Evolution, 46(1), 1992, pp. 92–106

LIFE-CYCLE COMPONENTS OF SELECTION IN *ERIGERON ANNUUS*: I. PHENOTYPIC SELECTION

DONALD A. STRATTON[1]
Department of Ecology and Evolution, State University of New York, Stony Brook, NY 11794 USA

Abstract.—The magnitude and direction of phenotypic selection on emergence date and seedling size in *Erigeron annuus* was measured to determine the heterogeneity of selection among sites and the proportion of fitness variance explained by seedling size and emergence date. Three disturbance treatments (open, annual vegetation, perennial vegetation) were imposed to test the hypothesis of stronger selection on seedlings in competitive environments. Selection was most heterogeneous early in the life cycle, with significant spatial heterogeneity in the magnitude of selection on a local scale. The disturbance treatments affected only fecundity selection gradients and selection was strongest in open plots. Significant variation in the sign of selection differentials on emergence date was observed for establishment and fall viability selection episodes; at later stages selection varied in magnitude but not direction. Seedlings in the earliest cohort experienced high mortality during establishment, but increased size and fecundity later in the life cycle. Both stabilizing and disruptive selection on emergence date were observed during establishment, but in general selection was purely directional. At Stony Brook most selection on emergence date operated indirectly through seedling size, whereas at the Weld Preserve direct selection was stronger. There were persistent effects of both seedling emergence date and rosette diameter on adult fitness components, and October rosette diameter explained 18% of the total phenotypic variance in fecundity. Overall, viability fitness components were much more important than fecundity selection. Winter survivorship was the single most important episode of selection.

Key words.—*Erigeron annuus,* fitness, germination date, phenotypic selection, seedling size.

Received July 8, 1990. Accepted June 28, 1991.

In most plant populations, many more seedlings germinate than become established (Grubb, 1977; Cook, 1979) and the seedling stage is often the period of maximum mortality. If seedling mortality is correlated with some phenotypic trait, large shifts in the population mean value of that trait (i.e., selection) may occur during the critical establishment phase of the life cycle. Harper (1977) labels this period the "environmental sieve." Conceivably, selection on seedlings may be strong enough to override conflicting selection pressures in later stages of the life cycle. If seedling characters are correlated with other phenotypes expressed later in the life cycle, selection may indirectly shift the distribution of adult characters not even expressed in seedlings.

Variation in seedling size may be one of the most important determinants of fitness during the early stages of the life cycle. Size hierarchies (skewed size distributions with a few large individuals) develop early and often become more skewed with time, resulting in a disproportionate contribution of zygotes from the few largest individuals (Solbrig, 1981; Cook and Lyons, 1983; Weiner, 1985). Small variations in the timing of germination or in the initial growth rate of seedlings may translate into large fitness differences (Stanton, 1985; Waller, 1985). Thus, seedling size may lock a plant into a position in the fitness hierarchy, so the final fitness distribution may be largely determined by events occurring in the first months of the life cycle.

Several studies have shown the importance of emergence time for seedling survivorship, as well as fecundity and lifetime fitness (Howell, 1981; Lee and Hamrick, 1983). The first seedlings to emerge get a head start on growth and may maintain their relative size advantage, exhibiting increased survivorship and fecundity at later stages of the life cycle (Ross and Harper, 1972; Waller, 1985). In some species early germination decreases viability, creating a tradeoff between size and initial survivorship (Arthur et al., 1973; Marks and Prince, 1981), while other studies have shown directional

---

[1] Present address: Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544 USA.

selection for early germination over all components of fitness (Howell, 1981; Kalisz, 1986; Miller, 1987).

The above studies have shown seedling size to be a trait highly correlated with fitness, and therefore expected to be under consistent positive directional selection. However, the magnitude of selection may vary among environments. In particular, selection on early seedling size may be more intense in dense populations with high intra- or interspecific competition (Shaw, 1986; Schmitt et al., 1987). Large seed size (which in part determines early seedling size) is favored in more closed habitats (Salisbury, 1942) and the magnitude of the seed size advantage increased in experiments with high levels of competition (Black, 1958; Stanton, 1984; Stratton, 1989).

The magnitude and even the direction of selection may not be constant across selection episodes (Clegg et al., 1978; Arnold and Wade, 1984*b*). Characters expressed at the seedling stage may affect some fitness components but not others, or there may be tradeoffs between fitness components. For example, early germination may increase seedling size (ultimately fecundity) but at the cost of increased mortality if there are unfavorable climatic conditions during establishment. By partitioning selection into the component episodes one can expose the critical stages of the life cycle for selection and identify potential life history tradeoffs, even when there is little or no net selection.

It is useful to separate natural selection into two components: the phenotypic covariance between a trait and fitness, which governs changes in phenotypic means within a generation, and the genetic variance for the trait, which allows a response to selection across generations (Lande and Arnold, 1983). The ecological interactions that determine a plant's survivorship, growth rate and ultimate fecundity depend on *phenotypes* and their interaction with the environment. Focusing solely on the mean response of genotypes, while important for evolution, obscures much of the ecological dynamics that determine the reproductive success of an individual. Here I address questions concerning the relationship between seedling phenotypes (germination date and seedling size) and fitness in the common weed *Erigeron annuus*. Specifically, 1) how does selection vary with the competitive environment? Previous data suggest that selection for early seedling size should be stronger in more competitive environments (Stratton, 1989; Schmitt and Erhardt, 1990). 2) Are there critical stages in the life cycle for selection on these traits? (i.e., which components of viability and fecundity most strongly covary with seedling size and emergence date?) Finally, 3) How much of the final variance in relative fitness can be explained by events at the seedling stage? Measurements of genetic variation are presented in a companion paper (Stratton, 1992).

MATERIALS AND METHODS

Erigeron annuus (Asteraceae) is a common early successional weed native to eastern North America. It is classified as a winter annual; seeds typically germinate in August, seedlings overwinter as rosettes and plants bolt and flower the following summer. Some plants do not reproduce first year but instead remain as rosettes until the second or third summer. *Erigeron annuus* is triploid and apomictic, reproducing solely by tiny wind-dispersed seeds. Seed production is high: a single plant may produce as many as 100,000 genetically identical seeds (Stratton, 1988).

The experiment was set up at two sites near Stony Brook, New York, USA. The Weld Preserve (WP) site was an old field, fallow approximately five years, and had a dense cover of primarily *Solidago* spp. The Stony Brook campus site (SB) was an old garden plot dominated by grasses, *Artemesia vulgaris,* and *Daucus carota.* The SB site was more mesic than WP, being partially shaded by an oak forest to the south, and the substrate was less sandy.

Each experimental block consisted of three 1 m^2 plots, each randomly assigned one of three disturbance treatments. The treatments included bare tilled soil ("open"), tilled soil with a sparse cover of summer annuals ("annual"), and natural vegetation with small 10 × 10 cm disturbances ("perennial"). Plots in the open and annual treatments were tilled one week prior to planting. For the annual treatment I transplanted 16 seedlings of *Ambrosia artemi-*

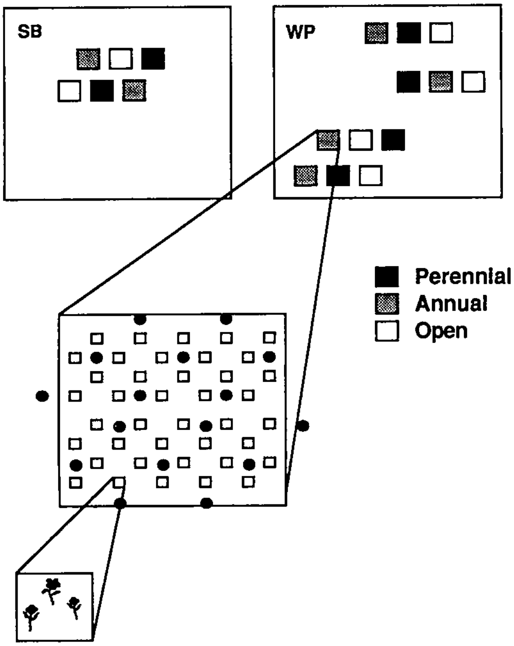

FIG. 1. Summary of the experimental design. Three experimental disturbance treatments (Open, Annual, Perennial) were replicated in six blocks at two sites, Stony Brook and Weld Preserve. Seeds were sown in 40 10 × 10 cm cells within each 1 m^2 plot and several seedlings were measured per cell. The solid circles show the position of *Ambrosia* plants in the Annual plots.

siifolia into the tilled plots immediately after the *Erigeron* seeds were planted (Fig. 1). The *Ambrosia* were about 25 cm tall when transplanted. This treatment resulted in a 50 cm canopy with sparse shade by two weeks after transplanting. During the first week, the open and annual treatments were very similar. In the perennial plots, I clipped the vegetation to 10 cm to facilitate planting but no tilling or whole-plant removal took place. The perennial cover grew back readily. These treatments correspond to conditions experienced by *Erigeron annuus* in successional environments ranging from newly fallow fields to three to five year old successional communities. All can be considered "natural" habitats of *E. annuus*. There were six blocks (4 at WP and 2 at SB) for a total of 18 plots (Fig. 1).

Each plot was divided into 40 10 × 10 cm cells, arranged in a checkerboard design. A plug of soil was removed from each cell and the resulting hole was refilled with autoclaved soil. A small "pinch" (600–900) of seeds was scattered over each cell and lightly covered with soil to help hold the seeds in place. I used seeds from 10 *Erigeron* genotypes, all collected from a large population at the Weld Preserve and there were two replicates of two maternal families of each. See Stratton (1992) for the genetic details. Seeds were planted between 31 July and 2 August 1987, near the end of the normal period of seed dispersal on Long Island. The plots were censused weekly for emergence and survivorship from 15 August to 6 September. Seedlings that emerged during each census week were defined as an emergence cohort. There were four cohorts. A subset of up to 10 seedlings in each cell were marked in each emergence cohort using color coded toothpicks. When more than 10 seedlings in a given cohort emerged, I randomly removed the excess seedlings. Because most of the excess seedlings emerged in cohort 1, thinning increased the variance in emergence date by an average of 13%. After seedlings were established and after most early mortality had occurred, I permanently marked a subset of the surviving seedlings and mapped their location within the cell. An average of three (maximum = four) seedlings in each cell were chosen such that they were approximately equally spaced and evenly divided among cohorts. Again, because initial densities were not controlled, I removed excess seedlings. Seedling removal in October increased the phenotypic variance of emergence date by only 3%.

I measured the maximum rosette diameter of each seedling and monitored survivorship during censuses in October 1987, March, May, July 1988, and April, July 1989. In the July censuses I estimated the seed production of each reproductive plant. Because of the large number of seeds produced per plant (25,900 ± 1,660 in this experiment), I counted the number of flower heads (capitula) on each plant and estimated the number of seeds/capitulum from the disk diameter. The number of florets per capitulum was determined by the equation: florets = 38.9 + 7.27(Disk Area) (in mm^2; $r^2 = 0.81$; Stratton, 1988). The disk diameter increases with the age of the capitulum, so all measurements were made on heads with dehiscent anthers in only the outer two or three whorls of disk florets. Each floret produces one single-seeded achene so, assuming equal seed set, fecundity is proportional to the total number of florets.

Selection Episodes and Fitness Components.—I divided the life cycle into a series of selection episodes that multiplicatively combine to determine lifetime fitness. Viability selection was divided into five components. The establishment episode was defined as emergence through the September census; fall, winter, spring, and second year viability selection episodes cover the periods September–October, October–March, March–July 1988, and July 1988–July 1989, respectively. The divisions are somewhat arbitrary but they correspond to the major phases of the life cycle of *E. annuus* (establishment, winter dormancy, spring growth) and represent periods of distinct environmental sources of mortality. Desiccation was a particularly important source of mortality during the establishment and fall selection episodes whereas frost-heaving was apparently the major source of mortality over the winter. Survivors of a particular selection episode were assigned a fitness value of one, otherwise fitness was zero for that episode. The fecundity component was estimated by the seed production of plants that survived to reproduce. Each replicate 1 m^2 plot was defined as a population for the purpose of computing relative fitness and estimating phenotypic selection.

Most estimates of lifetime fitness were zero because of the large number of plants that failed to survive to reproduction. I discounted the fecundity of second year plants by the population growth rate, using the equation: $w_i = \Sigma\, \lambda^{-x} s_{i(x)} m_{i(x)}$ where w_i is the absolute fitness of individual i, λ is the population growth rate, $s_{i(x)}$ is survivorship (0 or 1) and $m_{i(x)}$ is the fecundity of individual i at time x (Service and Lenski, 1982). I calculated λ separately for each of the 18 replicate plots by population projection of the Leslie matrix (**A**) until the estimates of λ (ratio of population sizes in successive generations) converged within 0.001 (Table 1). The transition matrix was of the form

$$\mathbf{A} = \begin{bmatrix} g \cdot s_1 \cdot r_1 \cdot f_1 & g \cdot s_2 \cdot r_2 \cdot f_2 \\ s_1 \cdot (1 - r_1) & 0 \end{bmatrix}$$

where g is the germination fraction, s is survivorship, r is the probability of reproduction, and f is the fecundity in each year. Fitness was made relative by dividing by the mean fitness in each 1 m^2 plot.

Measuring Phenotypic Selection.—While this experiment primarily focused on the covariance between phenotypes and fitness (descriptive and correlational), the three experimental disturbance treatments tested the hypothesis that the magnitude of directional selection on seedling size should be greater in the plots with high levels of competition (perennial) compared to the open and annual plots. In addition, the replicate plots within sites allowed ad hoc tests for spatial variation in the magnitude of selection between the Stony Brook and Weld Preserve sites.

For each character and for each selection episode I calculated the directional and stabilizing selection gradients from linear and quadratic regressions of relative fitness on the phenotype (Lande and Arnold, 1983). When multiple characters are considered simultaneously, the vector of partial regression coefficients estimates the direct selection on each character while controlling indirect effects of selection on correlated characters. I standardized all characters to unit variance before estimating selection. Standardized selection gradients have the advantage of being directly comparable among populations and characters. Because the seedling phenotypes were not measured simultaneously, the multiple regression approach could not be extended to analyses of lifetime fitness. Multiple regression of fitness on emergence date, October, and March rosette diameter could only include data from individuals that survived through March, thus ignoring earlier selection episodes. Instead the components of lifetime selection were estimated separately and lifetime selection was computed as the sum of selection gradients over all episodes (Arnold and Wade, 1984*a*). Selection gradients were made additive by substituting the initial phenotypic covariance matrix $\mathbf{P}_0$ for the conditional covariance matrix $\mathbf{P}_i$ observed at the beginning of each episode (Wade and Kalisz, 1990). The initial phenotypic covariance matrix was constructed by repeatedly solving for $\mathbf{P}_i$ in the equation

TABLE 1. Demographic parameters used in calculating the population growth rate in the 18 plots. The values of lambda are sensitive to the estimated germination fraction and thus to my estimate of the initial number of seeds planted (600–900/cell). I used the high estimate, but the actual value of λ may be as much as 50% higher. Higher values of λ will further decrease the value of delayed reproduction. N = total number of seeds that emerged per plot (germination fraction = $N/(900*40)$; s = survivorship; r = probability of reproduction, given that it survives through year 1 or 2; f = fecundity; λ = population growth rate.

		Year 1			Year 2			
Site Block	N	s_1	r_1	f_1	s_2	r_2	f_2	λ
Open								
SB 1	1,355	0.041	0.257	4,152	0.75	0.27	6,854	2.32
SB 2	1,246	0.036	0.476	6,216	0.86	0.55	7,220	4.21
WP 3	483	0.025	0.806	66,739	0.57	1.00	20,195	18.06
WP 4	387	0.027	0.829	43,839	0.62	0.80	20,036	10.64
WP 5	669	0.009	0.542	11,656	0.20	1.00	8,705	1.17
WP 6	146	0.009	0.875	47,053	1.00	0.50	13,949	1.54
Mean	714	0.025	0.631	29,943	0.67	0.69	12,826	6.32
Annual								
SB 1	1,187	0.048	0.229	4,572	0.58	0.18	24,241	2.77
SB 2	632	0.022	0.524	6,517	0.87	0.75	10,244	1.95
WP 3	298	0.033	0.971	54,990	1.00	1.00	10,952	14.63
WP 4	713	0.031	0.955	42,318	1.00	0.67	9,962	24.81
WP 5	881	0.004	0.800	6,870	0.67	0.50	6,321	0.61
WP 6	146	0.009	0.750	82,437	0.75	0.33	24,798	2.31
Mean	643	0.025	0.705	32,951	0.81	0.57	14,420	7.85
Perennial								
SB 1	169	0.016	0.143	6,583	0.83	0.60	5,490	0.46
SB 2	320	0.012	0.000	0	0.67	0.50	6,942	0.52
WP 3	643	0.017	0.636	11,534	0.46	0.67	58,541	2.92
WP 4	930	0.047	0.292	13,266	0.83	0.74	15,757	6.07
WP 5	600	0.014	0.000	0	0.21	0.00	0	0.00
WP 6	464	0.011	0.186	5,687	0.76	0.52	12,916	0.84
Mean	521	0.020	0.210	6,178	0.63	0.51	16,608	1.80

$$\mathbf{P}_{i+1} = \mathbf{P}_i + \mathbf{P}_i^{-1}\gamma_i\mathbf{P}_i - (\mathbf{P}_i\beta_i)^{\mathrm{T}}(\mathbf{P}_i\beta_i)$$

where γ is a 3×3 matrix of stabilizing selection gradients and β is a 3×1 vector of directional selection gradients (Lande and Arnold, 1983; Lynch and Arnold, 1988). Note that prior to the third census, γ and β are only partially observed. The unmeasured elements were assumed to be zero, under the assumption that selection can not act directly on characters before they are expressed (Lynch and Arnold, 1988). Given an estimate of $\mathbf{P}_0$, conditional selection gradients, β', were made additive by $\beta_i = \mathbf{P}_0^{-1}\mathbf{P}_i\beta_i'$ (Wade and Kalisz, 1990).

Statistical Analyses.—The distribution of lifetime fitness was highly nonnormal, having a large excess of individuals with zero fitness. Similarly, survivorship could only assume values of 0 or 1, violating the normality assumption of regression analysis. Thus, significance levels for selection differentials and selection gradients were computed from 1,000 bootstrap replications of the simple or multiple regression (Efron, 1982). The data were randomly resampled with replacement 1,000 times from the original distribution, restandardized, and used to compute new regression coefficients. I used the upper and lower 2.5% of the distribution of bootstrapped estimates to find the 95% confidence intervals for the selection gradients. Individual selection gradients were considered to be significant if their 95% confidence intervals did not include zero. Because there is a high probability that at least one of 18 selection gradients will be nominally significant during each episode, experimentwise error was controlled using the sequential Bonferroni method (Rice, 1989).

Overall significance of the selection gradients across the entire range of environments was tested via nonparametric signed ranks tests, using values from the 18 plots as observations. Even when individual estimates cannot be distinguished from zero, consistency of the sign of selection gradients provides evidence that selection is nonzero, and tests for repeatability of selection across environments.

Heterogeneity of selection was tested by drawing 300 bootstrap samples for each pair of plots and computing the difference for each bootstrap replicate. The two selection gradients were significantly different if the bootstrap confidence interval of the difference did not include zero (Dixon et al., 1987). The proportion of the 153 pairwise comparisons that were significantly different was used as an overall index of the heterogeneity of selection during a given episode. To correct for multiple comparisons, heterogeneity of selection was only considered significant when at least 12/153 pairs had nonoverlapping confidence intervals (from binomial probability; $P = 0.95$; $N = 153$). Note that this test tells nothing about *which* pairs of plots show heterogeneity, only that selection was heterogeneous overall.

Comparisons of the magnitude of selection among disturbance treatments and sites were tested by nonparametric Kruskal-Wallis tests or Friedman's method for randomized blocks (SAS, 1988) using the 18 selection gradients as observations. These do not just test for heterogeneity, but rather require consistent differences in the rank of selection gradients among sites or disturbance treatments.

RESULTS

Over 12,000 seedlings emerged in all plots. Of these, 6,251 were marked by cohort and censused for early survivorship; 2,160 of the survivors were individually numbered and measured for rosette diameter, growth rate, survivorship, and lifetime fecundity. Most seedlings emerged in the first germination cohort, which included 53% of all seedlings. Cohorts 2, 3, and 4 contained 12, 20 and 15% of all seedlings, respectively.

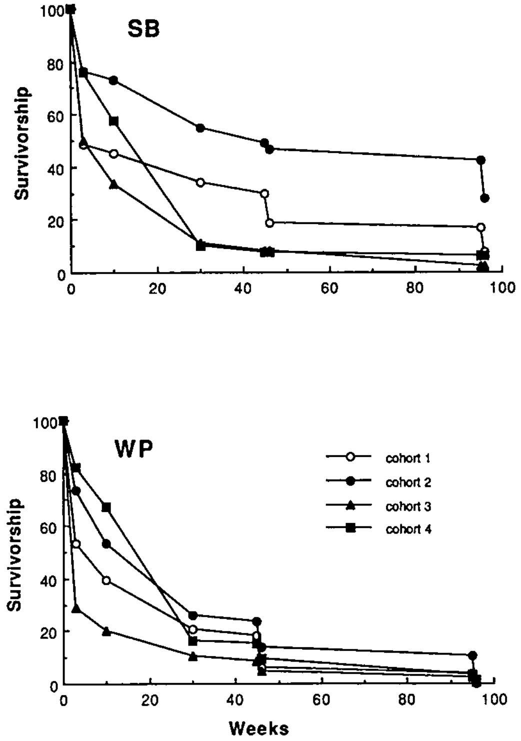

FIG. 2. Survivorship curves for four cohorts of *E. annuus*. Mortality was concentrated during the first few weeks after emergence. Episodes of high mortality at 46 and 95 weeks show flowering plants that died following reproduction.

Seedling mortality was concentrated during the first three weeks following emergence (Fig. 2). On average, 42% of all seedlings died within three weeks. Mortality during establishment accounted for nearly 50% of the total deaths from emergence to reproduction. A second period of high mortality occurred during the winter, especially for plants in later cohorts. The mean survivorship from October to March was 0.57.

Plants in the perennial plots were significantly smaller, had lower survivorship, and lower fecundity than plants in the open and annual treatments. The average seed production in perennial plots was 14.2×10^3 compared to 27.1×10^3 and 32.3×10^3 seeds in the open and annual plots ($F_{[2,440]} = 3.43$, $P < 0.05$). Only 19% of surviving plants reproduced as annuals in perennial plots, compared to 63% and 70% in the open and annual treatments ($F_{[2,12]} = 9.58$, $P = 0.003$). As a result, estimates of population growth rate showed declining populations ($\lambda < 1$) in 4/6 perennial plots (Table 1).

Selection on Emergence Date.—Directional selection on emergence date during the establishment phase was significantly

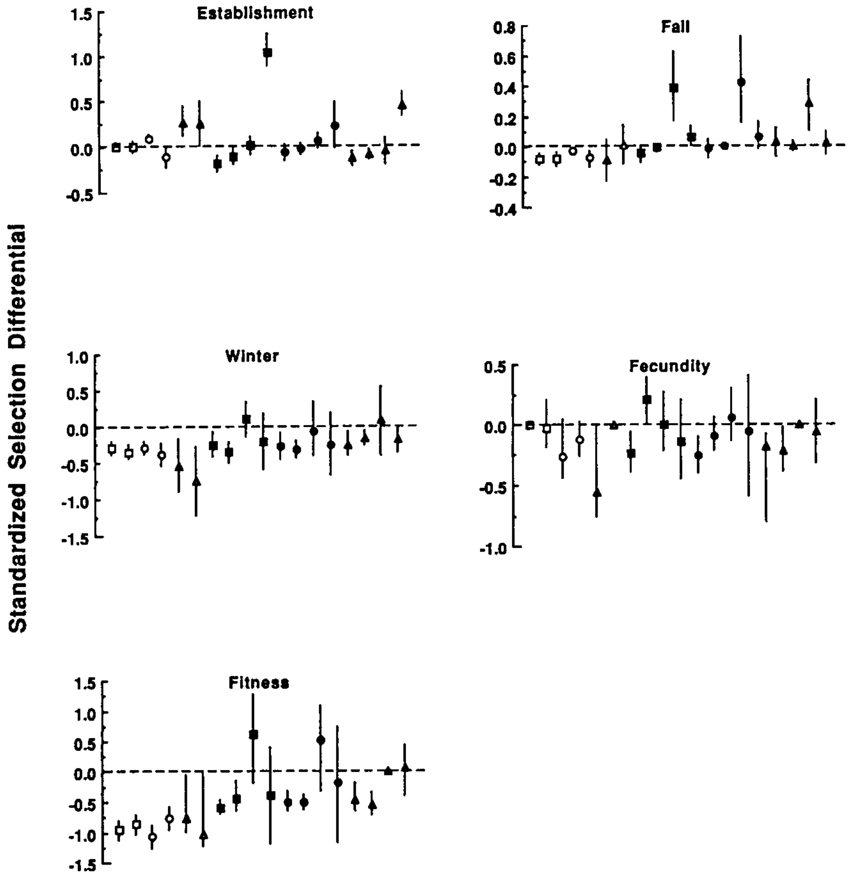

FIG. 3. Standardized selection differentials for selection on emergence date in 18 plots with 95% confidence intervals. The units are phenotypic standard deviations. In this and all other figures, open symbols show plots at Stony Brook and closed symbols show plots at the Weld Preserve. Squares are Open plots, circles are Annual plots and triangles are Perennial plots.

positive (favoring later emergence) in 6 of the 18 plots and significantly negative in 4 plots (Fig. 3). In addition, there were significant quadratic components to the fitness surface, indicating the presence of both stabilizing selection (four plots) and disruptive selection (three plots) during the establishment episode (Fig. 4). Four more plots had significantly positive quadratic components but the survivorship minimum was outside the range of phenotypes. Thus these plots had monotonic directional selection for late emergence, although the fitness surface was significantly curved. Both directional and stabilizing/disruptive selection differentials during establishment were significantly heterogeneous overall and showed spatial dependence among blocks (Table 2). However there was no significant variation in selection among disturbance treatments or between the two sites.

Three plots at the Weld Preserve had significant selection for later emergence in the fall selection episode (September to October) whereas early emergence was favored in four plots (all at Stony Brook) (Fig. 3). Disruptive selection on emergence date was present in three plots (Fig. 4). One more had a significantly positive quadratic coefficient but showed net directional selection for early emergence. There was no effect of disturbance treatment on the magnitude or shape of fall viability selection but there was significant spatial heterogeneity of directional and disruptive selection among blocks and sites (Table 2).

Once seedlings survived establishment and fall mortality, directional selection toward early emergence dominated all other selection episodes (Fig. 3) and there was no significant stabilizing or disruptive selection. Winter viability selection favored early emergence in 10/18 plots, with an average directional selection differential of -0.26 standard deviations. Winter survivorship was over twice as high for the first two emergence cohorts compared to the two later cohorts (0.70 versus 0.33; $G = 199.6$; $P < 0.0001$). Selection was stronger at Stony Brook than the Weld Preserve, but again there was no effect of the competitive environment on winter survivorship (Table 2). The net winter selection differential was partially the result of correlations with seedling size. On average, 51% of the selection differential was due to indirect selection through seedling size. Indirect selection was more important at SB, where it accounted for 87% of the total winter viability selection differential, compared to 19% at WP (Friedman's test, $P < 0.003$). Direct winter viability selection on emergence date was observed in seven plots (Table 3A). The three disturbance treatments had no significant effect on either direct or indirect winter viability selection on emergence date.

The timing of reproduction was highly dependent on the date of emergence. Of plants that reproduced, 78% of plants in cohort 1 flowered their first year (annual life cycle) compared to only 61% of plants in later cohorts ($G = 11.2$, $P < 0.001$). No plants that germinated after 20 August flowered at Stony Brook during year 1. Similarly, the probability of reproducing at all was much higher for plants in the earliest cohort compared to all others (0.235 versus 0.073, $G = 513.8$, $P < 0.0001$). Among plants that reproduced, early emergence resulted in increased fecundity at both sites (Fig. 3). Plants in cohort 1 had 26% higher fecundity at Stony Brook (7,420 versus 5,860) and 41% higher fecundity at the Weld Preserve (38,000 versus 27,000) compared to plants in later cohorts ($F_{[1,451]} = 10.2$, $P < 0.001$). Individual fecundity selection differentials were not significant, partly a result of the small number of plants that survived to reproduce, but selection was consistently negative across all plots ($P < 0.01$, signed ranks test). While the net fecundity selection differentials favored early emergence, direct selection gradients on emergence date (controlling for selection on size) were not significant but generally positive, especially in the open plots (Table 3A). Direct fecundity selection gradients on emergence date were significantly heterogeneous among the three disturbance treatments, but the pattern of heterogeneity did not support my a priori predictions of stronger selection in perennial plots (Table 3A). Most of the fecundity selection on emergence date operated indirectly through seedling size.

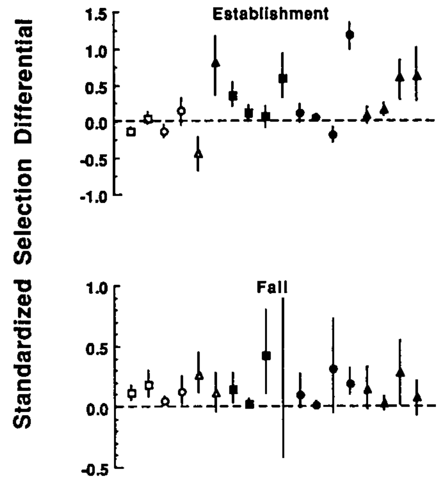

FIG. 4. Stabilizing and disruptive selection differentials on emergence date during the establishment and fall viability selection episodes. Negative selection differentials indicate stabilizing selection and positive selection differentials indicate disruptive selection. Open symbols = SB, closed = WP; squares = Open plots, circles = Annual plots, triangles = Perennial plots.

The cumulative effect of phenotypic selection on emergence date was to decrease mean emergence time in most plots, but blocks 5 and 6 at WP had net positive selection on emergence date (Fig. 5, upper). The cumulative selection differential was -0.69 standard deviations at SB. This corresponds to a decrease in mean emergence date of 5.2 days. Lifetime selection on emergence date had a significant positive quadratic component in 7/18 plots (Table 2), primarily because cohorts 3 and 4 both had uniformly low fitness (Fig. 6) rather than disruptive selection on emergence date. At SB, most of the lifetime selection on emergence date was the result of indirect selection through seedling size (Table 3C). In

TABLE 2. Heterogeneity of selection differentials. Heterogeneity of selection among sites, blocks, and disturbance treatments was tested via Kruskall-Wallis tests using the 18 selection gradients as observations. Heterogeneity among plots is given by the proportion of the 153 pairwise comparisons that are significantly different. Overall heterogeneity among plots may be considered significant if it is greater than 8% (see text).

	Disturbance treatments	Heterogeneity among			No. significant	
		Sites	Blocks	Plots		
	χ^2	χ^2	χ^2	%	+	−
Directional selection differentials						
Emergence date						
Viability						
Establishment	0.25	0.71	11.99**	51*	4+	3−
Fall	0.50	7.89**	13.66*	48*	3+	4−
Winter	0.14	8.43**	13.19*	17*		10−
Spring	1.13	0.43	1.56	11*	1+	
Year-2	2.71	0.13	1.33	35*	0	
Fecundity	2.47	1.38	10.35*	17*	0	
Lifetime fitness	0.18	11.00***	14.56*	54*		10−
October rosette diameter						
Viability						
Winter	0.78	0.56	9.59	16*	8+	
Spring	0.78	1.06	4.30	6	0	
Year-2	2.16	0.13	3.45	15*	0	
Fecundity	1.22	1.45	9.10	11*	1+	
Lifetime fitness	5.23	0.65	3.27	29*	9+	
Stabilizing/disruptive selection differentials						
Emergence date						
Establishment	1.27	2.25	9.94	70*	7+	4−
Fall	0.98	0.08	11.12*	20*	4+	
Lifetime fitness	0.57	0.82	4.29	29*	5+	
October rosette diameter						
Winter	2.14	5.93*	6.28	12*		6−

*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$.

contrast, most of the selection at WP acted directly on emergence date itself. In all plots, lifetime viability selection on emergence date was much stronger than fecundity selection (Table 3C).

Selection on Seedling Size.—Viability selection on October rosette diameter primarily operated through variation in winter survivorship. The mean directional selection differential was +0.41 standard deviations; winter selection differentials were significant in 8 of the 18 plots after adjusting for experimentwise error, but all 18 were nominally significant at $P \leq 0.056$ (Fig. 7). Most of the variation in phenotypic selection occurred among plots and among blocks ($P = 0.07$), and there were no significant effects of site or disturbance treatment (Table 2). Quadratic selection differentials were significant in 9/18 plots (all negative) but there was no evidence of an intermediate fitness maximum. Seedlings larger than 20 mm had uniformly high winter survivorship (Fig. 8). Although the fitness surface was significantly curved, there was net positive directional selection with a size threshold. The threshold effect was stronger at Stony Brook, resulting in significant heterogeneity of quadratic selection differentials among sites (Table 2). Overall, winter viability selection accounted for 80% of the lifetime selection differential (Table 3).

October rosette diameter had only a weak effect on spring viability, in part because of the low opportunity for selection. The variance in relative spring survivorship was 0.15, compared to 1.43 for winter viability. There was also no effect of October diameter on survivorship during the second year (Table 2).

On average, October rosette diameter explained 18% of the total variation in fecundity. Individual fecundity selection differentials were not significant in any plots, but

TABLE 3. Mean phenotypic selection gradients (A) and phenotypic correlations (B) for emergence date, October, and March rosette diameter. Because of heterogeneity within the Weld Preserve, means were computed separately for blocks 3,4 and 5,6. Asterisks denote significant heterogeneity among disturbance treatments or locations using Friedman's test for randomized blocks. Values in boldface indicate consistency of the sign of selection gradients within the location or treatment. Under h_0 of no selection, the probability that all six selection gradients have the same sign is $P = 0.03$. No stabilizing or disruptive selection gradients were significantly different from zero. The number of plots with individually significant selection gradients (after adjusting for experimentwise error) is shown at the right. Composite selection gradients (C) were calculated as the sum of selection over all component episodes.

	Site				Disturbance treatment				
Variable	SB	WP(3,4)	WP(5,6)		Open	Annual	Perennial		No. sig.
A) Viability selection episodes									
Establishment									
Emergence	0.0849	−0.0996	0.2926	***	0.1254	0.0306	0.1220		7
Fall									
Emergence	−0.0744	−0.0138	**0.3130**	***	0.0365	0.1092	0.0792	+	7
Winter									
Emergence	**−0.2933**	**−0.4320**	0.0763	***	−0.2152	**−0.3409**	0.0928	+	7
October	**2.8992**	0.1361	**0.7463**	***	**0.6696**	0.7312	**2.3809**		10
Adult (Spring + Year 2)									
Emergence	0.0321	0.0561	0.0543		0.0371	0.0592	0.0462		0
October	−0.2615	**0.1176**	−0.2942	**	−0.0056	−0.0864	−0.3461		0
March	**0.5443**	**0.1363**	**0.5761**	**	**0.3144**	**0.3549**	**0.5874**		3
Fecundity selection									
Emergence	0.0350	0.0707	0.2232		**0.2710**	0.0711	0.0158	**	0
October	−0.1391	0.3150	−0.0187	+	0.3124	−0.2451	0.1079	***	0
March	0.2181	0.1632	0.2707		0.2150	**0.4258**	0.0112	***	4
B) Phenotypic correlations									
Emergence—October	−0.534	**−0.473**	−0.277	+	−0.432	**−0.494**	−0.358		
Emergence—March	−0.443	**−0.329**	−0.162		−0.351	−0.310	−0.273		
October–March	**0.917**	**0.334**	**0.611**	***	**0.554**	**0.598**	**0.711**	**	
C) Composite selection gradients									
Emergence date									
Total indirect	−1.5044	**−0.3575**	−0.2213		−0.6527	−0.4679	−1.0737		
Total direct	−0.2157	**−0.4185**	**0.9595**	***	0.2547	−0.0709	−0.0815		
Total viability	−1.6980	−0.6424	**0.5190**	***	−0.4379	−0.6299	−1.0743		
Total fecundity	−0.0220	**−0.1335**	0.2192	+	0.0399	0.0911	−0.0808		
October rosette diameter									
Total indirect	**0.6720**	0.0513	**0.4949**	**	0.3145	**0.4865**	**0.4173**		
Total direct	2.4985	0.5688	**0.5438**		**0.9763**	0.3996	**2.5734**	**	
Total viability	**3.1253**	0.2744	**0.7735**	***	**0.8633**	**0.8609**	2.7881		
Total fecundity	0.0453	0.3457	0.1549		**0.4275**	0.0253	0.1117	+	

*** $P < 0.001$; ** $P < 0.01$; + $P < 0.05$ but not significant with Bonferroni adjustment.

overall fecundity selection was significantly greater than zero ($P = 0.02$, signed ranks test). In most plots, fecundity selection was much weaker than the total viability selection (Table 3A; Fig. 5, lower). The effect of seedling size on fecundity was much stronger among plants that reproduced the first year ($\beta = 0.26$; significant in 8/18) than the effect on the fecundity of second year plants (ns). Thus delayed reproduction decreased the total fecundity selection on seedling size. The three disturbance treatments differed in the direct fecundity selection on October rosette diameter (Table 3A). However the phenotypic selection for large seedlings was highest in open plots, a pattern opposite predictions.

The relationship between seedling size and lifetime fitness showed purely directional selection, with no evidence of curvature of

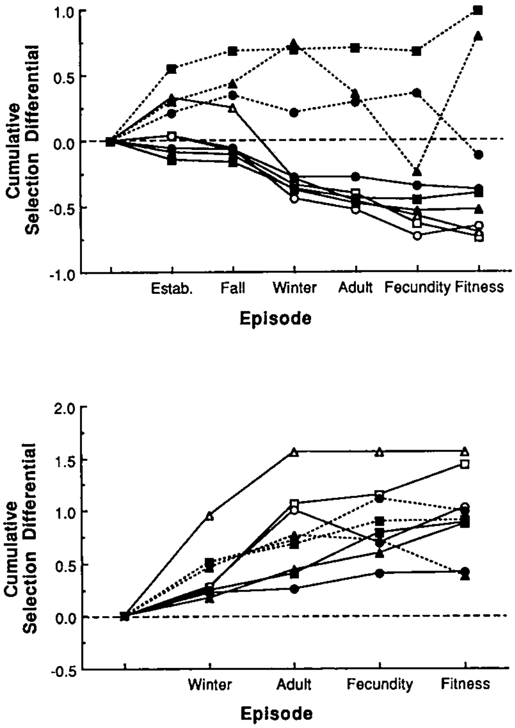

FIG. 5. Cumulative standardized selection differentials (±SE) for selection on emergence date (upper) and October rosette diameter (lower) at Stony Brook and Weld Preserve. Adult viability includes both spring and year-2 survivorship for plants that delayed reproduction. Open symbols = SB, closed = WP; squares = Open plots, circles = Annual plots, triangles = Perennial plots. Data from blocks 5 and 6 at WP are shown with dotted lines.

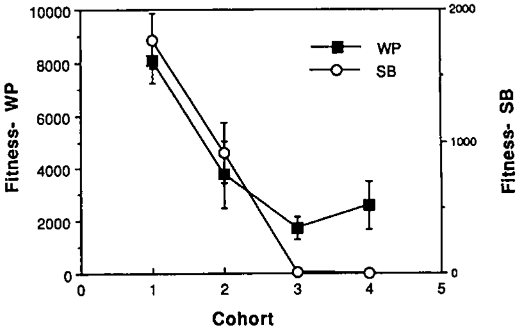

FIG. 6. Mean fitness (±SE) of plants in the four emergence cohorts at Stony Brook and the Weld Preserve. Note the difference in scale on the ordinate.

the fitness surface (Fig. 9). October rosette diameter explained 22% of the phenotypic variance in lifetime fitness.

DISCUSSION

Heterogeneous Selection.—The differences in the environment that cause the heterogeneity of selection among the replicate plots operate over a local scale, but remain unknown. I found few consistent differences in the magnitude of phenotypic selection with respect to the three disturbance treatments, so my a priori hypothesis of increased selection on seedling size in competitive environments was not supported by these data. There was significant heterogeneity among disturbance treatments for fecundity selection gradients for both seedling size and emergence date. However selection was weakest in high competition perennial plots, a pattern opposite to predictions. In contrast, Van der Toorn and Pons (1988) did report a trend for stronger selection on germination date closed habitats in two species of *Plantago*.

Fall and winter viability selection favoring early emergence cohorts was stronger at Stony Brook than at the Weld Preserve, which may be partially related to the competitive regime. One of the most obvious environmental differences between the two sites was the difference in percent vegetation cover. The plots at Stony Brook were all rapidly colonized by other species (primarily grasses, *Artemesia vulgaris,* and *Stellaria media*) and by October had >80% cover. Seedlings in later cohorts faced increased competition with these species which may partially account for the stronger selection on emergence date at SB. At the Weld Preserve the open and annual plots maintained low percent vegetation cover (<40%) throughout the experiment. At Stony Brook, the open plots resembled the perennial plots after two months and were not equivalent to the open treatment at the Weld Preserve. Because the three disturbance treatments did not remain distinct, it is not surprising that estimates of selection did not show consistent differences among treatments.

Within the Weld Preserve site, there were large and consistent differences in the pattern of selection between blocks 3 and 4 versus blocks 5 and 6. This spatial variation in selection was generally much larger than the biotic effects of the competitive environment. The relevant environmental dif-

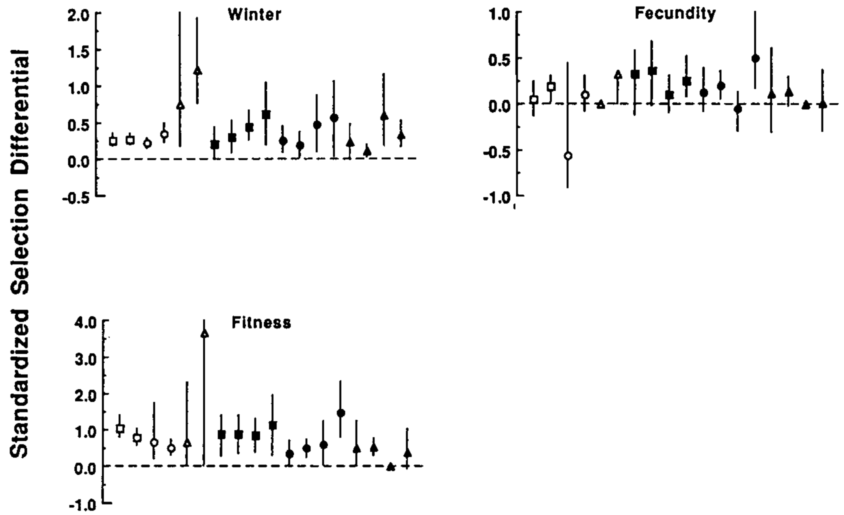

FIG. 7. Standardized selection differentials and 95% confidence intervals for October rosette diameter. Open symbols = SB, closed = WP; squares = Open plots, circles = Annual plots, triangles = Perennial plots.

ferences are not known, however blocks 5 and 6 appeared to have sandier soil that dried out faster during the fall and winter, suggesting the possible importance of abiotic factors. The severe desiccation may account for the large viability selection against early emergence in those blocks. However, such inferences about the causes of selective heterogeneity are merely speculative. To make causal statements about particular selective forces the consequences of abiotic variation in soil type must be tested experimentally, as was done for the competitive regime (cf. Wade and Kalisz, 1990).

Significant variation in the magnitude of selection was observed among the 18 plots in nearly all selection episodes. Selection was most heterogeneous early in the life cycle, with most of the variation occurring among blocks within sites. Several recent studies have examined the spatial heterogeneity of phenotypic selection within plant populations and these have shown similar variation in the magnitude and direction of selection among plots (Kalisz, 1986; Stewart and Schoen, 1987). The emerging consensus is that phenotypic selection on life history characters is strong and variable on a local scale, even within seemingly homogeneous populations (but see Mitchell-Olds and Bergelson, 1990). Unlike the other

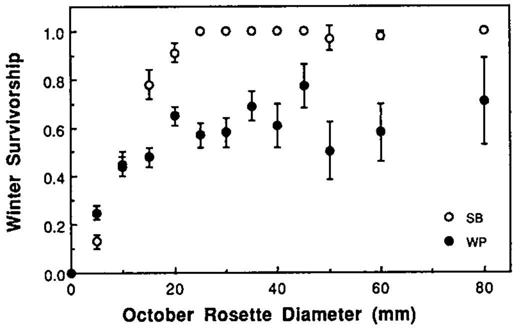

FIG. 8. Mean winter survivorship (±SE) as a function of October rosette diameter at Stony Brook and the Weld Preserve. Each mean is based on minimum of 12 plants.

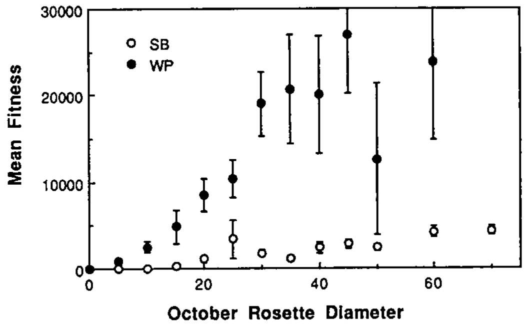

FIG. 9. Mean lifetime fitness (±SE) as a function of October rosette diameter at Stony Brook and the Weld Preserve.

studies, the fitness-related size characters examined in this experiment did not show variation in the direction of selection: large seedlings had higher viability and fecundity, as is expected of fitness-related traits.

The phenotypic selection on emergence date revealed an apparent tradeoff between the size advantage of early germinating individuals and survivorship during establishment. Similar patterns were observed by Arthur et al. (1973) and Marks and Prince (1981) for comparisons of fall vs. spring germinating plants. Viability versus fecundity tradeoffs with respect to germination date have generally not been observed in single season comparisons (Kalisz, 1986; A. Biere, pers. comm.), although such tradeoffs are often assumed for life history characters at equilibrium. Directional selection on seedling size may be expected to decrease the mean emergence date until this selection is balanced by conflicting viability selection against individuals that germinate too early. In blocks 1 through 4, negative directional selection at later stages of the life cycle was much stronger than the positive viability selection during establishment, whereas in blocks 5 and 6 at WP the net selection on emergence remained positive.

Shape of the Fitness Surface.—Quadratic coefficients were significant in early viability selection episodes, revealing both stabilizing and disruptive selection on emergence date. This resulted from large variation in the relative survivorship of cohorts 2 and 3 during establishment. The high mortality of cohort 3 was largely responsible for the observed disruptive selection. Later selection episodes showed only monotonic directional selection toward early emergence. Quadratic selection differentials were significant for lifetime selection on emergence date, and for winter viability selection on October diameter, but all had monotonic fitness functions. Following Mitchell-Olds and Shaw (1987) these are interpreted as directional selection. The lifetime selection on seedling size was very nearly linear. In the multiple regressions, no quadratic selection gradients were significant for any component of selection. Thus overall, there was little evidence for stabilizing or disruptive selection on seedling size or emergence date.

Direct versus Indirect Selection.—Much of the total selection on emergence date and October rosette diameter was the result of direct selection, in addition to indirect selection through effects on size at later stages of the life cycle. The large direct effects on seedling characters result from the importance of viability fitness components for lifetime selection in *Erigeron.* In contrast, Mitchell-Olds and Bergelson (1990) showed little direct selection on seedlings in *Impatiens,* where fitness was entirely determined by fecundity. In this experiment, the most important single contribution was that through winter survivorship. Winter viability differences explained over half of the selection on October rosette diameter and were twice as large as selection during the adult life stages.

There can not be "direct" fecundity selection on emergence date in the same sense that there can be direct fecundity selection on adult phenotypes. The direct fecundity selection gradients simply indicate that there are residual effects of emergence date that can not be explained by the increased fecundity of larger plants. In particular, if seedling size is held constant, late emerging seedlings must have grown faster. Presumably the positive fecundity selection gradients show a continuing expression of the faster growth rates of those seedlings.

Each of the selection gradients are measured with error and the errors are compounded when several selection gradients are combined. Quantititive conclusions about the precise magnitudes of the composite selection gradients may not be warranted. Nevertheless, the repeatability within each block (Table 3) provides evidence that the composite selection gradients are reasonably accurate indications of the major patterns of selection.

Others have used path analysis to assess the relative fitness effects of various causal paths (Crespi and Bookstein, 1989; Mitchell-Olds and Bergelson, 1990). Standardized selection gradients can be converted to path coefficients by multiplying them by the standard deviation of relative fitness. The techniques of path analysis could then be used to partition the determination of each major component of fitness. However, path analysis is less useful when fitness is measured in multiple episodes. Paths from major fitness components to lifetime fitness can not be included because path analysis assumes an additive model and fitness components are multiplicative (a logarithmic transformation does not work when individual survivorship is measured as 0 or 1). Also, in path analysis each fitness component is standardized to unit variance, so there can be no variation among fitness components in the opportunity for selection (Arnold and Wade, 1984*a*).

Phenotypic selection on the date of seedling emergence and subsequent seedling size was generally strong and was observed in all stages of the life cycle. There were not only immediate effects of these seedling characters on viability, but also persistent effects on adult fitness components. That large seedlings show increased survival and fecundity is not a new result (Harper, 1977 ch. 6; Cook, 1979; Solbrig, 1981). However, quantitative estimates of the proportion of fitness variance explained by seedling characters, the separation of effects of various fitness components, and tests for spatial heterogeneity of selection are less common. In total, the seedling size variation present in October explained 18% of the variance in fecundity of the plants that reproduced and 22% of the total phenotypic variance in lifetime fitness. Stanton (1985) and Miller (1987) also reported that seedling emergence date and seedling size explain about 20% of fecundity variation. Genetic variation is present for these traits (Stratton, 1991), so a substantial proportion of the fitness differences among genotypes may be determined by events in the first months of a seedling's life. However, heritabilities in the field are quite low (Stratton, 1992) so the evolutionary response to phenotypic selection will be slow.

ACKNOWLEDGMENTS

This work was improved by the comments and suggestions of many people, particularly J. Thomson, A. Biere, S. Kalisz, H. Young, and an anonymous reviewer. Special thanks to H. Young for braving ticks and hot sun and spending many hours helping me plant seeds and census seedlings. This research was funded in part by NSF grant BSR8601106. This is contribution 806 in Ecology and Evolution, State University of New York at Stony Brook.

LITERATURE CITED

ARNOLD, S. J., AND M. J. WADE. 1984*a*. On the measurement of natural and sexual selection: Theory. Evolution 38:709–719.

———. 1984*b*. On the measurement of natural and sexual selection: Applications. Evolution 38:720–734.

ARTHUR, A. E., J. S. GALE, AND M. J. LAWRENCE. 1973. Variation in wild populations of *Papaver dubium* VII. germination time. Heredity 30:189–197.

BLACK, J. M. 1958. Competition between plants of different initial seed size in swards of subterranean clover (*Trifolium subterraneum* L.) with particular reference to leaf area and the light microclimate. Aust. J. Agric. Res. 9:299–318.

CLEGG, M. T., A. L. KAHLER, AND R. W. ALLARD. 1978. Estimation of life cycle components of selection in an experimental plant population. Genetics 89:765–792.

COOK, R. F. 1979. Patterns of juvenile mortality and recruitment in plants, pp. 207–231. *In* O. T. Solbrig, S. Jain, G. B. Thompson, and P. H. Raven (eds.), Topics in Plant Population Biology. Columbia Univ. Press, N.Y., USA.

COOK, R. F., AND E. E. LYONS. 1983. The biology of *Viola fimbriatula* in a natural disturbance. Ecology 64:654–660.

CRESPI, B. J., AND F. L. BOOKSTEIN. 1989. A path-analytic model for the measurement of selection on morphology. Evolution 43:18–28.

DIXON, P. M., J. WEINER, T. MITCHELL-OLDS, AND R. WOODLEY. 1987. Bootstrapping the Gini coefficient of inequality. Ecology 68:1548–1551.

EFRON, B. 1982. The Jackknife, the Bootstrap, and Other Resampling Plans. Soc. Indust. Appl. Math. Philadelphia, PA, USA.

GRUBB, P. J. 1977. The maintenance of species richness in plant communities: The importance of the regeneration niche. Biol. Rev. 52:107–145.

HARPER, J. L. 1977. Population Biology of Plants. Academic Press, London, UK.

HOWELL, N. 1981. The effect of seed size and relative emergence time on fitness in a natural population of *Impatiens capensis* Meerb. (Balsaminaceae). Am. Midl. Nat. 105:312–320.

KALISZ, S. 1986. Variable selection on the timing of germination in *Collinsia verna* (Scrophulariaceae). Evolution 40:479–491.

LANDE, R., AND S. J. ARNOLD. 1983. The measurement of selection on correlated characters. Evolution 37:1210–1226.

LEE, J. M., AND J. L. HAMRICK. 1983. Demography of two natural populations of musk thistle (*Carduus nutans*). J. Ecol. 71:923–936.

LYNCH, M., AND S. J. ARNOLD. 1988. The measurement of selection on size and growth, p. 47–59. *In* B. Ebenman and L. Persson (eds.), Size Structured Populations. Springer Verlag, Berlin, Germany.

MARKS, M., AND S. PRINCE. 1981. Influence of germination date on survival and fecundity in wild lettuce *Lactuca serriola*. Oikos 36:326–330.

MILLER, T. E. 1987. Effects of emergence time on the survival and growth in an early oldfield community. Oecologia 72:272–278.

MITCHELL-OLDS, T., AND J. BERGELSON. 1990. Statistical genetics of an annual plant, *Impatiens capensis.* II Natural selection. Genetics 124:417–421.

MITCHELL-OLDS, T., AND R. G. SHAW. 1987. Regression analysis of natural selection: Statistical inference and biological interpretation. Evolution 41: 1149–1161.

RICE, W. R. 1989. Analyzing tables of statistical tests. Evolution 43:223–225.

ROSS, M. A., AND J. L. HARPER. 1972. Occupation of biological space during seedling establishment. J. Ecol. 60:77–88.

SALISBURY, E. J. 1942. The reproductive capacity of plants. G. Bell and Sons, London, UK.

SAS. 1988. SAS/STAT User's Guide release 6.03 edition. SAS Institute, Cary, NC, USA.

SCHMITT, J. A., J. ECCLESTON, AND D. W. ERHARDT. 1987. Dominance and suppression, size dependent growth, and self thinning in a natural *Impatiens capensis* population. J. Ecol. 75:651–665.

SCHMITT, J. A., AND D. W. ERHARDT. 1990. Enhancement of inbreeding suppression by dominance and suppression in *Impatiens capensis.* Evolution 44:269–278.

SERVICE, P. M., AND R. LENSKI. 1982. Aphid genotypes, plant phenotypes, and genetic diversity: A demographic analysis of experimental data. Evolution 36:1276–1282.

SHAW, R. G. 1986. Response to density in a wild population of the perennial herb *Salvia lyrata*: Variation among families. Evolution 40:492–505.

SOLBRIG, O. T. 1981. Studies on the population biology of the genus *Viola* II the effect of plant size on fitness in *Viola sororia.* Evolution 35:1080–1093.

STANTON, M. L. 1984. Seed variation in wild radish: Effect of seed size on components of seedling and adult fitness. Ecology 65:1105–1112.

———. 1985. Seed size and emergence time within a stand of wild radish (*Raphanus raphanistrum* L.): The establishment of a fitness hierarchy. Oecologia 67:524–531.

STEWART, S. C., AND D. J. SCHOEN. 1987. Pattern of phenotypic viability and fecundity selection in a natural population of *Impatiens pallida.* Evolution 41:1290–1301.

STRATTON, D. A. 1988. Life-cycle components of selection in *Erigeron annuus.* State University of New York, Stony Brook. Ph.D. Dissertation.

———. 1989. Competition prolongs expression of maternal effects in seedlings of *Erigeron annuus.* Am. J. Bot. 76:1646–1653.

———. 1991. Life history variation within populations of an asexual plant, *Erigeron annuus* (Asteraceae). Am. J. Bot. 78:723–728.

——— 1992. Life-cycle components of selection in *Erigeron annuus:* II. Genetic variation. Evolution 46:107–120.

VAN DER TOORN, J., AND T. L. PONS. 1988. Establishment of *Plantago lanceolata* L. and *Plantago major* L. among grass. II. Shade tolerance of seedlings and selection on time of germination. Oecologia 76:341–347.

WADE, M. J., AND S. KALISZ. 1990. The causes of natural selection. Evolution 44:1947–1955.

WALLER, D. M. 1985. The genesis of size hierarchies in seedling populations of *Impatiens capensis.* New Phyt. 100:243–260.

WEINER, J. 1985. Size hierarchies in experimental populations of annual plants. Ecology 66:743–752.

Corresponding Editor: J. Schmitt