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# SEED MORTALITY IN DAUCUS CAROTA POPULATIONS: LATITUDINAL EFFECTS[1]

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ABSTRACT

*Daucus carota,* a common herbaceous weed, grows over a wide latitudinal range in eastern North America. Viability and germination tests of mature seeds collected from 36° to 45°N were conducted to measure predispersal seed mortality. Viability and germination declined as latitude of the seed source decreased. Only 30–50% of the seeds from southern populations germinated owing to high embryo inviability and absence of embryos. Sixty to ninety percent of the seeds from northern populations germinated. Reciprocal planting of seeds in outdoor experimental plots at three latitudes and testing of seeds over two generations together showed that the environment in which seeds mature, rather than environmental preconditioning over generations or genetically-based differences among populations, explain this variation in germination ability. Within-latitude germination declined in experimental plots as population age of the seed source within latitudes increased. The data indicate that predispersal seed mortality can influence local population persistence and that seed mortality is an increasingly important factor in population regulation at the southern limit of the species' range.

ALTHOUGH MORTALITY can occur at the seed stage in a plant life cycle, we do not yet know how strongly this mortality regulates the size of natural plant populations. The loss of a few hundred seeds may be inconsequential in view of the thousands entering the seed pool (Harper, 1977). Conversely, seed death may reduce the seed pool so dramatically that it renders post-germination mortality "trivial" (Hickman, 1979). To assess better the role that seed mortality plays in regulating natural plant populations, ecologists have recently begun to quantify seed mortality and identify its causes. In *Minuartia uniflora,* mortality at the seed stage far surpasses mortality at any other stage (Sharitz and McCormick, 1973). Predation (e.g., Janzen, 1971; DeSteven, 1983) and abortion (e.g., Stephenson, 1981; Aker, 1982; Lee and Bazzaz, 1982) can both act at the flower, fruit, or seed levels to lower seed set, and seed predation can severely reduce seedling recruitment in *Haplopappus* (Louda 1982, 1983). To provide further information about seed mortality in natural populations, I here describe the variation in predispersal seed mortality in *Daucus carota* L. ssp. *carota* (Small, 1978) and examine the contributions of latitude and population age to this variation.

MATERIALS AND METHODS—The data come from four viability and germination experiments conducted on seed samples collected over the species' latitudinal range, from southern Canada to the Georgia piedmont, in eastern North America. Seed germination and viability studies are usually conducted to identify environmental conditions that induce germination in viable seeds (e.g., Ruhland, 1965; Kozlowski, 1972; Mayer and Poljakoff-Mayber, 1975; Harper, 1977; Baskin and Baskin, 1982) or to identify the provenance that produces seeds best suited for agricultural or forestry purposes (see Barton, 1967). In *D. carota,* germination tests can also be used to assess mortality during fruit development. Fruit development continues whether or not the embryo dies during development, and the seed mortality agent does not remove fruits from the plant (Flemion and Henrickson, 1949; Flemion and Olson, 1950; Robinson, 1954).

*Experiment 1: indoor germination tests*—During the summer of 1981 I sampled plants at four latitudes: Greensboro, NC—36°N, Charlottesville, VA—38°N, Ann Arbor, MI—42°N, and Ottawa, Canada—45°N. (Fig. 1). One population was sampled per latitude. The flowering season for *D. carota* spans approximately 2 months; in North Carolina flowering occurs

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Fig. 1. Approximate range of *D. carota* in eastern North America and location of study sites: 45°N—Ottawa (●), 42°N—Ann Arbor (■), 38°N—Charlottesville (●), 36°N—Greensboro (▲).

predominantly in June–July and in northern United States and Canada in July–August. Thus, to sample adequately each population over time, I marked in Charlottesville and Ottawa in late June and July, respectively, 20–30 plants in each of three developmental states: 1) terminal (uppermost) umbel likely to begin flowering in 1–2 wk, 2) only terminal umbel flowering, and 3) green developing fruits in the terminal umbel and first order lateral umbels flowering. In Greensboro and Ann Arbor, I marked plants in the latter two stages only.

I collected the mature (brown) terminal umbels from these samples in August and September and culled out umbels producing fewer than 100 mericarps (one-seeded half-fruits) because these umbels did not produce enough seeds to test for germination. From those remaining umbels, I chose ten at random for indoor germination tests. When samples did not contain ten umbels with at least 100 mericarps, I used all remaining umbels. From each umbel, I selected at random 25 mericarps and placed them on filter paper in a petri dish. Six ml of distilled water were added to each dish, and the seeds were allowed to germinate for two weeks in an incubator set at 26 C, 14-hr day and 20 C, 10-hr night. Additional water was added when needed to keep the filter paper moist. Previous studies of *D. carota* indicated both that these environmental conditions would maximize the amount of germination and that a 2-wk interval was sufficient to assess immediate germination potential (Hoefke, 1929; Borthwick, 1931; Durfee, 1948; Dale and Harrison, 1966). Since some seeds require several months of afterripening before they will germinate (Hoefke, 1929; Borthwick, 1931; Dale and Harrison, 1966), I repeated the germination tests monthly from September to December.

Total seed germination was recorded for each seed sample, and the arcsine-transformed data were analyzed with analysis of variance to determine the impact of latitude of source population and relative time of germination test (based on estimated number of days since flowering of the terminal umbel) on percent seed germination. I also examined the effects of seasonal flowering time on percent germination by assigning each sample a value from 1–4 depending on the flowering time of that sample relative to the two month flowering season for that latitude. The value 1 signifies the plants that flowered in the first 2 wk of the flowering season and 4 those that flowered in the last 2 wk. Seeds develop at approximately the same rate regardless of flowering time or latitude (Pace, 1981; Lacey, 1982); therefore these seasonal differences in flowering time also reflect differences in time of seed maturation and onset of dispersal.

*Experiment 2: viability test*—I also tested the samples directly for seed viability. In January 1982, I selected an additional 25 mericarps from each umbel used in the germination tests that still contained fruits. All had fruits except for some Greensboro umbels. Viewing the fruits through a dissecting scope, I sliced the mericarps longitudinally off center (through the endosperm) and soaked them in 2,3,5, triphenyltetrazolium chloride in the dark. Slicing the mericarp facilitated the movement of the dye to the embryo. After 2 hr I examined the mericarps again through the dissecting scope and scored each seed as either 1) viable, embryo pink to red, 2) inviable, embryo present but partially or completely white, 3) inviable, embryo absent. I then used the multivariate $G^2$ test (log-likelihood ratio) (Bishop, Fienberg

and Holland, 1975) to examine the effects of latitude of source population and relative flowering time on embryo condition.

*Experiment 3: outdoor reciprocal sowing across latitudes*—The outdoor reciprocal sowing experiment assessed the germination potential of different-aged populations under more natural conditions. In August and September 1979, I collected 25 terminal, fruit-laden umbels from three populations at each of three latitudes: Greensboro, NC (36°N), Ann Arbor, MI (42°N), and Ottawa, Canada (45°N). The fields in which these populations were found had lain fallow from 1 to approximately 8 yr in Greensboro and from 2 to at least 20 yr in Ann Arbor and Ottawa. The year of last planting (abandonment) was known exactly or was estimated to within 2–5 yr by the owner of each field. Because *D. carota* usually colonizes fields in the first 2 yr of abandonment (Pace, 1981; Lacey, 1982), these populations represented different stages in typical population growth and decline. All sampled plants had flowered in the 1st month of the flowering season.

For each of the three populations at each latitude, I counted 15 samples of 500 mericarps (20 mericarps/umbel), and in early October scattered these samples onto outdoor 0.5 × 0.5-m plots in a modified Latin square design. Five samples per population were scattered onto separate plots at each latitude. Thus each sowing site contained 50 plots, which included five control plots onto which no seeds were sown. These control plots tested for seed movement among plots and seeds already in the soil. The fields encompassing all plots had been plowed once that previous spring and once just before seed sowing; thus they resembled a disturbed, or recently abandoned, field, a common habitat for this species. I estimated seed germination by recording seedling numbers that autumn and the following spring, when most seeds germinate (Lacey, 1982). The square root-transformed data were analyzed with analysis of variance to determine the effect of latitude of sowing site, latitude of seed source, and relative age (ranked from 1–3) of source population within latitude on total seed germination. The relative age of the source population was determined by the age of field in which the population was found. Thus populations from fields abandoned for 2, 5 and 10–12 yr were ranked 1, 2, and 3 respectively.

*Experiment 4: genetic and environmental components*—To shed light on the transmission of germination potential from one generation to the next and thus to assess genetic and environmental contributions to latitudinal variation in potential germination, I allowed the seeds that germinated in the previous experimental plots to grow and reproduce. I then collected the terminal umbels from both annuals and biennials that flowered in these plots. Terminal umbels from annual plants were collected by original seed source (i.e., by latitudinal source of seeds initially sown onto the plots) from the Greensboro and Ann Arbor plots in 1980, and from biennials from each seed source growing in the Ann Arbor and Ottawa plots in 1981. The Greensboro plots in 1981 did not produce enough biennials for a collection.

All umbels were stored in plastic bags in boxes in the laboratory until March 1983, when I selected from each sample up to ten umbels that contained at least 25 mericarps. To minimize the effects of within-season flowering time I selected only umbels that had flowered in the 1st month of the flowering season in the Ann Arbor and Ottawa plots. Such selection was not possible for the Greensboro plots because the plants from the Greensboro seed sources all flowered earlier than those from Ann Arbor and Ottawa seed sources. From each umbel I took 25 mericarps and placed them under the same environmental conditions as in Experiment 1. Analysis of variance was used on arcsine-transformed germination data to determine the effect of planting site (latitude in which the seeds had been produced), original seed source (latitude in which the mother's seeds had been produced), and maternal flowering age (either annual or biennial) on percent germination.

RESULTS—The four latitudes differed significantly ($G^2 = 40$, $df = 6$, $P < 0.005$) in the number of umbels available for the indoor germination tests. Only 28% ($N = 43$) of the Greensboro umbels and 26% ($N = 27$) of the Charlottesville umbels produced 100 mericarps, in contrast to 70% ($N = 60$) and 65% ($N = 51$) of the Ann Arbor and Ottawa umbels, respectively. Although the Greensboro and Charlottesville umbels contained several hundred hermaphroditic flowers, few flowers produced fruits. Most flowers produced fruit in the Ann Arbor and Ottawa umbels.

Latitude, flowering time and month of performing the germination test all contributed significantly to the variance in percent seed germination for those umbels tested (Table 1). The later the test was performed, the higher the germination (Fig. 2). Regardless of month of the test, percent germination rose with in-

TABLE 1. *Three-way analysis of variance of arcsine-transformed seed germination shown in Fig. 2 and 3. Ten umbels were used per flowering time for all Ann Arbor and Ottawa flowering groups. Umbel no. for Greensboro flowering groups: flowering group (FG) 2 = 8, FG 3 = 4; for Charlottesville: FG 2 = 6, FG 3 = 10, FG 4 = 7. Twenty-five seeds sampled per umbel*

| Source | df | *F* statistic[a] |
|---|---|---|
| Seed source latitude (S) | 3 | 7.9*** |
| Relative flowering time (F) | 3 | 7.6*** |
| Time interval between flowering and germination time (G) | 3 | 13.1*** |
| S × F | 3 | 4.0** |
| S × G | 8 | 0.7$^{NS}$ |
| F × G | 7 | 0.5$^{NS}$ |

[a] $^{NS} = P > 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

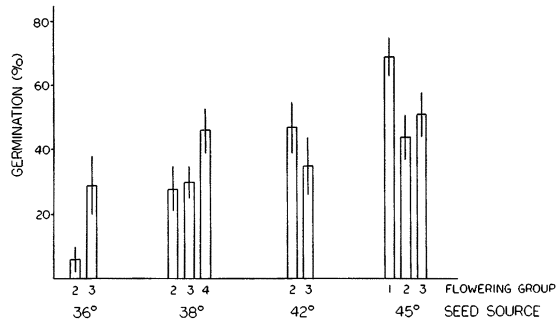


Fig. 3. Mean percent germination of seeds that were collected from plants flowering at different times and at different latitudes and that were tested 106–126 days after flowering. Flowering group: 1 = plants flowering in 1st 2 wk of flowering season to 4 = plants flowering in last 2 wk. These results typify results from all tests. Vertical bar is ±1 SE.

creasing latitude of the seed sample. For example, in the last test mean germination rose from 31% for Greensboro seeds to 64% for Ottawa seeds. The latitude × time between flowering and testing interaction was not significant, indicating that all latitudes responded similarly to the delay in testing. Within-season flowering time affected percent germination (Fig. 3), but the results are difficult to interpret. Germination increased as flowering was delayed in southern populations but decreased in northern populations; however, only two flowering times were sampled in Greensboro and Ann Arbor, so these differences should be viewed cautiously. The insignificant flowering time × time between flowering and testing interaction (Table 1) indicates that all flowering times responded similarly to the delay in testing; thus afterripening occurred at the same rate for all flowering times.

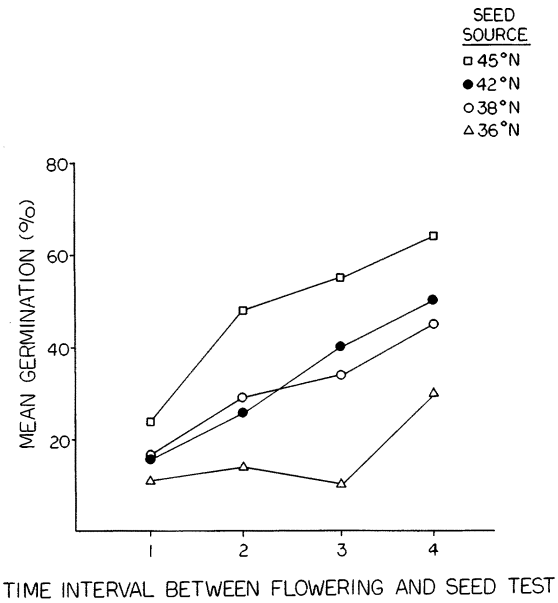


Fig. 2. Mean percent germination for tests conducted at different times after flowering of the terminal umbel: 1 = 66–85 days, 2 = 86–105 days, 3 = 106–126 days, 4 = 127–148 days. Statistics shown in Table 1.

Results of the seed viability test were consistent with germination test results (Fig. 4). Viability rose from 34% for Greensboro seeds to 81% for Ottawa seeds and the sharpest increase occurred between 38°N (Charlottesville) and 42°N (Ann Arbor). Concomitantly, the number of seeds with non-respiring embryos or lacking embryos decreased. These differences were highly significant within flowering times (Flowering group 2: $G^2 = 163$, df = 6, $P < 0.005$; Flowering group 3: $G^2 = 161$, df = 6, $P < 0.005$). The impact of flowering time depended on the latitude from which the seeds came ($G^2 = 53$, df = 6, $P < 0.005$). Late flowering plants produced more viable seeds than early flowering plants in Charlottesville and Ann Arbor, but in Ottawa produced fewer viable seeds. Flowering time did not affect viability in Greensboro.

The outdoor reciprocal sowing experiment showed that relative population age and latitude of seed source and sowing site all significantly influenced germination (Table 2). Germination ranged from 13–311 seedlings per plot (2–62%) over all plots, was highest in the Greensboro plots, and decreased as latitude of the sowing site increased (Fig. 5). In contrast, the Greensboro seed sources showed the poorest germination regardless of sowing site. The effect of seed source was most apparent in the Greensboro plots, where overall germination

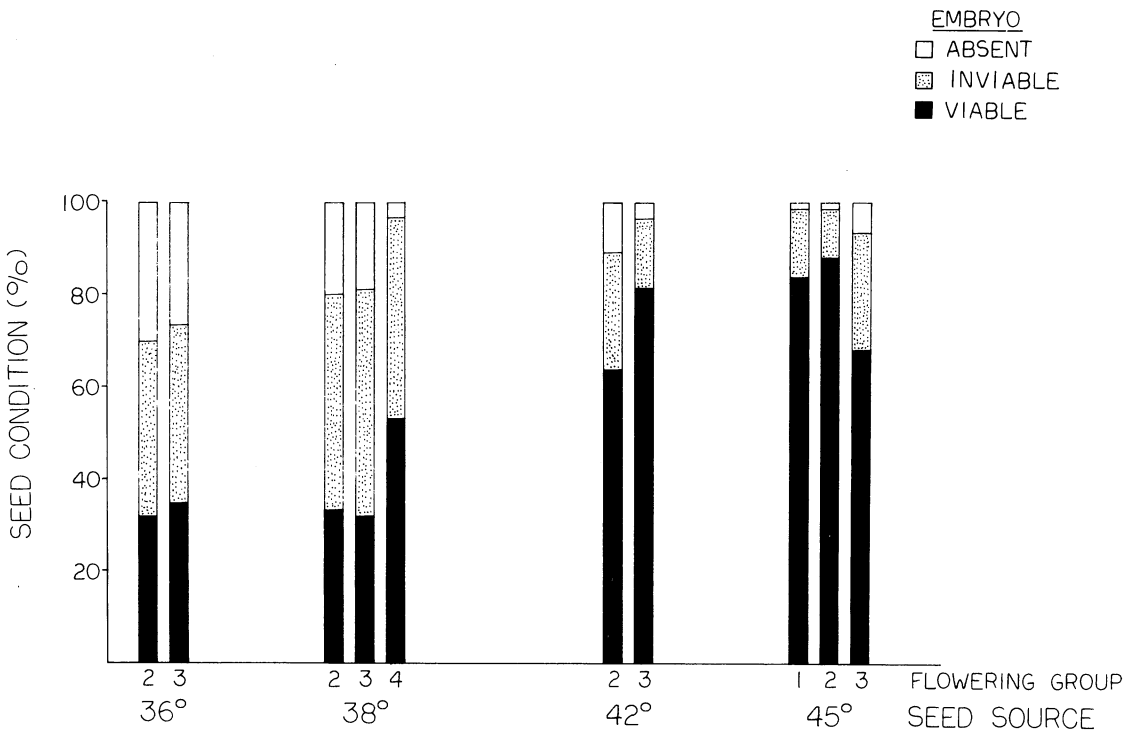


Fig. 4. Percent seeds with viable, inviable, or absent embryos for samples of seeds from plants that flowered at different times at four latitudes. Flowering group: 1 = plants flowering in 1st 2 wk of flowering season to 4 = plants flowering in last 2 wk.

was highest. Few seedlings were found in the control plots. Sixteen and twelve seedlings were recorded for two Ann Arbor plots, seven for one Ottawa plot, and the rest had 0–5 seedlings per plot.

Relative population age also affected germination. In 8 of 9 seed source-sowing site combinations, the oldest population showed poorer germination than the youngest. The probability of this occurring by chance alone is .039. Moreover, the effect of relative population age varied significantly among seed sources (Table 2). Germination declined more quickly with age among the Greensboro source populations than among the more northern populations (Fig. 5). Since the Greensboro population ranked no. 2 was approximately 4–5 yr old, whereas the Ann Arbor and Ottawa no. 2 populations were 9–10 yr and 12–15 yr old, respectively, the interaction of population age and latitude was even stronger than was detected by the statistical analysis.

TABLE 2. *Three-way analysis of variance of square-root transformed seed germination summarized in Fig. 5. Fourteen plots per population were used for the analysis. Five hundred seeds sown per plot*

| Source | df | *F* statistic[a] |
|---|---|---|
| Planting latitude (P) | 2 | 374*** |
| Seed source latitude (S) | 2 | 81*** |
| Relative population age (A) | 2 | 8*** |
| P × S | 4 | 3* |
| P × A | 4 | $2^{NS}$ |
| S × A | 4 | 8*** |

[a] $^{NS} = P > 0.05$, * = $P < 0.05$, *** = $P < 0.001$.

Examination of seeds produced by plants allowed to grow naturally in these outdoor plots showed that observed latitudinal differences in seed germination were not transmitted via the mother from one generation to the next (Fig. 6). The original seed source (i.e., latitude of seeds sown onto the plots) did not significantly influence percent germination of the seeds produced within sowing sites (Table 3). On the other hand, germination did differ significantly among sowing sites. As in the previous generation, seeds that matured in Greensboro showed the poorest germination. This is best seen by looking at annuals alone.

DISCUSSION—The most striking variation in the observed germination patterns can be at-

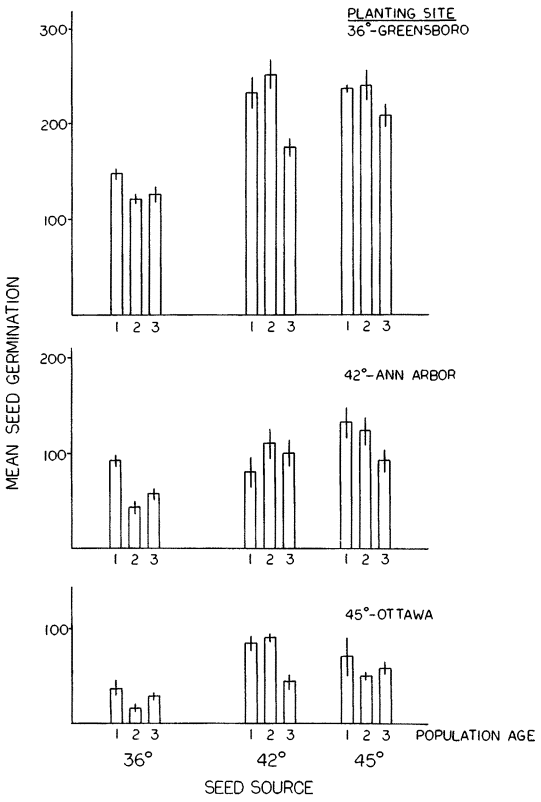


Fig. 5. Mean seed germination per plot of *D. carota* in Greensboro, Ann Arbor, and Ottawa plots shown by relative population age (1 = youngest and 3 = oldest) and latitude of each seed source. Five hundred seeds sown per plot. Vertical bar is ±1 SE. Statistics shown in Table 2.

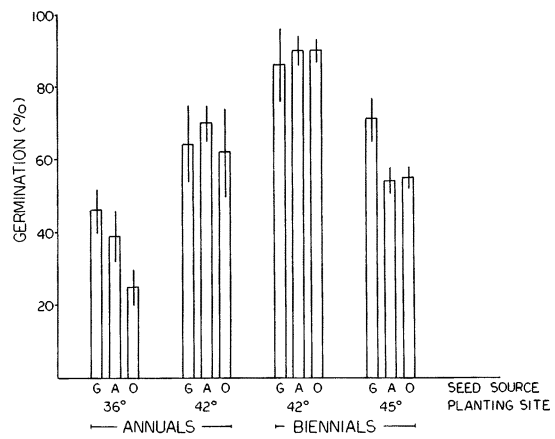


Fig. 6. Mean percent germination of *D. carota* seeds produced by annual and biennial mothers grown in plots at different sowing site latitudes. The germination values are broken down by original source of the seeds (G = Greensboro, A = Ann Arbor, O = Ottawa) that gave rise to the mother plants. Vertical bar is ±1 SE. Statistics shown in Table 3.

tributed to latitude. Southern populations produced proportionately fewer viable seeds than did northern populations in all germination and viability tests. The indoor germination tests performed repeatedly over 4 months showed that the latitudinal variation is manifested as soon as seed dispersal begins and persists during afterripening. There is no evidence for clinal variation in the rate of afterripening, which had been expected given the latitudinal variation in length of the autumn growing season. The viability test showed that the indoor germination results truly reflected variation in embryo quality rather than some unknown variable associated with the conditions used for seed germination. Moreover, the viability tests showed that number of seeds with inviable embryos and lacking embryos increased with decreasing latitude. The outdoor experiments showed that these latitudinal patterns are observed under natural conditions, where rudimentary embryos (Robinson, 1954) should have ample time to mature.

Dale (1970) reported no difference in germination of *D. carota* seeds collected from Canada to Virginia. His southernmost seed sample came from Blacksburg, Virginia (37.25°N, 640 m alt.), however, which has a cooler climate than does Charlottesville. Dale's findings are consistent with mine when viewed in the context of my data for the northern populations alone.

Latitudinal source of parents did not influence offspring seed germination in the outdoor plots. Thus, genetic differences among populations do not explain the latitudinal variation in germination. Some cross-pollination among latitudes may have occurred in the Ann Arbor and Ottawa experimental plots because flowering times of the seed sources overlapped.

TABLE 3. *Three-way analysis of variance of arcsine-transformed seed germination summarized in Fig. 6. Number of umbels sampled for annuals in Greensboro plots: by seed source, Greensboro (G) = 10; (A) = 10, Ottawa (O) = 4; annuals in Ann Arbor plots: G = 7, A = 10, O = 8; biennials in Ann Arbor plots: G = 10, A = 5, O = 10; biennials in Ottawa plots: G = 6, A = 10, O = 10. Twenty-five seeds sampled per umbel*

| Source | df | *F* statistic[a] |
|---|---|---|
| Planting latitude (P) | 2 | 23.7*** |
| Latitude of maternal seed source (S) | 2 | 0.9[NS] |
| Parental flowering age (F) | 1 | 18.7*** |
| P × S | 4 | 2.0[NS] |
| S × F | 2 | 0.8[NS] |

[a] NS = $P > 0.05$, *** = $P < 0.001$.

Thus, some genetic mixing may have occurred, diffusing genetic differences among seed sources. However, there was no genetic mixing between Greensboro and northern sources in the Greensboro plots (Greensboro plants flowered earlier), and the seeds produced by the northern parents still showed poor germination. Thus, there is no evidence for a genetic carryover in germination pattern or for a climatic pre-conditioning (Baskin and Baskin, 1973; Quinn and Colosi, 1977; Lacey and Pace, 1983) of seeds over more than one generation. The latitudinal differences appear to be due solely to environmental conditions acting directly upon parents after germination or upon developing seeds.

Because *D. carota* embryos develop over several weeks and quite slowly relative to the rest of the fruit (Flemion and Olson, 1950), they are potentially subject to environmental stress for a long time. Both abiotic and biotic factors may alter normal development during this period. For example, developing fruits in the south are subject to hotter weather even though southern populations flower earlier in the summer. The mean daily temperature in the month of greatest fruit maturation from 1971 through 1977 was 22 C in August in Ann Arbor but 25 C in July in Greensboro. Higher temperatures might block normal embryo development, as they can in other plant species (e.g., Levitt, 1972; Pollack and Roos, 1972; Scott and Longden, 1973). Although seed size was not recorded, seeds from southern populations do appear to be much smaller than seeds from northern populations (Lacey, pers. observ.).

Seed predators might destroy a larger portion of the seeds in southern populations. *Lygus* spp. bugs (Hemiptera) can reduce the germination capacity of cultivated and wild carrot seeds from 3–37% by feeding on embryos of developing fruits (Flemion and Henrickson, 1949; Flemion and Olson, 1950). Such fruits lacking embryos cannot be separated from normal fruits by size or weight. In my experiments the absence of embryos rose from 3% in Ottawa seeds to 30% in Greensboro seeds, suggesting that seed predation may intensify as latitude declines. I have not found *Lygus* on *D. carota* in Piedmont, North Carolina, but I have observed large numbers of a Corimelaenid bug (Hemiptera) feeding on developing fruits and flowers. If seed predation varies latitudinally, the variation is not likely caused by changing furanocoumarin concentration. *Daucus carota* seeds from New York lack furanocoumarins that deter many insect feeders (Berenbaum, 1981).

The reciprocal sowing experiment showed that percent germination declined with increasing population age, regardless of latitude. The reason for this is unknown. Other studies suggest that seed predation intensifies as populations age. *Lygus oblineatus,* a seed predator of wild and cultivated carrots, reproduces throughout the summer in New York and as its populations increase, seed predation rises. Thus, plants flowering late in the summer produce fewer viable seeds (Flemion and Olson, 1950). Because plants in old populations more likely flower late in the summer than plants in young populations (Lacey, 1982), probably because of limited nutrients (Lacey, unpubl.), old populations should suffer more predation. If *Lygus* populations overwinter locally as they do in cultivated carrot populations (Handford, 1949), then the bugs will increasingly lower the viability of the seed crop as the natural population ages; predation may accelerate the decline of the population. An alternative hypothesis is that site fertility declines as a population ages and that this decline alone causes the production of seeds with lower viability.

Within populations, regardless of age or latitude, germination varied up to 20% depending on flowering time. Because flowering phenology is in part determined by age of both individuals (Lacey, unpubl.) and populations (Lacey, 1982), it is difficult to identify the relationship between flowering time and germination based on data presented here. Studies have shown that late-flowering plants produce fewer germinating seeds in both New York (Flemion and Olson, 1950) and North Carolina (Lacey and Pace, 1983). The New York data are consistent with those presented here; however, the North Carolina data are not. Further experiments examining the independent effects of plant and population age and flowering time are needed.

This study has examined one phase of seed mortality, that occurring during fruit development. The extent to which this mortality retards population growth and limits the species' distribution depends on its effect relative to the total number of seeds produced. If total seed production in southern populations surpassed that in northern populations, the greater observed percent seed mortality might be inconsequential. Higher seed production in the South could offset the higher mortality. However, preliminary data indicate that southern populations produce fewer seeds. Only 27% of the terminal umbels collected from southern populations produced more than 100 seeds (most produced none); whereas 68% of

the northern umbels produced more than 100 seeds (few produced none). Plants from southern populations are on average, smaller and produce fewer umbels (pers. observ.). Both natural seedling and adult densities are lower in the South (Bastian and Lacey, unpublished data). The data indicate that mortality during fruit development increases as populations age and that mortality is higher in the southern part of the species' range. Pre-dispersal seed mortality appears to influence both the southern distribution and local population persistence of this species.

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