

SOURCES AND CONSEQUENCES OF SEED SIZE VARIATION IN *LUPINUS PERENNIS* (FABACEAE): ADAPTIVE AND NON-ADAPTIVE HYPOTHESES¹

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Seed size variation within species and individuals is common. This variation may be adaptive in heterogeneous landscapes if the fitness consequences of seed size differ among environments or through time. Variation may also arise from constraints that limit control of seed size. I manipulated resource availability in both maternal and offspring environments to test conditions underlying these explanations for seed size variation in the herbaceous perennial *Lupinus perennis*. A fivefold variation in seed size arose primarily from differences among individuals and within-plant variability rather than from environmental conditions manipulated in the experiment. Environmental conditions had little effect on mean seed size; in contrast, within-plant variation in seed size increased with reduced resources. Fitness benefits from large seed size were similar across offspring environments, suggesting that environmental heterogeneity alone may not maintain seed size variation in this species. Surprisingly, seed size affected long-term fitness measures, including a plant's size and probability of flowering through its second year. These results are consistent with non-adaptive but not adaptive explanations for seed size variation. They also suggest that offspring size variation per se may contribute to variation in maternal fitness.

Key words: drought; environmental heterogeneity; fitness components; germination; offspring size; resource availability; seed size variation.

According to classic life history theory, individuals are expected to produce uniformly sized offspring that optimize the trade-off between offspring size and number (Smith and Fretwell, 1974). However, ample evidence of substantial within-species and within-individual variation in offspring size has accumulated in the past few decades, especially for seed size variation in plants (e.g., Harper et al., 1970; Schaal, 1980; Stanton, 1984; Wulff, 1986a; Ågren, 1989; Winn, 1991; Mendez, 1997; Vaughton and Ramsey, 1997; Poulin and Hamilton, 2000; Simons and Johnston, 2000; Susko and Lovett-Doust, 2000; Einum and Fleming, 2002). Although less than the variation in seed size observed among species (Harper et al., 1970), within population and individual variation can be quite substantial; for example, seed size can vary ninefold within a species (Krannitz, 1997) and sixfold within an individual fruit (Stanton, 1984).

Both adaptive and non-adaptive hypotheses have been proposed to explain variation in seed size. Such variation could be the result of adaptive evolution if it provides direct fitness benefits to the parent, so that selection favors parents that produce multiple seed sizes. Producing offspring of different sizes could be advantageous if offspring vary in genetic quality and garner provisions differentially (Temme, 1986); if seed size effects on dispersal distance (Westoby et al., 1996), dormancy (Rees, 1996), or timing of germination (Schaal, 1980; Dolan, 1984; Simons and Johnston, 2000; Tremayne and Richards,

2000; Galloway, 2001) reduce competition among siblings; or if the optimal seed size varies through time or space (e.g., Janzen, 1977; Capinera, 1979; Thompson, 1984; Simons and Johnston, 2000; but see McGinley et al., 1987). Under certain conditions, seed size variation may be adaptive if the offspring environment is unpredictable (McGinley et al., 1987). Parental growing environment also can influence seed size (e.g., Platenkamp and Shaw, 1993; Meyer and Allen, 1999; Galloway, 2001), but relatively few studies have explicitly examined the correlation between parental and offspring environments, or the adaptive value of producing different seed sizes in contrasting environments.

Variation in seed size also may be non-adaptive in several ways. First, limits to parental control of seed size could contribute to seed size variability. Parental control may be limited if abiotic and biotic stressors contribute to developmental instability (Koops et al., 2003), if increased control over seed size incurs fitness costs due to pleiotropy (McGinley et al., 1987), or if variations in resources through time affect allocation to seeds (Haig and Westoby, 1988; Zimmerman and Pyke, 1988; Campbell and Halama, 1993). Second, weak selection or genetic architecture may prevent the evolution of uniform seed size. For example, antagonistic genetic correlations or limited genetic variation for seed size (Platenkamp and Shaw, 1993; Byers et al., 1997; Mojonner, 1998) may slow or prevent response to selection for constant seed size. Third, variation in seed size could arise from parent-offspring conflict over seed size, especially since selection on seed size is expected to differ for the embryo and the parent (reviewed in Mojonner, 1998).

In this study, I evaluate conditions that underpin two hypotheses for seed size variation in the perennial herb, *Lupinus perennis* L. I focus on adaptive hypotheses that posit a fitness benefit to producing variable offspring in a heterogeneous environment, and non-adaptive hypotheses that propose limited

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parental control over seed provisioning. First, I determine whether the fitness consequences of seed size vary among offspring environments, as predicted if seed size variation is adaptive because offspring disperse into environments that differ in optimal seed size. For example, the benefits of large seed size might increase as competition increases (Stanton, 1984) or resources decline. In addition, I determine how maternal environmental conditions affect seed size. If a less favorable maternal environment simply limits provisioning, differences in seed size or number might occur among plants in different maternal environments. If, instead, poor conditions in the maternal environment affect the equality of seed provisioning, variation in seed size might increase within plants growing in stressful environments.

To test these predictions, I manipulated both maternal and offspring environments in field experiments conducted over two seasons. I describe the magnitude and nature of variation in seed size, and examine sources of that variation including resource availability, water stress, phenology, and individual plant differences. I also investigate consequences of variation in seed size for seeds from maternal families grown in ambient and dry environments, and estimate selection on seed size under those two conditions.

MATERIALS AND METHODS

Natural history and site description—*Lupinus perennis* L. (Fabaceae) occurs on well-drained sandy soils across the northern United States often in oak savannas and pine barrens (Dirig, 1994; Celebrezze, 1996). An indeterminate herbaceous perennial, *L. perennis* reproduces both vegetatively and by seed. Several stems may emerge from a single rhizome (Dirig, 1994), re-sprouting shortly after snowmelt in April. Flowering begins and peaks in late May, although some individuals continue to bloom through June, especially on secondary flower stalks. The self-compatible flowers occur on a raceme that matures from the base up. Bees (*Bombus* spp.) are the most common floral visitors (Bernhardt, 2000; S. Halpern, personal observation), but others include ants, butterflies, beetles, and thrips (S. Halpern, personal observation). Fruits and seeds begin to mature in June and most plants enter seasonal dormancy by early August. Fruits contain 0–7 filled seeds, which disperse short distances via explosive dehiscence. Seeds may germinate the summer they mature or in subsequent springs (S. Halpern, personal observation), and can persist at least 3 yr in the seed bank (Zaremba, 1992, as cited by Celebrezze, 1996).

I established an experimental population in a common garden at the Aldo Leopold Memorial Reserve (LMR), a 567-ha privately owned and cooperatively managed reserve located in Sauk County, Wisconsin, USA (43°33' N, 89°40' W). The LMR includes restored prairies, forests, marshes, and a former old-field common garden site used in this study. The garden site slopes with an eastern exposure, and is fenced to reduce deer browse; otherwise, damage to flowering stalks is extensive (S. Halpern, unpublished data). Regionally, the soil is sandy-gravelly till deposited during the Wisconsin glaciation (Clayton and Attig, 1990); the garden site lies on Gotham loamy sand soils (Grundlach, 1980) that consist of 87% sand, 9% silt, and 4% clay (Hunt, 1987; Zolidis, 1987). The plots used in these experiments were treated with the herbicide Round-Up and tilled before initial plantings to reduce competition from weeds.

The climate at the LMR is typical temperate continental. From 1971 to 2000, mean temperatures ranged from -10.6°C in January to 20.6°C in July, and annual precipitation averaged 85.8 cm, with 70% arriving from April to September and about a third arriving during the peak growing season of *L. perennis*, from mid-April to mid-July (Wisconsin State Climatology Office, 2003).

Sources of variation in seed size—I examined sources of variation in seed size using 2-yr-old maternal plants grown in the LMR common garden. Ma-

ternal plants had grown from seeds that originated from several small populations within 30 km of the LMR site (S. Weber, Bluestem Farm, personal communication). I planted 10 blocks of three 1.5×1.5 m plots in April–May 1999. Each plot contained 36 individuals planted in 6 rows spaced 20 cm apart, resulting in 16 “center” plants (surrounded by conspecifics on all sides) and 20 “edge” plants per plot. Paths approximately 80 cm wide separated plots. During the 1999 growing season, I periodically weeded and watered plots to facilitate establishment of the 1080 plants.

I manipulated several aspects of the 2-yr-old maternal plants' growing environment during the 2000 growing season to test the effects of these conditions on the mean and variance in seed size. I manipulated resources indirectly by weeding within and around plots and mowing paths between plots, creating differences in inter- and intraspecific competition for plants on the edge of plots compared to those in the center. Specifically, center plants grew at higher conspecific densities and likely experienced greater intraspecific competition. I simulated herbivory and directly manipulated resources by clipping 50% of each new leaf weekly from five edge plants in each plot. Plants thus grew in one of three resource treatments: edge clipped, edge unclipped, or center unclipped. Plots also received an ambient or dry water treatment. Ambient plots received approximately 46.5 cm of natural rainfall over the three-mo growing season; from 1971 to 2000, mean precipitation during the same period was 29 cm (Wisconsin State Climatology Office, 2003). In dry plots, I withheld rainfall using temporary plastic rain-out shelters, deployed only during rainfall events. These shelters drained into gutters directed away from plots. Shelters intercepted 43 cm (92%) of the ambient rainfall and reduced soil moisture content in the top 70 cm by 37% (Halpern, 2003). However, physiological symptoms of water stress were not evident in adult plants in this experiment (Halpern, 2003), probably because their long tap roots accessed deep water resources. Although it appears that adults did not experience water stress, I include water treatment as a factor in analyses because it was a design element.

From 16 June to 7 July 2000, I collected all mature fruits as they ripened from all adults. Fruits from each maternal plant were stored separately and sorted into three harvest date categories: early (16–23 June), mid (23–30 June), and late (July). Seeds were stored in an air conditioned laboratory until March 2001, when they were cold-stratified at 4°C for at least 13 d before weighing. Using stratified random sampling, I selected 59 maternal plants distributed among the different water and resource treatment combinations. For each maternal plant, I counted the number of seeds produced and weighed up to 180 haphazardly selected seeds on a microbalance (Mettler AT261 DeltaRange, Columbus, Ohio, USA) at an accuracy of 0.01 mg; seeds were equally distributed among all harvests represented in that plant. I weighed all seeds for plants that produced ≤ 30 seeds; I weighed >30 seeds for the 40 plants included in the following experiment, which examined the effects of the size of a seed on the fitness of the individual that grew from it.

Consequences of variation in seed size—To determine the effects of seed size on seedling performance and fitness, I planted individually weighed and hand scarified seeds from 40 randomly selected maternal plants into plots in the same common garden site. The maternal plants included an equal number from dry and ambient plots, and from edge and center positions in the plots. To obtain additional data on germination, I planted 2 seeds/position (spaced 1 cm apart) from fecund families; if both seeds germinated, I randomly pulled one and measured all subsequent plant traits on the remaining individual. I planted seeds 8 cm apart in a hexagonal array on 18–19 April 2001. Each 1.7×1.7 m plot included six replicates per maternal family, in a completely randomized design. The experiment included 40 families \times 6 replicates \cdot family $^{-1}$ \cdot plot $^{-1}$ \times 3 plots/block \times 5 blocks, for a total of 3600 plants; double planting led to an additional 1600 seeds from which germination data were collected and analyzed.

Plots received one of three water treatments: watered, ambient, or dry. Ambient plots received approximately 28 cm of natural rainfall over the 3-mo growing season. Watered plots received supplemental watering by hand 7 times, for a total of approximately 7 cm additional water. To avoid run-off, I watered at least 3 d after a natural rainfall event. Watered and ambient plots did not differ in soil moisture or in plant traits (Halpern, 2003), so I combined

these treatments in all analyses. In dry plots, I again used temporary rain-out shelters, which intercepted 22 cm (79%) of precipitation and reduced soil moisture in the top 30 cm by 25%.

I surveyed individuals from April 2001 to June 2002 to estimate fitness effects of seed size in different moisture environments during a plant's first two growing seasons. I measured several components of fitness: germination (yes/no) and its timing, plant size in years 1 and 2, plant survival through years 1 and 2, and reproductive success. I surveyed for germination every 2–3 d from 22 April to 24 May, and then approximately once per week through mid-July. I measured germination rate as 1/number of days to germinate; a germination rate of 0 indicates the seed never germinated. After thinning double planted seeds, I surveyed for survival and counted the number of true leaves present on each plant on 17–20 May, 6–15 June, 29 June–5 July, and 12–15 August (a total of 3388 individuals, after excluding those damaged by animals or damaged during handling). I recorded presence of plants in May 2002, and separately harvested and dried reproductive and vegetative above-ground biomass in June 2002. I weighed dry vegetative and reproductive biomass and counted all fruits and seeds.

Data analysis—To describe variation in seed size in this population, I plotted histograms of seed size for the entire data set and separately for each maternal plant. I also tested these distributions for normality, kurtosis, and skew. I calculated the mean seed mass and the coefficient of variation in seed mass for each maternal plant. In separate analyses, I used linear regression to assess the relationship between seed number and either mean seed mass or the coefficient of variation in seed mass, weighted for the number of seeds measured for an individual plant.

Sources of variation in seed size—To determine whether maternal growing environment affected mean seed mass for a plant, I used restricted maximum likelihood to analyze the following model:

$$\begin{aligned} \text{seed mass} = & \text{block} + \text{trt}_w + \text{trt}_r + \text{harvest} \\ & + \text{maternal plant}(\text{block} \times \text{trt}_w \times \text{trt}_r) + \text{harvest} \\ & \times \text{maternal plant}(\text{block} \times \text{trt}_w \times \text{trt}_r) \end{aligned}$$

where trt_w is the water availability treatment and trt_r is the resources treatment. I treated maternal plant and the $\text{harvest} \times \text{maternal plant}$ interaction as random and all other effects as fixed. To test for statistical significance of random effects, I fit the full model, excluded random effects one at a time, and used likelihood ratios to test the difference in the fit to the data between the full and the reduced models. I tested for statistical significance of fixed effects using F -ratios from the full model, where maternal plant was the unit of replication. I used PROC MIXED in SAS version 8.0 to carry out these analyses.

I tested for effects of maternal environment on variation in seed mass using analysis of variance. Specifically, I tested the effect of water or resources treatments on the coefficient of variation, weighted for the number of seeds weighed for a maternal plant. Two planned contrasts were of interest: unclipped edge plants vs. unclipped center plants (testing for an effect of intra-specific competition, which is greater in the center of plots) and clipped edge plants vs. unclipped edge plants (testing for an effect of reduced photosynthetic tissue, holding competition constant). I also used analysis of variance and these planned contrasts to test the effect of maternal environment on seed number. These analyses were conducted in JMP version 5.0.

Consequences of variation in seed size—I examined the fitness consequences of variation in seed mass using general linear models. For continuous components of fitness (germination rate, plant size, and reproductive success), I fit linear mixed models in SAS version 8.0 using PROC MIXED. For each fitness component, I started with a model including all two-way interactions between main effects as well as one three-way interaction of interest:

$$\begin{aligned} y = & \text{intercept} + \text{block} + \text{trt}_w + \text{block} \times \text{trt}_w + \text{fam} + \text{sdm} + \text{fam} \\ & \times \text{trt}_w + \text{fam} \times \text{sdm} + \text{trt}_w \times \text{sdm} + \text{block} \times \text{fam} \\ & + \text{block} \times \text{sdm} + \text{trt}_w \times \text{fam} \times \text{sdm} \end{aligned}$$

where fam = maternal family, trt_w = water treatment, and sdm = seed mass. Block, family, and any interactions including them were treated as random effects, while seed mass and treatment were fixed effects. In PROC MIXED, treating block as random accounts for the split-plot design and appropriately tests for treatment effects over the whole-plot error (SAS Institute, 1999). $\text{Fam} \times \text{sdm}$ and $\text{trt}_w \times \text{fam} \times \text{sdm}$ had estimated variance components of zero, so I excluded them from further models. To determine the statistical significance of the other predictors, I used F -tests for fixed effects and likelihood ratio tests of random effects, following the procedure described above. Except for germination rate, these analyses only included individuals that survived to the stage and had the trait measured on them, and responses were transformed to natural logs to improve error structure. I used biomass of the flowering raceme as the measure of reproductive success because many individuals flowered but did not produce seeds. These individuals may have sired offspring, so seed count could underestimate their reproductive success. In addition, flowering biomass and seed number were highly correlated ($r = 0.94$, $P < 0.0001$ for both the entire data set and overwinter survivors only).

For binomial components of fitness (probability of germination, survival, and flowering), I did not use mixed-model analyses because PROC NL MIXED did not converge to a global maximum. Therefore, I determined the effect of seed mass on these fitness components with multiple logistic regression. I fit the following model:

$$\begin{aligned} y = & \text{intercept} + \text{block} + \text{trt}_w + \text{block} \times \text{trt}_w + \text{fam} + \text{sdm} \\ & + \text{fam} \times \text{trt}_w + \text{fam} \times \text{sdm} + \text{trt}_w \times \text{sdm} \end{aligned}$$

I used Type III tests of effects, and examined model goodness-of-fit using the Hosmer-Lemeshow test, which is the most appropriate test for models that include one or more continuous predictors (Agresti, 1996; SAS Institute, 1999). When interactions with treatment were at or near statistical significance, I reran analyses separately by treatment, including just main effects in the model. These models test for treatment and block effects over the residual, which is inappropriate because of the split-plot design of the experiment. Therefore, for each response variable, I calculated proportions by plot and tested for treatment and block effects using ANOVA. I arcsine square-root transformed the proportions prior to analysis and used Type III errors. Both logistic regressions and ANOVAs included all individuals that were planted into the experiment; double-planted seeds were excluded except for germination analyses. I also reanalyzed the subset of individuals that survived to the previous stage to determine the influence of seed mass on transitions between stages independent of prior effects. In these ANOVAs, I weighted proportions by the number of individuals still alive in the plot because mortality differed substantially among them.

Selection on seed size—I evaluated selection on seed mass for seedlings grown in the two water environments, using seed count in the second year as a measure of individual fitness. I estimated linear and quadratic selection gradients on seed mass using the methods of Lande and Arnold (1983). I regressed relative fitness (individual seed count/mean seed count) on standardized seed mass and I ln-transformed seed mass before analysis to improve variance structure. The model included block and treatment to account for their effects, and I tested for treatment effects over the block \times treatment interaction. I also tested for a treatment \times seed mass interaction; when present, this interaction indicates that selection on seed size differs among the two water treatments. These analyses included all individuals planted into the experiment. Because many individuals produced no seeds, often due to mortality, the error distribution is poor and significance tests should be interpreted cautiously.

RESULTS

Variation in seed size—Seed mass was highly variable in the 5839 seeds weighed from 59 maternal plants. Seed mass was normally distributed (Kolmogorov-Smirnov-Lillifors $D = 0.008$, $P > 0.15$) with a fivefold range in magnitude, from 8 mg to 41 mg (Fig. 1). The distribution is mesokurtic (kurtosis

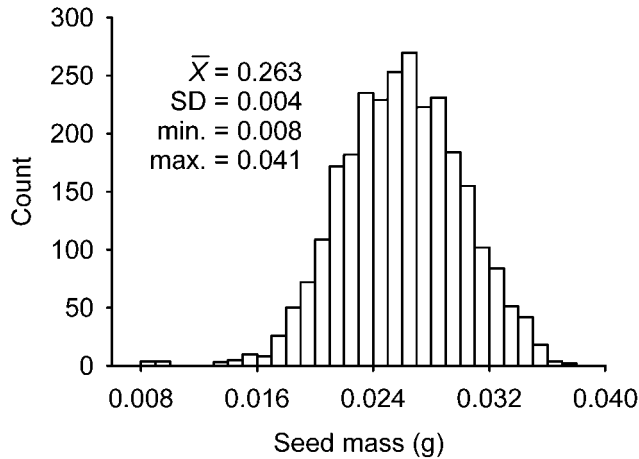


Fig. 1. Distribution of seed size in 59 plants ($N = 5939$ seeds).

= 0.27) and is not significantly skewed (skew = -0.08). Within individual plants, seed mass varied 1.2-fold to 4.5-fold, with the range of masses spanning 4–27 mg and the coefficient of variation ranging from 0.06–0.26. Seed size was normally distributed in 46 of the 59 individuals (78%). In 9 of the 13 individuals with non-normal distributions of seed mass, the distribution was skewed strongly to the left, while 11 had strongly leptokurtic distributions (i.e., heavy tails).

Sources of variation in seed size—Within plants, this study detected no relationship between maternal parents' seed number and seed size (weighted linear regression, $\beta = 3.8 \times 10^{-6}$, $t = 1.04$, $P = 0.304$) or between seed number and the coefficient of variation in seed size (weighted linear regression, $\beta = -3.8 \times 10^{-5}$, $t = 1.06$, $P = 0.295$; Fig. 2). Therefore, this study did not detect a trade-off between seed size and seed number, or a change in seed size variation with increasing seed number.

Water availability, resources (competition and clipping), and harvest date did not significantly affect mean seed size (Table 1). Because not all individuals matured seeds during all three harvest periods, I also tested for the effects of water availability and resources on mean seed mass within harvest periods. These analyses also detected no statistically significant effects of maternal growing environment on seed mass (results not shown). Maternal plants varied substantially in mean seed mass (Table 1), and the effect of harvest period on mean seed mass varied among families; in other words, timing of seed maturation had different effects on seed mass among maternal plants. In addition, seed number was not significantly affected by water availability ($F_{1,55} = 1.58$, $P = 0.228$), competition ($F_{1,55} = 1.94$, $P = 0.169$), or clipping ($F_{1,55} = 0.98$, $P = 0.327$).

In contrast, maternal growing environment did affect variation in seed size. Weighted ANOVA detected an effect of resource availability on the coefficient of variation (CV) in seed size ($F_{2,55} = 8.17$, $P = 0.0008$). Edge plants (with reduced intraspecific competition) had lower CV in seed size than center plants ($CV_{\text{edge}} = 0.096$, $CV_{\text{center}} = 0.123$, planned contrast $F_{1,55} = 12.13$, $P = 0.0009$). Although seeds from clipped plants also were more variable than seeds from unclipped plants ($CV_{\text{clip}} = 0.099$, $CV_{\text{control}} = 0.096$) this difference was not statistically significant (planned contrast, $F_{1,55} = 0.13$, $P = 0.78$). These results suggest that intraspecific com-

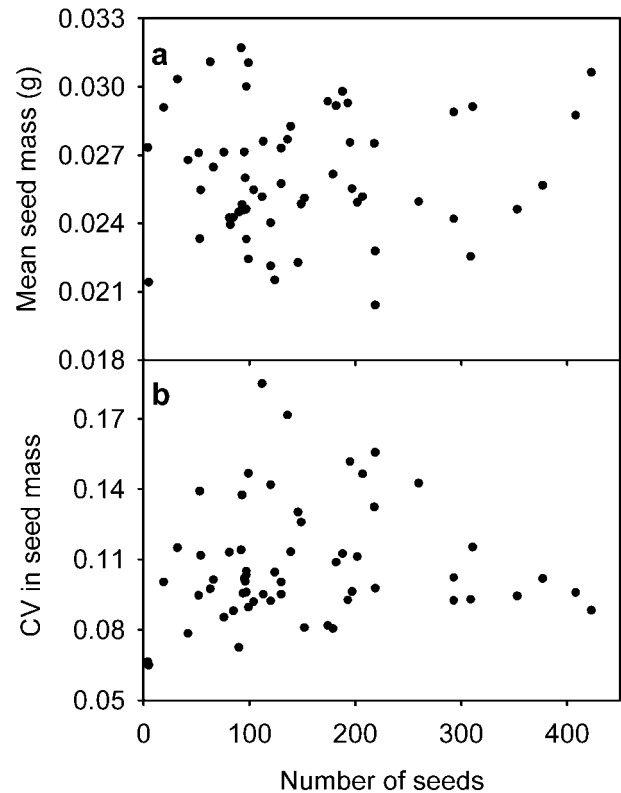


Fig. 2. Relationship between seed number and (a) seed size or (b) variation in seed size. Each point represents the mean or coefficient of variation for a single maternal plant ($N = 59$). Seed number was not a statistically significant predictor for either response ($P > 0.27$).

petition increases variation in seed sizes produced by an individual plant. It is possible that clipping also increases variation in seed size; the power to detect such differences was low in this study. The effect of water treatment on seed size variation also was not statistically significant (ANOVA, $F_{1,55} = 0.12$, $P = 0.73$); plants in ambient conditions had slightly

TABLE 1. Sources of variation in mean seed size for maternal plants growing in different environments. I tested for statistical significance using (A) F tests for fixed effects (tested over maternal plant error, denominator $df = 53$) and (B) likelihood ratio tests for random effects (model column indicates which predictor was excluded from the analysis, compared to the full model with all predictors). $N = 5839$.

A) Fixed effects			
Effect	Numerator df	F	P
Block	2	0.29	0.75
Water treatment	1	2.30	0.14
Resources treatment	2	1.82	0.17
Harvest	2	2.10	0.13
B) Random effects			
Model	$-2RLL^a$	$\Delta-2RLL^b$	P^c
Full	-51582.1		
Maternal plant ($b \times tr_t \times tr_w$) ^d	-51543.5	38.6	<0.0001
Harvest \times maternal plant ($b \times tr_t \times tr_w$) ^d	-51065.4	516.7	<0.0001

^a $-2RLL = -2 \times$ residual log likelihood.

^b $\Delta-2RLL =$ change in $-2RLL$ compared to full model.

^c P calculated from χ^2 distribution with 1 df.

^d $b =$ block; $tr_t =$ resources treatment; $tr_w =$ water treatment.

TABLE 2. Significance (*P*) of multiple logistic regression models that predict the categorical fitness components. (A) Full data set, including all seeds planted for germination (*N* = 5174 after accidental losses) and all seeds that remained after thinning of double-planted positions for other components (*N* = 3480 after accidental losses); analysis of germination post-thinning yields similar results, not shown. (B) Reduced data sets, including just those individuals that survived to the previous time step. *N* = 2990 (July), *N* = 2078 (ovw), *N* = 1356 (flower). germ. = probability of germination; July = survivorship to July 2001; ovw. = survivorship over the winter; flowering = probability of flowering.

(A) Source	Germ.	July	Ovw.	Flowering
Family	0.169	0.372	0.426	0.354
Family × treatment	0.007	0.641	0.763	0.978
Seed mass	0.973	<0.0001	<0.0001	0.009
Seed mass × treatment	0.002	0.539	0.507	0.164
Seed mass × family	0.206	0.332	0.632	0.375
(B) Source	July	Ovw.	Flowering	
Family	0.480	0.463	0.816	
Family × treatment	0.669	0.978	0.918	
Seed mass	<0.0001	0.442	0.898	
Seed mass × treatment	0.995	0.574	0.072	
Seed mass × family	0.409	0.502	0.571	

greater CV than plants in dry conditions ($CV_{\text{ambient}} = 0.107$, $CV_{\text{dry}} = 0.105$). The correlation between mean seed mass and the CV in seed mass was not significantly different than zero ($r = -0.084$, $P = 0.528$, $N = 59$)

Fitness consequences of variation in seed size—Seed mass affected all fitness components measured up to reproductive success (Tables 2, 3). For germination probability and germination rate, the effect of seed mass differed in the dry and ambient treatments (seed mass × treatment interaction; Tables 2A, 3). In the ambient environment, a 10-mg increase in seed mass tripled the odds of germination, while a 10-mg increase in seed mass had negligible effects in the dry treatment (Table 4A). A similar pattern occurred in germination rate: larger seeds germinated earlier in the ambient treatment, while the positive effects of seed mass on germination timing were smaller in the dry treatment (Fig. 3). Significance tests and effect sizes were similar when I reran germination analyses excluding double planted seeds (results not shown). Overall, germination was higher in the ambient treatment (92%) than in the dry treatment (61%). Larger seeds also had a higher probability of survival: a 10-mg increase in seed mass ap-

TABLE 4. Odds ratios (95% confidence limits) for effects of seed mass on probability of germination, survivorship, and flowering for (A) all data and (B) only survivors of the previous episode. The ratio gives the expected change in odds of success for a 10-mg increase in seed mass. Where the seed mass × treatment interaction was statistically significant, the odds ratio is presented for seed mass separately in each treatment.

A) All data	Odds ratio
Germination ambient	3.12 (2.08–4.68)
Germination dry	1.35 (0.96–1.90)
July survivorship	2.40 (1.70–3.38)
Overwinter survivorship	2.00 (1.40–2.84)
Flowering	2.02 (1.19–3.45)
B) Survivors	Odds ratio
July survivorship	2.22 (1.32–3.75)
Overwinter survivorship	1.27 (0.68–2.38)
Flowering ambient	2.03 (1.28–3.21)
Flowering dry	0.79 (0.28–2.30)

proximately doubled an individual’s probability of survival (Table 4A). After accounting for deaths in the previous stage, a 10 mg increase in seed mass still doubled an individual’s odds of surviving to July, although it had no effect on the probability of surviving the winter (Table 4B). The probability of flowering also doubled when considering all seeds planted. For just plants that survived the winter, increasing seed mass by 10 mg nearly doubled the probability of flowering in the ambient treatment but had a negligible effect in the dry treatment (Table 4B). Finally, increasing seed mass was associated with increasing aboveground plant size in both years 1 and 2 after excluding plants that had died. In contrast, seed mass had no detectable effect on reproductive biomass for those individuals that flowered (Fig. 3).

When detected, whole-plot effects (block and treatment) were strongest in the first year (Tables 3, 5). Except for maximum leaf number, all first-year traits were affected by treatment. A smaller proportion of seeds in the dry treatment germinated and survived when all individuals were included in the analysis (Table 5A). Seeds in the dry treatment also germinated later. When only survivors were included in the analysis, treatment effects were not detectable after July survival (Table 3, 5B). Therefore, the strong treatment effects arise primarily from impacts on early fitness components, germination, and establishment. If juveniles survived the first growing sea-

TABLE 3. Test statistics and significance (*P*) for sources of variation in continuous components of fitness. Random effects were analyzed using likelihood ratio tests, while fixed effects were analyzed with *F* tests. Random effects with estimated variances of zero were excluded from the model and do not appear as sources of variation. Except for germination rate, only survivors to the stage were included in the analysis. Analysis of germination excluding double planted seeds yields similar results.

Source	Germination rate (<i>N</i> = 5174)		Max. leaf number (<i>N</i> = 2333)		Total mass (<i>N</i> = 1159)		Flower mass (<i>N</i> = 518)	
	Test	<i>P</i>	Test	<i>P</i>	Test	<i>P</i>	Test	<i>P</i>
Family ^a	2.40	0.121	3.9	0.048	0.5	0.479	1.2	0.273
Treatment ^b	19.86	<0.0001	0.64	0.426	0.95	0.331	0.24	0.622
Seed mass ^b	14.91	0.013	20.04	<0.0001	11.19	0.001	0.91	0.342
Family × treatment ^a	1.5	0.273	4.2	0.040	0.3	0.584		
Block × treatment ^a	44.4	<0.0001	26.7	<0.0001	2.2	0.138	1.1	0.294
Seed mass × block ^a	2.8	0.094						
Seed mass × treatment ^b	10.23	0.002	1.42	0.234	0.23	0.633	0.00	0.987

^a Random effect; test statistic is $-2 \times$ residual log likelihood, tested against χ^2 distribution with 1 df.

^b Fixed effect; test statistic is *F*.

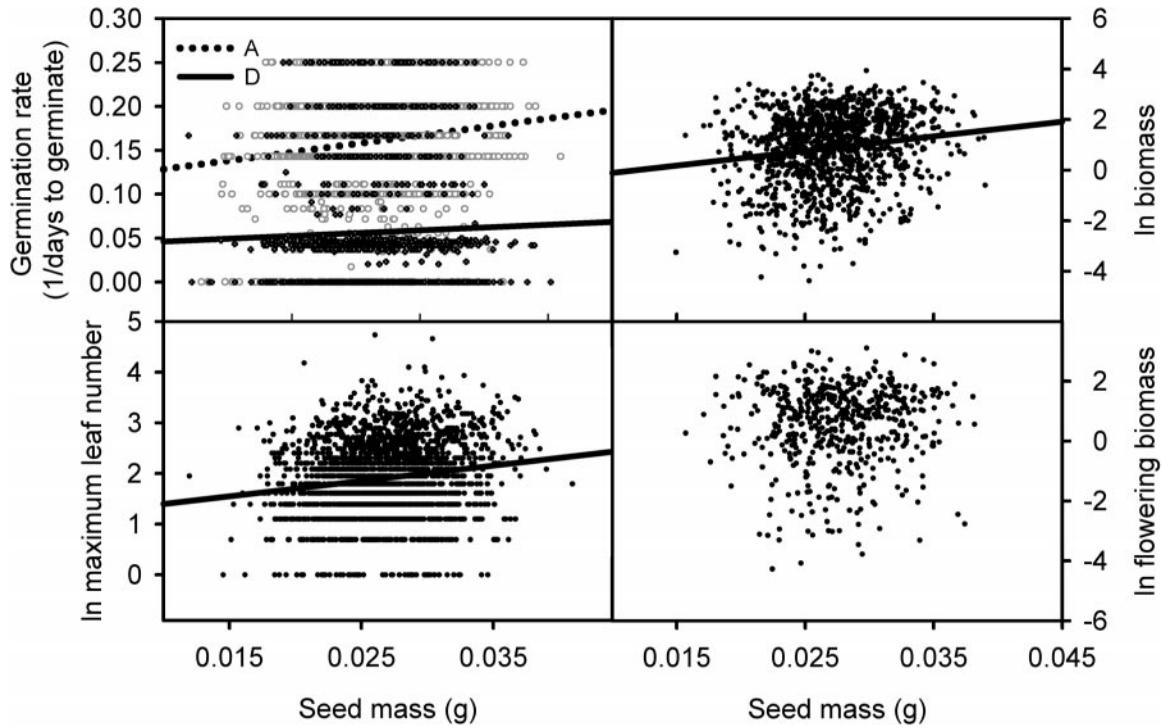


Fig. 3. Relationship between seed mass and continuous fitness components. For germination rate, A = Ambient and D = Dry.

son, effects of water limitation dissipated and were no longer detectable in terms of biomass or flowering. The only fitness component that varied among blocks was germination probability (Table 5A). However, treatment effects varied significantly among blocks for germination probability, germination rate, and maximum leaf number. This interaction suggests that the effects of water environment on these traits differed over the relatively small spatial scale of this experiment (7 × 11 m in total).

Selection on seed size—This experiment detected strong selection for increasing seed size ($\beta = 0.30$, $SE = 0.14$, $P < 0.0001$, $N = 2996$). Standardized linear selection gradients predict a shift of 0.30 standard deviations in mean seed mass per generation of selection. This analysis detected neither a treatment ($F_{1,4} = 0.10$, $P = 0.77$) nor a treatment-by-trait in-

teraction ($F_{1,2284} = 0.12$, $P = 0.73$). Quadratic selection gradients were not significantly different from zero ($\beta = 0.05$, $SE = 0.05$, $P = 0.29$, $N = 2996$). They provide no evidence for curvature in the fitness function, suggesting that selection on seed size is directional rather than nonlinear. Again, no treatment effect ($F_{1,4} = 0.08$, $P = 0.79$) or trait-by-treatment interaction ($F_{1,2983} = 0.10$, $P = 0.76$) were detected.

DISCUSSION

Sources of variation in seed size—The fivefold variation in seed size observed in this study was not associated with environmental conditions. Mean seed size differed substantially among individuals but not among maternal growing environments or seed maturation times. Many other studies similarly have found individual differences in seed size (e.g., Dolan,

TABLE 5. ANOVA on proportion seeds that germinated, survived or flowered in plots. Proportions were arcsine square-root transformed prior to analysis. (A) All seeds planted in the experiment. (B) Only those individuals that survived the previous episode; proportions weighted by the number of individuals surviving in the plot.

A) All data								
Source	Germination		July survival		Overwinter survival		Flowering	
	F	P	F	P	F	P	F	P
Block ^a	10.0	0.013	2.83	0.142	1.31	0.380	1.19	0.418
Treatment ^b	368	<0.0001	75.9	0.0003	6.75	0.048	3.49	0.121
Block × treatment ^a	12.8	0.008	2.61	0.61	0.79	0.579	0.32	0.854
B) Survivors								
Source	July survival		Overwinter survival		Flowering			
	F	P	F	P	F	P	F	P
Block ^c	1.25	0.399	0.27	0.884	0.23	0.909		
Treatment ^d	31.2	0.002	0.18	0.691	0.41	0.552		
Block × treatment ^c	1.53	0.322	0.32	0.866	0.66	0.645		

^a df = 4,14; ^b df = 1,14; ^c df = 4,14; ^d df = 1,1.

1984; Thompson, 1984; Fenster, 1991; Winn, 1991; Krannitz, 1997; Mendez, 1997; Vaughton and Ramsey, 1997, 1998; Castro, 1999; Simons and Johnston, 2000), which may arise from environmental maternal effects (Platenkamp and Shaw, 1993; Gutterman, 2000), genetic maternal effects (Byers et al., 1997), or both (Hereford and Moriuchi, in press). In contrast to this study, differences in seed size among environments are common, likely due in part to low heritabilities and strong environmental maternal effects in this trait (Platenkamp and Shaw, 1993; Byers et al., 1997). However, the effect of a particular environment is not clearly predictable across systems. For example, similar resource manipulations can affect mean seed size in different directions (Platenkamp and Shaw, 1993; Vaughton and Ramsey, 1998; Galloway, 2001): artificial defoliation reduces mean seed size in some species (Vaughton and Ramsey, 1997, 1998) but not in others (this study, Ågren, 1989; Krannitz, 1997); maternal plant size positively affects seed size in some species (Dolan, 1984) but not others (Krannitz, 1997; Vaughton and Ramsey, 1997); and seasonal effects on mean seed size vary from substantial (Fenster, 1991; Winn, 1991; Byers et al., 1997; Vaughton and Ramsey, 1998) to undetectable (Krannitz, 1997; Vaughton and Ramsey, 1997).

In contrast to mean seed size, maternal growing environment affected variability in the seed sizes produced by an individual *L. perennis* plant. Seed size variation was greater for plants growing at higher compared to lower densities of intraspecific competitors; a similar trend related to clipping was not statistically significant. These results are consistent with a scenario in which environmental conditions affect control over seed size. An increase in trait variation under stress usually is interpreted as maladaptive developmental instability (reviewed in Simons and Johnston, 1997). Therefore, variation in seed size in *L. perennis* may occur in part due to constraints on equitable seed provisioning when resources become more limiting. It is also possible that developmental instability might be a mechanism for producing adaptive variation (Simons and Johnston, 1997), and differences in variation between treatments occur because its expression changes across environments. Determining whether the observed variation is adaptive would require information about the relationship between fitness and seed size variation as a parental trait, which this study did not test.

In fact, variation in offspring size as a parental trait has received much less empirical attention than identifying sources of within-plant variation in seed size, and few studies have explicitly considered the effects of maternal environment on seed size variation within a plant. In plants, Krannitz (1997) found that a stressor, proportion of twigs browsed, was associated with variability in seed size in *Purshia tridentate* (Pursh) DC. Recent studies in trematodes (Poulin and Hamilton, 2000) and fish (Koops et al., 2003) also have explicitly studied variation in offspring size among environments. By correlating this variation with estimates of environmental predictability, Koops et al. (2003) argued that egg size variation within female trout arises as part of a bet-hedging strategy in unpredictable environments. Similar empirical work with plants could help clarify whether and when an individual that produces more variable seeds is favored.

Consequences of differences in seed size—For offspring, fitness consequences of seed size are dramatic and persistent in *Lupinus perennis*. Most fitness components measured in the first two seasons were affected by seed size, although some of

those effects weakened over time or after accounting for mortality in earlier stages. Larger seed size may allow for faster seedling growth, giving individuals a head start that carries over into greater survival and reproduction in subsequent years. For *L. perennis*, a head start may be important in terms of root establishment. Adult *L. perennis* avoid water stress despite growing in sandy, drought-prone soils, apparently because their long tap-roots reach deep water sources (Dirig, 1994; Halpern, 2003). Plants that reach deep water faster, having grown from larger seeds, may photosynthesize and grow continuously, while smaller plants from smaller seeds may be more dependent on rain and associated surface water.

Seed size effects are similarly persistent in some other plants, including *Lobelia inflata*, which has very small seeds (Simons and Johnston, 2000). However, seed size also is seen commonly as an important component of maternal effects whose influence tends to dissipate during the first few weeks of seedling establishment (Harper et al., 1970; Roach and Wulff, 1987). Evidence to support this conclusion comes from empirical examples where positive effects of seed size on germination and plant size only persist during early establishment (Dolan, 1984; Tremayne and Richards, 2000; but see Stanton, 1984; Simons and Johnston, 2000). The duration of seed size effects may vary in association with life history characteristics or habitat conditions, or it may be idiosyncratic. Comparative studies that control for similarities due to shared evolutionary history (Felsenstein, 1985; Martins and Hansen, 1996) could best test the importance of these potential explanations for differences in seed size effects.

In this study, it is somewhat surprising that seed size had little effect on germination probability in the dry treatment. Larger seeds often contain additional resources, which could be allocated to root growth in seedlings and thus could increase access to soil water. Indeed, *L. perennis* seeds that germinate in drier soils in the greenhouse have longer and heavier roots (Halpern, 2003). Alternatively, smaller seeds could be favored if they affected root:shoot ratios, and hence water losses to transpiration under drought conditions (Hendrix et al., 1991). Because seed size can affect dormancy (Murdoch and Ellis, 2000), it is possible that smaller seeds were likely to remain dormant in the dry treatment. In this experiment, however, it seems unlikely that seeds in the dry treatment entered the seed bank and remained viable: all seeds were hand-scarified, and I observed no new germinants in spring 2002, when treatments were no longer applied. Seed size can also affect probability of seed predation (Reader, 1993; Moegenburg, 1996; Alexander et al., 2001; Sousa et al., 2003). However, *L. perennis* seeds are not attacked by pre- or post-dispersal predators at this site (S. Halpern, unpublished data), so it is also unlikely that greater seed predation influenced germination rates differentially among treatments.

The large fitness benefits of increasing seed size did not differ between environments. The impact of seed size on fitness did not vary among ambient and dry environments for most fitness components, and selection on seed size did not differ among ambient and dry environments. Thus, this study provides little support for conditions underlying one common adaptive explanation for seed size variability, that temporal or spatial variation in establishment conditions creates a mosaic of optimal seed sizes on the landscape (Janzen, 1977; Capierna, 1979; reviewed in McGinley et al., 1987). These results contrast with several studies that manipulate environmental characteristics in other systems; for example, Eriksson (1999)

found some evidence that the positive benefits of larger seed size increased in *Convallaria majalis* L. when seedlings grew at higher densities of a competitor, while Wulff (1986b) reported differences in the magnitude of effects of seed size on seedling survival among habitat types for *Desmodium paniculatum* (L.) DC.

This study only measured the fitness consequences of seed size for offspring. Only one empirical study has simultaneously estimated selection on seed size for both parent and offspring (Mojonnier, 1998). She found high heritability but no selection on seed size for maternal plants of *Ipomoea purpurea* (L.) Roth, and low heritability but strong positive directional selection for seed size for offspring plants. If the same pattern holds in *L. perennis*, variation in seed size could persist because it is a neutral trait in terms of the maternal plant's fitness.

Seed size vs. number trade-off?—Life history theory predicts that resource limitations induce a fundamental genetic trade-off between number of offspring and offspring size (Smith and Fretwell, 1974), but evidence of trade-offs between seed size and number in plants is inconsistent. A genetic or phenotypic trade-off has been reported in numerous studies (e.g., Agren, 1989; Mehlman, 1993; Byers et al., 1997; Vaughton and Ramsey, 1997, 1998; Eriksson, 1999; Simons and Johnston, 2000) but not in others (e.g., Schaal, 1980; Mendez, 1997; Vaughton and Ramsey, 1997; Galloway, 2001; Karrenberg and Suter, 2003; reviewed in Venable, 1992), including this one (Fig. 2a). It is possible that differences in microenvironment or plant size affect resources available for seed provisioning, thus obscuring actual trade-offs among plants (van Noordwijk and de Jong, 1986; Venable, 1992). In this study seed number increased with plant size (measured as leaf number) ($r = 0.22$, $P = 0.006$, $N = 151$), although mean seed mass was not associated with plant size ($r = 0.09$, $P = 0.65$, $N = 24$). Therefore, this study provides no evidence for a trade-off but cannot rule one out. Similarly, plant modules such as racemes or fruits may experience different resource environments and therefore provision seeds differently. For example, Mehlman (1993) observed a size-number trade-off among fruits within individuals but not among individuals, and Simons and Johnston (2000) only detected a size-number trade-off after controlling for fruit size. Although the effects of position and plant modularity on seed size are well recognized (reviewed in McGinley et al., 1987), the implications for the evolutionary ecology of seed size and life-history trade-offs have not received as much attention.

Conclusion—The fivefold variation in seed sizes observed in this study with *Lupinus perennis* contributes to important and long-lasting differences in fitness among offspring. In addition, stressful conditions increase the variability in the size of seeds an individual produces. This pattern could arise from a lack of parental control over seed size that is magnified when resource limitation increases. Few studies have explicitly examined the causes of seed or egg size variation within an individual (but see Poulin and Hamilton, 2000; Koops et al., 2003), despite its potential importance in life history and seed evolutionary ecology. Although they present challenges, such studies could contribute to new insights about the evolution of seed size variation. Given the large differences among plants in their seed size variation, it also might be possible to examine selection on seed size variation per se in various en-

vironmental contexts, thereby explicitly testing the premise that increased variation is favored under some conditions.

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