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## Effects of pollination intensity on *Lesquerella fendleri* seed set: variation among plants

Received: 29 January 1996 / Accepted: 6 August 1996

**Abstract** The amount of pollen arriving on a flower can be an important determinant of seed production. I investigated the effect of varying pollen loads on seed set of the perennial desert mustard *Lesquerella fendleri*. To do this, I quantified the dose response relationship between stigmatic pollen load and seed set per fruit using over 400 flowers from 13 greenhouse-grown plants. Seed set per fruit generally increased with pollen up to about 100 pollen grains, then reached a plateau. A negative exponential regression of seed set on pollen load for the pooled data explained less than 10% of the observed variation in seeds per fruit. However, accounting for variation among individual plants in the dose-response relationship increased explained variation to 40%, indicating that plants responded differently to the same amount of available pollen. Plants varied little in the initial slope of the dose-response curve, but differed substantially in the asymptote, which ranged from 3 to 16 seeds. This limit is not imposed by ovule number, and may instead result from variation among plants in vigor, propensity to abort seeds, or in gender specialization. Such variation among plants in dose-response relationships has important consequences for understanding pollination limitation and pollen competition.

**Key words** Pollination intensity · Pollen dose-response · Pollen number · Non-linear regression · Seed set

### Introduction

The amount of pollen deposited on flowers can be an important determinant of plant reproductive success, affecting both seed number and seed quality. Seed number can increase with the number of pollen grains on a stigma ("pollen load") simply because each additional pollen grain may fertilize an otherwise wasted ovule. Seed qual-

ity can be affected by pollen load because the presence of more pollen increases the opportunity for gametophytic and zygotic competition and for mate choice by females (Snow 1986; Mulcahy and Mulcahy 1987; Winsor et al. 1987).

Understanding the effects of pollen load on plant reproduction requires more knowledge of how seed set per flower is affected by the amount of pollen deposited on an individual flower. This association is known as the pollen dose-response relationship. A number of studies have estimated these relationships, and with some notable exceptions (e.g., Silander and Primack 1978; Snow 1982; Shore and Barrett 1984), have found substantial variation in seed set that is not explained by pollen load alone (e.g., McDade and Davidar 1984; Kohn and Waser 1985; Campbell 1986; Snow 1986; Galen and Newport 1988; Waser and Price 1991a). One likely cause for such imprecision in the dose-response relationship is variation among individual plants in their ability to produce mature seeds even when given adequate pollen.

In this study I address two questions: (1) how is seed set per fruit affected by pollen load? and (2) does the effect of pollen load on seed set vary among plants? Elsewhere I consider the effects of pollen load on progeny quality (R.J. Mitchell, unpublished work).

### Materials and methods

#### Methods

*Lesquerella fendleri* (Brassicaceae) is a small herbaceous perennial common in the deserts of the southwestern USA. The 15-mm-diameter yellow flowers are simultaneously hermaphroditic, and are self-incompatible (R.J. Mitchell, unpublished work). Naturally pollinated flowers receive an average of 319 pollen grains (SE = 43,  $n = 17$  plants), and flowers typically contain 20.3 ovules (SE = 0.2,  $n = 433$ ) and produce 8.5 seeds per mature fruit (SE = 0.9,  $n = 60$ ). Pollination in the field is accomplished by small bees and bee flies foraging for nectar and pollen (R.J. Mitchell, unpublished work). Plants in both the field and the greenhouse frequently have 20 or more flowers open each day, and individual flowers last 1 day in the field, and 1–4 days in the greenhouse.

To assess the effects of pollen load on seed set per fruit, I artificially altered the amount of pollen applied to flowers on 13 pot-

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ted plants. These plants originated (as seeds or transplants) within 100 m of each other at the Sevilleta Long Term Ecological Research area (LTER), 80 km south of Albuquerque, New Mexico, United States, in fall 1992. I maintained these plants in 10-cm pots in a temperature controlled greenhouse in Albuquerque, watering and fertilizing as needed. All plants were treated similarly, and appeared to be comparable in health and vigor. In June of 1993, I pollinated freshly opened flowers using a 2-cm length of heavy monofilament fishing line attached to a wooden handle (Kearns and Inouye 1993). Each morning of pollination, I placed anthers from at least eight plants (not those used as maternal plants, but from the same source population) in a small petri dish, and swirled the fishing line in the dish to completely coat it with pollen. Then I either touched the line briefly to the stigma, or swiped it lengthwise along the stigma.

To produce a wide variation in the amount of pollen deposited from this bulk sample, I used the following seven pollination treatments in randomized order: unpollinated controls, touched once, touched twice, swiped once, swiped twice, swiped three times, and swiped four times. I re-loaded the line with pollen after each touch or swipe. I haphazardly assigned flowers to treatments, whenever possible using flowers from different flowering branches. Just before pollination, I removed anthers to allow unobstructed access to the stigma. I collected stigmas from tagged flowers 72–96 h after pollinations, leaving the rest of the flower on the plant. Trials on these same plants indicated that collecting stigmas at this time had no significant effect on subsequent seed set of pollinated flowers (R.J. Mitchell, unpublished work). I placed each sampled stigma separately on a labeled microscope slide with a drop of basic fuchsin dye (Kearns and Inouye 1993), and squashed it under a cover slip. I then counted the total number of pollen grains applied under  $\times = 100$ –200 magnification. Because pollen is frequently dislodged from the stigma while being squashed and stained, I considered the cloud of pollen on and near the stigma to represent that available to sire seeds. Preliminary counts from the first two replicates (applied 7 June) revealed substantial amounts of self pollen on unpollinated stigmas. In an attempt to reduce this, I repeated the treatments twice more (16–22 June) with careful emasculation of all flowers each morning before they opened. This did not significantly reduce self-pollen on stigmas of control flowers (unpubl. data), so I do not distinguish between the emasculated and unemasculated replicates below. This resulted in a total of four replicates, and 364 pollinated flowers (28 on each of the 13 plants), of which I recovered 273 intact (many fruits were lost when one plant was accidentally damaged). I collected fruits as they matured, about 1 month after pollination, then counted seeds, and weighed all seeds from each fruit.

#### Analysis

I analyzed these data in two ways. First, I used mixed model ANOVA (Proc GLM, SAS Institute 1989) to discern differences

among treatments in pollen loads, seed set per fruit, and individual seed mass per fruit (total seed mass/number of seeds). I considered maternal plant a random factor, and treatment and replicate fixed, so I tested treatment over the treatment by plant interaction, and replicate over the replicate by plant interaction (Sokal and Rohlf 1981). I made *a posteriori* comparisons using Duncan's multiple range test. I analyzed seed set from all recovered fruits, including those with no seeds. To ensure conservative ANOVA tests for effects of pollination treatment, I do not include unpollinated control flowers in statistical analyses, though I include them in figures for illustration. I used type III sums of squares throughout. Distributions of residuals were approximately normal, and plots of residuals against predicted values showed no strong heteroskedasticity.

To assess dose-response relationships, I fitted a saturating negative exponential model [seeds =  $A(1 - \exp^{-B \text{ pollen}})$ ] for the effect of pollen on seed set, using Proc NLIN (SAS Institute 1990). I calculated  $R^2$  for these analyses as  $1 - (\text{residual SS}/\text{corrected total SS})$ , as suggested by Kvålseth (1985). These data might instead be analyzed using linear and quadratic regression, but such phenomenological models can make biologically unrealistic predictions. For example, a linear model predicts that seed set increases without bound, and quadratic models can predict negative seed set. In contrast, a negative exponential model is mechanistically justifiable, in that it involves an asymptote beyond which any more pollen would not increase seed set (see Kohn and Waser 1985; Waser and Price 1991b). This is biologically more reasonable, since a limited number of ovules, ovary space, and resources are available to each flower.

To increase the sample size of pollen-seed pairs (for the NLIN analysis only), I also included data from another experiment (R.J. Mitchell, unpublished work) on the same plants. These supplemental flowers received the one-touch, one-swipe, or four-swipe treatments, for six replicate flowers on each plant for each treatment. I performed these pollinations on 8–13 June 1993. Most fruits from one plant were lost, so regression analyses are based on the other 12 plants, each of which had a minimum of 23 (maximum of 41) seed-bearing fruits (442 total).

There typically is a large amount of unexplained variation in published dose-response relationships, and one likely cause is variation among plants. To statistically evaluate the hypothesis that there is variation among plants in the dose-response relationship, I fitted a single non-linear analysis to the pooled data from all 12 plants with >20 pollen-seed data pairs, and output the residuals (differences between observed and predicted seed set). I then used ANOVA of the residuals to test for variation among plants in their deviation from the pooled negative exponential relationship (Waser and Price 1991b). Significant variation among plants in residuals would indicate that some plants mature consistently more or fewer seeds than expected based on the pollen load, and would demonstrate that plants vary in dose-response relationships. For heuristic purposes, I also used PROC NLIN to analyze data from each plant separately.

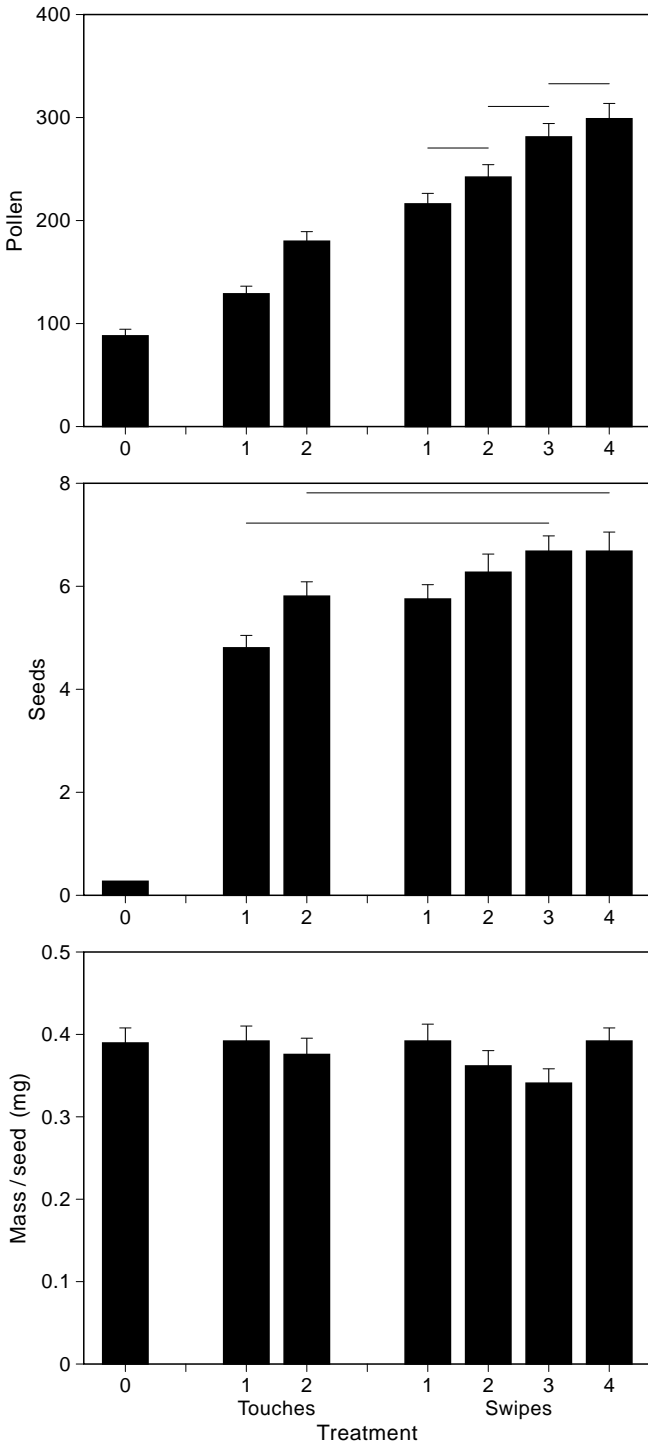
**Table 1** Analysis of variance for effects of pollination treatment. *F* values are for a mixed-model analysis with maternal plant considered a random effect and all other effects fixed, so that treatment effects are tested over plant  $\times$  treatment, and replicate is tested

Source	Pollen load $R^2 = 0.79$				Seed set $R^2 = 0.82$				Mass/seed $R^2 = 0.85$			
	<i>df</i>	SS	<i>F</i>	<i>P</i>	<i>df</i>	SS	<i>F</i>	<i>P</i>	<i>df</i>	SS	<i>F</i>	<i>P</i>
Maternal plant	12	1,360,613	3.7	<b>0.002</b>	12	3724	9.4	<b>0.0001</b>	12	1.76	9.1	<b>0.0001</b>
Treatment	5	606,557	20.3	<b>0.0001</b>	5	139	2.7	<b>0.03</b>	5	0.03	1.0	0.4
Replicate	3	57,123	0.6	0.6	3	524	4.6	<b>0.009</b>	3	0.13	2.2	0.12
Maternal plant $\times$ Treatment	59	352,167	0.7	0.8	54	543	0.8	0.7	52	0.36	0.8	0.8
Maternal plant $\times$ Replicate	30	994,371	4.4	<b>0.0001</b>	28	1052	3.2	<b>0.0001</b>	24	0.48	2.2	<b>0.006</b>
Treatment $\times$ Replicate	15	221,418	2.0	<b>0.02</b>	15	313	1.8	<b>0.04</b>	15	0.17	1.3	0.2
Error	138	1,031,692			120	1387			65	0.58		

over plant  $\times$  replicate. Each replicate included 2 flowers receiving each of the 6 treatments.  $R^2$  refers to variance explained by the total model (see Fig. 1). Degrees of freedom vary among response variables because of differences in sample size

**Results**

Pollen loads and seed set varied significantly among treatments, but seed size was unaffected (Table 1, Fig. 1). Multiple comparisons revealed strong effects of pollina-



**Fig. 1** Effects of pollination treatment. *Top panel* pollen applied to stigmas. *Middle panel* seed set per fruit. *Bottom panel* mass per seed. Means of plant means  $\pm$  SE are shown, so  $n = 13$  plants for each bar. Statistical analysis presented in Table 1. *Horizontal bars* denote values indistinguishable using Duncan's multiple range test

tion treatment on pollen load, but lesser effects on seed set, with only the highest and lowest pollen treatments differing significantly from one another. In general, application of more pollen was weakly associated with production of more seeds, with some indication of an asymptote. There is a surprisingly regular increase in pollen load and seed set with treatment, with each additional touch or swipe increasing the pollen load by  $\sim 30$  grains, and increasing seed set by one-half to one seed. Note that unpollinated flowers received substantial pollen ( $89 \pm 15$  grains,  $n = 13$  plants), probably through passive self-pollen deposition, and produced almost no seeds.

Aside from these treatment effects, all three response variables differed significantly among maternal plants, but significant maternal plant  $\times$  replicate interactions indicate that these differences varied among replicates. Furthermore, seed set varied significantly among replicates, probably reflecting resource limitation in response to the presence of prior fruits. Indeed, mean seeds per flower decreased over time (mean  $\pm$  SE seeds/flower =  $8.8 \pm 1.7$ ,  $6.6 \pm 0.8$ ,  $5.1 \pm 1.3$ ,  $4.8 \pm 1.5$  for the first, second, third, and fourth replicates, respectively). The significant treatment  $\times$  replicate interaction for pollen and seeds indicates that the effect of treatment varied among replicates.

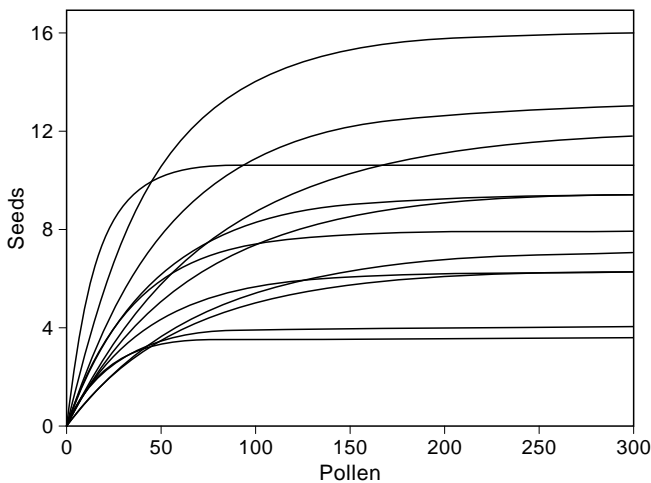
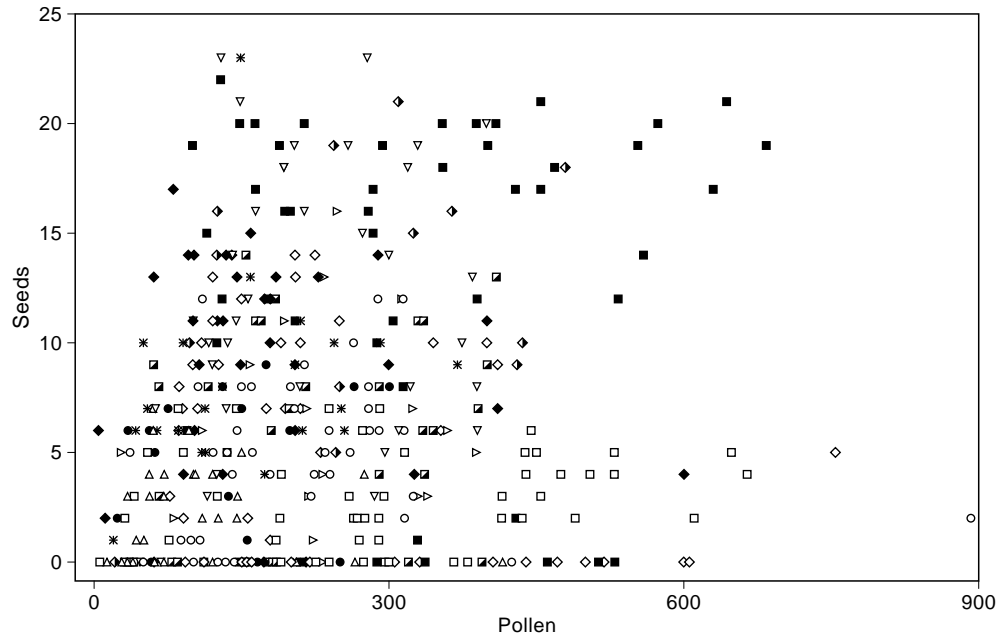
Fruit set (developed fruits/total pollinated flowers) was 75% overall ( $n = 273$  flowers), and did not vary significantly with pollination treatment (ANOVA  $F_{5, 54} = 1.8$ ,  $P = 0.1$ ). However, fruit set did vary significantly among maternal plants ( $F_{12, 54} = 6.6$ ,  $P = 0.0001$ ), with fruit set per maternal plant ranging from 35% to 100%.

Seed set increased with pollen load for the  $>400$  flowers on which I measured both traits (Fig. 2). The equation for this dose-response relationship is:  $Y = 7.78(1 - \exp^{-0.0123 \text{ pollen}})$ . In this equation, the first term (7.78) represents an asymptote on seed set, and the second dictates the rate with which that asymptote is reached as pollen loads increase.

Unfortunately, this negative exponential model explains less than 10% of the variation in seed set for the pooled data ( $R^2 = 0.054$ ). Linear and quadratic regressions explain even less of the variation, as do analyses which exclude fruits with no seeds (unpubl. results). One possible explanation for the large variance is that different plants have different dose-response relationships. For example, in Fig. 2, note that fruits from some plants never contain more than four or five seeds (empty squares), while fruits from other plants usually contain many more (filled squares). Examination of individual negative exponential curves fitted to each plant separately indicate this is a possibility (Fig. 3).

Analysis of residuals from the pooled NLIN analysis confirms that plants varied significantly in dose-response relationships ( $F_{11, 419} = 25$ ,  $P < 0.0001$ ,  $R^2 = 0.395$ ). This is a substantial increase in explained variation over the 0.054 for the pooled data, implying that a large fraction of the unexplained variation is due to plant-to-plant differences in the dose-response relationship. Nonetheless, each individual regression explains little of the variation within plants ( $R^2$  ranges from 0 to 0.18, mean = 0.09).

**Fig. 2** Scatter plot of dose-response relationships for 12 plants. Each distinct *symbol* represents a different plant. The best fit negative exponential model to the pooled data: seeds = 7.78 (1 - exp<sup>-0.0123 Pollen</sup>);  $R^2 = 0.054$ ,  $n = 442$  seed-pollen pairs)



**Fig. 3** Non-linear dose-response equations fitted to each of 12 plants separately:  $n$  for each regression = 21 to 43, individual  $R^2$  values range from 0 to 0.18, mean = 0.09. The corresponding scatter plot of the data is in Fig. 2. Note different axis scaling from Fig. 2

## Discussion

Application of more pollen to *Lesquerella fendleri* flowers was only loosely related to production of more seeds, even though I used the same bulk pollen samples for all plants. However, accounting for differences among plants in the dose-response relationship substantially increased explained variation. Together, these results indicate that differences among and within plants are important contributors to the overall variation, and these contributions may affect interpretations of events in the field.

## Variation among plants

Nearly 40% of the variation in the pollen dose-response relationship is attributable to differences among plants. Thus, although no clear relationship between pollen load and seed set is discernible when results from all plants are lumped (Fig. 2), individual plants differed substantially in their response (Fig. 3). Such strong differences among plants have been casually noted in the past (e.g., Bertin 1990), but to my knowledge have not been statistically confirmed. Indeed, they may be common, since differences among plants in maximal seed set per fruit occur in many species (Roach and Wulff 1987).

## Causes

What causes variation among plants in maximal seed set per flower? Possibilities that I will consider include variation among plants in gynoecium structure, in self-pollen receipt, in sex-allocation strategies, in patterns of seed abortion, and in plant vigor and resource availability. I consider only the last three likely in this study.

Variation among plants in structure of the gynoecium, such as ovule number or space in the fruit might possibly affect maximal seed set, but probably are not important here. Variation in ovule number cannot be an important component of variation for *L. fendleri*, since the asymptotes for all individual plant dose-response curves were <16, (Fig. 3), while average ovule numbers for *L. fendleri* are near 20 (see Methods), and only 9% of plants have fewer than 15 ovules per flower ( $n = 433$ ; R.J. Mitchell, unpublished work). Therefore the upper limit on seed set per flower was not commonly set by ovule number. It also is unlikely that seed set was limited by ovule fertilization, since the largest pollen loads applied in this experiment saturated the stigma, and some fruits

contained as many seeds as ovules (personal observations). Fruits appear to have adequate space in which to fit more seeds, and other morphological limitations also seem unlikely to explain these results (personal observations).

Variation among plants in the amount of self-pollen received (which occurred for unpollinated flowers, and therefore probably also for outcrossed flowers) might alter asymptotes, if self-pollen negatively affects seed set (see Waser and Price 1991b and references therein). Unfortunately, I was unable to emasculate flowers early enough in ontogeny to prevent self-pollen deposition. However, it is unlikely that differences among plants in the amount of passive self-pollen deposition caused the differences in dose-response relationships for two reasons. First, the effects of self pollen on seed set are small. When self pollen precedes cross pollen by 24 h (much longer than is likely in this experiment), seed set decreased by only 1.4 seeds per fruit (unpubl. data), which is insufficient to produce the strong differences among plants in asymptotes shown in Fig. 3. Second, plants with large amounts of self pollen on unpollinated flowers do not have lower asymptotes. Instead, the correlation between mean self-pollen loads and the magnitude of the asymptote is strongly positive ( $r = 0.72$ ,  $P = 0.01$ ).

Variation among plants in sex allocation strategies might also explain these results, if plants devoting more resources to male function do so at the expense of seed set. I have conflicting evidence on this topic. On one hand, I find no phenotypic correlation between pollen and ovule production per flower ( $r = 0.07$ ,  $n = 150$ ; R.J. Mitchell, unpublished work). On the other hand, there may be a tradeoff at the level of seed set. In a  $7 \times 7$  diallel cross (R.J. Mitchell, unpublished work), seed set per flower when acting as a maternal plant was strongly (though non-significantly) negatively correlated with seeds/flower as a paternal parent ( $r = -0.546$ ,  $n = 7$ ,  $P > 0.05$ ; analyzed following Schlichting and Devlin 1989). It is therefore possible that gender specialization is associated with variation in maximal seed set among plants, but more information is needed.

Variation among plants in propensity to abort developing seeds might also cause variation in the dose-response relationship. This might take two forms. First, abortion patterns could be non-random, with, for example, only the least vigorous zygotes being aborted. This would result in "choosier" females (those with lower asymptotes and higher abortion rates) having higher quality offspring; the decreased seed set per fruit could then be seen as a cost incurred to improve offspring quality at the expense of quantity (see also Björkman et al. 1995). This possibility is not supported by data. In a study of offspring of the same individual plants used in this experiment, I grew seedlings in a greenhouse for 55 days (R.J. Mitchell, unpublished work). The correlation between an estimate of the vigor of those plants (number of leaves) and an estimate of choosiness ( $-A$ ; the negative of the asymptote of each plant's dose-response equation) is not significant ( $r = 0.10$ ,  $n = 10$  plants for which

I had estimates of both variables). If abortion is non-random in this plant, it does not seem to improve the early vigor of offspring. Second, abortion patterns could be random, perhaps resulting from resource limitation or differences in gender specialization. This is possible, but has not yet been conclusively tested (but see Mitchell and Marshall 1995).

Variation among plants in vigor and resource availability might also be important. I intended to minimize this by using potted plants in a greenhouse environment (Silander and Primack 1978). Although such controls are never perfect (Potvin 1993), it seems unlikely that resources varied enough among these plants to account for the 5-fold variation in asymptotes (3–16 seeds/fruit) among plants.

However generated, variation among plants in the asymptote of the dose-response relationship appears to be more important in causing differences among plants in seed set than does variation in the "slope" parameter. This is true even at low pollen loads. For example, there is a strong correlation between predicted seed set for each plant (based on the individual non-linear analyses, pollen load size set at 25) and the estimated asymptote (Spearman's rank correlation = 0.77,  $P = 0.003$ ,  $n = 12$ ) but not between predicted seed set and the slope parameter (Spearman's  $r = 0.27$ ,  $P = 0.4$ ). Higher asymptotes are not achieved by decreasing individual seed size; if anything, mean mass/seed increases with the asymptote ( $r = 0.354$ ,  $n = 12$ ,  $P = 0.26$ ).

Overall, I interpret the variation among plants in dose response relationships to indicate that plants differed in propensity to abort seeds, in the extent of gender specialization, or in vigor/resource availability. Note that the ultimate goal of maximizing fitness by, for example, gender specialization, may be proximally achieved by, for example, a change in abortion rates.

### Consequences

What are the likely consequences of variation among plants in the dose-response relationship? This certainly depends on how the variation arises for each species, but in general I can think of three likely consequences: variation among plants in pollen limitation, variation among plants in pollen competition, and variation among plants in mating strategies.

First, plants within a population may differ in the extent of pollen limitation. For example, in Fig. 3, if pollen loads are near 50 grains/flower, some plants have achieved nearly full seed set (such that their dose-response curves have flattened out), while others would produce more seeds if they received more pollen. This may be more important for other plant species, but for *L. fendleri* only a fairly narrow window of pollen load sizes result in variation among plants in pollen limitation (roughly 0–120 grains, including selfs: Fig. 3). Since pollen loads in the field usually are  $\gg 120$  grains (see Methods), seed production for whole plants should rarely

be limited by pollen, as is indeed the case (R.J. Mitchell, unpublished work). This means that most flowers receive enough pollen to potentially have full seed set, regardless of the maximum seed set potential of any particular plant.

Second, plants within a population may differ in the extent of pollen competition. If increasing pollen number does not increase seed number, then a smaller subset of available pollen will be successful, increasing the advantage to fast growing pollen tubes, and the opportunity for non-random mating. The importance of this will depend critically on the schedule of arrival of pollen on stigmas in the field (Mulcahy et al. 1983; Snow 1986; Bertin 1990; Spira et al. 1992). I am currently quantifying these schedules for *L. fendleri*.

Third, plants within a population may differ in mating strategies, including both gender specialization and propensity to abort seeds. These are important components of plant mating systems (e.g., Campbell 1989; Rigney 1995), but I am not aware of any discussion of the possibility that such specialization might be indicated by variation in dose-response relationships among plants. Furthermore, although seed abortion can be an important cause of non-random mating in plants (e.g., Marshall and Ellstrand 1988; Rigney 1995), my results are consistent with the idea that abortion can exact a detectable cost by reducing seed set. Thus, the variation among plants in dose-response relationships may reflect functional gender variation within populations, and could be important in explaining variation in reproductive effort and success within populations.

#### Variation within plants

Although there are substantial differences among plants in the form of the dose-response relationship, there is still an enormous amount of unexplained variation (see Fig. 2). Thus, knowledge of pollen deposition is of limited utility in predicting seed set for *L. fendleri*, even over the wide range of pollen loads used in this experiment. This is also true for many other species (e.g., McDade and Davidar 1984; Kohn and Waser 1985; Campbell 1986; Snow 1986; Galen and Newport 1988; Waser and Price 1991a; N.M. Waser and R.J. Mitchell, unpublished work), although most studies to date have not distinguished among- from within- plant variation.

Why is there so much scatter in the relationship between pollen and seed set within plants? Kohn and Waser (1985) suggested a number of reasons, including differences among flowers in stigma and ovule receptivity, in the viability of the arriving pollen, in the genetic congruity between pollen and ovule, and in ovule number. To these might also be added effects of within-plant resource limitation, and of subtle damage to flowers and developing fruits (Stephenson 1981). Which of these may be important here is uncertain, although there are some clues. Variation among flowers in stigma receptivity (as quantified by flower age) can only account for two

seeds per fruit differences within plants (R.J. Mitchell, unpublished work), which is insufficient to generate all of the unexplained variation. Likewise, as mentioned above, variation in the amount and timing of self pollen arrival alters seed set only slightly. Other aspects of genetic congruity of ovule and pollen did not vary among flowers or within plants because of the experimental design, since the same mix of pollen from more than eight donors was used in all cases. Variation among flowers in ovule number also is relatively small (mean of within-plant SD = 2.2,  $n = 6$  plants, 51 flowers; R.J. Mitchell, unpublished work). Resource limitation within plants occurs, but can account for only about 4 seeds/fruit differences. It probably is the joint effect of many such disparate factors that causes the inexact relationship between pollen and seeds. Since variation among flowers in these factors should be even greater in the field, this appears to be an important drawback to the use of stigmatic pollen loads, pollen tubes, or other indirect measures as surrogates for seed set.

Overall, these results indicate that although seed number does generally increase with pollen load in this species, this is an extremely loose relationship. Much of the existing variation cannot now be attributed to specific causes, and understanding why so much variation exists is an important question for future research. However, I have argued that one important and identifiable cause for the inexactness of the relationship between seed number and pollen load is variation among plants, and that this variation may have important consequences for plant mating biology.

**Acknowledgements** Joy Avritt, Bob Cabin, Brenda Casper Ann Evans, Doug Furcht, Patty Gegick, Diane Marshall, Ellen Mitchell, Karen Mitchell, Bill Morris, Scott Orcutt, Nick Waser, and two anonymous reviewers provided help, support, and advice. The Sevilleta LTER and the Sevilleta National Wildlife Refuge provided permission to collect plants from the field. This research was supported by NSF grant DEB 92-03203. This is publication 85 of the Sevilleta LTER.

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