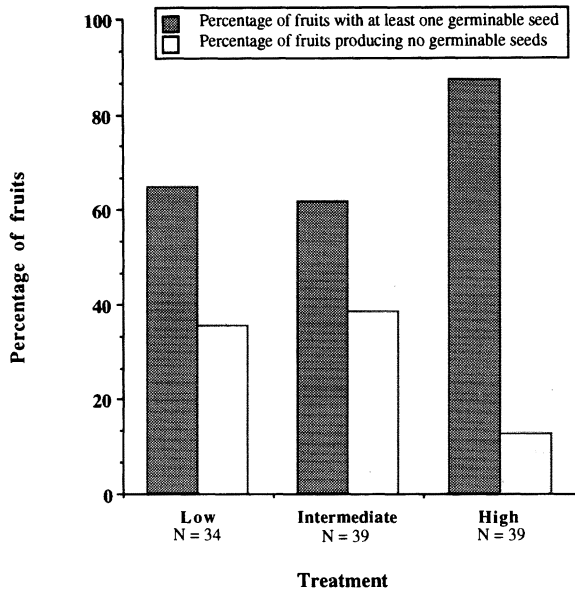


Fig. 1. The number of F1 fruits producing at least one germinable seed and no germinable seeds for three pollination intensities ($G = 8.02$, $P < 0.02$).

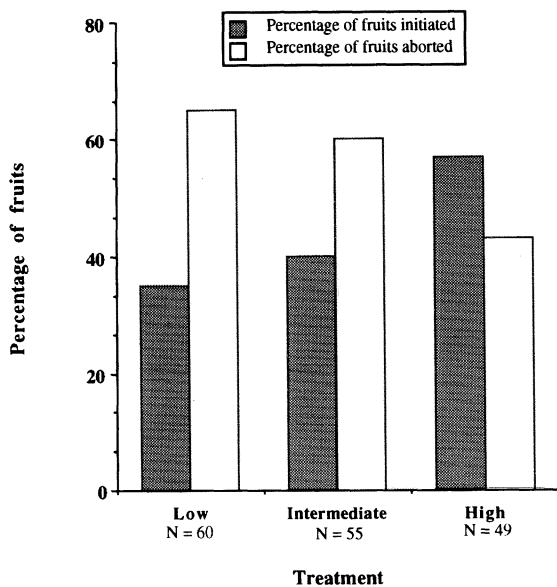


Fig. 2. The number of F2 fruits initiated and aborted for three pollination intensities (low vs high, $\chi^2 = 4.49$, $P < 0.03$; low vs intermediate, $\chi^2 = 0.13$, $P > 0.70$; intermediate vs high, $\chi^2 = 2.40$, $P > 0.10$).

treatments in seedling height at 20 d (Kruskal-Wallis, $P > 0.50$, $N = 90$).

Pollen load size was significantly and positively related to germination probability (Table 1). Heavy pollen application resulted in higher average germination per fruit than light and medium applications. Significant differences were found among treatments in the number of fruits producing germinable seeds (Fig. 1, G-Test, $P < 0.02$).

Table 2. Results of Kruskal-Wallis ANOVA among treatments for three measures of F2 sporophyte characteristics. $N = 21$, 23, and 28 for light, intermediate and heavy pollen loads, respectively. Data on aborted fruits are not included.

Variable	mean	S.D.	H	P
Seed number per fruit				
Low	5.43	3.93	0.55	>0.76
Intermediate	5.22	3.68		
High	6.43	4.80		
Total seed weight per fruit (mg)				
Low	6.88	5.32	0.25	>0.88
Intermediate	6.15	4.38		
High	7.50	5.86		
Percent germination per fruit				
Low	75.0	38.0	4.42	<0.10
Intermediate	52.0	40.0		
High	64.0	41.0		

Seed weight had no significant effect on germination probability among the size classes tested (G-Test, $P > 0.60$). Percent germination for small, medium and large seeds (mean weight = 0.79, 1.49 and 2.09 mg, respectively) was 80%, 90% and 80%, respectively.

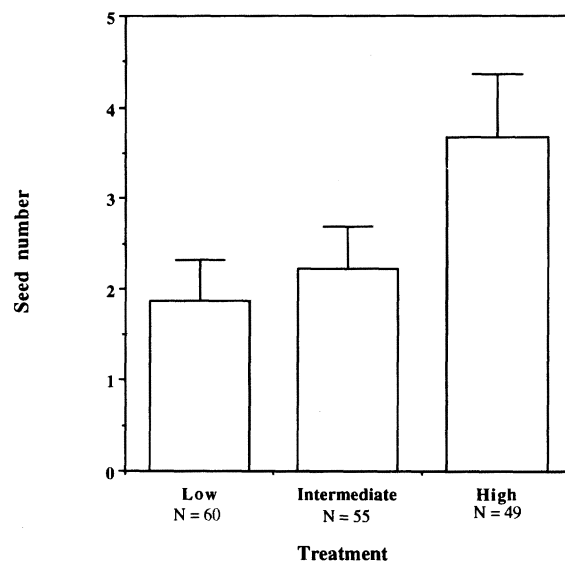


Fig. 3. The average number of seeds produced per pollination (includes 0's for aborted fruits) for crosses among F1 plants (Kruskal-Wallis $H = 6.17$, $P < 0.05$). Error bars show standard errors.

Second generation tests

Pollen donor type had no significant effect on the average number of seeds set per initiated fruit, average total seed weight per initiated fruit, and average percent germination per initiated fruit (Table 2) in the F2. However, treatments differed in the number of fruits aborted and initiated (Fig. 2) in the F2 generation. Fruits sired from the low selection (LF1) line were aborted significantly more frequently than fruits sired from the high selection (HF1) line ($\chi^2 = 4.49$, $P < 0.03$). No significant differences existed in the number of fruits aborted between the LF1 and IF1 (intermediate) selection lines or the IF1 and HF1 selection lines ($\chi^2 = 0.13$, $P > 0.72$; $\chi^2 = 2.40$, $P > 0.10$, respectively). As a result of differences in fruit abortion among treatments, the number of seeds set per pollen load application differed significantly among treatments (Fig. 3, Kruskal-Wallis, $P < 0.05$).

Discussion

The present study demonstrates that seed germination is significantly and positively related to pollen load in *Brassica campestris*. Additionally, to our knowledge it is the first study to provide evidence that the intensity of pollen competition under which a plant is sired can influence the ability of pollen from that plant to effect fruit and seed set. Pollen loads from plants sired under conditions of high pollen competition produced greater fruit set and greater numbers of seeds per pollination than equal sized pollen loads from plants sired under conditions of low pollen competition. This result confirms the potential for pollen selection in flowering plants.

The relationship between pollination intensity and sporophytic vigor demonstrated in the present study has been shown for a number of other species, including *Zea mays* (Ottaviano et al. 1980), *Cucurbita pepo* (Davis et al. 1987, Winsor et al. 1987), and *Campsis radicans* (Bertin 1990). While these results are suggestive of pollen competition, Walsh and Charlesworth (1992) point out that in the absence of a rigorous demonstration of cause-and-effect, relationships between pollen load and sporophytic characters are difficult to interpret. For example, fertilization success of pollen donors may be influenced by the stylar environment (Pfahler 1967), or different sized pollen loads may stimulate differential allocation of resources to fruits independently of pollen competition (Charlesworth 1988). Consequently, an effective test of gametophytic competition should involve comparison of fruits with the same number of seeds (Lee 1984). This criterion has been met in several studies (Mulcahy and Mulcahy 1975, McKenna 1986, Bertin 1990), although none of these studies tested for heritability of improved vigor in the F2 generation. In the present study, variation

in pollen load had no significant effect on the average seed number per fruit or total seed weight per fruit. These results suggest that maternal allocation to fruits was independent of pollen load size. Consequently, differential germination success of seeds likely resulted from pollen competition.

Two alternative explanations are possible for the increased germination of seeds produced under strong pollen competition. First, it is possible that differential allocation of resources within fruits (reviewed in Lee 1988) occurred but was not detected. We determined seed weight on a per fruit basis, rather than measuring the weights of individual seeds. Consequently, it is possible that variance in seed weight within fruits may have differed among fruits initiated under different competitive regimes. For example, consider a case in which a fruit resulting from low pollen load and a fruit resulting from high pollen load both contain ten seeds. If the fruit resulting from a low pollen load contained three large, vigorous seeds and seven low quality small seeds, while the fruit resulting from a high pollen load contained ten relatively vigorous medium sized seeds, differences in germination probability of seeds from these fruits could result from variation in seed weight alone (e.g., Stanton 1984). This scenario is unlikely for two reasons. First, we did not observe any consistent variability in seed size among fruits resulting from different treatments. Second, we performed germination trials on twenty seeds from each of three size classes in which roughly equivalent numbers germinated from each size class.

The second alternative is that fruits resulting from high pollen loads may be subject to undetected differential abortion, eliminating less vigorous zygotes and resulting in higher quality sporophytes (Charlesworth 1988). Since we cannot rule out the possibility of this indirect form of pollen selection, our results should be treated with caution.

Our second experiment involved comparisons of fruits sired by equivalent pollen loads from donors derived under low, intermediate and high pollen competition. Analysis of total seed number per application of pollen indicated that HF1 donors sired significantly greater numbers of seeds per pollination event than did pollen from LF1 donors. This difference is attributable to the increased frequency of fruit abortion in LF1 treatments. Since pollen loads were equivalent among treatments and each plant received at least one set of each of the three treatments, these results suggest that maternal plants allocated a greater proportion of resources to fruits sired by HF1 donors relative to LF1 donors. HF1 donors and LF1 donors differed only in the intensity of pollen competition under which they were sired in the first experiment. Thus strong pollen competition both increased the survivorship of the resultant F1 sporophytes through greater germination probability and resulted in increased ability of F1 pollen to initiate fruit set. These results indicate a strong paternal influence on plant fitness. Selective production of fruits based on paternity has been demon-

strated in *Campsis radicans* (Bertin 1982), while other studies have shown consistent differential success of particular pollen donors across a range of recipients (e.g., Bookman 1984, Marshall and Ellstrand 1986, but see Mazer 1987).

The mechanism through which maternal parents discriminate among HF1 and LF1 pollen loads of the same size is unclear. One possibility is that pollen from LF1 donors germinated less frequently than pollen from HF1 donors, resulting in fewer seeds per fruit which in turn resulted in an increased frequency of fruit abortion for these treatments. Many studies have shown a relationship between seed number and the probability of fruit maturation (e.g., Bertin 1982, Lee and Bazzaz 1982, Bookman 1984), indicating the potential for selective maturation of many seeded fruits by the maternal plant.

Evidence for second generation effects of previous pollen competition is limited. Snow and Mazer (1988) and Schlichting et al. (1990) concluded that the effect of pollen load on progeny vigor was not strongly heritable in *Raphanus raphanistrum* and *Cucurbita pepo*, respectively. In a study of *Petunia hybrida*, Mulcahy et al. (1978) found that previous pollen competition affected the phenotype of the F2 sporophytes, but it is difficult to generalize these results since the original crosses were performed using only one paternal clone and one maternal clone. Thus the present study provides the strongest evidence to date for differential fertilization success of pollen donors sired under different degrees of competition.

The present study has illustrated two main points. First, a seven-fold increase (between LF1 and HF1 donors) in pollen load size in the first experiment resulted in a 30% increase in germination probability for seeds sired under conditions of high pollen competition. Interestingly, the effects of pollen competition were not readily apparent until after the seeds had been germinated. This result points to the importance of conducting long-term experiments, since differences in offspring quality may become more pronounced with age (Stevenson and Winsor 1986, Bertin 1988). Second, the present study provides evidence that the competitive regime under which a plant is sired can affect the ability of that plant's pollen to effect seed set. The superior performance of HF1 pollen relative to LF1 pollen was apparently manifested through selective maturation of fruits sired by the former, and selective abortion of fruits sired by the latter. Pollen from plants sired under intense competition (HF1) sired twice as many seeds per application than did pollen from plants sired under relaxed (LF1) competition. These results suggest strong selection for pollen performance.

To understand the evolutionary implications of pollen competition more fully, future studies must address whether the strong selection demonstrated in the present study is possible in natural populations. While individual variability in pollen competitive ability has been demonstrated in a natural population of *Hibiscus moscheutos* (Snow and Spira 1991), heritability of pollen competitive

ability in nature remains to be documented. Indeed, if pollen competition is shown to be an evolutionarily important phenomenon in nature, the vexing question that remains is what maintains variability in pollen competitive ability if selection on pollen performance is strong (Walsh and Charlesworth 1992). This area of inquiry is surely an important one for our understanding of plant evolution in general.

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