Effect of parental flowering and dispersal times on offspring fate in *Daucus carota* (Apiaceae)

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Abstract:
Seeds collected from parents that flowered at different times were dispersed onto experimental plots at different times during the normal dispersal season. Parental flowering and dispersal times, which are correlated with each other, independently affected offspring germination, growth, and time of reproduction. Estimated population growth rates were highest for offspring that were dispersed early in the dispersal season and that came from early flowering parents. The data provide evidence that 1) an individual's fate is determined by the environment of the previous generation, and that 2) an individual's fitness should be calculated from life history data that span more than one generation.

Article:

Introduction

Although the concept of fitness underlies the study of evolutionary biology, no one has yet succeeded in measuring accurately the net fitness of any genotype in a natural habitat. One fundamental barrier has been identifying all components of fitness. Fitness is usually estimated from survivorship and fecundity data, however, Lewontin (1974) has pointed out that to measure the net fitness of a genotype accurately, we should measure also the probability that the genotype's offspring survive to reproduce. Rowe (1964) earlier articulated a similar idea, when he argued that an individual's phenotype may be determined by the environmental history of previous generations.

The extent to which one generation influences the phenotype, and therefore fitness, of individuals in another generation is unclear. Studies have shown that the parental environment can influence offspring germination and growth (e.g. Went 1959; Highkin 1958, 1961; Durrant 1958, 1962; Hill 1965; Evenari et al. 1966; Baskin and Baskin 1973), however, these studies have not demonstrated that such changes influence an offspring's ultimate fate or its contribution to future generations. To explore further the impact that events in one generation might have on another, we conducted an experiment to examine the effect of parental flowering and dispersal times on offspring fate in *Daucus carota* L. ssp. *carota.*

Biology and methods

Daucus carota L. ssp. *carota* (Apiaceae), commonly called wild carrot or Queen Anne's Lace, grows in disturbed habitats and old fields throughout much of temperate North America and Eurasia. Populations establish themselves quickly, usually by the second year, and persist for variable lengths of time (Lacey 1982). In North Carolina, populations may last for four to six years before being replaced by later successional species. Individual plants are short-lived monocarps that usually flower in the first, second, or third summer. Year of flowering is both genetically and environmentally controlled (Lacey unpublished ms.), and natural populations comprise a mixture of annuals, biennials and longer-lived individuals.

Flowering and dispersal times within years can vary greatly within and among populations (Pace 1981; Lacey 1982). In North Carolina most plants begin to flower during June and July. Flowers are produced in umbels that

reach anthesis sequentially with the terminal umbel, at the tip of the main stem, flowering first. Dispersal begins in early August and extends into the following year. The earliest flowering plants are the first to begin dispersing seeds, and the terminal umbel is the first within a plant to lose seeds.

On June 8th and 22nd and July 3rd, 1979, we marked in each of two populations near Greensboro, N.C. (Pace 1981) thirteen flowering terminal umbels. Then on August 4th we collected all seeds from the early June flowering umbels (the only ones with brown seeds), and on September 8th we collected seeds from the later flowering groups. After we thoroughly mixed the seeds within each flowering group from each population, we counted six samples of 500 seeds from the earliest flowering group and five from the later groups per population. Each sample was suspended in a mosquito net bag (an artificial umbel) approximately one meter above ground at the North Carolina Agricultural and Technical University Experimental Farm, Greensboro, N.C. Monthly, beginning in August for the earliest flowering group and September for the later groups, we scattered one sample per source onto one of 40 plots (0.5 m x 0.5 m) that lay near the suspended seeds. Seed samples were as-signed to plots at random, and eight plots were left alone, i.e., designated as controls to check for carrot seeds already in the soil and for seed movement among plots. Neighboring plots were separated from each other by 0.5 m. The area used for the plots had been plowed and cleared of weeds in the beginning of August and was bordered by grasses and weeds on two sides and plowed soil on the other sides. The area represented a common habitat of *D. carota,* a recently disturbed field.
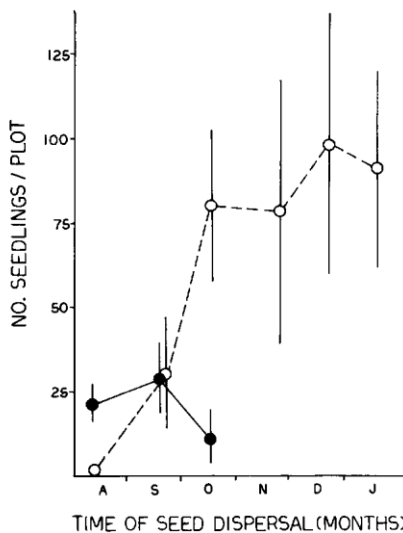

Fig. 1. Mean seed germination in fall 1979 (●) and spring 1980 (o) for each dispersal time. Standard deviation shown by vertical bar
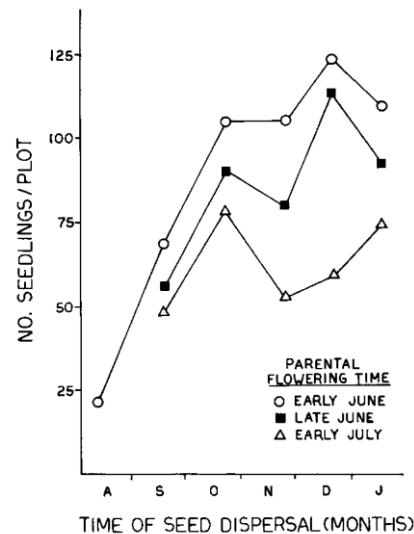
Fig. 2. Mean germination of seeds dispersed at different times and from plants flowering in early June (o), late June (■), and early July (Δ)

Throughout that following year we collected data on time and amount of germination, survivorship, and number of annuals in each plot. We also examined the growth of all individuals by measuring with calipers the root crown diameter of each to 0.1 mm. Root crown diameter provides a good estimate of total plant biomass (Gross 1981) and survivorship and is positively correlated with seed set (Lacey unpublished data).

To examine the differences among flowering — dispersal treatments we first analyzed separately the germination, survivorship, size, and flowering year data using analysis of variance and Chi-square tests. We present the ANOVA statistics and p values for Type I sums of squares when we considered September through January dispersal and Type IV values when we included the August dispersal data, which produced an unbalanced design. Unless indicated otherwise, the ANOVA statistics come from Type IV sums of squares.

Then we integrated our data to estimate the population growth rate for each treatment. Population growth rate (2), which we used as our fitness estimate was calculated from the matrix model:

$$\begin{bmatrix} 0 & 0 & S_A & S_B \\ L_{x_1}(1-P_A) & 0 & 0 & 0 \\ L_{x_1}(P_A) & 0 & 0 & 0 \\ 0 & L_{x_2} & 0 & 0 \end{bmatrix} \begin{bmatrix} S \\ NR1 \\ R1 \\ R2 \end{bmatrix} = \lambda \begin{bmatrix} S \\ NR1 \\ R1 \\ R2 \end{bmatrix}$$

where SA = average seed set per annual (within-season flowering time disregarded), S_B = average seed set per biennial (within-season flowering time disregarded), L_{x_1} =*probability* of surviving the first year, L_{x_2} =*probability* of surviving the second year, P_A= proportion of first year survivors that are annuals, S= seed number, $NR1$= number of one year old plants that do not reproduce, and $NR2$ = number of one year old plants that do reproduce.

The values of λ that were calculated from this model were constrained in two ways. First, the model assumed that individuals did not live past their second year. This assumption was quite reasonable given data from a neigh-boring experiment (Lacey, unpublished data) in which the same seed source were sown onto the same size plots at the same density in October of the same year. Survivorship was followed for three years in these plots and almost no rosettes survived to the third year. Second, because we did not collect data for all the parameters of the model, we had to hold some parameters constant and use data from the neighboring experiment to estimate these parameters. To estimate second-year survivorship, L_{x_2}, we used the survivorship values of different-sized fall rosettes in the neigh-boring plots. Because the survivorship values varied so little over the range of size (root crown diameter) classes found in our dispersal-flowering treatments, L_{x_2}= 0.37 for all treatments. The seed set values, S_A = 1162 and S_B= 5129, were the mean seed set values for annuals and biennials growing in the neighboring plots.
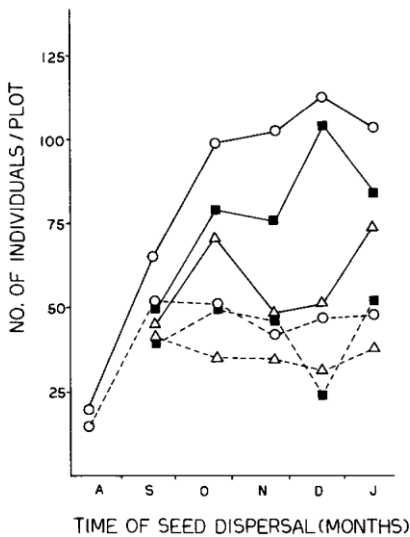

Fig. 3. Mean survivorship to August (solid line) and November (dashed line) of offspring from parents flowering in early June (o), late June (■), and early July (▲), shown by time of seed dispersal
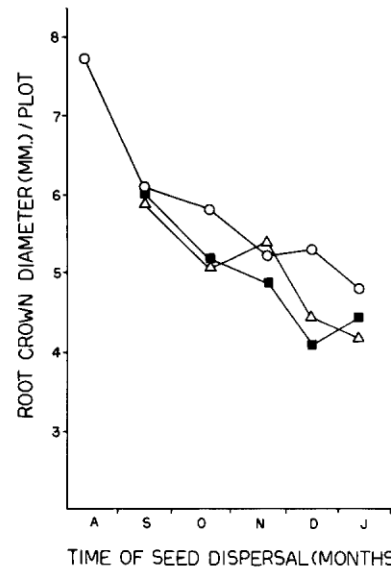

Fig. 4. Mean root crown diameter of offspring from parents flowering in early June (o), late June (■), and early July (▲) shown by time of seed dispersal

Results

Total seed germination increased significantly when we delayed seed dispersal from August through January (Fig. 1; August—January plots: df = 5, SS =13,506, F = 8.13, *P< 0.01;* September—January plots: df = 4, SS = 6,329, F = 4.76, *P<* 0.05). Autumn germination occurred only in plots sown with seeds in August, September, and October and did not vary significantly among these plots (df = 2, SS = 884, F = 4.29, *P>* 0.05). Subsequent spring germination occurred in all plots and did increase significantly with delay in sowing time (df= 4, SS =17,934, F =16.48, *P* < 0.001). Thus the variation in spring germination explains the variation ob-served in total germination. No seeds germinated in the control plots.

Delay in parental flowering time significantly reduced total offspring germination (Fig. 2: September—January plots: df= 2, SS = 8,002, F = 12.04, *P<* 0.01). The spring germination pattern accounted for this change because

it alone varied significantly over parental flowering groups (September—January plots: df = 2, SS = 7,141, F =13.12, $P < 0.01$). All flowering groups responded similarly to dispersal delays as there was no significant flowering-dispersal time interaction (September—January plots: df= 8, SS = 1956, F = 0.74, $P> 0.05$).
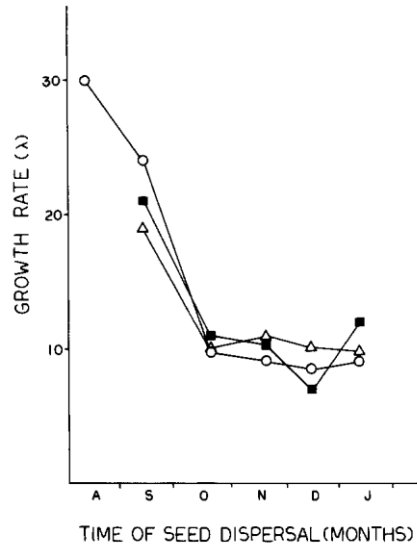

Fig. 5. Estimated population growth rate (λ) for each flowering-dispersal treatment. See text for further explanation. Symbols identified in Fig. 4

Rosette survivorship to mid-summer (August 1980) was quite high in all plots. Subsequently, however, many rosettes died, and the plots having the highest density suffered the greatest mortality. Consequently, by November the striking differences in initial density observed among dispersal-flowering treatments had completely disappeared (Fig. 3; dispersal effects: df= 5, SS =1,570, F = 1.32, $P> 0.05$; flowering effects: df = 2, SS = 616, F =1.30, $P> 0.05$). Most of the rosettes that died belonged to the spring cohort, which constituted 100% of the seedlings in the densest plots. Even in September dispersal plots where size of the fall and spring cohorts were similar, the spring cohort still suffered higher mortality (X^2 = 25.3, df= 1, $P <0.001$).

Dispersal time explained a significant amount of the variation in mean root crown diameter of the rosettes still alive in November (Fig. 4; df = 5, SS = 60,182, F = 79.75, $P < 0.0001$). Mean root crown diameter declined with delays in seed dispersal. Part of this dispersal effect may be attributed to the autumn cohort, which contained the largest rosettes and were present in only the August through October dispersal plots. Even within the spring cohort, however, delaying dispersal significantly reduced rosette size (df= 5, SS = 7274, F = 10.37, $P < 0.0001$).

The mean root crown diameter of the November rosettes also declined significantly with delays in parental flowering time (Fig. 4; df= 2, SS = 6,672, F = 22.1, $P < 0.0001$), and even within the spring cohort alone, earlier flowering plants produced, on average, larger offspring (September—January plots: df= 2, SS = 5,772, F = 20.54, $P <0.0001$). While the flowering — dispersal interaction was not significant when all plants were considered, it was significant for the spring cohort (September—January plots: df= 8, SS = 6,368, F = 5.67, $P < 0.0001$). Offspring from the earliest flowering group were less sensitive to the negative effect of delaying dispersal.

Dispersal and flowering times additionally affected the time when offspring reproduced. All annuals came from the autumn cohort, i.e., the August through October dispersal plots. Also, more annuals emerged from the plots with earlier dispersal among these plots having autumn germination ($\bar{x}_{AUG}= 17$, $\bar{x}_{SEP}= 22$, $\bar{x}_{OCT} = 1$; df= 2, SS= 1,131, F = 39.14, $P< 0.05$). To examine the influence of parental flowering time on number of annuals, we focused on the September plots, which uniquely had considerable autumn germination for all flowering groups. Within these plots seeds from the earliest flowering parents were most likely to develop into annuals (fraction of annuals from parents flowering in early June = 66/70, late June = 29/37, early July = 36/57; X^2=18.9, df= 2, $P < 0.005$).

The population growth rates, which integrated survivor-ship and reproductive data, varied greatly among flowering-dispersal treatments (Fig. 5). Projected growth was greatest for offspring dispersed by September and from the earliest flowering group. After September, growth rate dropped to an equivalent level for all flowering-dispersal treatments.

Discussion

Previous studies have shown that within-season flowering time can significantly affect seed set (e.g., Beattie et al. 1973; Schemske 1977; Waser 1978; Augspurger 1981 ; Arnold 1981) and germination (e.g., Gutterman 1973; Baskin and Baskin 1973), however, few studies go beyond germination. Those that do confound position effects of flowers on individual plants with temporal effects (e.g., Borthwick 1931; Hawthorne et al. 1962; Cavers and Harper 1966; Thomas et al. 1979; Gutterman 1980/81). In this study we have eliminated the position effect to look at the temporal effect alone, and found that parental flowering time influenced offspring germination, growth, and time of reproduction.

Dispersal time also influenced these fitness components. The negative relationship between dispersal time and germination was consistent with Schaal and Leverich's (1981) hypothesis that delaying dispersal should enhance germination. However, in our experiment, subsequent density-dependent mortality eliminated any numerical advantage that was gained by delaying dispersal. Previous work with *D. carota* (Lacey 1982) suggested that dispersal time would influence significantly offspring growth and reproduction, and it did. This study shows additionally that parental dispersal time, independently of flowering time, can influence offspring fate in spite of the fact that onset of parental flowering and dispersal are positively correlated (Lacey 1982).

The estimated population growth rates, which estimate fitness for the different treatments, summarize the flowering-dispersal effects. Fitness values were highest for seeds dispersed early and from the earliest flowering parents. Only the early dispersed seeds germinated in autumn, and only this cohort produced annuals. Also, the earliest flowering group produced the greatest number of annuals. Possibly the seeds from this group were larger, of higher quality, or more mature at time of germination; but in any case, only these seeds could be dispersed in August, which enhanced the opportunity for autumn germination.

The variation in population growth rate over treatments most reflects the variation in proportion of annuals *(PA)* in the fitness model. This is to be expected, first because growth rate is most sensitive to changes in length of the pre-reproductive period (Lewontin 1965), and second, second year survivorship and annual and biennial seed set were held constant in our model. Even if these parameters had varied over treatments, the variation should have exaggerated the differences in growth rates among treatments rather than reduced them. Seeds dispersed early and from the earliest flowering parents produced the largest " one-year olds", which should have a higher probability of survival and produce more seeds the second summer.

Because our experimental data come from only one year, it is important not to place too much weight on the absolute differences in growth rates among treatments. Had the experimental plots not suffered a severe drought from August through November, first-year survivorship of the later dispersed seeds might have been higher. Further, survivorship of autumn- and spring-germinating cohorts can vary considerably over years (Lacey 1982). In spite of this limitation, the data show that the environment of one generation can influence the fitness of another.

We have treated flowering and dispersal times as parental attributes even though flowering time is correlated with time of zygote formation, offspring birth, and dispersal time produces an environmental change during early embryo development. The critical aspect of these events is their control. Parental time of flowering determines when offspring birth and dispersal can occur, and time of flowering is determined by the environment in which the juvenile parent is growing. Low nutrient availability delays flowering (Lacey unpublished ms.), and offspring do not maintain parental differences in flowering time when grown in the same environment (Lacey 1982). Therefore the control of offspring birth and dispersal is influenced by the environmental history of the parent prior to initiation of the offspring generation.

Thus far we have discussed the impact of the parental environment on offspring fate. The data, however, also ad-dress the causes of variation in parental fitness and show that parental fitness can vary with time of reproduction and dispersal within a growing season. If *D. carota* is not unique, realistic fitness estimates should include fitness components that measure phenological effects beyond fecundity, such as the reproductive success of the next generation. The long-term impact that one generation can have upon the fitness of individuals in another, i.e., the number of generations that need to be considered, is unclear. The environment can produce effects that span several future generations in potato (Went 1959) and flax (Durrant 1962) crops, but so far no studies have addressed these effects in natural populations. Clearly this component of fitness is ripe for further study.

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