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Effects of male sterility on reproductive traits in gynodioecious plants: a meta-analysis

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Abstract Female fecundity advantage in gynodioecious plants is required for the spread and maintenance of this reproductive system. However, not all reproductive characters show female advantage in all species. We used a meta-analysis to summarise differences between females and hermaphrodites reported from the literature for several reproductive traits. Further we tested three hypotheses, (1) that female plants of species with many ovules produce more seeds per fruit while those with few ovules produce heavier seeds, (2) that females are more pollen limited than hermaphrodites, and (3) that floral sexual size dimorphism is more pronounced in species with few ovules, either because female reproductive success is less limited by pollen availability in such species or because flowers with few ovules require a smaller floral structure to protect the carpels. Overall, females compared to hermaphrodites produced more but smaller flowers, had higher fruit set, higher total seed production, and produced heavier seeds that germinated better. Species with many versus few ovules differed in female advantage for flower size dimorphism, flower number, fruit set and total seed production. However seed size, seed set per fruit and seed germination differences between females and hermaphrodites did not differ significantly between species with few and many ovules. We also found no evidence for differential pollen limitation between females and hermaphrodites. Degree of floral sexual size dimorphism differed significantly between species with few and many ovules. Though pistillate flowers were generally smaller than those of hermaphrodites, species with many ovules showed less difference in flower size between the sexes, suggesting either that the protective role of the perianth constrains

the evolution of sexual size dimorphism in species with many ovules or that selection for adequate pollination in species with many ovules impedes the reduction in flower size of females.

Keywords Female advantage · Pollen limitation · Seed set · Fruit set · Seed germination

Introduction

Gynodioecy, the co-occurrence of female and hermaphrodite individuals within plant populations, is a reproductive system found in numerous plant families. It is common in the Lamiaceae and the subfamily Silenoidea of the Caryophyllaceae. In other plant families gynodioecy may only appear as a rare and occasional breeding system. Models for the evolution of gynodioecy that consider nuclear inheritance of male sterility find that females can only spread in populations if they are more than twice as fecund as hermaphrodites. On the other hand, if cytoplasmically inherited genes control male sterility, which is the case in most gynodioecious species investigated (Charlesworth and Laporte 1998), females can spread and be maintained even with minimal female fecundity advantage (Lewis 1941).

Female advantage may result from reallocation of resources saved from pollen production in male sterile individuals or from avoidance of inbreeding by females unable to self-pollinate (Darwin 1877). Females may also produce higher quality offspring if pistillate flowers provide a more intensely competitive sieve for pollen, allowing only the best genotypic combinations to give rise to zygotes (Shykoff 1992). Indeed females and their offspring, can differ from hermaphrodites and their offspring, in several ways that may influence their fitness, including seed production, seed size, seed germination ability, seedling survival, plant size, flower production and survival (see Appendix). Recent reviews of sexual dimorphism in reproductive characters indicate that perfect flowers of hermaphrodites are generally larger

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than pistillate ones on females, but for nectar production the difference is equivocal (Delph 1996; Delph et al. 1996; Eckhart 1999).

Many examples of female advantage for various traits are available in the literature, allowing for a synthesis of the general effects of male sterility on reproductive effort and life-history variation in gynodioecious plants. Furthermore, evidence for female advantage is equivocal for some characters, such as seed production and seed size (see Appendix). To determine whether male sterility generates a common average effect on a variety of reproductive traits it is necessary to synthesise the available information across a range of independent studies and species in an objective and quantitative manner, such as that provided by meta-analytical methods (Arnqvist and Wooster 1995). These methods allow the combination of information across studies while weighting by sample sizes to give a general overall measure of effects. Furthermore meta-analysis allows the testing of precise hypotheses involving various grouping variables.

Here we investigate the general effects of male sterility on different female reproductive functions including fruit set, seed set, total plant seed production, and seed germination ability. Further we test for general effects of male sterility on flower production and flower size. To gain insight into patterns of resource allocation within pistillate plants and other ecological and evolutionary consequences of male sterility we test the following hypotheses about patterns of expression of these effects:

1. Gynodioecy is particularly common in plant families with small fixed numbers of ovules per flower such as the Lamiaceae and Plantaginaceae. Females of such species cannot increase seed set per fruit or flower beyond the strict bounds fixed by the number of available ovules. If resources saved from pollen production are reallocated within the flower, then such plants might be expected to produce larger seeds than do the hermaphrodites, whereas in plant species with many ovules per flower, resources could go into producing more seeds. If, on the other hand, the resources are placed into a whole-plant pool, such species might produce more flowers than their hermaphrodite counterparts. Such a finding could give insight into the patterns of resource reallocation, indicating whether resources move more freely between organs within flowers or among flowers of the same plant.
2. Male sterile individuals in gynodioecious populations are obligate outcrossers and may be more pollen limited than their hermaphrodite counterparts (Charlesworth and Charlesworth 1981). Is there a general pattern that female fecundity advantage is greater under hand-pollination with ad libitum pollen than under open-pollination regimes?
3. Three hypotheses have been proposed to explain sexual size dimorphism between pistillate and perfect flowers: (1) developmental correlations between stamens and petals, (2) a protective role of the petals for

the pollen-bearing structures, or (3) pollinator attraction serving male reproductive success (Delph 1996). The last one, that floral display is generally considered to be more important for male than female function in hermaphrodite plants (Bell 1985), predicts that loss of male function may allow the evolution of sexual dimorphism in flower size, with pistillate flowers becoming smaller. Pollen limitation may be differentially severe for plant species with many versus few ovules per flower, and this may have ramifications for flower size evolution. Do species with abundant ovules, where seed set of females is more likely to be pollen limited, show less sexual dimorphism in flower size than those with few ovules per flower?

Materials and methods

Literature search and data extraction

We searched the bibliographic databases BIOSIS and Web of Science from the last 20 years for all papers with “gynodioecy”, “gynodioecious”, or “male sterility” and “plants” in the title, keywords or abstract. Older papers were found in the citation lists of these articles. Further we contacted colleagues who work on problems of gynodioecious reproductive systems in plants and asked for data on reproductive characteristics of female versus hermaphrodite individuals. We included all data from all papers to which we had access and for which the necessary information was available. Since we performed an analysis of the raw data using the program MetaWin 2.0 (Rosenberg et al. 2000), we required sample sizes, mean trait values, and SDs for females and hermaphrodites, respectively. SDs were calculated from SEs or 95% confidence intervals (CIs) where these were given. In the few cases where the author did not state which measure of dispersion was given, we assumed that the reported values were SDs. Studies, for which the necessary information could not be extracted, either from tables, text, or figures, were omitted. For papers that reported results for several independent plant populations we took two approaches. First we included all data, treating multiple data from the same species and studies, but different plant populations or years, as independent observations. Second, to prevent bias from pseudoreplication we chose the one population with the most balanced sample size for females and hermaphrodites from each study and excluded all others from the analyses. Further, there is no possibility to correct for phylogenetic dependence. Our data set comprises studies of 23 different plant families of varying phylogenetic proximity, and there are several observations for numerous families, particularly the Caryophyllaceae.

Calculating effect sizes

We calculated Hedges' d , the standard meta-analytical metric, using the program MetaWin 2.0 (Rosenberg et al. 2000). Since we were interested in two kinds of grouping variables or classes, effect sizes were then combined across studies separately for these two grouping variables used in our analyses. The grouping variables were: (1) for all traits considered, whether plants had a large variable number or a small (one to five) fixed number of ovules per flower; and (2) for fruit and seed traits only, whether plants (both females and hermaphrodites) had been hand-pollinated or left for open-pollination. For these analyses we employed two different reduced data sets. The first, for the comparison of species with contrasting ovule numbers, included only a single study from each species from natural open-pollination. The second, for comparing pollination regimes, included a single study that presented data

from natural open- and hand-pollination for the same species. All our analyses used the random-effects model approach in MetaWin 2.0. This approach assumes random variation in the effect of interest among the studies and tests whether groups differ in effect size by calculating the heterogeneity between groups.

Seed size can influence seed germination characteristics (Giles 1990) so we examined whether species with larger female advantage for seed size also had a larger female advantage for germination by testing the relationships between the Hedges' d for seed size and for seed germination with the Spearman rank correlation. To investigate the relationship between sexual size dimorphism and pollination we tested whether in species where pistillate flowers were much smaller than perfect ones, i.e. with larger sexual size dimorphism, the pistillate flowers set relatively fewer seeds than the perfect ones. A single population for which we had both germination and seed size data or flower size and seed set data was used for each species.

Results

Females bore consistently smaller flowers than hermaphrodites summarised over all 52 comparisons (Table 1, Fig. 1), or when only considering the 29 comparisons using a single observation from each study, as revealed by the positive overall Hedges' d . Females showed higher proportional fruit set over all studies and for the reduced data set, and similarly had higher total plant seed production. They also produced larger seeds that germinated better than those produced by hermaphrodites. On the other hand, seed set per fruit did not show consistent differences between females and hermaphrodites, as shown by the 95% CIs for Hedges' d overlapping with 0 (Table 1).

Flower size and number, fruit set and total plant seed production varied differently between females and hermaphrodites for plant species with few versus many ovules. Those with few ovules produced relatively more,

Table 1 Summarised Hedges' d from a random-effects model meta-analysis for the seven traits analysed. The *first row* for each trait represents all data, including multiple observations per study and species. The *second row*, the reduced data set, includes only a single observation per species, retaining the study with the largest sample size among open-pollination data. When d is *negative* females have a larger effect size than hermaphrodites, when d is *positive*, a smaller effect size. If 95% confidence intervals (CIs) do not include 0 the effect is significant over all studies

| Trait | d | 95% CI | n |
|-----------------------|--------|------------------|-----|
| Flower size | 2.573 | 2.287 to 2.860 | 52 |
| | 2.272 | 1.883 to 2.662 | 29 |
| Flower number | 0.028 | -0.174 to 0.229 | 63 |
| | -0.444 | -0.786 to -0.102 | 25 |
| Fruit set | -0.977 | -1.332 to -0.622 | 88 |
| | -2.344 | -3.223 to -1.466 | 29 |
| Seed set per fruit | -0.025 | -0.271 to 0.220 | 75 |
| | -0.480 | -1.098 to 0.138 | 24 |
| Total seed production | -0.422 | -0.728 to -0.115 | 22 |
| | -0.681 | -1.129 to -0.234 | 13 |
| Seed size | -0.406 | -0.567 to -0.245 | 39 |
| | -0.392 | -0.629 to -0.156 | 20 |
| Seed germination | -0.521 | -0.996 to -0.047 | 14 |
| | -0.711 | -1.151 to -0.071 | 10 |

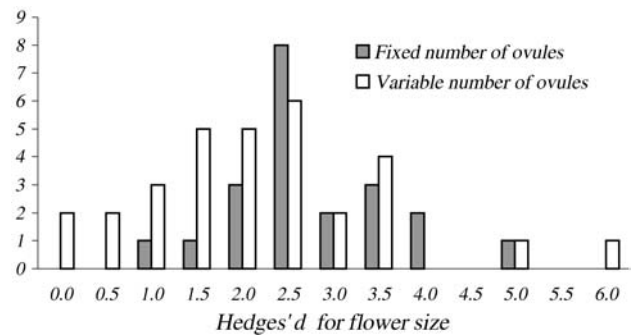


Fig. 1 Frequency distribution of dimorphism in flower size between females and hermaphrodites for plant species that produce a small fixed number versus a large variable number of ovules per flower using all data available ($n=52$). Large values of Hedges' d indicate large sexual dimorphism, with female flowers much smaller than those of hermaphrodites

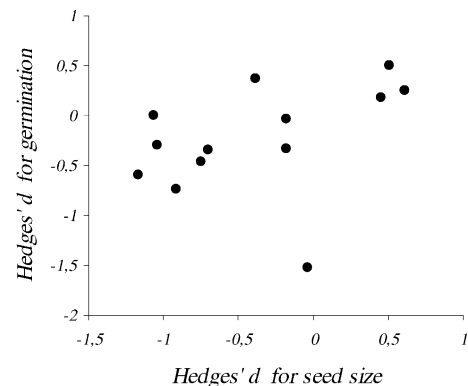


Fig. 2 The relationship between the difference between hermaphrodites and females in seed size and seed germination using all data available. Negative values of Hedges' d represent female advantage, positive values hermaphrodite advantage. Species for which females increased seed size more also showed a greater increase in germination rates of seeds from female plants ($r_{\text{spearman}}=0.49$, $n=13$, $P=0.086$). If the outlier (*Ochradenus baccatus*) is removed this correlation becomes significant ($r_{\text{spearman}}=0.698$, $n=12$, $P=0.012$)

smaller flowers than did those with many ovules, that is, the degree of sexual flower size dimorphism between females and hermaphrodites was greater for species with few ovules per flower. Species with many ovules showed greater female advantage than did those with few for fruit and total seed set. Female advantage for seed size, seed set per fruit, and seed germination, on the other hand, were not significantly different between plant species with few versus many ovules (Table 2).

We found no support for our hypothesis that females are generally more pollen limited than hermaphrodites in natural populations, since there was no significant heterogeneity between hand-pollinated and open-pollinated comparisons between female and hermaphrodite plants (Table 2).

Plant populations and species that showed greater female advantage in seed size also showed a tendency for greater female advantage in seed germination (Fig. 2;

Table 2 Hedges' d from a random-effects model meta-analysis for the seven traits analysed, employing the reduced data set, which includes only a single observation per species, retaining the study with the largest sample. Two grouping variables were considered. First the ovule number, i.e. whether each flower contains a small fixed number of ovules (*Few*) or a large variable number (*Many*); only results from open-pollination were used here. Second the pollination regime, whether flowers were open- or hand-pollinated. The heterogeneity statistic, Q_B , and its associated probability show whether the groups differ or not

| Trait | Grouping variable | d | 95% CI | n | Q_B | P |
|--------------------|-------------------|--------|------------------|-----|--------|-------|
| Flower size | Few ovules | 3.246 | 2.450 to 4.0421 | 9 | 11.356 | 0.001 |
| | Many ovules | 1.859 | 1.389 to 2.329 | 20 | | |
| Flower number | Few ovules | -0.859 | -1.351 to -0.367 | 14 | 7.053 | 0.008 |
| | Many ovules | -0.035 | -0.517 to 0.587 | 11 | | |
| Fruit set | Few ovules | -0.748 | -2.102 to 0.606 | 14 | 13.06 | 0.003 |
| | Many ovules | -3.904 | -5.207 to -2.600 | 15 | | |
| | Open-pollination | -1.163 | -1.828 to -0.498 | 29 | | |
| | Hand-pollination | -0.315 | -1.931 to 1.301 | 7 | | |
| Seed set per fruit | Few ovules | 0.077 | -1.516 to 1.670 | 6 | 1.109 | 0.292 |
| | Many ovules | -0.680 | -1.449 to 0.089 | 18 | | |
| | Open-pollination | -0.544 | -1.102 to 0.013 | 24 | | |
| | Hand-pollination | -0.350 | -1.358 to 0.658 | 9 | | |
| Total seed | Few ovules | -0.291 | -0.706 to 0.123 | 9 | 15.451 | 0.000 |
| | Many ovules | -1.627 | -2.544 to -0.709 | 4 | | |
| Seed size | Few ovules | -0.378 | -0.744 to -0.012 | 10 | 0.023 | 0.881 |
| | Many ovules | -0.413 | -0.795 to -0.032 | 10 | | |
| | Open-pollination | -0.365 | -0.590 to -0.140 | 20 | | |
| | Hand-pollination | -0.310 | -0.851 to 0.230 | 6 | | |
| Seed germination | Few ovules | -0.990 | -2.017 to 0.037 | 6 | 0.973 | 0.324 |
| | Many ovules | -0.386 | -1.864 to 1.092 | 4 | | |
| | Open-pollination | -0.705 | -1.332 to -0.078 | 10 | | |
| | Hand-pollination | -0.101 | -8.004 to 7.802 | 2 | | |

$r_{\text{spearman}}=0.49$, $n=13$, $P=0.086$). We found no such relationship between differences in seed set per flower and differences in flower size between females and hermaphrodites ($r_{\text{spearman}}=-0.146$, $n=15$, $P>0.5$).

Discussion

Overall female advantage was found for several traits. Females produced more flowers, set more fruits, and produced more seeds that were larger and germinated better than those of hermaphrodites in the same populations, but no difference was found for seed set per fruit (Table 1). Thus, it appears that resources saved by not producing pollen do not contribute to greater seed production for each fruit. Instead, female plants have greater reproductive potential, producing more flowers, and these flowers are more successful at giving rise to fruits containing higher quality seeds than hermaphrodites. This suggests reallocation of resources saved from pollen at the whole plant rather than the flower level.

Female advantage may result from a combination of three mechanisms: reallocation of resources saved from pollen production in male sterile individuals, less inbreeding because of selfing avoidance, or higher quality zygotes produced by female plants through more intense pollen competition. The meta-analysis cannot distinguish among these mechanisms that may generate female advantage, and focused experiments and investigations would be necessary to test among these possibilities.

Where detailed information on nutrient content in seeds was available no difference was detected in resource provisioning or embryo size between seeds produced by females and hermaphrodites in *Silene acaulis* (Delph et al. 1999). This suggests that large differences in

seedling survival found for this species (Shykoff 1988) are probably not due simply to better resources in seeds from females, and that other mechanisms must be invoked (Shykoff 1992; Delph et al. 1999).

We found a tendency for a relationship between female advantage for seed size and seed germination. Thus in plant species for which females made much larger seeds than hermaphrodites, females also tended to enjoy a germination advantage. Indeed, seed size is positively correlated with many fitness traits of the resulting plants (Giles 1990 and references therein). Here resource reallocation may play a common role in seed size and seed viability, and plants with access to more additional resources can allocate to both of these functions. On the other hand, inbreeding depression or zygote quality can influence both seed size and seed germination, so the observed relationship could equally result from differences in levels of inbreeding or offspring genetic quality between females and hermaphrodites.

We hypothesised that plant species with few versus many ovules could differ in female advantage for flower production or seed size and seed set per fruit, and that this would allow insight into patterns of reallocation of resources saved from pollen. We found no difference in female advantage for seed size or seed set, but female plants of species with few ovules produce more additional flowers than those of species with many ovules. This, together with the global result that female plants produce more seeds overall, but do not produce more seeds per fruit, suggests resource reallocation at the whole plant level. Alternatively, seed size and seed set per fruit may be limited by factors other than resources, such as pollen availability or genetic quality of the growing seed. Furthermore reproductive allocation, possibly including seed size and seed set, can vary strongly with position on

the plant (Carroll and Delph 1996) and this uncontrolled within-plant variation may mask effects at the plant level.

Pollination regime, i.e. whether plants had been open-pollinated or hand-pollinated did not significantly influence female advantage for either fruit set, seed set, seed size or seed germination. This implies that pollen limitation did not differ between females and hermaphrodites for any of these characteristics. Models of the dynamics of gynodioecious populations find that cytoplasmically inherited male sterility factors will spread in populations until seed production of females becomes severely pollen limited. At this point, a mutation that restores male function will be strongly selected for, and this process will generate cyclical dynamics for population sex ratios and patterns of pollen limitation (Gouyon et al. 1991). Natural gynodioecious populations will be situated at varying positions on cycles of a spread of cytoplasmic male sterility factors or nuclear restorers, hence a global effect of pollen limitation of females would, perhaps, not be expected. Further, spatial variation in sex ratios among and within populations will influence equilibrium sex ratios and the evolutionary dynamics of gynodioecy (McCauley and Taylor 1997). Indeed sex ratio variation in natural (Widén and Widén 1990; Graff 1999) and artificial (McCauley and Brock 1998) populations strongly influences pollen limitation of females, with females in patches of highly local female frequency being more pollen limited.

Females produced smaller flowers than hermaphrodites in almost all species (Fig. 1, Table 1). Delph (1996) elaborates three hypotheses to explain this sexual size dimorphism in gynodioecious species: (1) greater importance of pollinator attraction for the male function of hermaphrodites (see also Bell 1985), (2) developmental correlation between stamens and petals (see also Darwin 1877; Plack 1957) or (3) protection of the pollen-bearing anthers. In many dioecious species, on the other hand, pistillate flowers are larger than those of males, possibly because of the protective role the perianth plays for the carpels (Delph et al. 1996). We found that plant species with a small fixed number of ovules per flower showed stronger sexual size dimorphism in flower size, producing much smaller pistillate than hermaphrodite flowers. Species with many ovules per flower, on the other hand, bore pistillate flowers that were closer in size to those of hermaphrodites (Fig. 1). This result can be explained in the light of either the protection or the attraction hypotheses above. A double protective role of flowers for both the stamens and carpels might mean that in plants with large ovaries containing a large number of ovules, size dimorphism will be constrained and pistillate flowers cannot become greatly reduced in size. Alternatively, if pollinator attraction is important for the evolution of floral dimorphism, the difference between females and hermaphrodites in floral morphology should be most pronounced in species with only few ovules per flower. Such species will readily have their stigmas saturated, receiving sufficient pollen to fertilise all available ovules, and most pollinator visits would serve to remove rather than deliver pollen. For species with many ovules, on the other hand, multiple pollinator visits might be required to

provide enough pollen for total fertilisation, so selection via the female and the male pathway on floral traits should be less divergent. This suggests that though sexual selection on male function can generate evolution of sexual dimorphism (Queller 1983), natural selection for fecundity on female function in plants with many ovules can prevent the evolution of marked sexual size dimorphism and strong diminution of pistillate flowers. Indeed, pollen receipt increases with increasing flower size, and multiple pollinator visits are required for maximal pollination in *Fragaria virginiana* (Ashman 2000). However, we found no general relationship between degree of sexual dimorphism in flower size and per flower seed set differences between the sexes. Thus flower size dimorphism did not appear to have a general influence on differential pollination success and thereby seed production between the sexes. The general pattern we found of differences in sexual size dimorphism between gynodioecious species with few and many ovules is more probably due to the protective role of the perianth. Additional experiments such as those of Ashman (2000) on flower size manipulations and pollen export and receipt and experiments to test the effect of flower size on carpel protection will be necessary to understand the role of these two selective factors in the evolution of sexual size dimorphism between pistillate and perfect flowers.

In summary, the meta-analysis approach allowed us to identify consistent differences in reproductive characters between females and hermaphrodites of a broad phylogenetic range of gynodioecious species. We found no support for our hypothesis that females of species with few ovules should produce significantly larger seeds relative to their conspecific hermaphrodites than those of species with many ovules, despite constraints in producing additional seeds. This, together with the lack of an overall female advantage for seed production per fruit, suggests that reallocation of resources saved from pollen production takes place at the whole plant rather than the flower level. Similarly we found no evidence that females are overall more pollen limited than hermaphrodites in natural populations. Significant heterogeneity of species with many versus few ovules, together with a lack of a relationship between sexual size dimorphism and seed set per fruit, suggest that evolution of sexual size dimorphism is constrained by a protective role of the perianth for the carpels rather than pollinator-driven selection in gynodioecious taxa (but see Ashman 2000). For all these three findings an experimental approach will be necessary to determine real causal links. Meta-analysis is a powerful tool for detecting overall patterns summarised over a large number of studies, but it is a correlative approach, useful for identifying hypotheses. For example, bud removal experiments could test for local versus whole plant resource reallocation, further pollen addition experiments should be carried out in populations or patches with varying sex ratios (McCauley and Brock 1998; Graff 1999) to see whether pollen limitation can indeed drive the evolution of nuclear restorer genes, and finally the role of flower size on carpel protection should be tested with floral manipulation experiments.

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Appendix

Summary

Table 3 shows a summary of the studies included in the metaanalysis.

Table 3 Summary of studies included in the metaanalysis. Species are classified as to whether each flower contains a small fixed number of ovules (*Few*) or a large variable number (*Many*). *NS* No significant difference between females (*F*) and hermaphrodites (*H*),

F≤*H* or *F*≥*H* both significant and non-significant differences found for different populations, *F*>*H* or *F*<*H* significant differences, * denotes results of supplemental hand pollination

| Family | Species | Study | Ovule number | Flower size | Flower number | Fruit set | Seed set per fruit | Total seed | Seed size | Seed germination | |
|---------------------------------------|-------------------------------|--|--------------|-------------|---------------|-----------|--------------------|------------|-----------|------------------|-----|
| Apiaceae | <i>Gingidia decipiens</i> | Lloyd et al. (1980) | Few | | | | NS | | | | |
| | <i>Gingidia montana</i> | Lloyd et al. (1980) | Few | | | | NS | | | | |
| | <i>Scandia geniculata</i> | Lloyd et al. (1980) | Few | | | | NS | | | | |
| Asteraceae | <i>Cirsium chikushiense</i> | Kawakubo (1994) | Few | NS | | | | | | | |
| Boraginaceae | <i>Echium vulgare</i> | Klinkhamer et al. (1991) | Few | | | | F>H | | | | |
| | | Klinkhamer et al. (1994) | Few | | NS | | | F>H | F>H | | |
| | <i>Eritrichium aretioides</i> | Puterbaugh et al. (1997) | Few | F<H | | | | | F>H | | |
| | | Puterbaugh (unpublished data) | Few | | NS | | NS | NS | | | |
| Caryophyllaceae | <i>Arenaria merckoides</i> | Sugawara and Horii (1995) | Many | F<H | | | NS | F>H | | | |
| | | Shykoff et al. (1997) | Many | F<H | | | | | | | |
| | <i>Dianthus silvester</i> | Sugawara et al. (1994) | Many | F<H | | | | F≤H | | | |
| | <i>Dianthus superbus</i> | Collin et al. (2002) | Many | F<H | | | | NS | F>H | NS | |
| | <i>Dianthus sylvestris</i> | Collin (unpublished data) | Many | F<H | | F<H | F>H | NS | | NS | |
| | | López-Villavicencio (unpublished data) | Many | F<H | | | | NS | | | |
| | <i>Gypsophila repens</i> | Shykoff (unpublished data) | Many | | | | NS | | | NS | |
| | <i>Moehringia lateriflora</i> | Sugawara (1993) | Many | F<H | | | | F≥H | | | |
| | <i>Paronychia pulvinata</i> | Puterbaugh (unpublished data) | Few | F<H | | NS | | F>H | F>H | | |
| | | Sakai et al. (1997) | Many | | | NS | F>H | F<H | | F>H | F≥H |
| | <i>Schiedea adamantis</i> | Shykoff (1988) | Many | | | | F>H | NS | F>H | NS | NS |
| | <i>Silene acaulis</i> | Hermanutz and Innes (1994) | Many | F>H | | | | | | | |
| | | Delph et al. (1999) | Many | | | NS | F>H | | | NS | |
| | <i>Silene italica</i> | Delph and Carroll (2001) | Many | | | | F>H | | | | |
| Lafuma and Maurice (unpublished data) | | Many | | | F≤H | F≥H | | | F>H | | |
| <i>Silene littorea</i> | Gutián and Medrano (2000) | Many | | | | F≥H | | | | | |
| <i>Silene nutans</i> | Jürgens et al. (1996) | Many | F<H | | | | F<H | | | | |
| | Desfeux (1996) | Many | | | NS | F>H | NS | | F≥H | | |
| <i>Silene stockenii</i> | Talavera et al. (1996) | Many | F<H | | | | F≥H | | | | |
| <i>Silene vulgaris</i> | Dulberger and Horovitz (1984) | Many | F<H | | | | NS | | F>H | | |
| | Jolls and Chenier (1989) | Many | | | | | | | F>H | | |
| | <i>Stellaria longipes</i> | Jürgens et al. (1996) | Many | F<H | | | F<H | | | | |
| | | Charlesworth unpublished | Many | | | F≤H | NS | F≤H | | F≥H | |
| | <i>Stellaria longipes</i> | Philipp (1980) | Many | | | | F<H | | | | |
| Celastraceae | <i>Euonymus europaeus</i> | Lloyd et al. (1980) | Few | | | | NS | | | | |
| Fabaceae | <i>Trifolium hirtum</i> | Molina-Freaner and Jain (1992) | Few | | | | NS | F≤H | F>H | NS | |

Table 3 (continued)

| Family | Species | Study | Ovule number | Flower size | Flower number | Fruit set | Seed set per fruit | Total seed | Seed size | Seed germination |
|------------------|---|---|--------------|-------------|---------------|-------------|--------------------|------------|-----------|------------------|
| Geraniaceae | <i>Geranium maculatum</i> | Ågren and Willson (1991) | Few | F<H | F≤H | F≥H | F>H | F>H | NS | |
| | <i>Geranium richardsonii</i> | Williams et al. (2000) | Few | F<H | | | | | | |
| | <i>Geranium sylvaticum</i> | Shykoff and Widmer (unpublished data) | Few | F<H | | | | | | |
| Hydrophyllaceae | <i>Phacelia dubia</i> | Del Castillo (1993) | Many | | F>H F>H* | F<H F>H* | NS | | F<H | F<H |
| | <i>Phacelia linearis</i> | Eckhart (1992) | Many | F<H | | | | | | |
| Iridaceae | <i>Iris douglasiana</i> | Uno (1982) | Many | | | | NS | | | |
| Lamiaceae | <i>Glechoma hederacea</i> | Widén and Widén (1990) | Few | | NS | F≤H | F≤H | | | |
| | <i>Thymus vulgaris</i> | Widén (1992) Gigord et al. (1999) | Few Few | F<H | F≥H | F≤H | F≤H F>H | | F>H | F>H |
| Liliaceae | <i>Chionographis japonica</i> var <i>kurohimensis</i> | Maki 1993 Maki (1996) | Few Few | | F<H F<H | | | F>H | | |
| | <i>Chionographis japonica</i> var <i>hisauchiana</i> | Maki (1996) | Few | | NS | | | | | |
| | <i>Limnanthes douglasii</i> | Kesseli and Jain (1984) | Few | F<H | | | | | | |
| Lobeliaceae | <i>Lobelia siphilitica</i> | Dudle (1999) | Many | | F≤H | F≥H | | | | |
| Malvaceae | <i>Nototriche compacta</i> | Garcia-Franco and Arroyo (1995) | Many | NS | | NS | NS | | | |
| | <i>Sidalcea oregana</i> | Ashman and Stanton (1991) | Many | F<H | F>H | | | | | |
| | <i>Sidalcea hendersonii</i> <i>Sidalcea malviflora</i> | Marshall (1997) Graff (1999) | Many Many | F<H F<H | NS | NS F>H | F≥H F>H | F>H | F≥H | |
| Onagraceae | <i>Fuchsia microphylla</i> | Arroyo and Raven (1975) | Many | F<H | | | | | | |
| | <i>Fuchsia thymifolia</i> | Arroyo and Raven (1975) | Many | F<H | | | | | | |
| Plantaginaceae | <i>Plantago coronopus</i> | Koelwijn (1996) | Few | | F>H | | F<H | F>H | F>H | |
| | <i>Plantago maritima</i> | Dinnetz and Jerling (1997) | Few | | | | F>H | NS | F<H | F<H |
| Poaceae | <i>Chionochloa bromoides</i> | Connor (1990) | Few | | NS | NS | | | | |
| | <i>Cortaderia richardii</i> | Connor (1965) | Few | | NS | NS | | | F≥H | F>H |
| | <i>Cortaderia selloana</i> | Connor (1973) | Few | | F>H | F>H | | | | F>H |
| Resedaceae | <i>Ochradenus baccatus</i> | Wolfe and Schmida (1997) | Many | F<H | NS | | | F>H | F>H | F>H |
| Rosaceae | <i>Fragaria virginiana</i> | Ashman (1999a) Ashman (1999b) | Many Many | F<H F<H | F<H F<H | F>H | | | | |
| | <i>Prunus mahaleb</i> | Ashman (2000) Jordano (1993) | Many Few | F<H | | | F<H NS* | | F>H | NS |
| | <i>Bequaertiodendron magalismontanum</i> | Steyn and Robbertse (1990) | Few | | | | F>H | | | |
| Saxifragaceae | <i>Saxifraga granulata</i> | Stevens (1988) Stevens and Richards (1985) | Many Many | F<H | NS | | F<H | | F>H | |
| Scrophulariaceae | <i>Hebe stricta</i> | Delph and Lively (1992) | Many | NS | | | | | | |
| | <i>Hebe subalpina</i> | Delph and Lloyd (1991) | Many | | | F>H | F>H | | | |
| Thymelaeaceae | <i>Daphne laureaola</i> | Alonso and Herrera (2001) | Few | | NS | NS | | NS | | |
| | | Alonso and Herrera (unpublished data) | Few | F<H | | | | | NS | NS |

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