BRIDGING THE GENERATION GAP IN PLANTS: POLLINATION, PARENTAL FECUNDITY, AND OFFSPRING DEMOGRAPHY

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Abstract. Despite extensive study of pollination and plant reproduction on the one hand, and of plant demography on the other, we know remarkably little about links between seed production in successive generations, and hence about long-term population consequences of variation in pollination success. We bridged this "generation gap" in *Ipomopsis aggregata*, a long-lived semelparous wildflower that is pollinator limited, by adding varying densities of seeds to natural populations and following resulting plants through their entire life histories. To determine whether pollen limitation of seed production constrains rate of population growth in this species, we sowed seeds into replicated plots at a density that mimics typical pollination success and spacing of flowering plants in nature, and at twice that density to mimic full pollination. Per capita offspring survival, flower production, and contribution to population increase (λ) did not decline with sowing density in this experiment, suggesting that typical *I. aggregata* populations freed from pollen limitation will grow over the short term. In a second experiment we addressed whether density dependence would eventually erase the growth benefits of full pollination, by sowing a 10-fold range of seed densities that falls within extremes estimated for the natural "seed rain" that reaches the soil surface. Per capita survival to flowering and age at flowering were again unaffected by sowing density, but offspring size, per capita flower production, and λ declined with density. Such density dependence complicates efforts to predict population dynamics over the longer term, because it changes components of the life history (in this case fecundity) as a population grows. A complete understanding of how constraints on seed production affect long-term population growth will hinge on following offspring fates at least through flowering of the first offspring generation, and doing so for a realistic range of population densities.

Key words: density dependence; experimental seed augmentation; Ipomopsis aggregata; *life history; long-term demographic monitoring; matrix model; pollen limitation; population growth; scarlet gilia; seed limitation; survivorship.*

INTRODUCTION

Flowering plants, being sessile, rely on abiotic or biotic agents to move male gametes (pollen) from male structures of one flower to female structures of another during sexual reproduction. Pollination is a highly variable process (e.g., Price et al. 2005), and pollen deposition on stigmas is often insufficient for full seed set (Burd 1994, Ashman et al. 2004). By constraining fecundity, pollen limitation can be expected to affect not only the fitness of individual plants, but also the dynamics of plant populations. One might suppose, therefore, that the population-level consequences of variable pollination and pollen limitation would have been well studied. Surprisingly, this is not the case (Ashman et al. 2004); the study of plant demography has remained relatively separate from that of pollination

and plant reproductive ecology, and pollination ecologists have rarely looked beyond fruit and seed set.

A parallel situation holds for plant–consumer interactions (Kauffman and Maron 2006, Maron and Crone 2006). From research at the individual plant level we know that consumers often affect growth, survival, seed output, and seed survival. But we still know rather little about the extent to which these individual-level effects scale up to the population level, because most studies to date have looked at only part of the entire life cycle, and/or have not been designed to detect density dependence (for exceptions see Rose et al. [2005], Kauffman and Maron [2006]). Although there have been many seed-addition experiments aimed at determining whether plant population growth is seed limited, few have gone beyond establishment of new recruits to determine their survival to reproduction and reproductive success. Even fewer have examined whether recruitment, survival, or reproduction depends on population or seed-input density. As a consequence, we still do not know whether the increased recruitment

that often results from increased seed input (which suggests that seed limitation is common in plant populations) is transient and will disappear in time (e.g., Turnbull et al. 2000, Young et al. 2005, Ehrlén et al. 2006).

To understand long-term population consequences of consumer- or pollination-mediated variation in seed production, we need to look over the entire life cycle and over a range of population densities (Ashman et al. 2004, Maron and Crone 2006), ideally over multiple generations. Population growth rate or density may not respond to increased pollination success and the resulting increased seed production for a variety of reasons (e.g., Harper 1977). If "safe sites" that are suitable for germination and establishment are limiting, establishment will increase with seed production until safe sites are saturated, then level off at greater levels of seed input. Even if safe sites are not limiting, competition may limit survival, growth, or reproductive success at high population densities; or herbivores and pathogens may preferentially attack dense stands. If density dependence is fully compensatory, increased seed production will have no effect at the population level.

Understanding how plant populations respond to variation in seed production is important for progress in several disciplines. It is critical for our efforts to conserve endangered species (e.g., Pavlik et al. 1993, Menges 2000, Hobbs and Yates 2003), to manage for biodiversity (e.g., Chesson 2000, Harms et al. 2000), and to control invasive species (e.g., Maron and Crone 2006, Stokes et al. 2006). It is critical for evolutionary studies as well. Estimates of pollinator- or herbivore-mediated natural selection generally use flower, fruit, or seed production as proxies for maternal fitness (e.g., Galen 1989, Campbell 1991). These measures may overestimate true fitness differentials if density-dependent processes reduce lifetime success of offspring from fecund mothers.

Here we describe two seed-augmentation experiments with the montane wildflower *Ipomopsis aggregata* that to our knowledge are the first ones designed explicitly to examine links between pollination success and subsequent population growth. In the 2× Experiment we explored how offspring survival and reproduction might differ between naturally pollinated populations vs. those freed from pollen limitation (sensu Ashman et al. 2004). To do so, we sowed seeds at a density that mimics seed production in typical pollen-limited populations, vs. twice that density, which mimics seed production under full pollination. In the 10× Experiment, we asked whether density dependence occurred over a greater (10-fold) range of seed input densities that still falls within the natural range of seed inputs. For both experiments we characterized the complete life histories of the offspring to determine how population growth is likely to respond to variation in pollinator service and seed production.

METHODS

Study species

Ipomopsis aggregata Pursh (V. Grant) subsp. *aggregata* (scarlet gilia, Polemoniaceae) is a monocarpic (=semelparous) perennial wildflower that is widely distributed in mountains of the western United States (Grant and Wilken 1986). It is a good choice for studying links between seed production and offspring demography because monocarpy and virtual absence of seed dormancy make population growth particularly sensitive to recruitment of seedlings from currently produced seed (Louda and Potvin 1995). Monocarpy also allows one to measure lifetime fitness directly (e.g., Waser and Price 1989, Campbell 1997) while studying the perennial habit common to many plants. Scarlet gilia plants are self-incompatible (Sage et al. 2006) and depend for seed set on hummingbird and insect pollinators (Price et al. 2005). Pollination is highly variable across years (Price et al. 2005) and often, along with nutrients, limits seed production (Hainsworth et al. 1985, Campbell 1991, Campbell and Halama 1993).

Plants flower from late June through August and shed seeds from August to September at our study sites near the Rocky Mountain Biological Laboratory (RMBL, 2900 m elevation) in western Colorado, USA. Seeds lack specialized dispersal structures, and fall beneath maternal parents. Seed and seedling shadows around isolated plants have similar leptokurtic distributions, with mean dispersal distances ~0.5 m. Seeds germinate and emerge as seedlings after snowmelt the following spring. By the end of the first growing season, seedlings grow into a small rosette of leaves. Surviving plants grow for 1–10+ years after germination, flower once and then die; iteroparity is rare (Waser and Price 1989, Campbell 1997).

Effects of sowing density on offspring life history and demography—the 2× Experiment

To examine how enhanced pollinator service might translate into population-level effects through the next generation, we sowed seeds at densities that mimic fecundity of populations experiencing typical levels of natural pollination vs. those freed from pollen limitation. In 1997 we chose three sites separated by 150–575 m in dry meadows with resident *I. aggregata* populations (see also Price et al. 2005). We established six pairs (=six blocks) of 3 × 3 m experimental plots, two pairs in each of the three study sites, and assigned treatments at random to plots within blocks. Previous studies showed that augmenting natural pollination with hand pollination approximately doubles whole-plant seed production on average, and has no effect on seed mass. For example, in 1987 hand pollination increased seed set per flower from 0.63 to 1.95 seeds (Campbell 1991), and in 1990 from 3.12 to 4.48 seeds, while not affecting flower number (Campbell and Halama 1993). Multiplying these figures by an average of 84 flowers per plant

(Campbell 1989) yields estimates of 53–262 seeds (mean = 158 seeds) per naturally pollinated plant, vs. 164–376 (mean = 270 seeds) per fully pollinated plant. We approximated these values with treatments of 150 vs. 300 seeds per plant. At the RMBL, a 3×3 m area typically contains five flowering plants. Thus, we multiplied 150 or 300 by 5, to yield sowing densities of 750 or 1500 seeds per 3×3 m plot.

During years of experimental seed addition we removed flowering stalks from within 1.5 m of each plot to eliminate natural seed input. We collected the requisite mature seeds from plants growing within 10 m of plots, bulked them, and counted out aliquots to sow into each plot. A single person sprinkled seeds by hand into each plot, half on one day, and the remainder 4–5 days later, to approximate gradual seed drop as it occurs in nature. No seeds were spread within the central 1-m^2 portion of a plot, which served as a place to kneel during subsequent censuses. Seeds were scattered haphazardly across the remaining 8 m^2 of each plot in an attempt to produce random spatial dispersion. When known seed shadows of individual plants are overlapped at a spacing of five plants per 8 m^2 to simulate a typical population, the result is a statistically random distribution (N. Waser and M. Price, *unpublished data*). We sowed seeds in August 1997 and again in August 1998 into plots containing undisturbed resident plant communities that comprise ~85 species dominated by perennial graminoids and forbs (e.g., Price and Waser 2000).

Effects of sowing density on offspring life history and demography—the 10× Experiment

Natural seed rain varies beyond the twofold range just described. To examine the functional relationship between seed rain and offspring success over this wider range of densities, we established seven 3×3 m plots at a fourth site lying 120–560 m from the other three sites, and assigned them at random to be sown with 300, 450, 750, 1000, 1500, 2000, or 3000 seeds. This 10-fold range falls within the range in natural seed rain ($0–11.3 \times 10^3$ seeds per 8 m^2) estimated near the 2× Experiment plots in the same years as this study (M. Price, N. Waser, A. Brody, and D. Campbell, *unpublished data*). More of this natural variation derives from variation in the density of flowering individuals than from variation in flower number or seeds per flower. Plots were sown once, in August 1998; other methods followed the 2× Experiment.

Census methods

In the summer after seeds were sown we mapped emerging seedlings and preexisting plants, which are clearly distinguishable. Before sowing seeds we had removed all flowering *I. aggregata* plants within plots, and for a radius of 1.5 m around them. Even large plants disperse most seeds <1 m, and seed dormancy is minimal (e.g., Campbell 1997), so we could safely assume that seedlings emerging in June came from seeds sown the previous autumn. We took map coordinates of each

plant relative to permanent markers at the corners of 1×1 m subplots within each 3×3 m plot, and returned in subsequent summers to census mapped plants, which were distinguished from later recruits by map position and root-crown size. We did not map or follow these later recruits. When we terminated the experiment in 2005, 7–8 years after beginning the two experiments, only four individuals survived (two each in high- and low-density treatments in the 2× Experiment, about one-thousandth of the 3369 seedlings originally mapped.

During censuses at the start of each summer, we checked map locations of plants known to be alive in the previous year's census. We scored plants as dead (presence of a dead rosette or missing), vegetative, or flowering (with an elongating inflorescence). For vegetative plants we counted the number of basal rosettes (multiple rosettes may develop if apical meristems are damaged; Brody et al. 2007), number of leaves in each rosette, and length of the longest leaf. We marked flowering plants and returned later in the season to count flowers. By these means we recorded numbers of seedlings that emerged in experimental plots from experimentally sown seeds and followed each one's entire life history. Because we did not individually monitor recruits that established after our focal seedling cohorts, we limit our analysis to the first generation after seed addition.

Analysis

For both experiments we first asked whether seed-sowing density affected numbers of seedlings emerging, numbers surviving to flower, age at flowering, preflowering size, or flower production. For the 2× Experiment we pooled the two cohorts (arising from 1997 and 1998 sowing) after finding no difference between them (see *Results*, below), and used a nonparametric sign test to compare low and high seed-sowing treatments within blocks. We analyzed the same dependent variables for the 10× Experiment, but used linear and quadratic regression because there were seven input densities and no replication of the treatments.

To determine whether population growth varied with seed-input density, we used data from each experimental plot to parameterize a density-independent, age-structured matrix model; because we had data on the complete life history of plants of known age, we could use an age-structured rather than stage-structured model. The dominant eigenvalue, λ, of a population projection matrix measures the per capita contribution to population growth. It is a function of the probability of survival to age x and of age-specific fecundity (Caswell 2001) and should vary with input density if any of these life-history components is density dependent. We used D. Alstad's POPULUS software (*available online*)[6] to calculate λ from post-breeding, birth-

pulse population projection matrices whose elements were p_x (the probability of survival from year $x - 1$ to year x) and F_x (fertility $= p_x m_x$; m_x is the mean fecundity of plants of age x) (Caswell 2001).

We analyzed λ from two perspectives. First we asked what the demographic impact of persistent full pollination would be in a typical population, compared to natural levels of pollen limitation (as in Ashman et al. 2004). For this analysis we used observed plot-level values of age-specific survival p_x from the 2× Experiment, but estimated m_x as the observed proportion of surviving offspring that reproduced at age x, multiplied by the average number of seeds made by either fully or naturally pollinated plants (270 vs. 158 seeds; see *Methods: Effects of sowing density … the 2× Experiment*, above), as appropriate for the plot in question. Second, we looked for any evidence of density dependence in the actual life histories of first-generation offspring. For this analysis, which we performed for both the 2× Experiment and the 10× Experiment, we used observed values for age-specific survival, but estimated m_x as the observed number of flowers per plant. Since combined male and female fecundity increases close to linearly with flower number in *I. aggregata* (e.g., Campbell 1998), this approach gives reliable relative measures of λ (hereafter "flower-based λ") as a function of seed-input treatment.

For the 2× Experiment we used a sign test to compare effects of treatments, which were nested within blocks, on the flower-based λ calculated for each cohort and plot. To examine whether results depend on the cohort, we also used univariate repeated-measures ANOVA, with cohorts as the repeated measures (see Littell et al. [2002] for justification of a univariate approach when there are only two periods of measurement). The model included block as a random factor and seed input treatment, cohort, and their interaction as fixed factors. To analyze the 10× Experiment we regressed flower-based λ on seed input, over the 10-fold range of input densities. Finding density dependence in λ (see *Results: Effects of sowing density on modeled λ …*, below), we quantified the importance of demographic variables to this treatment effect. We first determined elasticities, responses of λ to proportional changes in elements of the population projection matrix (Caswell 2001). However, actual contributions of age-specific survival and fecundity to a treatment effect on λ can differ from elasticities. They are calculated with demographic-perturbation analysis (Caswell 2001) as the element-by-element product of the matrix of differences between the projection matrices for the two treatments, multiplied by the matrix of sensitivities (responses of λ to absolute changes in elements of the projection matrix), evaluated at a point midway between the two matrices being compared.

RESULTS

Effects of sowing density on offspring demography

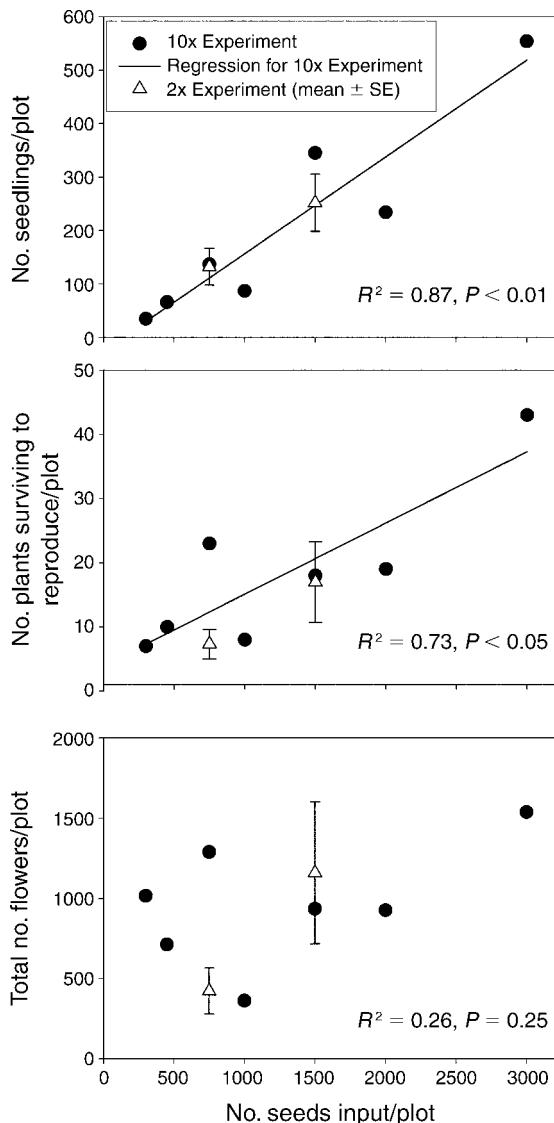The 2× Experiment mimicked a seed rain equivalent to that observed with full pollination (1500 seeds per

FIG. 1. Number of *Ipomopsis aggregata* seedlings, number of plants surviving to reproduce, and total number of flowers produced per 3 × 3 m plot as functions of seed-input density in the two experiments. Data for the 2× Experiment (involving a two-fold variation in seed-input density) are means ± SE. Linear regression lines are shown for the 10× Experiment (involving a 10-fold variation in seed-input density) when the slope differed significantly from zero.

plot) vs. natural pollination (750 seeds) of a typical population. More seedlings emerged from the high-density (full pollination) than the low-density (natural pollination) plot in each of the six blocks, and more individuals survived to flower (Fig. 1: open triangles; means = 252 vs. 132 seedlings and 17 vs. 7 flowering plants; both $P < 0.05$, sign test). Age at flowering was similar in high- vs. low-density plots (means = 3.4 vs. 3.8 years, $P > 0.05$, sign test). Plants that flowered grew to similar rosette sizes (estimated as summed length of all leaves) in the summer before flowering, and produced
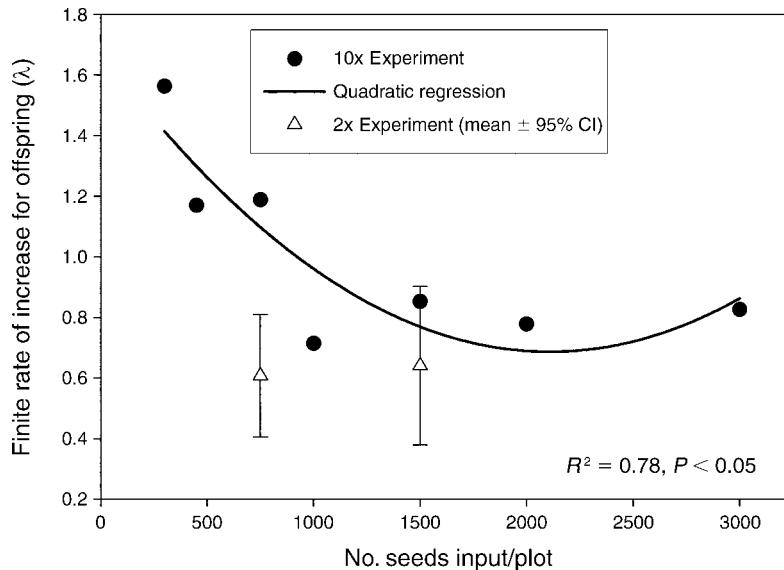
FIG. 2. A relative measure of per seed contribution to population growth (λ, based on flower production) as a function of seed-input treatment in the two experiments. A quadratic regression is shown for the 10× Experiment.

similar numbers of flowers per capita, in high- vs. low-density plots (means = 82.1 vs. 69.4 cm and 69 vs. 62 flowers; both $P > 0.34$, sign test). As a consequence, more total flowers were produced in high-density plots (Fig. 1; means = 1159 vs. 422 flowers per plot, $P < 0.05$, sign test). The two annual cohorts had similar treatment responses, although fewer flowers were produced by the later (1998) cohort in 8 of the 12 plots.

The 10× Experiment, with its wider range of seed inputs, generated results similar to those from the 2× Experiment for numbers of seedlings and individuals surviving to flower. Both increased linearly with seed input (Fig. 1: closed circles; linear regression coefficients $P < 0.05$, quadratic term not significant), and intercepts were not significantly different from zero (both $P > 0.25$). Again, age at flowering did not vary across treatments ($P = 0.27$ for regression with linear and quadratic terms). However, rosette size in the year before flowering tended to decline with seed-input density (slope estimate = −0.036 cm per seed sown, $P = 0.14$) as did flower number per individual (slope estimate = −0.04 flowers per seed sown, $P = 0.064$). Consistent with this apparent density dependence, total numbers of flowers per plot did not increase significantly with sowing density (slope estimate = 0.2 flowers per seed sown, $P = 0.25$; Fig. 1).

Effects of sowing density on modeled λ, the finite rate of increase

The 2× Experiment showed no detectable density dependence. Survival to flowering, age at flowering, and flower number per plant were indistinguishable for treatments mimicking full vs. natural pollination. As a result, under a scenario in which the offspring continue to experience the same pollination regime and seed sets

as the parents (i.e., 270 vs. 158 seeds per fully vs. naturally pollinated plant), a fully pollinated population would have λ = 1.14 (positive growth), vs. λ = 0.94 (negative growth) for a naturally pollinated population. Under an alternative scenario in which offspring do not experience the parental pollination regime and per flower seed sets are equivalent across treatments, flower-based estimates of λ were insensitive to sowing density (Fig. 2). Averaged over the 1997 and 1998 cohorts, the flower-based λ was lower in the high-density treatment in three of the six blocks, and higher in the other three, and repeated-measures ANOVA revealed no significant effect of seed input treatment, cohort, or their interaction (all $P > 0.10$).

In contrast to the 2× Experiment, flower-based λ in the 10× Experiment was approximately halved from the lowest (300 seeds/8 m²) to highest (3000 seeds) seed-input treatment, yielding a significant linear component ($P < 0.05$) in quadratic regression of λ on sowing density ($R^2 = 0.78$; quadratic term $P < 0.075$; Fig. 2). This density dependence is consistent with the lack of increase in total flowers per plot as a function of sowing density (Fig. 1: bottom panel).

By averaging age-specific survival and fecundity (estimated as flower number) across the seven seed-input densities of the 10× Experiment (Appendix A), we obtained an average population projection matrix with λ = 1.17. Analysis of this matrix suggested that λ would respond most to early survival: the elasticity components for survival comprised 65% of the total elasticity (Appendix B, Fig. B1: panels A, B). However, elasticity to fecundity was substantial as well (35% of total elasticity), particularly at age 3, the age at which most plants flower (Appendix B, Fig. B1: panels B, C; see also Brody et al. 2007).
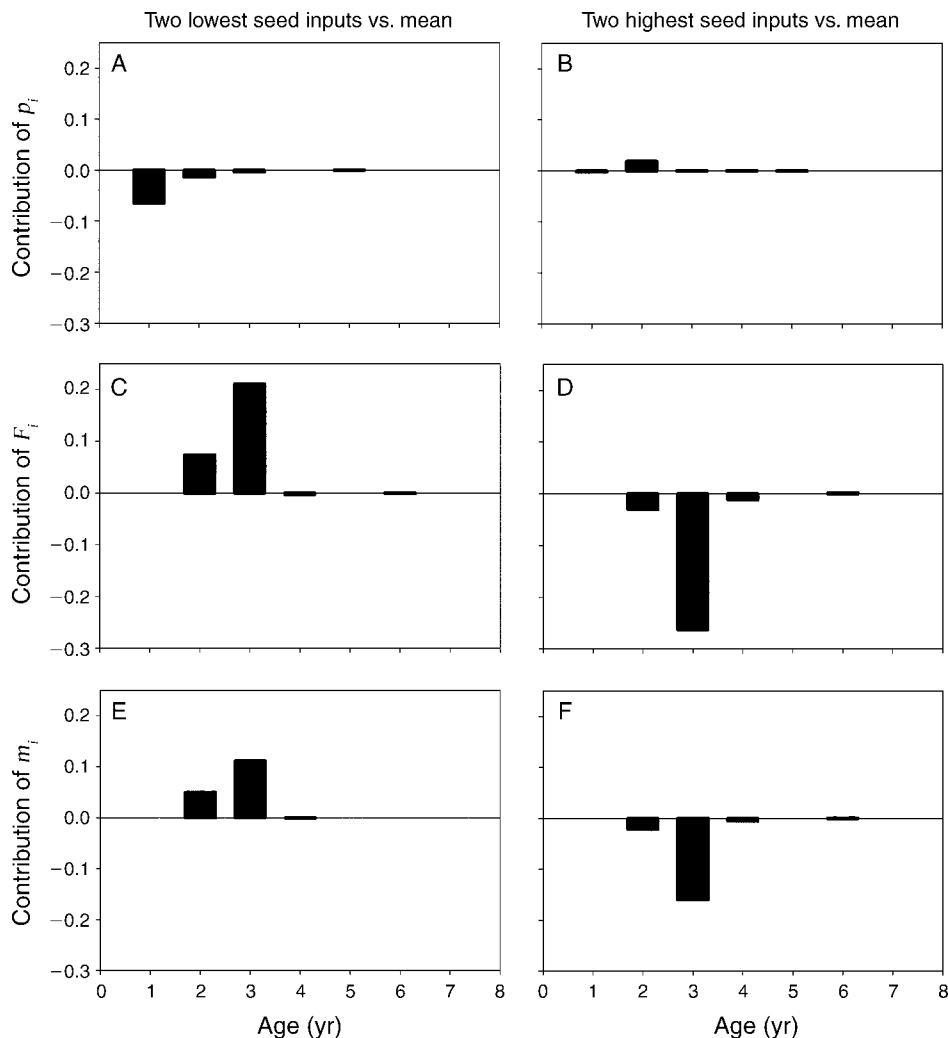
FIG. 3.   Contributions of (A, B) survival from age $i - 1$ to i (p_i), (C, D) fertility (F_i), and (E, F) reproductive (flower) output (m_i) to treatment effects on λ. All matrix calculations to determine these contributions were performed with procedure IML in SAS (SAS Institute 2006). Left-hand panels (A, C, E) compare the two lowest seed inputs (300 and 450 seeds) to the mean of all seven seed-input treatments in the 10× Experiment. Right-hand panels (B, D, F) compare the two highest seed inputs (2000 and 3000 seeds) to the mean of all seven treatments.

Since λ varied with treatment in the 10× Experiment, we used demographic perturbation analysis to calculate contributions of age-specific survival and fecundity to this treatment effect. We compared the average projection matrix for the two lowest seed input densities (300 and 450 seeds), and for the two highest (2000 and 3000 seeds), to the mean matrix for all treatments. Despite high elasticity to early survival, the larger λ in low-density plots was due entirely to higher fecundity as estimated by flower production (Fig. 3). The proportion of seeds emerging as seedlings was lower in the low-density than in the high-density plots, yielding a negative contribution for survival from seed to seedling (p_1). The largest contribution to treatment differences between low- and high-density plots came from fecundity at age 3 (60 and 37 flowers per 3-yr-old plant in the 300-seed and

450-seed treatment, vs. 9 and 5 in the 2000- and 3000-seed treatments).

DISCUSSION

Density independence and density dependence

In the literature on plant demography, "seed limitation" refers to a situation in which numbers of established offspring are determined by the numbers of seeds shed by parents, rather than by (or in addition to) some density-dependent process such as availability of suitable microsites, intensity of post-dispersal seed predation, or herbivory of offspring. Our experiments indicate that (pollen-limited) populations of *Ipomopsis aggregata* at the Rocky Mountain Biological Laboratory (RMBL) are seed limited: adding more seeds always yielded more emerging seedlings and more individuals

surviving to flower in the offspring generation. There was no detectable density dependence in these components of offspring demography. Furthermore, even though different meadows were involved, values for the 2× Experiment fell close to the overall regression lines from the 10× Experiment, in which recruitment increased linearly with sowing density. This seed-limited recruitment is consistent with seed-augmentation studies of other monocarpic perennials of open habitats (Turnbull et al. 2000), and with other species whose recruitment is determined by strong pollen or herbivore limitation of seed production (e.g., Ackerman et al. 1996). It indicates that scarlet gilia populations released from pollen (or herbivore) constraints on seed production should grow, at least over the short term.

But what would happen if there were no pollen limitation over the longer term? Could enhanced recruitment into a population eventually yield densities high enough that recruitment would become limited by microsite availability (sensu Turnbull et al. 2000, Stokes et al. 2006) or seed output by intraspecific competition? We did not monitor individuals or populations past the first generation, and have no direct evidence for this. However, from the 2× Experiment alone we might answer in the negative: seedling recruitment was not limited by microsites suitable for germination, and per capita offspring fecundity was unaffected by input density, causing overall flower production in a plot to increase with sowing density. The 10× Experiment, on the other hand, indicates that such density independence would be transient, because average pre-flowering size and flower number declined at higher sowing densities, causing total offspring flower production of plots to stop increasing with seed-input density. These results come from an unreplicated experiment, and so must be interpreted cautiously. Nonetheless, they call to mind the "law of constant yield" derived from many demographic experiments (e.g., Harper 1977), and they suggest that population-level seed output would reach a limit, or even decline, if pollen or herbivore limitation were permanently removed.

In contrast to fecundity, the 10× Experiment revealed no detectable density dependence in survival over an order of magnitude increase in seed input—a testimony to the tolerance of I. aggregata to crowding. This does not mean, however, that we can dismiss compensatory mortality in thinking about long-term population responses to increased seed production. We followed single seed cohorts through one generation (or two overlapping generations with the 2× Experiment), but it was impractical to continue on to simulate persistent increases in seed production with a "press" design (sensu Bender et al. 1984) across many generations. In a true "press" scenario, juveniles would experience ever-greater competition from individuals of all size classes as population density increased. Two studies of monocarpic plants suggest that compensatory mortality in I. aggregata is plausible, even though recruitment is not strictly microsite limited. From long-term demographic monitoring in unmanipulated populations of a monocarpic thistle (an approach that we are also pursuing with I. aggregata), Rose et al. (2005) found that recruitment was a decelerating function of seed production the previous year; this form of density dependence would eventually erase any recruitment signal of enhanced seed production as population density increased. An experiment with I. aggregata ssp. candida also suggests that increased mortality of juvenile plants might eventually result from persistent increases in seed production. Juenger and Bergelson (2000) found that seedling densities increased with density of the seed rain (seed limitation), but also with soil disturbance (suggesting additional microsite limitation). Survival to the year after emergence declined with rosette density in their experiment. We speculate that Juenger and Bergelson detected density-dependent mortality because they used much higher sowing densities (2400 seeds/m^2) than ours (maximally 3000 seeds/8 m^2 = 375 seeds/m^2). They did not follow plants to flowering, so we cannot know whether there would have been further density dependence in survival to flowering or flower production.

Some conservation implications

In seed-limited species such as I. aggregata, management for increased seed production has conservation value, even if enhanced recruitment and population growth are transient. Population density in such species should often increase in the short term, reducing risk of stochastic extinction. The converse argument holds for management of seed-limited invasive species: reducing seed production should be an effective strategy for reducing population density or rate of spread (e.g., Marone and Crone 2006, Stokes et al. 2006). In the specific case of I. aggregata, our observation that per capita flower production of offspring increased at the lowest sowing densities also suggests that populations might be buffered at low density against an Allee effect, as long as pollinators do not discriminate against sparse populations. Although I. aggregata is not currently threatened, suggestions of recent declines in some of its hummingbird pollinators (Nabhan 2004) and in the hawkmoth pollinators of its congener, I. tenuituba (Campbell et al. 1997), suggest that its status in the longer term is far from secure.

Seed set as a measure of Darwinian fitness

Our results support the assumption that greater seed production from enhanced pollination success will translate into higher average λ in I. aggregata populations—at least in the short term, and for a typical range of seed-rain densities. Unfortunately, this by itself does not justify a parallel assumption, made by many pollination ecologists (ourselves included) studying natural selection on floral traits, that seed set serves as a good proxy for the Darwinian fitness of individual

plants. Seed set is a good proxy for fitness only if there is no strong trade-off with fitness through male function, and only if there is no strong trade-off between offspring number and offspring success (measured as offspring λ). Our seed-sowing experiments were designed to evaluate consequences of population-wide variation in seed production due to variable pollination services of the kind reported by Price et al. (2005), rather than the consequences of variation in seed production at the individual-plant level. It is conceivable, for example, that compensatory density dependence within the seed shadows of high-fecundity plants would cause total progeny fitness to be insensitive to maternal seed production. To truly evaluate the assumption that seed set is a measure of fitness, we must compare the life histories of known offspring dispersed from high- and low-fecundity plants, as did Louda and Potvin (1995). We hope to report on such a study in the future.

The value of the long term

It is critical to follow offspring through their entire life history if one wants a complete accounting of the ecological or evolutionary consequences of altered seed production (e.g., Louda and Potvin 1995, Jules and Rathcke 1999, Turnbull et al. 2000, Ehrlén et al. 2006). Our experiments illustrate this point. In the 10× Experiment, fecundity at age 3 made the greatest contribution to effects of sowing treatment on the finite rate of increase, followed by fecundity at age 2 and early survival. The central contribution of fecundity variables to treatment differences in λ is consistent with other demographic studies of *I. aggregata* (Waser et al. 2000, Brody et al. 2007). We would have missed this effect if our study had measured only the survival of offspring up to some pre-reproductive age, as is commonly done in demographic studies.

Conclusions

Coupling comparative demography with matrix modeling, as we do here, provides a powerful way to extrapolate from relatively short-term studies to long-term population dynamics (also see Ashman et al. 2004, Kauffman and Maron 2006, Maron and Crone 2006). As a consequence, this approach is increasingly being used to understand the ecological and evolutionary consequences of antagonistic or mutualistic interactions that affect plant survival, growth, and fecundity (e.g., Ehrlén 2003, Rose et al. 2005, Kauffman and Maron 2006). It has the clear virtue of being more feasible than alternatives, such as manipulating and then monitoring populations over multiple generations. On the other hand, model predictions are only as good as their demographic input. We have improved on common practice by following offspring through their entire life histories and over a range of densities, but our experimental treatments manipulated only one form of density (effects of seed-input density), which in nature might be supplemented by other forms (e.g., increasing

density of all ages and sizes) that have different demographic consequences. Further progress in understanding the long-term population consequences of pollen limitation will therefore hinge, as Maron and Crone (2006) emphasized, on characterizing how density dependence manifests itself throughout the life cycle, and incorporating realistic density-dependent functions into structured population models.

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APPENDIX A

A table showing age-specific survival (l_x) and flower production (m_x) averaged across the seven seed-input densities in the 10× Experiment (*Ecological Archives* E089-095-A1).

APPENDIX B

A figure showing elasticities of λ in the 10× Experiment (*Ecological Archives* E089-095-A2).