



Density-dependent demographic responses of a semelparous plant to natural variation in seed rain

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The link between reproductive and vegetative ecology of flowering plants is rarely explored, despite its importance for understanding population processes and fitness. This link can be studied by using experimental or natural variation in seed input to the soil to assess how reproductive success affects vital rates of offspring. We previously reported for *Ipomopsis aggregata* that per-seed probability of germinating is insensitive to density of seeds sown into plots, whereas per capita flower production among adults that grow from the seedlings declines in nonlinear fashion with density. Here we describe a parallel non-experimental study. We related seedling emergence to estimated natural seed input ('seed rain') in three populations across ten summers and monitored seedlings that emerged in the first two summers throughout their life histories. Seedling emergence in 1996 was linearly related to seed rain from plants that flowered in 1995. This density independent seed-to-seedling transition recurred over the next nine summers, but the slope varied with springtime precipitation. Total numbers of 1996 seedlings that survived to flower and numbers of flowers they produced increased linearly with seed rain in one population, but did not vary detectably in the other two, consistent with negative density dependence. In consequence λ (the dominant eigenvalue of a population projection matrix) decreased from high values at low densities of seed rain to a relatively constant low value with greater seed rain. We also detected density dependence in the 1995 seedling cohort in survival and flower production. The similarity of results from natural and experimental studies supports a conclusion of nonlinear density dependence and shows that characterizing it requires the full life history. For this plant species and others, studies of pollination and fecundity alone may not suffice to draw conclusions about population change or fitness.

Animal antagonists and mutualists are intimately involved in the reproductive success of higher plants, but it does not follow that they drive plant population processes and microevolution. As Harper (1977) pointed out, even dramatic seed consumption by herbivores may lack demographic consequence if the seeds would otherwise be lost to density dependent mortality later in the life history. Harper's point applies equally to pollination. Some pollination studies strive to forecast population growth or viability from average pollination success (Aizen and Feinsinger 1994, Kéry et al. 2000, Ehrlén et al. 2006), but this endeavor depends critically on the links between pollination and subsequent numbers of seeds, seedlings, juveniles and adults. Other studies aim to measure natural selection on floral traits (Campbell 1989, Ashman et al. 2004, Irwin 2006, Burkle et al. 2007, Mitchell and Ashman 2008), but here again the link between reproductive success of individuals and performance of their offspring might play an important role.

The relationship between variable herbivory and plant demography has now been explored for several systems (Ehrlén 2002, Kauffman and Maron 2006, Maron and Crone 2006).

In contrast, studies that relate variation in pollination success to demography of seed offspring remain rare (Ehrlén 2002, Hegland and Totland 2007, Price et al. 2008). Some workers have combined estimates of pollen limitation of seed production with demographic modeling (reviewed by Ashman et al. 2004, Knight 2004), but whereas some of them did measure the seed-to-seedling link, they did not use methodology that allowed density dependent vital rates to be quantified.

In studies spanning more than a decade we have sought to characterize natural variation in pollination success in the montane wildflower *Ipomopsis aggregata* (Price et al. 2005) to relate pollination to patterns of seed production (unpubl.) and to determine how variation in reproductive success translates into the number and reproductive success of individuals in the seed generation. We previously reported on experiments in which we mimicked various levels of pollination limitation by sowing seeds at different densities into natural populations to see how this 'seed rain' affects vital rates (Price et al. 2008). Whereas per capita probabilities of seedling emergence and survival to flowering were insensitive to seed rain, size and flower production of reproductive plants declined

with increasing seed rain, leading to a nonlinear decline in λ , the dominant eigenvalue of a population projection matrix.

An experimental approach has the benefit of controlled seed input that can be randomized across study sites, but it cannot perfectly mimic the temporal and spatial properties of the natural seed rain. Thus a useful complement is a non-experimental study. Here we describe a study of this kind with *I. aggregata*. Its intent again was to examine density dependence in the demography of the seed generation. In permanent plots at three sites we mapped all seedlings emerging in two successive annual cohorts and characterized the lifetime fates of the more than 5000 mapped individuals. We simultaneously estimated the density of natural seed rain that gave rise to the second of these cohorts. We also estimated seed rain and counted emerging seedlings in the plots over nine subsequent summers. Results suggest that density mostly affects final number of reproductive individuals, yielding a relationship between λ and density that resembles the result of our parallel experimental study.

Material and methods

Study species

Ipomopsis aggregata (scarlet gilia, Polemoniaceae) is a subalpine plant of western North America that grows from Arizona to British Columbia and from the Pacific coastal ranges to the Rocky Mountains (Grant and Wilken 1986). It is most common at elevations above 1500 m a.s.l., and we have found populations up to 3500 m near the Rocky Mountain Biological Laboratory (RMBL, 2900 m) in western Colorado, USA. Plants lack clonal spread and recruit from seeds, which are shed about one month after flowers senesce. At the RMBL, few seeds (usually < 4%; Campbell 1997, Waser et al. 2000) remain dormant beyond the first winter after seed drop. By the end of one growing season surviving plants have formed a small rosette of leaves that increases in size until the plant flowers. Because the snow-free summer growing season is short, most individuals at the RMBL take several years, sometimes more than ten, to flower (Waser et al. 2000). Flowering adults are attacked by insect and vertebrate herbivores as well as insect seed predators (Zimmerman 1980, Freeman et al. 2003, Brody et al. 2007). Most individuals near the RMBL flower once and die; very few (usually < 1%) flower a second time (Campbell 1997, Waser et al. 2000), usually in response to earlier damage in vegetative stage (Brody et al. 2007). Limited iteroparity and modest life-span make it possible to estimate lifetime fitness. The red, tubular flowers secrete nectar and are cosexual, protandrous, and highly self-sterile due to late-acting self-incompatibility (Sage et al. 2006). They are pollinated mostly by hummingbirds, with additional contributions from various insects (Mayfield et al. 2001, Price et al. 2005). Pollination services vary in time and space (Price et al. 2005) and often limit seed production (Hainsworth et al. 1985, Campbell 1991, Campbell and Halama 1993).

Study sites and census methods

In the summer of 1995 we located three dry subalpine meadow sites, hereafter 'P', 'T' and 'V', in which we also

carried out part of our parallel experimental study (the "2 \times experiment" of Price et al. 2008). The sites are separated from one another by 180–575 m and are representative of areas around the RMBL that support *I. aggregata*, even though they differ in slope, compass aspect, soil depth, and in details of their floras. At each site we established nine study plots, each containing four 1 \times 1 m sub-plots whose corners were permanently marked. Emerging seedlings, identified by presence of cotyledons, were mapped in 1995 and 1996 with reference to these permanent corners within 24 of the 27 plots (we counted but did not map seedlings in three plots at site V). In total we mapped 2543 seedlings in the 1995 cohort (614, 877 and 1052 in P, T and V, respectively) and 2804 individuals in the 1996 cohort (1377, 617 and 810 in P, T and V, respectively). We then returned annually to check mapped plants, until (summer 2005) none remained alive. We recorded presence or absence of each mapped individual, if present its life stage (vegetative or reproductive), and if reproductive the number of flowers it produced. We estimated size of vegetative rosettes as the product of number of leaves and length of the longest leaf (Price et al. 2008).

Estimating the seed rain

The seed rain into each study plot in each summer was estimated as follows. We first chose a sample of 4–26 flowering plants in each site each summer, beginning in 1995 and ending in 2004 (mean \pm SD = 8.0 \pm 3.91 plants per sample, n = 10 summers \times 3 sites = 30 samples) that were found growing > 1 m from any plot. We harvested all expanded fruits from these plants and counted the number of viable seeds in each, thereby obtaining a mean value of seeds per fruit for each site. We then counted expanded fruits on each flowering plant inside and within 1m of each study plot and multiplied these values with those for mean seeds per fruit to estimate the seed crop of each plant. Most primary seed dispersal is \leq 1 m (Waser and Price 1983), so we concluded that flowering individuals inside plots but \leq 1 m from their borders would shed some seeds outside the plots, and vice versa for individuals outside the plots but \leq 1 m from their borders. To account for such seed shadows we imagined points spaced 25 cm apart in a grid covering an entire study plot as well as a 1 m-wide buffer on all sides of the plot. We then calculated the fraction of a circle of radius 1m centered on each of these points that intersected the central study plot. These fractions were averaged to estimate the mean proportion of the seed crop of a flowering plant inside the plot that would fall within that plot, and the same for a plant outside the plot but within the 1m-wide buffer; these proportions were respectively 42.3% and 11.5%. Multiplying these proportions by estimated seed production of the 'inside' and 'outside' plants for each of the 27 study plots in each year yielded an estimate of the seed rain into each plot from 1995 through 2004.

Demography: seed-to-seedling transitions

Estimates of the seed rain into each study plot in each year, as just described, were then compared to the counts of seedlings emerging in each plot one growing season later, from 1996 through 2005 (we only mapped these seedlings

in two summers, 1995 and 1996, and so obtained more complete demographic information only for those cohorts). Thus we obtained seed-to-seedling transitions on a plot-to-plot basis for ten summers.

Analyses

Demographic information was most complete for the 1996 cohort because we had estimates of the seed rain that produced this cohort as well as of survival and final fecundity within it. For each plot we combined these estimates into a summary statistic λ , the dominant eigenvalue of a population projection matrix. We used flower number as a proxy for fecundity. Because the sum of female and male fecundity increases nearly linearly with flower number in *I. aggregata* (Campbell 1998), this provides a reliable relative estimate of λ . A relative estimate suffices for our goal of looking for density dependence in vital rates, and was comparable to our approach in experimental studies (Price et al. 2008). To measure fecundity as seed set would have eliminated our chance to estimate the ongoing natural seed rain contributing to later cohorts, as required for investigating this link over the longer term.

Values of λ were calculated by entering age-dependent survival and fecundity for each study plot into a population projection matrix. The dominant eigenvalue of this matrix measures per capita contribution to rate of population change, λ (Caswell 2001), which should vary with density of the seed rain if any subsequent component of life history is density dependent. We used POPULUS software (Alstad 2003) 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 = $p_x m_x$, where m_x is the mean fecundity of plants of age x , estimated as flower number). For the 1996 cohort we examined four additional demographic parameters for each plot: number of seedlings, number of plants that survived to reproduction, number of flowers produced, and mean age at reproduction.

The effect of seed rain on λ and the other demographic parameters (numbers of seedlings, survivors and flowers) were examined with ANCOVA models that took into account variance across the three study sites. In each case, we began with the full model:

$$Y = c + \text{site} + \text{seeds} + \text{site} \times \text{seeds} + \left(\text{seeds} - \overline{\text{seeds}} \right)^2 + \text{site} \times \left(\text{seeds} - \overline{\text{seeds}} \right)^2 + \varepsilon$$

where Y is the demographic parameter, site is a categorical variable, seeds (= density of the seed rain) a continuous variable, c the intercept constant, and ε the residual. The quadratic terms allowed us to test whether the effect of seed rain was nonlinear, and were centered on the mean to reduce collinearity. We then removed insignificant terms in reverse order from their listing above until only terms with significant ($p < 0.05$) contributions remained, except that if an interaction was significant whereas one of its components was not, we left that main effect in the model. Note that interpretation of this statistical model differs depending on whether the dependent variable is a number of individuals

(e.g. number of seedlings) or a per capita measure (λ). In the former case, a linear increase with seed rain indicates density independence and curvature or a line with zero or negative slope indicate density dependence. For per capita measures such as λ , any demonstrable effect of seed rain indicates some form (negative or positive) of density dependence. For direct comparison with of the parallel “10× experiment” of Price et al. (2008), in which we sowed seeds at seven densities at a single site, we also ran a quadratic regression of λ on seed rain per m^2 ignoring site as a factor.

Because our study began in 1995, we lacked an estimate of the seed rain that produced the 1995 seedling cohort. We could, however, compare the 1995 and 1996 cohorts with respect to the number of seedlings that survived to reproduce and the total number of flowers they produced. We used the same statistical approach described above.

For the decadal study of seed-to-seedling transitions, we analyzed seedling emergence at two levels: (1) within sites in a given year, and (2) across years. We first ran a model with categorical factors of site, germination year, and their interaction, as well as the continuous variable of seed input and all interactions. Because there were strong interactions we removed the variation due to site, germination year, and the interaction in a preliminary two-way ANOVA to investigate seedling emergence at the within-site level. In a final model we related the residuals for seedling emergence to seed rain nested within site and germination year. We did not allow for nonlinearity in these models because seedling emergence in this study (Results) and in our previous experiments (Price et al. 2008) was consistently a linear function of seed input. We also examined variation in seedling emergence from year to year. For this analysis we looked for correlations between the fraction of seeds that germinated that year and available environmental data from a weather station that is within 500 m of each study site. We investigated three variables: (1) precipitation during May–June, which is when almost all seeds germinate; (2) total water content of winter precipitation; and (3) date of snowmelt.

Results

1996 seedling cohort

The number of seedlings in the 1996 cohort that emerged within a given study plot increased in direct proportion to the estimated density of the natural seed rain into that plot during 1995 (Fig. 1, top). The final model contained only a linear term ($F_{1,22} = 12.72$, $p < 0.01$) and explained 37% of the variance. The linear increase in seedling number shown in Fig. 1 indicates an absence of density dependence at the stage of seed germination in our study populations.

The number of plants surviving to flower exhibited a more complex response. We detected no quadratic effect of seed density on number of survivors ($p > 0.05$), but in our final model the observed relationship with seed density varied across sites (Fig. 1, middle, interaction between site and seed density, $F_{2,18} = 7.49$, $p < 0.05$). In a model that included effects of site and seed rain nested within site, the number of survivors increased linearly with seed number at the P site (one additional survivor to flowering for every 17

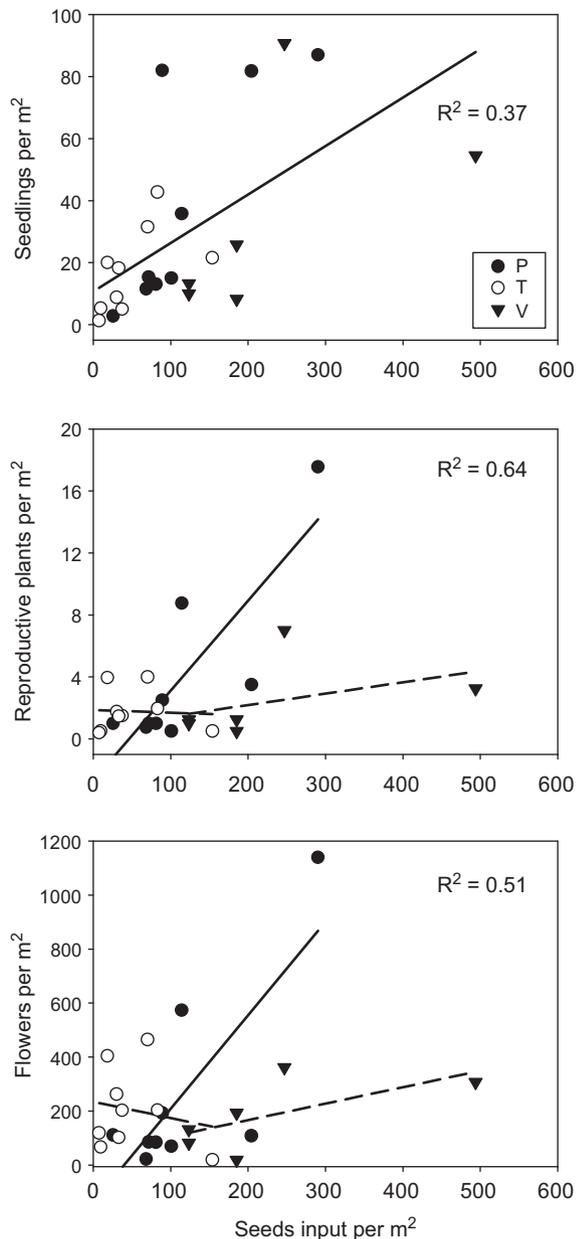


Figure 1. Relationships for the three study sites between density of the seed rain into plots and numbers of seedlings emerging the next summer (top), numbers of individuals surviving to flower (middle), and total numbers of flowers produced by those reproductive individuals (bottom). Separate regressions are shown for each site in cases where the site \times seeds interaction was significant. In these graphs, density independence appears as a linear increase with seed rain. A negative slope or slope indistinguishable from zero is consistent with density dependence (although the latter might also reflect unexplained variation).

additional seeds, $t_{18} = 5.19$, $p < 0.0001$), indicating density independent viability throughout the life history. In contrast, the slopes of the relationships for T and V did not differ significantly from zero, consistent either with negative density dependence or unexplained variation. To distinguish these alternatives, we asked whether per-seed survival to flowering varied with site and seed rain nested within site. Per capita survival declined significantly with seed rain

only at site T ($t_{18} = -2.20$, $p < 0.05$). A similar pattern is seen in the total number of flowers produced in a plot (Fig. 1, bottom). With effects of site and of seed rain nested within site included in the model, total flowers produced in a plot increased significantly with seed rain at P ($t_{18} = 4.12$, < 0.001), but not at T or V (both > 0.25). This implies negative density dependence in plot-level fecundity at least at the T site, where per-seed flower production decreased with density of the seed rain ($t_{18} = -3.33$, $p < 0.01$).

We detected no overall effect of seed input on mean size of individual plants in the summer before they flowered ($p > 0.05$ in all cases for the initial full model and all simplified models). Thus, flowering individuals appeared to remain roughly constant in size across the range of seed input at each site. This size constancy agrees with the finding that, at each site, plot-level production of flowers (Fig. 1, bottom) showed a relationship to seed input that was similar to the relationship seen for number of survivors (Fig. 1, middle), rather than being attenuated as would be expected if denser plots also had smaller flowering plants.

As did size prior to flowering, mean age at reproduction showed no effect of seed input. In linear regression, the density of the seed rain explained only 3% of the variation in this parameter ($F_{1,22} = 0.65$, $p = 0.43$). The final model after removing non-significant effects contained the effect of site ($F_{2,21} = 7.47$, $p = 0.004$): plants flowered significantly later at P (mean age = 3.8 years) than at T (mean age = 2.6 years, Tukey comparison $p < 0.05$), while V was intermediate (mean age = 3.1 years).

The combined effect of these responses was that λ was density dependent at the T site, since it declined strongly there with seed rain (Fig. 2). As λ is a per capita measure, the slopes indistinguishable from zero at P and V are consistent with density independence. Fitting a model with effects of site and seed rain nested within site indicated that λ declined significantly with seed input at T ($t_{18} = -4.31$, $p = 0.0004$), but not at the other two sites (both $p > 0.20$).

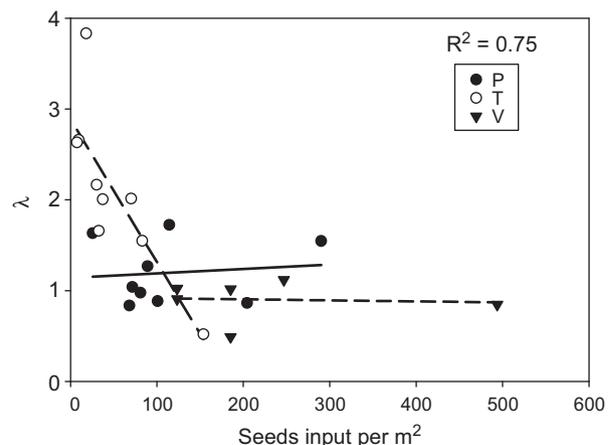


Figure 2. Relationships for the three study sites between density of the seed rain into plots and λ . Estimates of λ are based on flower number as a measure of fecundity and therefore produce relative rather than absolute values, as explained in the text. Because λ is a per capita measure, density independence and dependence would appear respectively as relationships of zero slope and of negative slope.

Although the three study sites therefore appear to differ in density dependence of λ for the 1996 seedling cohort, this difference might be explained by site-to-site variation in the density of the seed rain that produced this cohort. Plots at the T site experienced the lowest seed input densities, those at P somewhat higher, and those at V the highest, so that taken together plots spanned a range from few to ca 500 seeds m^{-2} . Assuming that differences in apparent density dependence across sites might stem from these differences in seed input rather than from other site differences, we examined the overall relationship, ignoring site as a factor. The resulting pattern strongly resembles the relationship we reported previously from the “10 \times experiment” of Price et al. (2008), which was done at a different site near the RMBL but involved a very similar range in seed rain. The overall relationship had significant curvature (quadratic term in a regression ignoring site, $t_{1,21} = 3.06$, $p < 0.01$ for the 1996 cohort; Fig. 3) in both studies. An ANCOVA with ‘study’ (the 1996 cohort in this study vs the 10 \times experiment) as a categorical variable, and including both linear and quadratic effects of seed rain, failed to detect any interaction between study and seed rain ($p = 0.12$ and $p = 0.75$ for interactions with the linear and quadratic terms, respectively), indicating that the two studies resembled each other closely in the relationship between λ and seed input.

Comparing the 1995 cohort to 1996

Although we could not calculate λ for the 1995 cohort since we lacked an estimate of seed input, an examination of vital rates other than seed-to-seedling survival revealed two cases of density dependence. First, we detected a significant interaction between site and the number of seedlings in a plot in their effect on survival of seedlings to flowering ($F_{2,18} = 4.84$, $p = 0.021$). When separate slopes were fitted for each site, T was the only site in which number of survivors increased significantly with seedlings ($F_{1,18} = 3.72$, $p = 0.002$), indicating density independence there and suggesting density dependence at the other two sites. Second, total number of

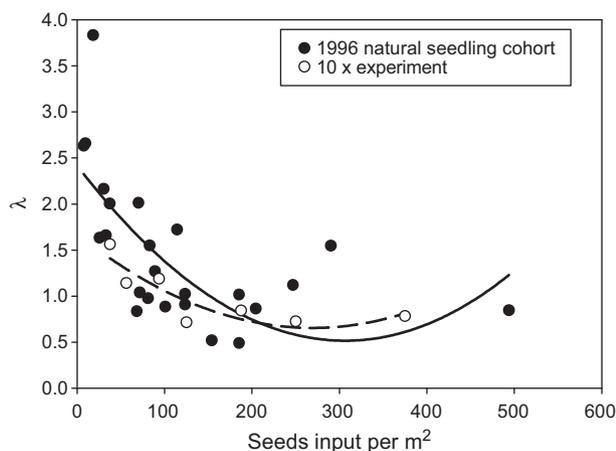


Figure 3. A comparison of the relationship shown in Fig. 2, but with the three study sites considered as a single entity, and of the curvilinear density dependence of λ on seed input from the “10 \times experiment” of Price et al. (2008). In both cases λ declines most strongly at the lowest densities of seed input, and at higher densities declines more slowly. Quadratic best-fit functions are shown.

flowers in a plot produced by members of the 1995 cohort was consistent with density dependence at all sites in that it failed to increase with number of seedlings ($F_{1,20} = 2.34$, $p = 0.14$ in ANCOVA). Density dependence appeared to be highest at site P for the 1995 cohort, with a slightly negative slope of total flower number on number of seedlings.

We can compare these results with analogous ones for the 1996 cohort, using analyses that begin at the seedling stage. Even though our earlier analyses (see ‘1996 seedling cohort’ above) had indicated density dependence from seed to flower number, analyses beginning with seedlings yielded linear increases in both number of individuals surviving to flower ($F_{1,22} = 17.51$, $p < 0.001$, $R^2 = 0.44$) and total number of flowers produced in a plot ($F_{1,22} = 9.20$, $p < 0.01$, $R^2 = 0.29$). For neither demographic parameter did we detect an interaction of site with number of seedlings (all $p > 0.50$), even though the earlier analysis of flower number did reveal such an interaction and indicated density dependence at site T (Fig. 1, bottom).

Over all analyses, site T in the 1996 cohort showed evidence for density dependence in flower production, whereas in the 1995 cohort this was true for site P instead. In both cases, however, this was the site with the lowest overall seedling density. Site P in the 1995 cohort had an average density of 68 seedlings per plot versus 97 and 175 for the other two sites, and site T in the 1996 cohort had an average of 67 per plot versus 135 and 153 for the other two sites. This result is consistent with the overall patterns in λ from the 1996 cohort, which decreased strongly with increasing density of seed input at low densities, and then leveled off (Fig. 3).

Seedling germination over a decade

Over the 10-year period from 1996 through 2005, seedling emergence always increased linearly with density of seed rain into a study plot. For all 30 site-by-year combinations, the estimated slope was positive, and 15 values were significant at $p < 0.05$, far higher than expected by chance alone. The overall effect of seed rain on seedling number was highly significant ($F_{30,236} = 3.69$, $p < 0.0001$) in a model that nested seed input within site-by-year combination. The percentage germination varied greatly across years, however, from a low of 0.1% in 2002 to a high of 25% in 1996. This percentage was highly correlated with precipitation at the RMBL during May and June (Spearman rank correlation = 0.77, $p < 0.01$), and the apparent step form of the relationship (Fig. 4) suggests that germination is low unless a threshold precipitation of about 50 mm is received during a critical time just before seedlings appear. Percentage germination did not correlate significantly ($p > 0.05$) with either the water content of winter precipitation or the date of snow-melt (rank correlations = 0.58 and 0.40, respectively).

Discussion

The considerable temporal and spatial variation in natural seed rain during our study presumably reflected variation in densities of flowering individuals, in pollination services to flowers, in activity of floral antagonists, and in availability of pollen within populations (Price et al. 2005). Seedling emergence was consistently a linear function of the seed rain,

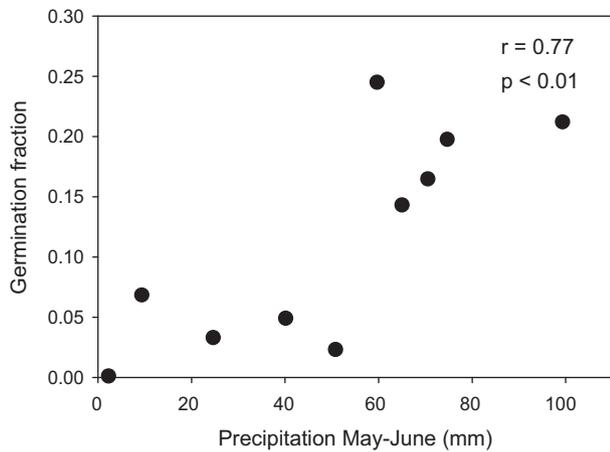


Figure 4. The apparent step-function relationship between spring precipitation and the fraction of seeds germinating, averaged across all study sites, in our decade-long study (1996–2005).

as it was in our parallel experimental studies (Price et al. 2008). Thus no density dependence appears at this initial stage in the life history of *I. aggregata* at the RMBL, and recruitment into populations is seed-limited (Turnbull et al. 2000). Recruitment also was correlated with spring precipitation. This is intuitively logical: soil moisture early in the growing season has been implicated as critical for this and other dry alpine and subalpine systems (Price and Waser 2000).

In contrast, density dependence began to appear at later life stages, including the probability of surviving to flower and the total number of flowers finally produced in a plot. We would not have detected density dependence if we had examined only early life stages. As others have stressed (Ehrlén 2002, Fowler et al. 2006, Hegland and Totland 2007, Morris et al. 2007, Ramula and Buckley 2009), it is crucial to study the effects of species interactions on plant demography over the entire life cycle!

Because sites varied in seed input densities, we must pool across them to get an overall picture of density dependence. When we do this for λ (which depends on survival and flowering across the life cycle) and the 1996 cohort (for which we have the most complete life-history information), we see a curvilinear, concave-upward relationship between λ and density of the seed rain. Two lines of evidence suggest that this is a true signal of density dependence, rather than an artifact of covariation between site-specific environment and seed rain. First, the sites at which density dependence appeared differed between the 1995 and 1996 cohorts, but in both cases were the lowest-density sites: P in 1995 and T in 1996. Second, the curvilinear relationship strongly resembles the one observed in our parallel experimental study, which assigned seed input treatments to plots at random (Price et al. 2008).

A concave-upward form of density dependence may not be uncommon. Smith (1963), Watkinson (1997) and Sibly et al. (2005), among others, reported similar shapes of relationships between per capita growth rate and population size (see also Reynolds and Freckleton 2005). Perhaps such a shape derives in our studies from the simple geometry of space use as numbers of recruits into a population are increased. If per capita resource availability to each of n seedling recruits scales as $1/n$ of total resources in the area

in question and λ is strongly related to per capita resources, then the function could be concave upward (i.e. $1/1$, $1/2$, $1/3$, $1/4$. . .). More generally, nonlinear density dependence in vital rates might derive from several causes, and its shape might depend on those rates most strongly affected. For example, if survival is the major fitness component that responds to density in a given species (not the situation in our studies), and if individual differences among plants confer variable tolerance to density, less-tolerant individuals might be lost rapidly as density increases, leading to concavity. Whatever the mechanism, finding that λ is relatively insensitive to change in density at relatively high seed input densities does not mean that this would persist at even higher densities. Juenger and Bergelson (2000), for example, detected strong density dependence in early survival of *I. aggregata* plants at densities ca 4–5 times higher than the maximum values for natural seed rain estimated here.

The results of this study, and of our previous experiments, carry a cautionary message for pollination ecology: equating pollinator visitation, pollen delivery, or even fruit or seed set to ‘fitness’ or population viability is questionable in the absence of demographic information (Ehrlén 2002 makes an analogous point for plant–animal interactions more generally). In the case of *I. aggregata*, curvilinear density dependence means that the effect of a change in pollination service, all else equal, will depend on population density. Seed inputs corresponding to average natural pollination and to plants having received supplemental pollen above natural levels both occupy the range in which λ is relatively independent of density (Price et al. 2008), so that a year with above-average pollination service might be followed by a short-term increase in population size. Populations that fall to low densities might be somewhat buffered from further decline, even without above-average pollination, due to higher values of λ brought about from density dependence of vital rates at those densities. But in general we do not know the implications of low seed set for population dynamics. As explained earlier our measures of λ are relative rather than absolute, and even though our experimental study did report some absolute measures (modeled λ in Price et al. 2008), longer-term population trends cannot necessarily be inferred from immediate responses.

What is the solution to this problem of possible nonlinearity between seed set on the one hand and fitness and short-term population change on the other? One can hardly insist that every pollination biologist take up demography (although more such studies would be welcome), any more than those who point out the cosexual nature of most plants should insist that every pollination biologist measure fecundity through the male sex function. Both undertakings are often impractical. At the least, however, one can acknowledge the possible complexities due to density dependence of links between pollination, reproduction, and the rest of the plant life cycle.

Our decade-long study of the relationship between pollination and offspring demography has produced results that are intriguing in their consistency across methods of study in the form of density dependence and in its appearance later in the life cycle. Just as pollination biologists are recognizing that pollen delivery is influenced by factors such as pollen availability and the action of pollen thieves in addition to availability of pollinators (Price et al. 2005, Irwin 2006); just as they are recognizing complexities in the transition from pollen delivery to seed set due to effects of pollen quality

and resource limitation (Haig and Westoby 1988, Campbell and Halama 1993, Aizen and Harder 2007); we urge them to recognize that what happens in the next generation can modify what they might conclude from studying pollination and reproduction of the parental plants alone.

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