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(Scrophulariaceae)**



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## VARIABLE SELECTION ON THE TIMING OF GERMINATION IN *COLLINSIA VERNA* (SCROPHULARIACEAE)

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*Abstract.*—Natural selection on the timing of seed germination was investigated in a natural population of the winter annual *Collinsia verna* (Scrophulariaceae) for two years. The goal was to quantify 1) the importance of the timing of seed germination to life history evolution in this population and 2) variation in selection in time and space. During fall germination, seedlings were assigned to cohorts on the basis of their dates of germination. Growth, survivorship, and reproduction were censused throughout both years. Selection on the timing of germination was quantified using linear and quadratic regressions during three ecologically important periods in the life cycle, using the techniques of Lande and Arnold (1983) and Arnold and Wade (1984a, 1984b). Comparisons were made between years and on two spatial scales within years. Overall, selection favored early-germinating plants in the first year. The primary determinant of the relationship of the timing of germination to fitness was fecundity selection, rather than viability selection on seedlings. Fecundity selection was responsible for from 54% to 80% of the change in the mean time of germination. Significant disruptive selection characterized the second field season, again mediated mainly through fecundity selection. There was also temporal and spatial heterogeneity in selection on this character. Transects and quadrats differed significantly in the direction and magnitude of natural selection. In addition, the direction of selection changed between episodes for the transects. The results illustrate the importance of the timing of germination to life-history evolution in this annual plant and the complex action of natural selection on this character.

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A general understanding of the direction, magnitude, and constancy of selection acting on the phenotypic variation in natural populations remains an unrealized goal in evolutionary biology. Studies of genetic differences among populations or sub-populations in morphological, phenological, and electrophoretic traits (Jain and Bradshaw, 1966; Clegg and Allard, 1972; Hamrick and Allard, 1972; Wu and Antonovics, 1976; Law et al., 1977; Primack and Antonovics, 1981; Schemske, 1984) have been used to exemplify the results of the evolutionary processes. Generally, these differences are attributed to past differences in natural selection that might have acted to create the observed distributions of phenotypic variation. Few studies have measured contemporary selection in natural plant populations (Endler, 1986). An understanding of the processes influencing evolution (and adaptation) requires realistic estimates for the magnitude, direction, and timing of natural selection. A coupling of the study of de-

mographically and ecologically important characters with a quantification of natural selection on such characters can provide new insights into the evolution of life histories.

Life-history evolution results from selection on the distribution of age- or stage-specific mortality and birth schedules in a population. Quantitative-genetics theory and methodology have recently been applied to the study of life-history evolution (Stearns, 1980, 1982a, 1982b; Etges, 1982; Dingle and Hegmann, 1982; Lande, 1982), with an emphasis on the measurement of phenotypic and genetic covariances among major components of fitness and life-history traits. To understand how evolutionary processes shape life histories, we must determine 1) how different stages, or stage-specific characters of the life cycle, are correlated with fitness and 2) how these characters are correlated among themselves. The stages during which these characters are expressed can be considered selective focal points in the shaping of life histories. The strength of selection on any particular life-history stage and the effects of early selection on the fitness of later life-history stages are poorly understood in natural populations, although the existence of such stage-specific

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effects is implicit in the widely used concept of life-history "trade-offs" (e.g., Pianka, 1983).

The timing of seed germination is expected to be correlated with seedling survival and, therefore, with fitness (Harper, 1977; Solbrig, 1980). Demographic studies of plant populations have demonstrated that far more plants germinate than survive to the next stage (Sharitz and McCormick, 1973; Mack, 1976; Solbrig et al., 1980). Phenotypic variation in the timing of seed germination, both within and between populations, has been demonstrated for several species (Salisbury, 1963, 1965; Cavers and Harper, 1966; McWilliams et al., 1968; Palmblad, 1969; Arthur et al., 1973; Wulff, 1973; Howell, 1981). Variation in the timing of seed germination within a population has been shown to influence subsequent survivorship and reproductive success, with several studies documenting an apparent trade-off between low survivorship and high reproduction for early germinating plants (Baskin and Baskin, 1972; Cook, 1980; Howell, 1981; Marks and Prince, 1981). In addition, the timing of germination has been shown to influence plant competitive ability in both field and laboratory experiments (Black and Wilkinson, 1963; Ross and Harper, 1972; Harper and White, 1974; Harper, 1977; White and Harper, 1970; Cook, 1980; Fowler, 1984), with early germinating plants attaining a larger initial size and consequent competitive advantage. Since the time of seed germination has been shown to influence plant fitness, it is expected to be under selection and to be a crucial trait in the shaping of plant life histories.

In this paper, I quantify the direction and magnitude of natural selection on the timing of seed germination in *Collinsia verna* (Scrophulariaceae), a winter annual. The specific aims of this research were to 1) quantify at which points in the life cycle the timing of seed germination was selectively important and 2) determine the spatial and temporal variation in selection in a natural population. I hypothesized that the timing of seed germination would have its greatest fitness effects on seedling survival and that the lower survivorship of early germinating seeds in conjunction with lower reproductive success of the late germinating individ-

uals would be detectable as selection for an intermediate germination phenotype.

#### *Study Species Life History*

*Collinsia verna* (Scrophulariaceae) is a winter annual of floodplains along small rivers and creeks. Its geographic range extends from the eastern coast of the United States west into Missouri, south to Tennessee, and north into New York. Seeds germinate throughout the fall. Seedling growth ceases in late fall, and the plants become dormant. One or two sets of true leaves and the cotyledons are present by the winter. In the spring, the plants grow rapidly, produce floral buds, flower, set seed, and senesce. Plants in the field produce from zero to more than 100 flowers. All plants are dead by early June. Most seeds are passively dispersed and lie dormant on the soil surface until the following autumn, when the first germination occurs. Long-term seed dormancy exists in this population, with some seeds remaining viable in the soil for up to three years (Kalisz, unpubl.). The life cycle of *C. verna* is characterized by two distinct growth periods, fall and spring, interrupted by a period of plant dormancy in the winter and seed dormancy in the summer. The plants experience extremely different abiotic and biotic conditions in the fall/winter and spring.

#### *Study Site*

The study was conducted in the Raccoon Grove Forest Preserve near Monee (Will County), Illinois from June 1982 to June 1984. The 154 hectare preserve is composed of an upland oak-hickory forest and a larger, floodplain forest. *Collinsia verna* is found only in the floodplain. *Acer saccharum*, *Celtis occidentalis*, *Juglans nigra*, and *Populus deltoides* are the dominant tree species on the floodplain, and these form a dense canopy in some areas. Other parts of the floodplain are open and receive direct sunlight. A secondary canopy of *Urtica dioica* is found on most of the floodplain. *Collinsia verna* is abundant in the various floodplain environments, with an estimated 1,000,000 reproductive individuals in a 4 hectare portion of the floodplain in the spring of 1982.

## MATERIALS AND METHODS

*Field Study*

A longitudinal field study was conducted during two complete life cycles of *C. verna* from June 1982 through June 1984. Three 75-meter transects were marked in the first year to span the range of environments in which *C. verna* grows. Every three meters along each transect a 40 × 40 cm quadrat was permanently marked, yielding 25 quadrats/transect and 75 total quadrats. All germinating seedlings in these quadrats ( $N = 14,523$ , 1982;  $N = 8,070$ , 1983) were tagged with a numbered band at regular census intervals; every ten days in the fall of 1982 and every seven days in the fall of 1983, until germination ceased. Individuals were assigned to germination cohorts on the basis of their germination date during the fall censuses. A single germination cohort included all seedlings that had emerged since the previous census. For an individual plant, germination time was defined with respect to the census interval during which it germinated, termed "cohort." The first day that germination was noted in the field was defined as the first day of cohort 1 in each year. Survivorship of all seedlings was monitored at each census. Growth, survivorship, and reproduction of the plants were censused weekly the following spring. The adult plants have extremely fragile and tangled stems at the time of fruit production. To census reproduction accurately, I harvested all adults from half of the quadrats. All plants from 36 quadrats (12/transect) were harvested before seed dispersal in June 1983 (end of year 1).

These plants ( $N = 1,256$ ) were disentangled and measured for vegetative and reproductive characters in the laboratory. The quadrats used in the first year were not used in the second field season, since the destructive harvesting methods used in these quadrats disturbed the normal seed input. Instead, plants emerging in the remaining quadrats were tagged and censused. In the late spring of 1984 (end of year 2), all plants ( $N = 2,439$ ) in the remaining quadrats were collected and scored as in the previous year. Since I was interested in the selective importance of the timing of germination to later life stages, I focused on two major com-

ponents of fitness: 1) viability (juvenile and adult) and 2) fecundity (adults). I divided the life cycle of *Collinsia verna* into three distinct episodes: fall/winter survivorship, survivorship to fruit production, and reproduction (scored as the number of fruits produced). These episodes correspond, respectively, to three important events in the life cycle of these annuals: 1) establishment and winter dormancy, 2) competition and vegetative growth in the early spring, and 3) fruit production in the late spring.

*Data Analysis*

Evolution by natural selection is characterized by two distinct components. First, phenotypic variation is acted upon by selection, resulting in differential survivorship and/or reproduction among phenotypes. Second, if the variation has a genetic basis, selection can produce a change in gene frequencies. This study focused on the first of these components: the characterization of selection on phenotypic variation in a natural population. Techniques for quantifying natural selection have been discussed by Lande and Arnold (1983) and Arnold and Wade (1984a, 1984b). A univariate analysis of selection on the timing of seed germination,  $z$ , was performed using these methods.

Four basic parameters are of interest in the measurement of natural selection: 1) the selection differential ( $S$ ) (Lush, 1945; Falconer, 1981), 2) the selection intensity ( $i$ ) (Falconer, 1981), 3) the directional selection gradient ( $\beta$ ), and 4) the stabilizing selection gradient ( $\gamma$ ).  $S$  describes the change in the mean value of a character,  $i$  describes the change in the mean in units of phenotypic standard deviations,  $\beta$  quantifies the direction and strength of directional selection on that character, and  $\gamma$  quantifies the direction and strength of stabilizing/disruptive selection. If  $\beta$  is negative, then low values of  $z$  were favored; if it is positive, then high values of  $z$  were favored. After correcting for the change in the variance due to directional selection, if  $\gamma$  is negative, then selection has decreased the variance (stabilizing), if it is positive, selection has increased the variance (disruptive) (Lande and Arnold, 1983). These parameters were used to quantify how selection acted to modify the phenotypic

distribution of germination dates ( $z$ ) within a generation. The force of directional selection,  $\beta$ , acting on a character was measured as the regression of relative fitness on  $z$ . The effects of stabilizing/disruptive selection,  $\gamma$ , were estimated from the partial regression of relative fitness ( $w$ ) on the quadratic terms,  $z^2$  (Lande and Arnold, 1983).

Both the total selection differentials and the selection gradients can be partitioned into  $m$  episodes of selection which are additive. The additivity allows the calculation of episode-specific selection effects for any number of episodes (Arnold and Wade, 1984a, 1984b). For  $m$  episodes of selection,

$$S = \sum_{k=1}^m S_k = \sum_{k=1}^m \text{Cov}(z, w_k) \quad (1)$$

and

$$\beta_{\text{total}} = \sum_{k=1}^m (\beta_k), \quad (2)$$

where  $w_k$  is the relative fitness and  $\beta_k$  is the selection gradient for the  $k$ th episode of selection. The  $\beta_k$  values as defined in Arnold and Wade (1984a) are not partial regressions and are not true selection gradients if character variances and covariances are changed by selection. The  $\beta_k^*$  given later in that same section (p. 712), although true partial regressions and true selection gradients, are not additive. Wade and Kalisz (unpubl.) have found that the  $\beta_k^*$ , when properly weighted to correct for the change in the variances and covariances, can be made additive in the following way:

$$\beta_{\text{total}} = \sum_{k=1}^m a_k \beta_k^* \quad (3)$$

where

$$a_k = \mathbf{P}^{-1} \mathbf{P}_k \quad (4)$$

and  $\mathbf{P}$  is the phenotypic variance/covariance matrix. In the univariate case  $a_k$  reduces to the ratio of the phenotypic variance after selection to the phenotypic variance before selection,  $\sigma_k^2 / \sigma_{k-1}^2$ .

Individual relative fitnesses,  $w_k$ , (Robertson, 1966), were calculated at each episode using  $W_k$ , the absolute fitness value of each individual present at the beginning of that episode divided by the mean absolute fit-

ness for that episode,  $\bar{W}_k$ . Relative fitnesses of the three episodes were: 1) relative winter survivorship  $w_1$ , 2) relative spring survivorship  $w_2$ , and 3) relative fruit production  $w_3$ . Individual plants were given a fitness score of 1 if alive and 0 if dead for the episodes of winter and spring survivorship. Individual fitness was scored as the number of fruits during the episode of reproduction. Directional selection during the  $k$ th episode,  $\beta_k$ , was calculated using the univariate linear regression model:

$$w_k = (\beta)z + \text{error}. \quad (5)$$

To quantify stabilizing/disruptive selection, I used the model

$$w_k = (\beta')z + (\gamma/2)z^2 + \text{error} \quad (6)$$

where  $\beta' \neq \beta$  if the distribution of  $z$  before selection is skewed (Lande and Arnold, 1983). Since the survivorship data can only take values of 0 or 1, it should be noted that the regression of relative survivorship on the timing of germination are approximations. Total  $\gamma$ s were calculated by treating the entire life cycle as one episode and regressing the original distribution of cohorts on relative fruit production.

The analyses were performed for both years, providing a comparison of the magnitude and direction of natural selection on a temporal scale. I calculated polynomial fitness functions for the time of germination for both field seasons using a maximum  $R^2$  improvement to fit the regression of total relative fitness on germination cohort. Plant total relative fitness is defined as the product of the relative fitness value over all episodes,  $w_1 w_2 w_3$ .

In addition, I analyzed spatial variation in natural selection on two micro-geographical scales. Variation in selection on a larger scale (among transects) was compared for each year. Transect-specific relative fitnesses were calculated using data on individuals from each transect separately. The regression models used to determine these selection gradients were those of Equations (5) and (6). Smaller-scale variation in selection (among quadrats within transects) was compared for both years. Quadrat-specific relative fitnesses were calculated using data from each quadrat separately. The regression model was that of Equation (5). Dif-

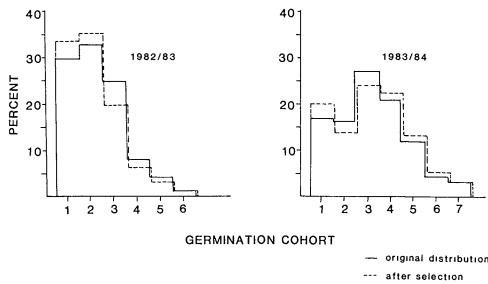


FIG. 1. Distributions of the germination phenotypes before and after selection during a two-year field study. Solid lines indicate the original distribution, dotted lines indicate the distribution after selection. Germination cohort = all of the seedlings which germinated during the ten-day census interval in 1982/1983 and the seven-day census interval in 1983/1984.

ferences in directional selection among transects or quadrats were compared using a test for heterogeneity of slopes (Zar, 1984).

The effects of transect and quadrat (nested within transect) on the timing of seed germination were investigated with a nested analysis of variance performed for each year. All analyses were performed using SAS statistical package (SAS Institute Inc., 1982).

### RESULTS

The original distributions of germination dates for the entire population in each year are shown in Figure 1. Seeds of *C. verna* germinated over a seven-week span in the autumn of 1982 and over a six-week span in 1983. The mean dates of germination ( $\bar{z}$ ) were day 23, (SD = 11.4 days) in year 1, and day 25, (SD = 10.8) in year 2. The distributions for the plants which survived

TABLE 2. Mean ( $\bar{z}$ ) and variance ( $\sigma_z^2$ ) for the timing of seed germination (cohort) for the entire population for two years. Episodic and final means are reported. Cohorts were ten-day intervals in year 1 and seven-day intervals in year 2.

Episode	1982/1983		1983/1984	
	$\bar{z}$	$\sigma_z^2$	$\bar{z}$	$\sigma_z^2$
Winter survivorship	2.26	1.14	3.20	1.54
Spring survivorship	2.18	1.09	3.22	1.61
Reproduction	2.23	1.11	3.25	1.65
Final	2.08	1.12	3.20	2.57

to fruiting are also shown in Figure 1. A comparison of the distributions of seed germination dates before and after selection illustrates the direction of selection during each year. The mean values of the fitness components ( $W_k$ ) at each episode are given in Table 1 and were used to calculate individual relative fitnesses ( $w_k$ ). The mean and variance of  $z$  are also reported by episode in Table 2.

#### Temporal Variation in Selection

The strength and direction of selection on the timing of germination varied both within and between years for the overall population (Table 3). Directional selection occurred during all three episodes of year 1, but the magnitude and the direction of selection changed over the course of a single generation. Viability selection over the winter favored early germination, as indicated by the negative directional selection gradient ( $\beta_1 = -0.06$ ), whereas viability selection during the spring favored late germination

TABLE 1. Mean values for fitness components by episode in two consecutive years. Data are reported by transect and for each year as a whole. For winter and spring survivorship, the entries in the table indicate the probability of survival through the episode in question. Fruit production is the mean number of fruits produced by an individual that survives to reproductive maturity. Variances in mean fitness components are given in parentheses.

Year	Selection episode	Transect			Overall
		1	2	3	
1982/1983	Winter survivorship	0.75 (0.19)	0.76 (0.18)	0.85 (0.13)	0.78 (0.17)
	Spring survivorship	0.92 (0.07)	0.36 (0.24)	0.41 (0.24)	0.60 (0.24)
	Fruit production	1.21 (6.86)	3.07 (17.51)	4.77 (28.15)	2.18 (14.31)
	Total	0.83 (5.15)	0.84 (6.79)	1.66 (14.75)	1.02 (7.85)
1983/1984	Winter survivorship	0.42 (0.24)	0.43 (0.25)	0.50 (0.25)	0.44 (0.25)
	Spring survivorship	0.74 (0.19)	0.61 (0.24)	0.75 (0.19)	0.68 (0.22)
	Fruit production	0.66 (2.96)	1.20 (7.05)	1.64 (6.05)	1.12 (5.45)
	Total	0.21 (1.01)	0.31 (2.13)	0.62 (0.34)	0.34 (1.91)

TABLE 3. Directional selection gradients ( $\beta$ ) and stabilizing/disruptive selection gradients ( $\gamma$ ) for the time of germination in 1982/1983 and 1983/1984.  $N$  = number of individuals at the beginning of each episode.

Selection episode	1982/1983			1983/1984		
	$N$	Directional $\beta$	Stabilizing/ disruptive $\gamma$	$N$	Directional $\beta$	Stabilizing/ disruptive $\gamma$
Winter survivorship	5,583	-0.062***	-0.016	8,088	+0.012	+0.054***
Spring survivorship	4,324	+0.045***	-0.006	3,568	+0.010	+0.024**
Reproduction	2,580	-0.179***	-0.032	2,440	-0.101***	-0.042
		-0.198***	0.014		-0.079*	0.010

\*  $P < 0.05$ ; \*\*  $P < 0.001$ ; \*\*\*  $P < 0.0001$ .

as indicated by the positive directional selection gradient ( $\beta_2 = +0.05$ ). Fertility selection favored early germinating individuals ( $\beta_3 = -0.18$ ). No significant stabilizing or disruptive selection was evident during any of the episodes in the first year.

The results for year 2 contrast with those of year 1. The only significant directional selection observed was for fruit production ( $\beta_3 = -0.10$ ). There was weak, positive directional selection during the first two episodes. Weak, but statistically significant, disruptive selection acted at both episodes of viability ( $\gamma_1 = +0.05$  and  $\gamma_2 = +0.02$ ). In general, the force of directional selection on timing of seed germination was much weaker in year 2.

Selection differentials and intensities of selection are reported in Table 4. In year 1, fecundity selection generated the major selective force on timing of seed germination, representing 63% of the total selection during that year and a change in the mean of -0.21 standard deviations (about 2 days earlier). Natural selection in winter and spring, respectively, accounted for 21% and 15% of the cumulative shifts in the mean. During year 2, the episodes of viability selection had approximately equal contributions to  $S$ , 11% and 9% of the total selection differential. Fecundity selection made the largest contribution to  $S$  and moved the mean -0.13 standard deviations (about 2 days earlier). Survivorship accounted for less

TABLE 4. Directional selection differentials ( $S$ ) for time of seed germination following each episode of selection for individual transects and the population as a whole. Intensities of selection ( $i$ ) are given in units of phenotypic standard deviations. Percentages are calculated as the proportion of the sum of the absolute values of the separate  $i_k$  values.

Selection episode	Selection differential $S_k$		Selection intensities $i_k$			
	1982/1983	1983/1984	1982/1983		1983/1984	
Overall						
Winter survivorship	-0.080	+0.027	-0.070	21%	+0.018	11%
Spring survivorship	+0.057	-0.024	+0.052	16%	-0.015	9%
Reproduction	-0.233	-0.221	-0.210	63%	-0.134	80%
Total selection	-0.256	-0.170	-0.228	100%	-0.101	100%
Transect 1						
Winter survivorship	-0.103	+0.060	-0.092	39%	+0.039	16%
Spring survivorship	-0.006	-0.062	-0.005	2%	+0.038	16%
Reproduction	-0.150	-0.264	-0.139	59%	-0.160	68%
Total selection	-0.259	-0.266	-0.236	100%	-0.083	100%
Transect 2						
Winter survivorship	-0.094	+0.023	-0.084	14%	+0.015	8%
Spring survivorship	+0.212	-0.044	+0.198	32%	-0.029	15%
Reproduction	-0.374	-0.234	-0.328	54%	-0.149	77%
Total selection	-0.256	-0.256	-0.214	100%	-0.163	100%
Transect 3						
Winter survivorship	-0.051	-0.035	-0.046	13%	-0.021	21%
Spring survivorship	-0.114	+0.008	-0.108	31%	+0.005	5%
Reproduction	-0.224	-0.032	-0.194	56%	-0.074	74%
Total selection	-0.389	-0.059	-0.348	100%	-0.035	100%

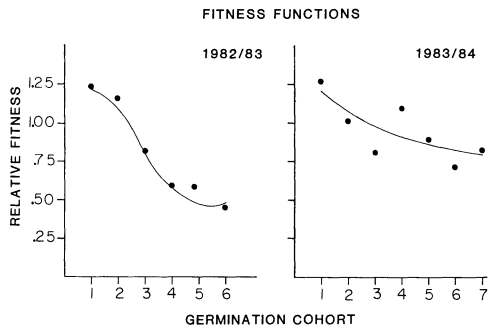


FIG. 2. Fitness functions for time of seed germination during 1982/1983 and 1983/1984. Solid circles indicate the cohort relative fitnesses. The regressions equations are  $y = 1.314 - 0.084x^2 + 0.010x^3$ ;  $R^2 = 0.96$  for 1982/1983 and  $y = 1.360 - 0.154x + 0.011x^2$ ;  $R^2 = 0.63$  for 1983/1984.

than 39% of the total selection differentials in each year. Fecundity is the primary determinant of the relationship between the timing of germination and fitness in this study. The net relationship of the timing of seed germination to plant total relative fitness is shown in Figure 2.

#### *Spatial Variation in Selection*

The heterogeneous nature of selection is evident from the analysis of selection on different spatial scales. The three transects differ in the importance of the timing of seed germination to plant fitness (Table 5). In all three transects in year 1 there was significant directional selection for earlier germination during the first episode. In addition, there was significant disruptive selection in transect 2 and highly significant stabilizing selection in transect 3 during the winter. In contrast, viability selection during the spring was disruptive in transect 1, directional and positive in transect 2, and both negatively directional and stabilizing in transect 3. All three transects showed highly significant negative directional selection during the third episode. The total strength of directional selection,  $\beta$ , was greatest in transect 3 ( $\beta = -0.33$ ), with transect 1 and transect 2 of equal magnitude ( $\beta = -0.20$ ). The directional regression coefficients (Table 5) were tested for heterogeneity (Zar, 1984) and were found to be significantly different among the transects for winter survivorship ( $P < 0.02$ ) and spring survivorship ( $P <$

0.001), but not for fruit production ( $P < 0.21$ ).

In year 2, variation in selection among transects was not as great, nor were the selection coefficients of the same magnitude as in year 1. During the first episode, directional selection for late germination was observed in both transects 1 and 2, but weak disruptive selection was also detected. No significant selection on germination time was measured in transect 3. For spring survivorship, significant positive directional selection was measured in transect 1, with disruptive selection in the remaining transects. Fertility showed significant negative directional selection in transects 1 and 2, but directional selection was not detectable in transect 3. The cumulative directional selection was negative in all transects, with no significant heterogeneity among transects. Overall, the stabilizing/disruptive selection gradients differed in sign among the transects during the episodes, but the total magnitudes were generally small.

The three transects varied in the selective importance of the timing of germination in year 1 (Table 4). Large differences in the intensity of selection were measured among transects at both episodes of viability selection (juvenile and adult). In transect 1, winter viability accounted for 39% of the total selection differential, but only 14% and 13% were due to winter viability in transects 2 and 3, respectively. Conversely, spring mortality selection in both transects 2 and 3 was responsible for 32% and 31% of the total shift in the mean, respectively, but only 2% of the selection differential in transect 1. Fecundity selection accounted for 54% to 59% of the total selection differential in the three transects. Variance in fitness among germination cohorts during the winter shifted the mean time of germination from  $-0.05$  to  $-0.10$  SD. The spring episode shifted the mean from  $-0.11$  to  $+0.20$  SD. The magnitude of the change in the average germination time was greatest for the third episode ( $-0.14$  to  $-0.33$  SD).

The results of year 2 are similar to those of year 1 in the relative importance of the three episodes, but the magnitude and direction of the shifts were more variable among the transects (Table 4). Winter viability selection was responsible for 8% to

TABLE 5. Directional selection gradients ( $\beta$ ) and stabilizing/disruptive selection gradients ( $\gamma$ ) for the three transects. Results reported for two years of study.  $N$  = number of individual plants present at the beginning of each episode of selection.

Transect	Selection episode	1982/1983			1983/1984		
		$N$	Directional $\beta$	Stabilizing/disruptive $\gamma$	$N$	Directional $\beta$	Stabilizing/disruptive $\gamma$
1	Winter survivorship	2,302	-0.081***	-0.016	2,861	+0.026	+0.074***
	Spring survivorship	1,730	-0.005	+0.028**	1,199	+0.026	+0.007
	Reproduction	1,599	-0.115**	-0.032	885	-0.108	-0.024
	Total selection		-0.201***	-0.002		-0.062*	+0.044
2	Winter survivorship	2,133	-0.076***	+0.032*	3,474	+0.011	+0.065***
	Spring survivorship	1,614	+0.170***	-0.063	1,508	-0.021	+0.025
	Reproduction	590	-0.308***	+0.158*	913	-0.106*	-0.044
	Total selection		-0.214***	+0.035		-0.116*	+0.037
3	Winter survivorship	1,148	-0.042***	-0.054***	1,753	-0.013	-0.016
	Spring survivorship	980	-0.095**	+0.192***	861	+0.003	+0.032*
	Reproduction	391	-0.190**	-0.019	642	-0.046	-0.064
	Total selection		-0.327***	+0.054		-0.056	-0.019

\*  $P < 0.05$ ; \*\*  $P < 0.001$ ; \*\*\*  $P < 0.0001$ .

21% of the change in germination time, but the direction of the shifts was from  $-0.02$  to  $+0.04$  phenotypic standard deviations. Spring viability selection accounted for 5% to 16% of the shift, or between  $-0.03$  to  $+0.04$  phenotypic standard deviations. The largest changes, 68% to 77% of the total shift in the mean, occurred during the episode of fecundity selection, with values ranging from  $-0.07$  to  $-0.16$  phenotypic standard deviations.

#### *Fine-Scale Variation in Selection: Quadrat Analyses*

Directional selection during fruit production accounted for from 42% to 80% of the total selection differentials in both the population- and transect-level analyses. Because the primary selection on germination time occurred through variation in adult fecundity (see Tables 4 and 5), I calculated only directional selection gradients for fecundity to compare selection intensities among quadrats. The entire life cycle was considered as one episode, with relative fruit production as the measure of fitness, calculated on an individual quadrat basis. The regression model was that of Equation (5). The results of the regression analyses for individual quadrats are shown as a histogram of directional selection coefficients,  $\beta$  for year 1 and year 2 (Fig. 3). Because the collection of these data required sacrifice-

sampling of quadrats, any single quadrat was measured in one year only. The quadrats were 2.6 meters apart.

The direction and force of selection on germination time varied even over the spatial scale of a few meters. Values of  $\beta$  ranged from  $-0.55$  to  $+0.20$  in the first year and  $-0.96$  to  $+0.68$  in the second. Shifts in the quadrats means,  $S$ , ranged from  $-0.60$  to  $+0.30$  during the two years. These represent changes in mean from eight days earlier to four days later. In concordance with the regression results for the entire population, early cohorts had higher fitness in the majority of the quadrats (21/32 in year 1; 20/31 in year 2). When tested for heterogeneity of slopes among quadrats, there was significant heterogeneity among quadrats in year 1 ( $P < 0.01$ ), but not in year 2 ( $P < 0.89$ ).

The effects of large- and small-scale variation in microsite on germination time were analyzed using a nested analysis of variance (Table 6). Both transect and quadrat-within-transect explained significant portions of the variance in germination date ( $P < 0.001$ ) in both years. Overall, the models explained small proportions of the total variance in germination time ( $R^2 = 0.08$  year 1;  $R^2 = 0.19$  year 2). The results suggest that microenvironmental conditions play some role in the creation of the phenotypic variation in the timing of seed germination in this population.

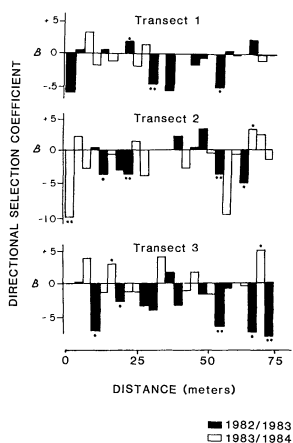


FIG. 3. Directional selection gradients for the timing of seed germination for individual quadrats. The position of the bars along the horizontal line indicate the relative positions of the quadrats along the 75-meter transects. Black bars indicate quadrats studied in year 1, white bars indicate quadrats studied in year 2. The height of the bars indicate the magnitude of directional selection. Positive  $\beta$  values are shown above the horizontal, negative  $\beta$  values are shown below the horizontal. \* =  $P < 0.05$ , \*\* =  $P < 0.01$  (significance levels for directional selection gradients).

## DISCUSSION

### Selection

Overall, seeds that germinated early had higher fitnesses than did seeds that germinated later, both during episodes of viability selection and fecundity selection. Strong directional selection is expected for characters that are highly correlated with fitness (Fisher, 1958). The observed directional selection contrasts with the expectation of an intermediate germination date exhibiting the highest fitness.

Several factors potentially influenced survivorship and fecundity in this population. Germination begins when the amount of light reaching the forest floor is increasing as the trees drop their leaves, but the average daily temperature, day length, and the spectral quality of light are all decreasing. A window of possible germination dates exists in which there is sufficient light, heat, and moisture available for establishment and growth. Early germinating plants experience the most favorable conditions and lower density-dependent competition among conspecifics, which could directly affect plant size. The fitness differentials

TABLE 6. Analysis of variance for germination cohort for two field seasons. Transect = transect in which seedlings germinated. Quadrat (transect) = quadrat nested within transect.

Year	Source	<i>df.</i>	Mean square	<i>F</i> value
1982/1983	Model	31	17.9	14.9***
	Transect	2	106.5	88.7***
	Quadrat (transect)	29	9.3	7.7***
	Error	5,550	1.2	—
1983/1984	Model	74	50.1	25.7***
	Transect	2	22.6	23.6***
	Quadrat (transect)	71	48.6	25.2***
	Error	8,070	1.9	—

\*\*\*  $P < 0.001$ .

among the germination cohorts observed in this study could in part be due to indirect selection on correlated characteristics such as plant mating system. In a greenhouse study comparing the performance of plants produced by selfing versus those produced by outcrossing, selfed seeds germinated later and were significantly less fecund than outcrossed seeds (Kalisz, 1985). Therefore, the variance in fitness among the cohorts in the field could be a function of inbreeding depression or hybrid vigor. The fitness differentials could be due to variation in the amount of competition as well. If density of conspecifics is an index of competition, individuals which germinate early experience lower densities of conspecifics than do plants which germinate later.

Although the average direction of selection in both years favored early germination, the magnitude and direction of this selective advantage was variable in time and space. The relative importance of germination time clearly changed between years (Fig. 2). The difference in the value of total relative fitness between the first and last cohorts estimated by the fitness functions was 0.74 in year 1 but only 0.41 in year 2. This fitness differential represented nearly a 2½-fold decrease in average relative fitness from the earliest to the latest germination cohort in the first year and a 1½-fold decrease in the second. This between-year variation in the selection gradient is most likely a reflection of large-scale differences in density-independent, abiotic factors. An autumn

flood, little snow cover, and record cold temperatures characterized the first year's winter. In the second year, there was a heavy snowcover and the flooding took place in the spring. These differences in winter weather may explain the differences in fitness between years. In general, the differences in the selection gradients among transects within years were smaller than those for any particular transect between years.

The direction and strength of selection changed among episodes and between years, even within the same transect (Table 4; e.g., transect 2). In this study, I investigated selection acting only on the timing of seed germination. However, the change in the distribution of the timing of seed germination may have been influenced by selection acting on this character and on correlated characters. Lande and Arnold (1983) indicate how selection may operate to reduce the intensity of directional selection on correlated characters. These correlations may be positive or negative and could explain the switch of the sign of the selection gradients between episodes. Thus, selection operating not only directly on the timing of germination, but also indirectly on correlated characters (such as selfing [Kalisz, 1985]) could be one explanation of the observed variable selection within a life cycle.

There have been few studies of the effects of the timing of seed germination on total lifetime fitness. Baskin and Baskin (1972), Howell (1981), and Marks and Prince (1981) concluded that early-germinating seeds experience lowered survivorship but higher fecundity when compared to later cohorts. My results of both higher survivorship and higher fecundity of early-germinating individuals contrast with these results. This indicates that the relationship of survivorship and fecundity to the timing of germination differs among species and that no general pattern is likely to exist.

#### *Phenotypic Variation in the Timing of Seed Germination*

The range of germination dates in both years spanned nearly two months, often within the same 16 × 16 cm quadrat. Coefficients of variation (CV) for the quadrats ranged from 37 to 62 with an average CV of 47. Phenotypic variation in the timing of

seed germination may be the result of genetic or environmental factors. The timing of seed germination is under variable selection pressure both on a spatial and temporal scale in this population. Variable selection in space and time have been postulated as mechanisms for the maintenance of genetic and phenotypic variation, and have received much theoretical attention (Levene, 1953; Haldane and Jayakar, 1963; Levins, 1968; Gillespie, 1974; Gillespie and Langley, 1974; Slatkin, 1978; Grant and Price, 1981; Via and Lande, 1985). If spatial heterogeneity in selection is retained among years, it has the ability to produce genetic subdivision of the population. Genetic variation could be maintained through the presence of dormant seeds or genotypes with varying degrees of dormancy which were produced during various kinds of selective regimes. Temporal variation in selection (between years) could affect the variance in date of seed germination (within a year) if a dormant seed population were present. This seed pool (the combined dormant seed production of several years) would have diverse germination requirements if the control of the timing of seed germination within a season had a genetic basis. This could occur whether or not genetic variation for long-term dormancy itself was present. Seed pools, in conjunction with variable selection, could result in the maintenance of genetic variation and evolutionary stasis (Epling et al., 1960). My work with natural and artificial seed pools in this *C. verna* population has demonstrated the existence of age structure due to the carry-over of dormant seeds between years (Kalisz, unpubl.). The observed diversity in the timing of seed germination within both field seasons may represent only a sample of the diversity of selective pressures experienced within the population over an extended number of generations. In addition to its effects on phenotypic variation in the population, this age structure in the population's seed pool can alter the response of the population to selection (Templeton and Levin, 1979; Charlesworth, 1980). The observed phenotypic variation in the timing of germination could be solely a function of changes in the direction and magnitude of selective forces between generations.

Habitat heterogeneity can directly cause environmental variance in the timing of seed germination and plant growth (e.g., Hartgerink and Bazzaz, 1984). Year-to-year changes in factors such as rainfall, average temperature, or percentage cloudcover produce overall changes in the microenvironment of a seed. Small-scale differences in the physical environment, such as soil topography, soil quality, amount of leaf litter, amount of surrounding vegetation, and depth of the seed in the soil, also create heterogeneity in the germination cues for seeds. Factors which are properties of the seed can also influence the timing of seed germination. Many seeds require scarification, cold-treatments, after-ripening, leaching of germination inhibitors, or a combination of such treatments to induce germination (e.g., Newman, 1963; Mayer and Poljakoff-Mayber, 1975). Diversity in germination requirements of seeds and a diversity of seed environments can produce a range in the timing of seed germination within a population.

#### *Response to Selection*

The rate of evolution by natural selection is a function of the amount of genetic variance for a character, its genetic covariance with other characters, and the strength of direct and indirect selection acting on it. Total fitness is expected to have very low additive genetic variance due to repeated episodes of strong directional selection (Fisher, 1958). I estimated the heritability of the timing of seed germination using a maximum likelihood option for variance component estimation (SAS Institute Inc., 1982 PROC VARCOMP). The estimated heritability was 0.06 with a standard error of 0.10 (Robertson, 1959), although the power of the estimate is low due to small sample size. The estimate represents a range of possible values of  $h^2$  for the population from 0 to 0.26. With this range of heritability, response to selection in this character would be possible in this population, as would a correlated response to selection on characters which are genetically correlated with the timing of germination. The range of germination dates in the field is likely to be a combination of both additive genetic and environmental variances. It is possible that

the phenotypic variation in the character is maintained through variable selection in time and space. The optimum date of germination appears to change from year to year in this population. Averaged over many generations, there may exist a net stabilizing selection acting on the timing of germination.

It was surprising that there were no individuals which germinated in an extreme left tail of the distribution. Clearly, individuals which germinate too early would be at a selective disadvantage with regard to interspecific competition, drought, and high temperatures present in late summer. Since germination in this species is cued by diurnal temperature fluctuations in the fall, individuals which were hypersensitive to this cue may have been culled from the population previously.

#### *Life-History Evolution*

The timing of seed germination had fitness effects throughout the lifetime of an individual. Although germination cohort can influence fitness at all episodes, the most profound effects were manifested late in the life cycle via fruit production (Table 4).

As evidenced in this study, both the direction and force of selection may change over the course of a generation. If selection is viewed as acting in a single episode, the perceived importance of a stage or character to life-history evolution could be diminished. Reversal of the direction of selection within a generation will produce an overall reduction in the magnitude of the selection differential. Therefore, if selection is measured at the end of the life cycle only, there exists the potential to mask the importance of a character expressed early in the life cycle. If selection is strong during one episode, followed by repeated episodes of weak selection in the opposite direction, there will appear to have been little or no selection acting on the character. Measuring and analyzing selection episodes expands our ability to understand and interpret not only how natural selection acts to create changes in phenotypic distributions, but also the selective importance of individual traits. When used in a multivariate study, these methods permit a partitioning and weighting of the selective impact of ecologically important

characters and their relation to the evolution of life histories.

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