TIMING OF SEED PRODUCTION AND DISPERSAL IN
GERANIUM CAROLINIANUM: EFFECTS ON FITNESS[1]

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Abstract. The importance of the timing of seed production and of seed dispersal to the fitness of an annual plant was examined using *Geranium carolinianum* in the piedmont of North Carolina. Mature seeds were collected from naturally growing plants on four dates in May and June and were then sown back into the population on five dates in late May, June, and July. The mean mass of seed produced varied during the growing season and this had important consequences for fitness. Seeds produced early were heavier, but lighter seeds germinated earlier. Seedlings that emerged earlier developed into larger plants with relatively higher reproductive output. Timing of seed dispersal had no effect on date of emergence, plant size, or fecundity.

Key words: fitness; Geranium carolinianum; *North Carolina piedmont; path analysis; seed dispersal; seed maturation date.*

INTRODUCTION

Fitness, or an individual's genetic contribution to future generations, is usually estimated through measurements of different components of fitness within a single generation. Survival, the number of offspring, offspring quality, and timing of reproduction are considered to be the most important components of fitness (Lotka 1913, Cole 1954). For organisms with overlapping generations and increasing population size, offspring produced earlier are more valuable than offspring produced later (Cole 1954, Lewontin 1965). However, the optimal timing of reproduction and its effects on offspring quality for an annual plant with discrete generations are not obvious. In contrast to the situation for perennials, seeds produced early by annuals do not increase the growth rate (r), because all seed from one generation will remain dormant in the soil for several months and germination is more or less synchronous. Schaal and Leverich (1981) suggested that if the quality of seed produced during the growing season remains constant and if there is a constant risk of seed mortality in the soil, then in annuals, offspring produced relatively late may have a higher fitness than offspring produced earlier.

There are, however, limitations to how long reproduction can be delayed. Growth and reproduction in annual plants are often limited at the end of the life cycle by unfavorable environmental conditions (Cohen 1971). Winter annuals, for example, that flower in late spring or early summer can encounter hot, dry summer conditions if they begin reproduction too late. On the other hand, if there is a positive correlation between plant size and fecundity (Werner 1975, Werner and Caswell 1977), then a plant that flowers too early may not be large enough to produce many seeds.

One assumption of many theoretical life history models is that all progeny within a particular reproductive event are of equal quality (Gadgil and Bossert 1970). However, in some plants, such as *Daucus carota*, seed produced earlier is of higher quality and has a higher germination percentage than seed produced later (Lacey and Pace 1983).

This study experimentally examined the importance of the timing of seed production and the timing of seed dispersal to the fitness of an annual plant. Specifically it asked how the timing of seed maturation and the timing of seed dispersal affect seed size, date of emergence, size of the plant, and fecundity in *Geranium carolinianum*.

METHODS

Geranium carolinianum L. (Geraniaceae) is a winter annual that grows in fields and waste places throughout much of the United States. In the piedmont of North Carolina, *G. carolinianum* germinates in September–October and persists as a rosette through the winter months. It bolts to an erect plant, 7–36 cm tall, in April, and flowers in late May. Each fruit is a five-seeded schizocarp.

Mature seeds were collected from naturally growing plants, in the Botany Experimental Plot on the campus of Duke University, on the following dates: 19 May, 27 May, 3 June, and 16 June 1982. These dates spanned the entire seed maturation period in the plot. Fifty seeds from each collection date were randomly selected, weighed, and returned to the collection. Until sowing, the seeds were stored in envelopes at room temperature in the laboratory. Seeds were sown in two blocks in the plot using a randomized block design. Twenty seeds from each available collection were sown in each block on 25 May, 29 May, 4 June, 17 June, and 22 July 1982. The dates spanned the period
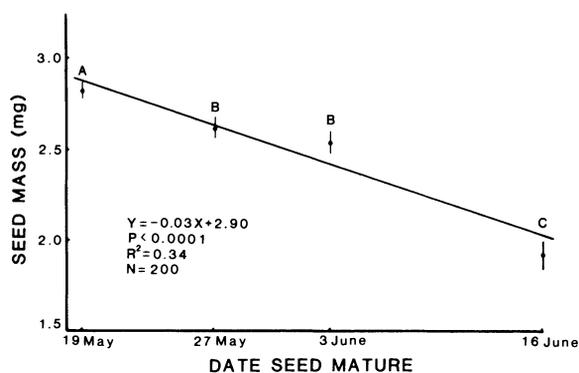
FIG. 1. Regression of seed mass on date of seed maturation ($\bar{X} \pm$ SE). Different letters indicate significant differences between means as determined by Duncan's multiple range test.

of dispersal in the plot, except for the last date, which was $\approx$4 wk after natural dispersal. On the last two sowing dates, seed from all of the collection dates were represented, but the earlier sowings were necessarily incomplete designs. Each seed was marked with a color-coded toothpick and an identification label. Date and percentage of emergence, plant size, fecundity, and phenological traits were recorded. During the time when plants were emerging, daily censuses were taken in order to reduce the chance of missing ephemeral individuals. After emergence, the plants were censused every 4 d until the end of the growing season. Size of the plant was defined as the product of two perpendicular widths of the plant and was measured nondestructively at the rosette and the adult, flowering stage. Regressions of total plant mass (y) on size (x) were highly significant: for the rosette stage, $y = 16.80x + 0.01$, $P < .0001$, $r^2 = 0.90$; for adult plants, $y = 2.34x + 6.49$, $P < .0001$, $r^2 = 0.50$. Date of bolting was defined as the date at which the stem of the plant was 5 mm long. Fecundity was quantified by counting the number of flowers that produced mature seeds. Each flower produces five seeds and there is no seed abortion.

For the analysis of the effect of sowing date on the phenological and size traits, an unconventional analysis of variance was used because of the unbalanced structure of the design. The null hypothesis for the

effect of sowing time was that all $\mu_{ms} = \mu_m$, where $m =$ date seed matured and $s =$ date seed was sown. In other words, the hypothesis tested was that there was no main effect of sowing date and no significant interaction between sowing date and date of seed collection. This model is equivalent to the hypothesis tested in a nested analysis of variance, with date of sowing nested within date of seed maturation. For the ANOVAs, transformations of the data were made when necessary to improve the fit to normality.

A goodness-of-fit G test was used to compare percent emergence as a function of maturation and sowing dates. Path analysis (Wright 1934) was used to measure the direct effect of one trait on another trait expressed at a later stage of the life cycle. This technique has been widely used in agronomic studies (Dewey and Lu 1959, Adams 1967, Grafius 1978), and recently has been applied to ecological data (Maddox and Antonovics 1983). The choice of paths in this type of analysis is often arbitrary, but in this case was based on ontogeny. The regression equations for the path analysis are as follows:

$$X_2 = P_{21}X_1 + e_2$$
$$X_3 = P_{32}X_2 + P_{31}X_1 + e_3$$
$$X_4 = P_{43}X_3 + P_{42}X_2 + P_{41}X_1 + e_4$$
$$X_5 = P_{54}X_4 + P_{53}X_3 + P_{52}X_2 + P_{51}X_1 + e_5,$$

where $X_1 =$ date of seed maturation, $X_2 =$ date of emergence, $X_3 =$ rosette size, $X_4 =$ adult size $X_5 =$ fecundity, $P_{ij} =$ path coefficient between variables X_i and X_j, and $e_i =$ residual error in each equation.

RESULTS

Seeds produced earlier in the growing season were heavier than seeds produced late (Fig. 1). The mean mass of mature seeds collected on 19 May was $\approx$46% greater than that of mature seeds collected on 16 June. By Duncan's multiple range test, the mean masses of mature seeds collected on 27 May and 3 June were not significantly different from each other, but means for all other dates were significantly different from each other (Fig. 1).

An analysis of variance showed that date of seed

TABLE 1. ANOVA results showing the effect of block, date of seed maturation, and date seed sown on phenological and size traits. Date seed sown is nested within date of seed maturation (see Methods).

Source of variation	Date of emergence		No. of rosette leaves		Rosette size‡		Date of bolting		Adult height		Adult size		Fecundity	
	F	df	F	df	F	df	F	df	F	df	F	df	F	df
Block	0.01	1	0.85	1	0.66	1	0.00	1	2.75	1	3.22†	1	0.97	1
Date seed mature	10.48**	3	1.38	3	1.49	3	2.31	3	3.26†	3	1.59	3	0.59	3
Sowing date	0.45	10	0.88	10	0.93	10	1.25	10	0.59	10	1.43	10	1.53	10
Error	⋯	172	⋯	134	⋯	134	⋯	120	⋯	102	⋯	102	⋯	107

† $P < .10$; ** $P < .01$.

‡ Product of two perpendicular widths of the rosette.

TABLE 2. Mean emergence date (±SE) for each date of seed maturation. Different letters denote significant differences between means as determined by Duncan's multiple range test.

Date seed mature	Emergence date	N	
19 May	21 October ± 2.4 d	60	A
27 May	21 October ± 2.1 d	57	A
3 June	16 October ± 2.2 d	47	A
16 June	7 October ± 2.7 d	23	B

maturation had a significant effect on date of emergence (Table 1), but a Duncan's multiple range test showed that only the mean emergence date of seed collected on 16 June was significantly different from the other mean emergence dates (Table 2). Seeds collected 16 June had a mean emergence date of 7 October, whereas seeds collected 19 and 27 May had a mean emergence date of 21 October. The emergence percentage was equivalent among seeds maturing on different dates ($\bar{X} \pm$ SE: 33 ± 4%; $G^2 = 1.97$, $P > .10$).

Date of emergence was correlated with a number of traits. Seedlings that emerged early developed into plants with more leaves and larger rosettes. Individuals larger as rosettes bolted earlier, attained larger adult stature, flowered earlier, and had higher fecundity (Table 3).

There were no effects due to block or sowing date, and interaction terms between sowing date and date of seed maturation were not significant (Table 1). There was no significant effect of sowing date on percentage emergence ($\bar{X} \pm$ SE: 34 ± 5%; $G^2 = 3.20$, $P > .10$).

From the regression equations presented above, a path diagram was constructed (Fig. 2). Each path is unidirectional, and the coefficient is a measure of the direct causal effect of one trait on another trait expressed at a later stage of the life cycle. The sum of the products of the path coefficients for all possible paths between any two traits is then the total causal component of the correlation between those traits. Using the path coefficients (Fig. 2) and the correlation coef-

ficients (Table 3), 92% (0.083/0.09) of the correlation between seed maturation date and fecundity is causal according to this model. However, 93% of this effect is an indirect effect of seed maturation date on fecundity via emergence date and later plant size. Furthermore, of the causal component to the correlation between date of emergence and fecundity, 97% is indirect through the effect of date of emergence on later plant size.

DISCUSSION

There is no evidence that timing of dispersal (sowing) is a significant component of fitness in *G. carolinianum*. It has been suggested that delayed reproduction would be advantageous for an annual plant that experiences a constant mortality of its seed in the soil (Schaal and Leverich 1981). This constant probability of mortality would be evident in a decreased germination percentage for seeds dispersed early. In this study with *G. carolinianum*, however, there were no differences in percentage emergence of seedlings from seed sown on different dates. It may be that in order to show a significant advantage of delayed dispersal sensu the Schaal and Leverich model, seeds must remain in the soil for a longer period of time to show differential mortality. Seeds of *G. carolinianum* survive in the soil for at least 2 yr; thus the importance of seed mortality in the soil for *G. carolinianum* may only be evident for seeds that germinate two or more years after being dispersed. The effect of timing of dispersal may also be dependent on environmental factors, as suggested in two studies with *Daucus carota*. In one study the emergence percentage decreased with delayed dispersal (Lacey 1982), but in a second study under different environmental conditions, the emergence percentages increased with delayed dispersal for the spring-germinating seed (Lacey and Pace 1983). Given such variation within one species, it may be difficult to determine the biological importance of the timing of seed release.

In the present study, effects of timing of dispersal

TABLE 3. Correlation coefficients between phenotypic traits at different stages of the life cycle (all $n \geq 100$). Because there are multiple correlated test of significance in this matrix, a Bonferroni inequality test at the $\alpha = .05$ level was used to determine the significance of the individual correlations (Miller 1981).

	Date of seed maturation	Sowing date	Date of emergence	No. of rosette leaves	Rosette size†	Date of bolting	Adult height	Adult size
Date of emergence	−0.26*	−0.15						
No. of rosette leaves	+0.15	+0.06	−0.28*					
Rosette size	+0.10	+0.08	−0.31*	+0.69*				
Date of bolting	−0.20	−0.07	+0.31*	−0.33*	−0.26			
Adult height	+0.15	+0.05	−0.27	+0.50*	+0.77*	−0.46*		
Adult size	+0.06	−0.01	−0.18	+0.48*	+0.68*	−0.03	+0.58*	
Date flowered	−0.09	+0.04	+0.15	−0.08	−0.36*	+0.26	−0.47*	−0.28
Fecundity	+0.09	+0.05	−0.24	+0.54*	+0.84*	−0.06	+0.67*	+0.91*

* $P < .05$.

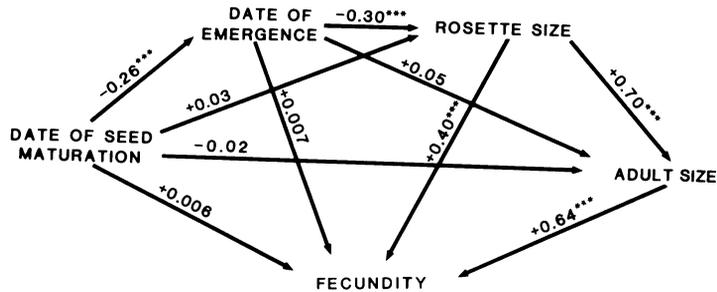† Product of two perpendicular widths of the rosette.

FIG. 2. Path analysis diagram. Each coefficient is a measure of the direct causal effect of the trait at the base of the arrow on the later occurring trait pointed to by the arrowhead.

and timing of maturation were measured independently. Without experimental separation of these effects, observed differences in timing of seed dispersal may be derived either from differences in the time at which the seed is ripened or from differences in the time of retention of ripe seed before it is dispersed. For example, variation in seed viability that has been attributed to differences in dispersal timing may be due to variation in the quality of seed produced during the growing season or to the advantage of early reproduction for a plant that can germinate immediately after dispersal (Baskin and Baskin 1978, Lacey and Pace 1983). Lacey and Pace (1983) found a significant effect of timing of seed maturation and dispersal on offspring growth and timing of reproduction. Seeds that were produced earlier and were sown earlier had an opportunity to germinate earlier, and subsequently to develop into larger offspring. Some seedling emergence from early-dispersed seeds occurred before later-dispersed seeds had been sown; thus there were seasonal advantages to early dispersal. In an annual plant, such as *G. carolinianum*, seasonal advantages are not important because all seeds remain dormant in the soil during the summer months and there is only a relatively short period of time during which germination occurs.

The date of seed maturation in *G. carolinianum* has its most significant effect on individual fitness indirectly through its effect on timing of germination and seedling emergence. Seedlings from seeds matured later emerge earlier, and early emergence gives an individual a longer life-span relative to its neighbors and, most importantly, allows an individual to grow for a longer period of time and thus to accumulate more resources before flowering. Large individuals are then more fecund. Timing of emergence has also been shown to have a significant effect on plant size, survival, and fecundity in other studies. Ross and Harper (1972) suggest that the success of an individual in dense stands is directly related to its emergence date relative to its neighbors. Late-emerging individuals are often smaller and have decreased survival probabilities and lower fecundity (Kasperbauer and Sutton 1977, Cook 1980, Naylor 1980, Howell 1981, Wanjura and Minton 1981).

There are cases, however, in which early germination will not be favored. For example, in an extreme case germination that is too early is not advantageous. Seeds of *G. carolinianum* that germinated in midsummer, after a period of low temperatures and high moisture, all died later in the summer during a dry spell (Baskin and Baskin 1971). Also, in cases where there is a constant size-independent risk of mortality, later-emerging individuals will have a higher probability of surviving to the time of reproduction (Fletcher 1975).

Large and small seeds produced at different times of the growing season may be advantageous under different conditions. Late-maturing seeds were smaller but they germinated earlier. Similar results have been found in other studies, where it has been suggested that when germination is limited by seed coat impermeability, smaller seeds will germinate earlier than larger seeds due to a higher surface-to-volume ratio (Harper and Obeid 1967, Edwards and Hartwig 1971, Cideciyan and Malloch 1982, Wulff 1982). Larger seeds have been shown to have an advantage when buried at greater depths because of their greater food reserves; however, when both sizes of seed are sown at the surface, smaller seeds germinate earlier (Harper and Obeid 1967). Larger seeds may also be advantageous if there is a positive correlation between seed size and seedling dry mass (Harper and Obeid 1967, Schaal 1980). Such an advantage has been found with *G. carolinianum* (Roach 1984). Variation in seedling size due to seed size differences could have the same effect as variation in date of emergence in dense stands (Ross and Harper 1972). In *G. carolinianum* there is not a trade-off between the mean seed size (y) and the number of seeds produced by an individual plant (x): $y = 0.0009x + 2.83$, $P > .10$, $r^2 = 0.03$, $n = 20$ (Roach 1984).

The success of an individual seed therefore depends on the interaction between seed mass and the environmental conditions during germination. The variation in seed size created by different seed maturation dates increases the chances that some of the offspring of an individual will be successful. In years with relatively synchronous germination, individuals with larger seeds will have an advantage; but in years with limited rainfall in the autumn, small seeds may emerge

earlier. If the risk of mortality is not increased by earlier emergence, then the individuals from small seeds will have the advantage of a few weeks growth. It is these differences in seed size and the interaction between seed size and the environmental conditions that regulate germination, hence emergence, that later determine which individuals become the largest, flower earliest, and produce the most seeds—in other words, which individuals will have the highest fitness.

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