

Consequences of Intraspecific Competition and Environmental Variation for Selection in the Mustard *Sinapsis arvensis*: Contrasting Ecological and Evolutionary Perspectives

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ABSTRACT: Alternative models of plant life-history evolution differ in their views of how abiotic stress and competition interact to shape the evolution of plant life-history traits. To address this debate, which crosses traditional boundaries between community ecology and population biology, we grew wild turnip families from three selection histories in a field experiment in which we manipulated conspecific density and sun exposure. Hot spring conditions caused neutral shading to reduce drought stress, resulting in a greater mean and variance for lifetime fertility at low density and greater intensity of competition at high density. The variance in relative fitness among individuals or families was least in partial shade at low density. Prior selection under shade stress in the greenhouse reduced lifetime fitness in the less stressful partial-shade treatment under field conditions. Patterns of selection and predicted trait evolution were more similar between high and low densities than between the two light environments. Partial shade favored the proliferation of large leaves early in development, especially at high density. Selection in the stressful full-sun treatment favored reduced pathogen susceptibility at both densities and early flowering at low density. Because direct selection on traits changed principally in magnitude rather than in direction, genetic correlations for fitness were generally positive between light and density treatments. Greater intraspecific competition led to more rapid predicted trait evolution in the partial-shade environment but not in the stressful full-sun treatment.

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Ecologists and evolutionary biologists are deeply interested in understanding how physical and biotic features of the environment shape the evolution of life-history traits. Ecologists using a comparative approach take note of correlations between habitat attributes and the life-history characteristics of species within those habitats to make inferences about the selection pressures that favor some species while excluding others (Raunkiaer 1934; Grime 1979). Experimental investigations of life-history strategy theory may test alternative mechanisms contributing to such community-level differences (e.g., Campbell and Grime 1992; Wedin and Tilman 1993; Peltzer et al. 1998; Keddy et al. 2001) or may demonstrate that ecotypes with different life histories are each adapted to habitats characterized by different levels of disturbance, competition, attack by natural enemies, and/or abiotic stress (Law et al. 1977; Solbrig and Simpson 1977; McGraw 1987; Volis et al. 2002). In this article, we extrapolate from these community- and ecotype-level analyses by asking whether life-history strategy theory can inform us about how interactions between competition and abiotic stress alter the evolutionary trajectories of single plant populations via contrasting selection pressures, changes in genetic architecture, or some combination of these factors.

Alternative views of life-history evolution vary with respect to the important axes of environmental variation across which adaptive differentiation is thought to occur and the suites of traits expected to evolve under contrasting conditions. In the C-S-R (or triangle) model of plant life-history evolution, Grime (1977, 1979) considers two orthogonal axes of environmental variation, one defined by disturbance frequency and the other by habitat productivity (also see Taylor et al. 1990). Grime's framework explicitly distinguishes decreases in plant growth potential caused by disturbance (which includes tissue loss due to

enemies or mechanical damage) or competition from those caused by excesses or deficiencies of abiotic factors (abiotic stresses). These axes of variability are thought to select for three contrasting life-history strategies: competitive (C), stress-tolerant (S), and ruderal (R). In the C-S-R view and in related models (e.g., Greenslade 1983; Southwood 1988; Keddy 1990), stable but unproductive habitats are thought to favor conservative life-history traits such as slow growth, delayed reproduction, and increased allocation to stored reserves. This prediction arises from the assumption that reduced competition in chronically unproductive habitats will weaken selection for traits that enhance competitive ability, especially if there is a trade-off between stress tolerance and either growth or metabolic rate (Hoffman and Parsons 1989; Chapin et al. 1993; Arendt 1997).

A competing perspective, developed principally by Tilman (1988, 1990), also envisions variation in habitat productivity as an axis along which plant communities and life histories diverge. However, in contrast to the C-S-R model, supporters of this "resource-ratio" model contend that competition is neither less intense nor a less important selective force in unproductive habitats (also see Newman 1973). Rather, they suggest that traits enhancing competition for belowground resources will be favored in less productive (and less densely vegetated) habitats, whereas traits enhancing competition for light will be most critical in fertile, late successional habitats. The resource-ratio model has most often been used to explain shifts in plant life histories occurring through successional changes in community composition (Reynolds and Pacala 1993). However, ecophysiological models (Givnish 1986) and population-focused empirical studies indicate that changes in competition for light versus belowground resources can also drive adaptive life-history differentiation within species (Dudley 1996; but see Scheiner and Teeri 1986; Schmitt 1993).

Competing views of the interaction between habitat productivity and competition lie at the heart of the debate between proponents of the C-S-R versus resource-ratio models of plant life-history evolution (Tilman 1987; Thompson and Grime 1988). Accordingly, a number of plant ecologists have studied whether the intensity of competition consistently changes along natural or manipulated fertility gradients by documenting the degree to which average plant performance is enhanced when neighboring plants are removed experimentally. The interpretation of these studies has varied widely, in part because some workers have measured competition intensity as the absolute increase in mean individual performance caused by release from competitors while others have argued that the proportional change in performance is a better measure (Goldberg and Scheiner 1993; Grace 1995). Although neighbor removal quite consistently leads to greater ab-

solute increases in fitness under fertile conditions, studies measuring how competitors proportionately decrease performance vary widely in demonstrating an increase, decrease, or no change in the intensity of competition in more productive sites (reviewed in Gurevitch et al. 1992; Grace 1995).

These strictly ecological analyses have been used to argue that basic tenets of the C-S-R model or the resource-ratio model are either supported or not (e.g., Ditommaso and Aarssen 1991). However, approaches of this kind cannot explicitly examine the consequences of variation in habitat productivity, environmental stress, and competition for the evolution of life-history traits (Stewart and Schoen 1987). Because measuring the impact of competition on average fitness cannot reveal its selective consequences, we must also ask how environmental productivity and plant density influence the relationship between heritable trait variation and relative fitness. Few studies have examined effects of competition or abiotic stress on genetic architecture and/or the opportunity for selection (Wade 1979) within plant populations (but see Shaw et al. 1995; Stanton et al. 2000).

Alternative life-history strategies are thought to evolve because contrasting selection regimes keep strategies distinct (reviewed in Futuyma and Moreno 1988; Roff 1996). Accordingly, it is important to determine which axes of environmental variation change patterns of selection on traits and whether genetic correlations for fitness, measured across environments thought to select for divergent life histories, are in fact negative (Rose 1982; Scheiner and Teeri 1986). Extending the C-S-R model to adaptation within species leads to two predictions: first, that lineages adapted to chronically unproductive conditions will be at a selective disadvantage when competition is intense and second, that competition will have a greater effect on trait evolution in more productive habitats. In contrast, extrapolation from the resource-ratio model might predict that adaptation to low light and plentiful soil resources will enhance performance in habitats with intense aboveground competition and that patterns of selection will be more sensitive to changes in the ratio of above- versus belowground resources than to changes in conspecific density.

In this article, we present results from a field study in which paternal half-sibships of a weedy mustard were planted at two different densities into two experimental settings that differed with respect to direct sunlight and, concordantly, in the level of environmental stress and productivity. Paternal families were derived from one of three selection histories: either of two experimental selection regimes in the greenhouse or natural selection under field conditions. Experimental plants were grown outside during an unusually hot and dry spring. The neutral shade

treatment reduced drought and heat stress, changing the ratio of aboveground to belowground resources and resulting in substantially greater growth and maximum lifetime seed production. Using the C-S-R and resource-ratio models for context, our aim in this article is to compare the ecological effects of conspecific density and shading on average plant performance with the evolutionary impacts of these factors on the opportunity for selection, patterns of genetic variation, and the predicted evolution of life-history traits.

We focus on the following specific questions: To what extent do light and conspecific density change mean fertility and fertility variance among individuals? Specifically, is the intensity of competition greater in the less stressful partial-shade treatment, as predicted by the C-S-R model? Do these ecological differences correspond with changes in the opportunity for selection, measured as variation in relative fitness?

Does the recent history of selection influence responses of experimental plants to conspecific density and shading? For example, does past selection under shade stress increase or decrease performance in the highly competitive, partially shaded environment?

How do levels of competition and light influence patterns of genotypic selection? Do the traits favored in different environmental treatments match predictions arising from either the C-S-R or resource-ratio models? Do patterns of direct selection on traits change markedly, as the resource-ratio model predicts, when the ratio of above- to belowground resources is manipulated?

To what extent does the pattern of predicted life-history trait evolution, as estimated by genetic selection differentials, conform to expectations based on alternative plant life-history strategy theories? Does increased competition have more dramatic effects on trait evolution in the more productive environment, as predicted by the C-S-R model?

Methods

Genetic stocks used in the field study. Wild turnip (*Sinapsis arvensis* L.; = *Brassica kaber*, *Brassica arvensis*) is an obligately outcrossing annual species that is native to Eurasia. It is a common weed in open, fertile, disturbed sites throughout California's central valley (Rollins 1981). In California, it grows as a winter annual, germinating with rains from November to February and setting seed by mid-June. The genetic stocks used in this study were derived from a bulk seed collection made within a very large, naturalized *S. arvensis* population 1 km north of the University of California, Davis (Yolo County) in 1993. As part of a larger study on the phenotypic and evolutionary consequences of abiotic stress (Roy and Stanton 1999; Roy et al. 1999; Stanton et al. 2000; Steinger et al.

2003), a sample of those seeds was subsequently divided among six treatments in which individually grown plants were subjected to three generations of natural selection under greenhouse conditions. Plants from two greenhouse selection regimes were used in this study. Lineages from the "shade stress" selection history experienced three generations of selection under neutral shade canopies in the greenhouse (a treatment that dramatically reduced growth and lifetime fertility), whereas plants from the "control" selection treatment received full ambient light. Belowground competition was eliminated during greenhouse selection by subirrigating individually potted plants with fertilizer water. In a fourth generation, we grew plants from both experimental selection regimes as well as from the original field seed collection under common greenhouse conditions to minimize maternal environmental effects (for details, see Stanton et al. 2000). We included families derived from the original seed stock to test for potential effects of inadvertent selection in the control greenhouse regime.

During this "common garden" generation, we conducted hand pollinations between randomly chosen individuals within each selection history to produce paternal half-sib families. For the experiment described in this article, we randomly selected among paternal half-sibships for which at least 32 viable seeds from at least two recipients were available.

Late in 1996, seeds to be used in the experiment were placed individually into clear, 96-well cell culture trays. Each tray represented an 8-seed \times 12-seed section of an experimental subplot to be planted in the field, within which seed locations were randomly assigned. Image analysis was used to estimate the cross-sectional area of each seed. Once the field site was ready for planting, seeds were induced to germinate by a short exposure to 1,000 ppm gibberellic acid. Six days before planting into the field, treated seeds were transplanted from cell culture trays into plug flats filled with Pro-Mix (Premier Horticulture, Quebec) and kept in a greenhouse, still in their randomized positions. We recorded the day on which each seedling emerged (March 4–10, 1997), and on March 7–9, we transplanted young seedlings (or in some cases, unemerged seeds) within their plugs into the prepared field site.

Design of the field experiment. The experiment was established in a fallow field on the University of California, Davis, campus. Extremely wet conditions caused by an strong El Niño event delayed soil preparation and transplanting of experimental seedlings until early spring, by which time nearby populations of *S. arvensis* seedlings had been growing for 2–3 months. The result of this delay was that our plants experienced hotter-than-average conditions during early life stages, although flowering in our plots

overlapped broadly with that in local populations of *S. arvensis*.

Two levels of light and of conspecific density were assigned within a replicated split-plot design, with light level as the full-plot factor and density as the subplot factor. After we tilled the ground thoroughly, two blocks were designated on the eastern and western sides of the field. Each block was divided into two 10 × 20-m plots separated by ~3 m. A metal hoop frame was erected over the northern plot in each block and then covered with a neutral shade cloth that blocked 60% of direct sunlight. The nonrandom assignment of plots to the two light treatments was necessary to prevent shading of nearby full-sun plots by the ~2.5-m-tall shade canopies. Within each plot, we suppressed weeds with a water-permeable barrier. Small holes (2–3 cm) were burned through the weed barrier to permit planting of experimental *S. arvensis* seedlings at different densities within each subplot: 7-cm spacing in the high-density subplot (232.2 plants m⁻²) and 20-cm spacing in the low-density subplot (36 plants m⁻²). Seeds from all families and selection histories were fully randomized within each subplot. To reduce edge effects on conspecific density, we planted a single row of background seedlings around the perimeter of each subplot. In all, 7,665 experimental seedlings representing 94 paternal half-sib families were included in the experimental design.

As seedlings grew, we continuously monitored their growth, phenology, and symptoms of disease. After El Niño rains subsided, the weather was unusually hot and dry. Based on 100 years of data from California's central valley, the period of March–May 1997 was the third hottest and second driest on record (2.8°C above the mean daily temperature and 7.85 cm below the mean for precipitation; National Climatic Data Center, 1898–1997 data for Fresno). As a result, the partial-shade treatment, which we anticipated to be a stressful environment based on greenhouse studies (Stanton et al. 2000; Steinger et al. 2003), actually provided a respite from heat and drought stress in our experiment. When signs of wilting were observed in the full-sun plots, we used overhead sprinkling to water plants in all plots.

On March 19–20 and again on March 31–April 3, we counted the number of expanded true leaves and measured the length of the longest leaf (in cm) on each individual. We calculated the relative change in leaf number and maximum leaf length as the difference between their log-transformed values recorded at the second and first census, divided by the number of days between measurements. Flowering began on April 2, and surveys were conducted three times per week thereafter to record the day on which each plant produced its first flower. Honeybees were abundant visitors to flowers in the full-sun plots. As flowering began within the shade canopies, we conducted hand pol-

linations haphazardly among reproductive individuals within the same enclosure. In mid-April, once flower densities on shaded plants were great enough to sustain pollinators, we enclosed a small (queen-rearing) hive of honeybees within each shade tent to pollinate the experimental plants.

Twice during the prereproductive growth period, we recorded ordinal scores for disease symptoms on leaves for each living individual, ranging from 0 for plants with no visible leaf lesions to 4.0 for plants with obvious leaf curling and necrosis. The two scores were summed for each plant to calculate a cumulative leaf disease score. Diseased plants in the full-sun treatment, especially at low density, showed lesions typical of infection by *Phytophthora* (IPM Manual Group of the Statewide IPM Project 1992), probably contracted from spores in the soil. In contrast, most diseased leaves in the partial-shade treatment exhibited the purple lesions and abaxial pustules characteristic of infection by *Albugo candidans* (Alexander and Burdon 1984; IPM Manual Group of the Statewide IPM Project 1992). Severity of disease symptoms on reproductive structures (staghead disease caused by *A. candidans*) was scored during peak flowering in each environment, ranging from 0 for no signs of disease to 2.0 for plants exhibiting severely deformed reproductive stems. After plants had matured their fruits in early June, we harvested whole plants. Over the next 2 years, we weighed the viable seeds produced by each individual. The total weight of viable seeds, a direct measure of female fertility, serves as our estimate of lifetime fitness.

Statistical Analyses

Effects of light treatment and intraspecific competition on lifetime fertility. A series of mixed-model analyses based on the split-plot design was used to test for environmental and genetic effects on the lifetime fertility of individual plants. Light level (the whole-plot factor) and density (the subplot factor) were fixed effects in the model, as was selection history (shade stress, control, and original lineages). Block, sire, dam, and all their interaction terms were considered random. Because of unequal variances among treatments (a serious problem for mixed-model analysis), we conducted a weighted ANOVA for testing the effects of fixed and random factors on absolute fitness (Freund et al. 1986; Snedecor and Cochran 1989; Neter et al. 1996). We used weighted ANOVA rather than the log-transformation method commonly used by ecologists grappling with heteroscedastic data. Within treatments, weighted ANOVA does not muddy comparisons between absolute fitness and relative fitness variation and does not change the quantitative relationship between fitness and trait values (also see Stanton et al. 2000).

We first analyzed lifetime fertility (an estimate of absolute fitness) with a split-plot mixed-model ANOVA in the GLM procedure of SAS, using the RANDOM/TEST option for testing hypotheses (Freund et al. 1986). The absolute values of residuals from that analysis were then used as the outcome variable in a second ANOVA of the same structure. This procedure, based on the Levene's test (Levene 1960), identifies the main effects or interactions showing significant heteroscedasticity. For our data, the greatest inequality of fertility variance was associated with the interaction between shading and conspecific density. Next, the inverse of residual variance for each level of this interaction was used to weight each observation in a third analysis of the same design, using the WEIGHT statement in the GLM procedure of SAS (Littell et al. 1996). This procedure accounts for heteroscedasticity in testing hypotheses about sources of variation in lifetime fertility.

Consequences of light level and density for fitness variance and the opportunity for selection. Because fitness variation provides the raw material for natural selection, heteroscedasticity for variance in lifetime fertility is of potential evolutionary importance in its own right, and so we also present results from the Levene's test described previously to focus attention on how environmental treatments and selection history influenced variance in absolute fitness (lifetime fertility). In this analysis and in analyses of the opportunity for selection (next paragraph), we applied the sequential Bonferroni correction (for $\alpha = 0.05$) to determine significance of pairwise differences between levels of light, density, and selection history calculated by the PDIFF option in GLM (Rice 1989).

When trying to document the strength of natural selection, it is variance in relative fitness that is of primary interest, and so we detail here how Levene's test was used to compare the opportunity for selection among environments. To analyze effects of light and density on the opportunity for selection among individuals, we first calculated mean individual fertility within each of the four light and density treatments, and we then computed each plant's relative fitness within that environment as its own fertility divided by the treatment mean. Fitness was relativized to treatment means rather than to the grand mean across all treatments because our aim was to compare the opportunity for selection among populations experiencing these alternative environments rather than to evaluate relative fitness in a single population occupying an environment heterogeneous for light and density. Individual relative fitness was used as the outcome variable in the same mixed-model ANOVA used previously for absolute fertility. The residuals for relative fitness were output from the analysis, and the absolute values of those residuals were then used as the outcome variable in a second ANOVA model of identical design. Significant effects of treatment

on residual variance in this second ANOVA indicate differences in the opportunity for selection between treatments and/or selection histories.

Because variance in relative fitness among individual plants is likely to be influenced by both genetic and environmental heterogeneity, we also measured the effects of treatments and selection histories on additive genetic variance in relative fitness. Within each subplot, we first calculated the mean fertility for each of the 94 paternal half-sib families and from those family means calculated mean fertility within that subplot. The relative fitness of each family within each subplot was then calculated and used as the outcome variable in a split-plot ANOVA model with light, density, and selection history as fixed factors and block (and the block \times light interaction) as random factors. Absolute values of residuals from this analysis were used as the outcome variable in a second ANOVA of the same design in which significant effects indicate significant variance in relative fitness among paternal half-sib families.

Genetic variation for phenotypic traits in contrasting environments. To estimate the effects of light level and conspecific density on heritability for lifetime fertility and for life-history traits, we used the VARCOMP procedure in SAS (SAS 1999) to obtain restricted maximum likelihood estimates for components of phenotypic variance. Within each combination of light and density, we conducted two analyses for lifetime fertility and for nine phenotypic traits measured on each individual. In the first analysis, variance components were estimated for selection history, sire nested within selection history, and dam nested within sire and selection history. In the second analysis, selection history was excluded from the analysis. In each analysis, heritability was estimated as four times the proportion of phenotypic variance explained by sire (Lynch and Walsh 1998). Comparing the two estimates indicates the degree to which including plants from different selection histories in the study population increased additive genetic variances.

Consequences of shading and density for patterns of genotypic selection. Within each treatment, we calculated the mean relative fitness and mean phenotype values for each paternal half-sibship and then used the REG procedure in SAS (SAS 1999) to regress the relative fitness of families on their standardized mean trait values (Lande and Arnold 1983). The partial regression coefficients from this analysis estimate the linear gradients for directional selection on the breeding value of each trait, reducing effects of environmentally mediated covariance between phenotype and fitness that may complicate interpretation of a purely phenotypic selection analysis (Rausher 1992). Selection gradients deemed significant were those for which the 95% confidence intervals, based on 1,000 bootstrapped resamplings of the data within each combination of light and

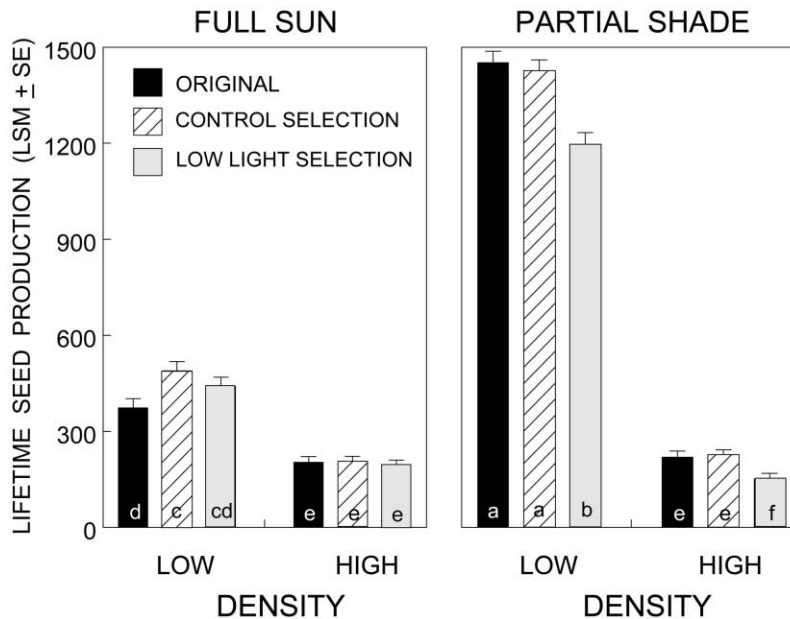


Figure 1: Effects of shading, conspecific density, and selection history on lifetime fertility in *Sinapsis arvensis*. Plants from three experimental selection histories (*original*, *control*, and *low light* [shade stress]) were grown under two levels of light and at two densities in the field. Fertility values not sharing the same letter are significantly different at $\alpha = 0.05$, corrected for multiple pairwise comparisons across all environments and selection histories. Least square means and standard errors were estimated using the REML option of the MIXED procedure in SAS, based on the split-plot model structure shown in table 1. Sample size for standard errors ranged from 621 to 651.

density, did not include 0. A full analysis of nonlinear genetic selection gradients would have included 90 quadratic terms (Lande and Arnold 1983), which was impractical for this data set. In a partial exploration, we found no significant nonlinear selection on traits under direct selection.

We used three methods to compare patterns of directional selection among treatments. First, to test for significant heterogeneity in direct selection across all combinations of light and conspecific density, we conducted an ANCOVA that included paternal half-sibship means for each trait within each light/density treatment, treatment as a class variable with four levels, and all trait-by-treatment interactions. Second, we calculated Pearson's product-moment correlation between the nine selection gradients measured in pairs of treatments, comparing correlations across densities within each light level and then within light levels at each conspecific density. Selection gradients are not independent within or between treatments, and so we use these correlations to summarize similarity in selection across treatments but do not test their statistical significance. Third, to determine whether competition intensifies directional selection in less stressful environments, we compared selection gradients measured at high and low density in the two light regimes. This

comparison was relatively straightforward because conspecific density typically affected the magnitude rather than the sign of direct selection. First, we expressed the selection gradient for each trait in each experimental environment as its absolute value. Then, within each light treatment, we subtracted the absolute selection gradient for each trait measured at low conspecific density from that measured at high density. A positive value for this difference (D_C) indicates stronger direct selection with increased intraspecific competition.

Genetic correlations within and between environments. For each trait within each experimental environment, we used derivative-free restricted maximum likelihood (MTDFREML; Boldman et al. 1995) to derive a best linear unbiased predictor for the breeding value of each sire. The model included both block and dam information. We estimated genetic correlations from the Pearson product-moment correlations between sire breeding values for each pair of phenotypic traits within a treatment. Similarly, cross-environment genetic correlations for fitness were estimated from product-moment correlations of sire breeding values for lifetime fertility between each pair of the four experimental treatments. A genetic correlation was deemed statistically significant if, based on analysis of

Table 1: Environmental and genetic effects on lifetime fertility in *Sinapis arvensis* grown under full sun or partial shade at two densities in a replicated split-plot design

Source of variation	Numerator df	Denominator df	F	P
Light	1	15.0	508.92	<.0001
Density	1	91.7	1,177.79	<.0001
Light × density	1	92.0	747.68	<.0001
Selection treatment	2	91.4	3.79	.0262
Light × selection treatment	2	91.6	7.06	.0014
Density × selection treatment	2	91.5	1.98	.1440
Light × density × selection	2	91.7	4.08	.0201
Block	1	1	.04	.8803
Block × light	1	6,624	1.89	.1696
Sire (selection treatment)	91	56.7	1.43	.0749
Sire × light	91	88.8	1.13	.2852
Sire × density	91	82.8	1.35	.0842
Sire × light × density	91	157.1	2.20	<.0001
Dam (sire selection treatment)	156	83.7	1.20	.1769
Dam × light	156	156	1.30	.0518
Dam × density	156	156	1.18	.1500
Dam × light × density	156	6,624	.87	.8700

Note: Because treatments resulted in dramatic inequality of fitness variances (table 2), each observation was weighted by the inverse of residual fertility variance within each level of shading and conspecific density. Light level is the full-plot factor, so only its interactions with block are included in the model. The weighted analysis was conducted using the RANDOM/TEST statement within the GLM procedure in SAS (Littell et al. 1996; SAS 1999) to account for random factors in the model.

1,000 bootstrapped resamplings of the data, its 95% confidence intervals did not overlap with 0.

Expected evolutionary change in life-history traits. To predict how selection in each combination of light and density would change trait values across generations, we estimated direct genetic selection differentials in each environment as the covariance between the relative fitness of a paternal half-sibship and its mean value for a given trait (expressed in units of standard deviation from the trait mean within that treatment; Lande and Arnold 1983). These differentials predict the magnitude and direction of change in that trait from the current to the next generation, accounting for patterns of genetic variance and covariance (reviewed in Rausher 1992) and assuming that counteracting selection does not occur during the postdispersal seed stage. Differentials within each environment were deemed significant if their 95% confidence intervals, derived from 1,000 bootstrapped resamplings of the data, did not overlap with 0. As a rough indication of how strongly manipulations of conspecific density or light level change predicted patterns of trait evolution, we calculated product-moment correlations for the nine selection differentials measured between pairs of treatments. To test the hypothesis that competition has a greater impact on trait evolution in less stressful environments, we measured how increasing conspecific density changed the predicted rate of trait evolution in the full-sun versus the partial-shade envi-

ronment. Within each light treatment, we subtracted the absolute selection differential measured for each trait at low density from that measured at high density; a positive value for this difference (D_D) predicts more rapid evolution of that trait with increased intraspecific competition.

Results

Effects of light level, intraspecific competition, and selection history on lifetime fertility. Under the unusually hot conditions from March through May, plants in partial shade had much greater reproductive potential than those in the full-sun treatment (fig. 1). At low conspecific density, average lifetime fertility in the partial shade was approximately three times that in full sun, giving rise to a highly significant main effect of light treatment on seed production (table 1). Plants in the full sun experienced substantial levels of heat and drought stress. Average midday soil and air temperatures were significantly higher in the full-sun treatment (soil: 24.96°C vs. 19.37°C, $F = 77.00$, $df = 1, 21$, $P < .0001$), and plants in the full sun inevitably wilted before those under the shade canopies between supplemental waterings.

Consequences of light environment for the intensity of competition. Greater conspecific density significantly reduced mean fitness in both light regimes, but the intensity of competition was much greater in the partial-shade treat-

ment than in the more stressful full-sun treatment. In full sun, increasing conspecific density reduced mean individual fertility by 53.1%. In partial shade, the same increase in conspecific density reduced lifetime fertility by 95.5% (fig. 1), generating a highly significant interaction between light and density in affecting lifetime fertility (table 1).

Consequences of treatments for fertility variance and the opportunity for selection. We observed a strong, positive correlation between mean fertility and the variance in fertility across environments. In both full sun and partial shade, increased competition resulted in significant decreases in absolute fitness variance among individual plants, mirroring decreases in mean individual fertility (cf. figs. 1, 2A). The Levene's test indicated that variance in lifetime fertility (absolute fitness) was significantly affected by density and by the interaction between light and density (table 2). Averaged over density treatments, light level alone did not significantly change variance in lifetime fertility.

Our results demonstrate that greater variance in lifetime fertility does not imply more intense or effective natural selection. Based on relative fitness variation, the opportunity for selection among individuals (fig. 2B) and among paternal half-sib families (fig. 2C) was strongly influenced by light and/or its interaction with conspecific density (table 2) but was not correlated with variance in absolute fertility (fig. 2A). For example, whereas variance in individual lifetime fertility was greatest for plants grown in partial shade at low density (fig. 2A), the variance in relative fitness among individual plants (fig. 2B) and among paternal half-sib families (fig. 2C) was least in this treatment. The effect of conspecific density on the opportunity for selection was dramatically reversed in the two light environments. Under less stressful partial-shade conditions, greater intraspecific competition tripled variance in relative fitness among individuals, and a nonsignificant effect of similar magnitude was observed for variance among paternal families. In the full-sun treatment, increased conspecific density reduced the opportunity for selection among individuals by 20%–35% and among paternal families by as much as 75%. Plants derived from the original seed stock exhibited reduced levels of among-family variance in relative fitness in the stressful full-sun treatment compared with those from shade stress and control selection histories (fig. 2C).

Effects of selection history on variation in phenotype and fitness. Levels of additive genetic variation within the experimental population were enhanced by including families from different greenhouse selection histories. Averaged across all traits and all levels of light and conspecific density, heritability estimated from the proportion of all variance attributable to sire increased by approximately 15% when all paternal families were pooled without regard

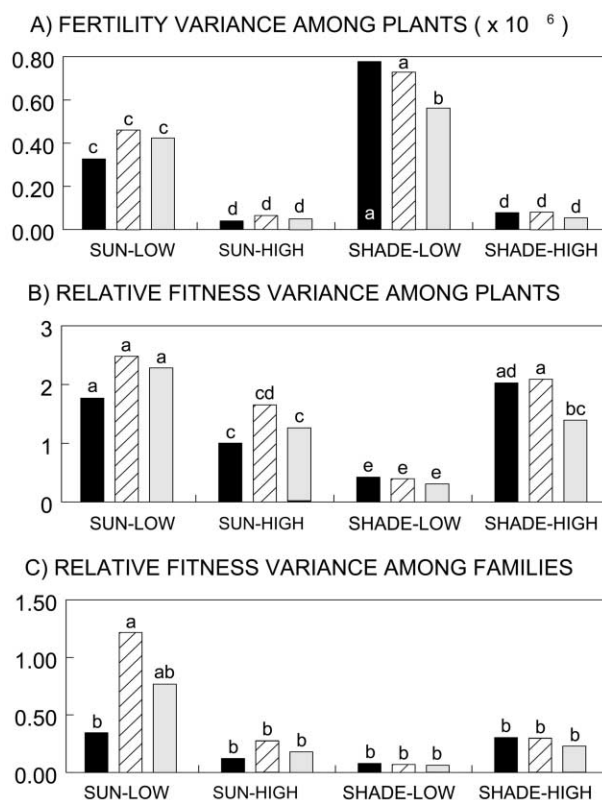


Figure 2: Effects of shading, conspecific density, and selection history on variance in absolute fertility and on the opportunity for selection in *Sinapsis arvensis*. A, Variance in lifetime seed production indicates absolute fitness variation among individual plants (sample size range: 621–651). B, Variance in relative fitness among individuals reflects the opportunity for phenotypic selection (sample size range: 621–651). C, Variance in relative fitness among paternal half-sibships indicates selection among genotypes (sample size range: 166–168). Treatments are abbreviated; for example, SUN-LOW represents full sun at low density. Raw variances are shown. Bar colors represent different selection histories, as in figure 1. Groups not sharing the same letter have significantly different variances at $\alpha = 0.05$, corrected for pairwise comparisons among all treatments and selection histories.

for their selection history (table A1 in the online edition of the *American Naturalist*). In a few instances, the enhancing effect of selection history on heritability estimates was substantial, but the correlation between the two heritability estimates was very high for all traits across the experiment as a whole (Pearson's $r = 0.993$). Because the inclusion of families from different selection histories influenced patterns of inheritance quantitatively but had similar effects across environments, our subsequent analyses take advantage of the increased statistical power provided by examining variation among all sires, pooled across the three selection histories.

Past selection history had modest but significant impacts

Table 2: Effects of shading, conspecific density, and selection history on variance in absolute and relative fitness measures in *Sinapis arvensis*

Source of heteroscedasticity	Variance in absolute fitness among individuals <i>P</i>	Variance in relative fitness among individuals <i>P</i>	Variance in relative fitness among paternal families <i>P</i>
Light	.0713	<.0001	.3437
Density	<.0001	.0534	.1014
Light × density	<.0001	<.0001	<.0001
Selection treatment	.1346	.1166	.0344
Light × selection treatment	.0095	.0676	.0224
Density × selection treatment	.9774	.0780	.5630
Light × density × selection	.1062	.9111	.5620
Block	.4013	.1826	.5249
Block × light	.0051	.3730	.0005
Sire (selection treatment)	.1640	.2481	
Sire × light	.3497	.1365	
Sire × density	.3060	.2057	
Sire × light × density	.0736	.3955	
Dam (sire selection)	.8262	.7689	
Dam × light	.2067	.3716	
Dam × density	.2003	.3157	
Dam × light × density	<.0001	<.0001	

Note: Absolute fitness for each plant was estimated as the total weight of viable seeds produced over its lifetime. Each plant's relative fitness was calculated by dividing its lifetime fertility by the mean fertility for all plants within that combination of shading and density. To allow for the split-plot model structure, relative fitness for each paternal half-sibship was calculated by dividing the mean fertility of its members within a given treatment block by the mean fertility of all plants within that treatment block. To conduct a Levene's test for variance inequality, a split-plot ANOVA was first conducted on each of these three fitness measures, and then the absolute residuals from each analysis were reanalyzed using the same statistical model. For analyses of individual fitness values, block, sire, dam, and all their interactions were treated as random effects. In analyzing relative fitness variance among paternal half-sib families, block was the only random factor included in the model. Probability values are from the GLM procedure in SAS, using the RANDOM/TEST option to account for the mixed-model ANOVA structure.

on plant responses to the experimental treatments. Overall, plants from the low-light stress selection history had significantly reduced lifetime fertility compared with those from the control selection history or from the original seed stock (fig. 1). As indicated by significant interactions between selection history and light level (table 1), this fitness disadvantage of plants from the low-light stress selection regime was seen primarily in the less stressful partial-shade environment (fig. 1). Plants from the control greenhouse selection regime generally performed similarly to those one generation removed from the original *Sinapis arvensis* population.

Effects of light level and conspecific density on the genetic architecture of life-history traits. A central goal of this study is to describe how experimental treatments modified direct selection on, and the predicted evolution of, life-history traits in *S. arvensis*. The relationship between directional selection and the evolutionary response to selection depends on genetic variances and covariances among traits (Lande 1979; Lande and Arnold 1983). Accordingly, although the C-S-R and resource-ratio models make no explicit predictions about environmental effects on patterns

of genetic variance, we briefly summarize how light and intraspecific competition altered the genetic architecture of focal traits in our experimental population.

In both partial-shade and full-sun environments, heritability for lifetime fertility was decreased by 60%–70% at high levels of conspecific density, compared with that in the low-density treatment (table A1). Reduced heritability for fertility at high density helps explain why variance in relative fitness among paternal half-sib families tended to diminish in the high-density treatment compared with variance in relative fitness among individuals (cf. fig. 2B, 2C).

Heritability for most of the phenotypic traits showed modest sensitivity to light and density treatments (table A1), but the pattern of change varied among traits. There was very substantial additive genetic variation for the days to first flower and for leaf number at the first census in all light and density treatments (also see Stanton et al. 2000). Additive genetic variance for the length of the longest leaf increased at high density, especially in the full-sun treatment. Heritability estimates for leaf disease scores and *Albugo* staghead disease scores were negligible in the

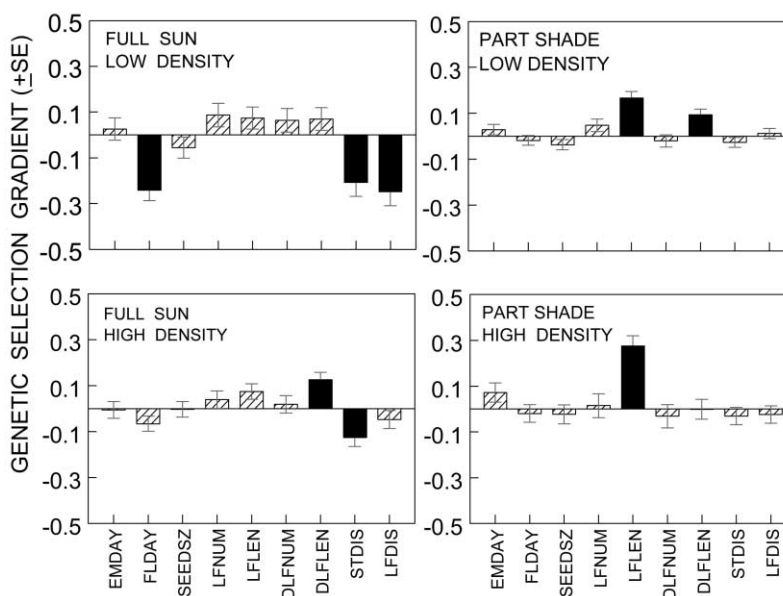


Figure 3: Linear genetic selection gradients for nine traits at different levels of shading and conspecific density. Within each experimental environment, gradient estimates and standard errors were obtained by regressing mean relative fitness within each paternal half-sibship on mean standardized trait values for that family. Gradients shown to be statistically different from 0, based on 1,000 bootstrapped replications, are distinguished as black bars. Trait abbreviations are as follows: *EMDAY* = days from planting to emergence; *FLDAY* = days from planting to first flower; *SEEDSZ* = estimated cross-sectional area of the seed; *LFNUM* = number of expanded true leaves at first census; *LFLEN* = length of the longest leaf at the first census; *DLFNUM* = relative change in leaf number between the first and second census; *DLFLEN* = relative change in length of longest leaf between the first and second census; *STDIS* = *Albugo* staghead disease score for reproductive parts; *LFDIS* = cumulative score for leaf disease symptoms.

partial shade but were relatively high in the full-sun treatment, especially at low density. Heritability for days to emergence and seed size were uniformly low.

Genetic correlations between some traits were relatively consistent in all four experimental environments (table A2 in the online edition of the *American Naturalist*). As expected from their mathematical interdependence, the length of the longest leaf at the first census was negatively correlated with the relative change in leaf size by the second census. This same pattern occurred for leaf number and relative change in leaf number. Other correlations seemed to reflect ecological associations. Families represented by larger seeds tended to emerge later. Later emergence, in turn, was consistently associated with reduced early leaf size and, to a lesser extent, with production of fewer leaves by the first date on which leaves were counted.

For other sets of traits, light level and/or conspecific density substantially changed the magnitude and even the direction of genetic correlations among them (table A2). In the full-sun treatment, there was a strong positive genetic correlation between a family's mean leaf disease score and *Albugo* staghead disease score, indicating that these two traits would be unlikely to evolve independently. In contrast, the genetic correlation between these traits was

negligible in the partial-shade treatment. At both densities in the full sun, the genetic correlation between length of the longest leaf and leaf number was nearly 0, indicating the potential for these two vegetative characters to evolve quite independently. In contrast, in the partial-shade treatment, selection for families with large leaves would consistently result in correlated selection for greater numbers of leaves. In the full-sun treatment, but not in the shade, families that flowered earlier had significantly faster rates of leaf proliferation and a tendency toward increased leaf and staghead disease symptoms.

Effects of light and conspecific density on the direction and magnitude of genotypic selection. Patterns of direct genotypic selection on several traits varied as a function of light level and conspecific density (fig. 3). ANCOVA indicated that the four treatments significantly changed directional selection on days to first flower ($F = 8.37$, $df = 3, 375$, $P < .0001$), the length of the longest leaf at first census ($F = 6.37$, $df = 3, 375$, $P = .0003$), leaf disease score ($F = 6.64$, $df = 3, 375$, $P < .0002$), and *Albugo* staghead disease score ($F = 4.02$, $df = 3, 375$, $P = .0079$). Decreasing direct sunlight exposure by 60% changed directional selection on the focal traits more than did our more than sixfold manipulation of con-

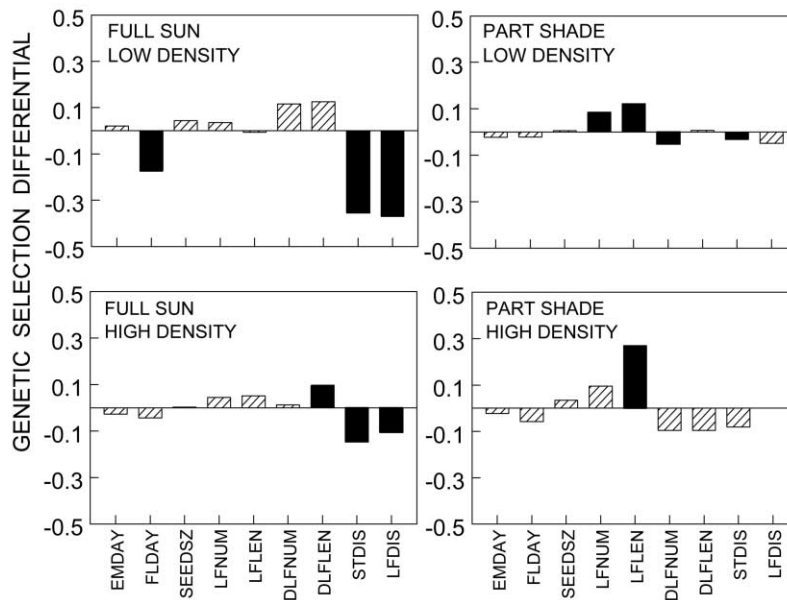


Figure 4: Genetic selection differentials for nine traits at four different levels of shading and conspecific density. Within each experimental environment, differentials were calculated as the covariance between the mean relative fitness of each paternal half-sibship and the standardized family mean for a given trait. Differentials shown to be statistically different from 0, based on 1,000 bootstrapped replications, are distinguished as black bars. Trait abbreviations are explained in the legend for figure 3.

specific density. In the partial shade, direct selection gradients for the nine traits were highly correlated across densities ($n = 9$ traits; $r = 0.868$), and the same was true across densities in the stressful full-sun treatment ($n = 9$ traits; $r = 0.898$). In contrast, correlations between selection gradients measured within the contrasting light regimes were relatively low at both high ($n = 9$; $r = 0.320$) and low ($n = 9$; $r = 0.355$) conspecific densities. Reversals in the direction of direct selection were rare between treatments (fig. 3). In the full-sun treatment, increased conspecific density tended to reduce the strength of directional selection (for nine gradients, high density–low density: mean $D_G = -0.063$), but density had little impact on selection gradients in the partial-shade treatment (mean $D_G = 0.004$).

Quantitative patterns of selection on genetically based trait variation differed markedly between the stressful full-sun environment and the partial-shade environment. Selection for families that flowered earlier was stronger in full sun than in partial shade and was statistically significant only at low density in the full sun. Selection against families with high cumulative disease scores was far stronger in the stressful full-sun environment. In the partial shade, there was strong selection for families that had produced large leaves by our first census, especially in the high-density treatment. In the full sun, direct selection for early large leaves was positive but not significant at either

density. Families that more rapidly increased maximum leaf size were selected for in the full-sun treatment, but this was only significant at high density. In contrast, significant genotypic selection for rapid increase in leaf size was seen in the partial shade at low density, but not at high density.

Expected evolutionary change in characters under selection. The predicted changes in trait values across generations, as estimated by genetic selection differentials, were similar (but not identical) to the patterns of direct genotypic selection we measured in the four experimental environments (cf. figs. 3, 4). Under these conditions, selection should result in an evolutionary shift toward earlier flowering in the full sun at low density. Across generations, selection in the full-sun regime would also be expected to decrease susceptibility to disease, especially in the low-density treatment. The strong, positive genetic correlation between leaf and staghead disease scores in the full-sun environment reinforces the effects of direct selection on those two traits, helping to overcome unfavorable genetic correlations with days to flowering (table A2; fig. 3). Similarly, the strongly positive genetic correlation between leaf number and leaf length in the shaded environment should result in an evolutionary increase in both traits, even though direct selection is significant only for increased leaf length. Patterns of genetic correlation appear to limit the evolutionary response of relative change in leaf length to

Table 3: Estimated genetic correlations for fitness across two levels of light and intraspecific density in the field

	Full sun, low density	Full sun, high density	Partial shade, low density
Full sun, high density	.510		
Partial shade, low density	.267	.474	
Partial shade, high density	.117	.344	.506

Note: Product-moment correlations are shown, based on best linear unbiased predictors of breeding value for the lifetime fertility of 94 sires, whose half-sib progeny were split among the four experimental environments. Correlations shown to be statistically significant by bootstrapping are in bold.

significant direct selection on this trait in the partial shade at low density.

Light levels had greater effects on predicted patterns of trait evolution than did conspecific density treatments. Measuring the correlation between genetic selection differentials across light treatments suggests that different life histories would tend to evolve in the full-sun and partial-shade environments (for nine selection differentials, Pearson's $r = 0.36$ and 0.32 across light levels in the low- and high-density treatments, respectively). In contrast, changes in conspecific density had little impact on the qualitative responses of these traits to selection (Pearson's $r = 0.87$ and 0.90 for selection differentials across densities within the partial-shade and full-sun treatment, respectively).

Overall, increased conspecific density had a greater impact on predicted trait evolution in the partial-shade treatment than in the stressful full-sun treatment. On average, increasing density in the full sun reduced the predicted magnitude of trait evolution (for nine traits, mean $D_D = -0.079$), whereas increasing density tended to accelerate trait evolution in the partial shade (mean $D_D = 0.040$).

Genetic correlations for fitness across environments. We found no evidence for genetically based fitness trade-offs between the levels of light and intraspecific density used in our experiment. Estimated genetic correlations for fertility were positive across all treatments and were statistically significant in all pairwise treatment comparisons except between full sun at low density and shade at high density (table 3). It is this same treatment pair for which patterns of predicted trait evolution were least correlated (for nine selection differentials, Pearson's $r = 0.11$).

Discussion

The distinct life-history strategies that characterize plant communities occupying habitats that vary for levels of disturbance, environmental stress, and competition are likely to arise via two processes: species replacement and environment-specific adaptation within species (e.g., McGraw and Chapin 1989; Poorter 1990; Taylor et al. 1990;

Tilman 1993). In this study, we investigate the latter of these processes by comparing the evolutionary impacts of contrasting environments on *Sinapis arvensis*, a ruderal species that is amenable to ecological manipulation and genetic analysis. In addition to contrasting the ecological and evolutionary impacts of light and intraspecific competition, we discuss the extent to which our findings support alternative models of plant life-history evolution that make contrasting predictions about how environmental productivity and competition interact to change selection on plant life-history traits (Grime 1977; Tilman 1988).

The intensity of competition does not necessarily predict the intensity of selection. Because of the unusually hot and dry conditions under which our field experiment was conducted, partial shade provided much more favorable conditions for growth than did full sun. The intensity of competition, measured as both the absolute and proportional decrease in average fertility at high density, was much greater in the productive, partial-shade treatment than in the more stressful full-sun treatment (fig. 1). Results of this type have been used to argue that competition is a more important force shaping plant life histories within communities characteristic of productive habitats, as assumed in the C-S-R model (Wilson and Keddy 1986; Kadmon and Shmida 1990; Campbell and Grime 1992). We caution that extending this ecological interpretation to life-history adaptation within species is premature unless supported by genetic analysis.

The dramatic impacts of shade and density treatments on average lifetime fertility of *S. arvensis* were mirrored by treatment effects on variance in absolute fertility among individuals (fig. 2A). In the absence of explicit genetic data, increased fertility variance might be construed as indicating greater potential for evolutionary change. In contrast to this expectation, we found that the environment causing the greatest variance in absolute fertility among individuals (low density in partial shade) also resulted in the least opportunity for selection (fig. 2), as defined by variance in relative fertility among individuals or among paternal half-sibships (Arnold and Wade 1984). The heritability of lifetime fitness decreased with greater conspecific density

in both light treatments (table A1), and experimental treatments also changed patterns of genetic correlation between traits (table A2). When environments change patterns of selection as well as the architecture of genetic variation, the evolutionary impact of increased competition cannot be predicted simply by comparing the ecological intensity of competition in environments of varying productivity.

Past selection under abiotic stress reduces fitness under more competitive field conditions. Selection history had a significant impact on the responses of *S. arvensis* to light and density treatments. Lineages that had undergone three generations of selection in the greenhouse under shade stress had significantly reduced lifetime fertility under the less stressful partial-shade treatment, compared with control selection lines and families from the original seed stock (table 1; fig. 1). Performance of shade-selected and control lineages were indistinguishable in the full-sun treatment, where drought stress was apparent. This pattern provides some support for the C-S-R model (Grime 1977), in that selection under shade stress significantly reduced the ability of those lineages to exploit partially shaded field conditions that promoted luxuriant growth.

Light regime changed directional selection on traits more than did changes in conspecific density. Our experimental manipulations of shading and conspecific density significantly altered patterns of directional selection on genetically based trait variation (fig. 3). Genetic selection gradients for nine traits were more highly correlated between high and low conspecific densities (Pearson $r = 0.836$ – 0.839 for the two light levels) than between the full-sun and partial-shade environments (Pearson $r = 0.434$ – 0.557 for the two levels of density). This finding is broadly consistent with a basic assumption of the resource-ratio mode, namely, that changes in the ratio of above-versus belowground resources rather than changes in the level of competition per se select for contrasting life histories in productive versus infertile habitats.

Competition had a greater net impact on predicted trait evolution in the more productive partial-shade environment. Comparing genetic selection differentials across environments (fig. 4) showed that increasing density tended to increase the rate at which our nine focal traits should evolve in the partial shade ($\bar{x}_D = 0.040$), whereas increasing density slowed adaptive character change in the full sun ($\bar{x}_D = -0.079$). This finding is in accord with a fundamental prediction of the C-S-R model, namely that competition should have a greater impact on plant life-history evolution in productive habitats than under chronically stressful conditions (fig. 3). The greater evolutionary impact of increased density in the partial-shade treatment was due principally to more intense directional selection for large early leaves.

Contrary to what one might predict based on either the

C-S-R or resource-ratio models for plant life-history evolution, we found no evidence for genetically based trade-offs in performance across these levels of shading and competition. Although some selection gradients changed significantly across treatments, our manipulations of light and conspecific density principally changed the magnitude rather than the sign of directional selection on focal traits (fig. 3). Accordingly, genetic correlations for fitness were all positive and mostly significant across pairs of treatments (table 3; also see Richards 1978; Schmitt 1993; Shaw and Platenkamp 1993; Andersson and Shaw 1994).

Effects of light and competition on the predicted evolution of specific life-history traits: direct selection, genetic architecture, and predicted change. Some theoretical models predict that increases in the ratio of belowground to aboveground resources, as tend to occur during secondary succession, will favor plant species with greater proportional allocation to shoots and leaves (Tilman 1988; Rees and Bergelson 1997). Extrapolating from this community focus to the process of life-history adaptation within species (e.g., Givnish 1986) leads to a prediction that environments with reduced light levels will select for genotypes that excel in competition for light. Our shading treatment created an opportunity to examine this prediction. Light was abundant in the full-sun plots, but the frequent wilting of plants in that treatment indicated that soil moisture was scarce. Direct sunlight was reduced by 60% in the partial-shade treatment, but soil temperature was lower and drought stress conspicuously less than in the full sun.

The patterns of predicted trait evolution we observed in the partial-shade treatment were largely consistent with the resource-ratio model but were also influenced by environmental changes in the genetic architecture of life-history traits. Genetic selection differentials indicate that increases in the number of leaves produced early in development should evolve under the partial-shade regime, along with early allocation to larger leaves, especially at high conspecific density (fig. 4). Producing large leaves early may allow these rosette-forming plants to capture photons at the expense of their near neighbors (Lantinga et al. 1999). There was also strong directional selection for rapid increases in leaf length over time in the partial shade at low density (fig. 3), but the evolutionary response of this trait is constrained by its strong negative genetic correlation with early leaf size (fig. 4; table A1).

In contrast to the partial-shade environment, selection differentials for early leaf size were negligible in the stressful full-sun treatment at both high and low densities (fig. 4). Patterns of genetic correlation appear to constrain the predicted evolution of large early leaves despite direct selection favoring this trait under full-sun conditions (fig. 3). For example, at low conspecific density, where pathogens had the greatest selective impact, families with large

early leaves also showed more symptoms of *Phytophthora* infection (leaf disease score, table A1). Many plants responded to full sun at high density by producing relatively horizontal rosette leaves that were close to the ground. Larger rosette leaves may have been more susceptible to pathogens because of heat stress and/or greater exposure to soil-borne pathogen spores. In contrast to early leaf size, more rapid increases in leaf size with age were not genetically associated with greater susceptibility to pathogens and would be predicted to evolve in the full-sun treatment, especially at high conspecific density (fig. 4).

To the extent that seedlings from large seeds are more competitive for above- or belowground resources, both the C-S-R and resource-ratio models might predict the evolution of larger seeds in productive habitats where plant densities are high. Many ecological studies have shown that large seed size can confer a competitive advantage in fertile habitats (Stanton 1984; Wulff 1986; Turnbull et al. 1999). However, seed size showed little evolutionary change in response to increased intraspecific competition in our experiment (fig. 4), reflecting low heritability for seed size variation as well as a consistently positive genetic correlation between large seed size and late emergence date (table A2).

We documented much stronger selection for resistance to pathogens in the stressful full-sun environment than in the more productive partial-shade treatment (fig. 3), lending support to the view that the evolutionary impact of natural enemies may be increased under conditions of chronic abiotic stress (Grime 1979; Coley et al. 1985; De Jong 1995). The greater expense of replacing lost tissues in unproductive habitats is one reason why reduced vulnerability to natural enemies is expected to evolve in stressful environments. In our study, strong selection for reduced disease susceptibility in the full sun was reinforced by the greater heritability of disease susceptibility in that environment (table A1).

In this experiment and in a previous greenhouse study (Stanton et al. 2000), we found that *S. arvensis* plants grown with minimal competition under environmental stress evolve toward earlier flowering time (fig. 4). This apparent stress-avoidance adaptation contrasts with the pattern of delayed reproduction seen in comparative studies of mostly perennial stress-tolerant species (Grime 1979), providing further support for the idea that short-lived and long-lived plants may evolve alternative life histories under selection imposed by chronic stress rather than converging on a single stress-tolerant strategy (Taylor et al. 1990; Grime 1993). Moreover, we found that selection for earlier flowering in the full-sun treatment was weakened by increasing plant density (fig. 3). Competition may change selection on flowering time if early flowering is genetically correlated with reduced leaf production and/

or height growth (Geber 1990; Dorn and Mitchell-Olds 1991).

Conclusion. Most empirical explorations of plant life-history strategy theory compare the performance of different species under contrasting conditions of disturbance, competition, and/or habitat productivity (Campbell and Grime 1992; Wedin and Tilman 1993; Peltzer et al. 1998; Keddy et al. 2001). These studies reveal patterns and/or mechanisms of species replacement across communities in different habitat types but do not necessarily shed light on how alternative life histories evolve. Changes in either competition (Shaw and Platenkamp 1993; Miller 1995; Shaw et al. 1995; Cheplick 1997) or habitat productivity (Farris 1988) have been shown to change selection on plant traits, but we know very little about how competition and habitat productivity interact to mold life-history characters. Because this interaction is at the core of a continuing debate over plant life-history strategy theory, further study of genetically tractable systems is needed to understand its evolutionary consequences.

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