Timing of seed dispersal in Daucus carota

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Lacey, E. P. (1982) Timing of seed dispersal in Daucus carota L. (Apiaceae). Oikos 39: 83-91.

Abstract:
This study describes the temporal pattern of seed dispersal in *Daucus carota* and examines the fate of seeds dispersed at different dates in SE Michigan. Plants varied greatly in both time of onset and rate of dispersal. Onset was directly related to flowering time, a phenotypically plastic character, and tended to occur earlier in newly established populations. Dispersal rate was similar for different-aged populations and for plants flowering at different times. The latter indicates that later-flowering plants dispersed a greater proportion of seeds in winter. Seed germination in outdoor plots declined when dispersal was delayed experimentally. Winter dispersal distances over snow surpassed autumn dispersal distances. However, only in some years did conditions (high winds and snow cover) required for longer distance dispersal occur while many seeds were still viable. Survival and reproduction of autumn-versus spring-germinating offspring varied greatly among years in experimental and natural populations.

The fate of seeds dispersed at different times is unpredictable, which may explain the extended dispersal pattern observed in *D. carota.* Individual variation in dispersal rate is associated with environmental uncertainty in 1) timing of conditions suitable for dispersal over snow and 2) relative success of autumn- versus spring-germinating offspring. Early onset of dispersal, more common in the youngest populations, improves chances for local population expansion; late onset of dispersal found in older populations improves chances for new site colonization.

Article:
Introduction
Plant ecologists have long recognized that propagule dispersal is an important aspect of the regulation of plant populations. Not only does it help maintain and expand extant populations, it also facilitates the establishment of new ones. Most research has viewed dispersal as a spatial phenomenon, and studies of propagule number, size, and morphology (e.g., Kerner 1895, Guppy 1912, Ridley 1930, Salisbury 1942, van der Pijl 1972, Harper 1977) abound because these characteristics influence how far the propagules, or offspring, may travel after leaving the parent plant. In contrast, less attention has been given to the timing of dispersal. Timing may also be important, however, because the environment and the propagules, themselves, may change during the time span over which the propagules leave the parent. For example, potential dispersal distances may change. LeBarron (1948) collected viable black spruce seeds dispersing from trees in both autumn and winter in Minnesota and postulated that winter-dispersed seeds could move much farther, over snow, than their autumn counterparts. Second, conditions suitable for germination may change. Extreme examples are pines that release their seeds only after a fire when germination conditions are excellent (Fielding 1964, Smith 1970). Kerner (1895) gives other anecdotal examples. Further, dispersal time may affect seed viability (Duncan 1954, Hawthorne 1973) and seed mortality (Harper 1966, Smith 1970).

To provide more information about the ecological significance of dispersal timing, I have studied seed dispersal in *Daucus carota* L., a weedy herb. *D. carota* populations disperse seeds over many months from Au-gust through the following winter in the midwestern United States. Here I describe the temporal dispersal pattern and

present data showing the time of onset and rate of seed loss once dispersal has begun for individual plants flowering at different times. I also describe the differences in flowering and dispersal patterns among populations of different ages. Finally, to determine whether dispersal timing affects offspring success, I present the result of experiments designed to examine the fate of seeds dispersed at different times. In particular, I present information about seed germination, seedling survivorship, and dispersal distance.

Biology of Daucus carota

Daucus carota L. (Queen Anne's Lace or wild carrot), a common weed of abandoned fields and disturbed habitats, belongs to the informal group *D. carota* ssp. aggregate *carota* (Small 1978) in the family Apiaceae (Umbelliferae). Introduced from Europe, it has spread across the continent in the northern United States and southern Canada and as far south as Georgia. Although always semelparous, it may be an annual, biennial or longer-lived. In SE Michigan germination occurs both in autumn and spring, usually after snowmelt or heavy rains. Some seeds can germinate immediately upon dispersal in early autumn; others must undergo a period of afterripening that prevents germination until the following spring (Robinson 1954). Most plants begin flowering from early July through August. The terminal umbel (Fig. 1) at the tip of the main stem reaches an-thesis first and umbels on branches follow predictably two and four weeks later (Lacey 1978). Seed set per umbel declines with delay in flowering both within and among plants (Lacey 1978).
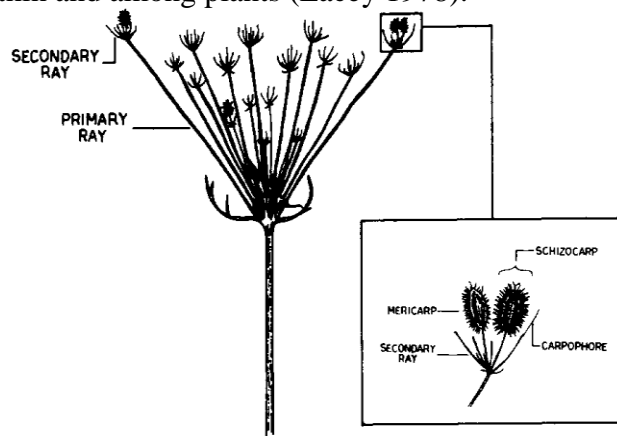

Fig. 1. Compound umbel with four fruits (schizocarps) remaining. A mericarp is one half a schizocarp.

The dispersal of seeds, primarily by wind (Lacey 1981), begins in late summer and continues through the following winter. The fruit, a schizocarp, usually splits into two mericarps, which disperse separately (Fig. 1). Because each mericarp contains one seed, I refer to "seed" rather than "mericarp" dispersal. Hygroscopic movement of outer primary rays of the umbel influences dispersal distance and rate (Lacey 1980). Umbels of the same plant release seeds at approximately the same rate. Plants collected in November 1976 and January 1977 ranked similarly with respect to number of seeds left whether rank rested on seeds in the terminal umbel or in other umbels, (Spearman rank correlation coefficient):

$r_{s \text{ Nov.}} = 0.72$, N = 8, p <0.05;

$r_{s \text{ Jan.}} = 0.83$, N = 10, p <0.01);

therefore, I use data only from terminal umbels.

Study sites

In SE Michigan, *D. carota* grows in a variety of different-aged fields. My data come from four fields in 1976, aged 2, 5, 7-8, and > 30 yr and from six fields in 1977, aged 1, 2, 2, 8-9, 10-12, and > 30 yr (Lacey 1978) (The 7-9 and > 30 yr old fields were used both years). These ages indicate time since a major disturbance such as plowing or disking. Common neighbors of *D. carota* in fields 1-5 yr old were *Erigeron annuus, Lactuca scariola, Cirsium arvense, C. vulgare, Ambrosia artemisitfolia,* and *Rumex crispus,* and in older fields *Phleum*

pratense, Sohdago sp., *Poa pratensis, Bromis inermis, Vitis* sp., *Aster* sp., plus scattered *Crataegus* and *Juniperus* trees (Lacey 1978).

Methods

I examined three aspects of dispersal: time of onset, its relationship to flowering time, and rate of seed loss once dispersal had begun. For all aspects, I marked plants that flowered at one of three times and designated sub-sets within each group to be examined for seed loss at different times later that year (Tab. 1). At each collection time I bagged and brought to the lab the terminal umbel of the marked plants. After noting whether any seeds had dispersed, I removed, mixed, and weighed the seeds left in each umbel; then to estimate the number of remaining seeds, I weighed a random sample of 100 seeds, divided the total by the sample weight and multiplied that value by 100. The mean error and standard deviation of the estimation technique were 3% ± 2% (N= 14, error = (actual seed no. — estimated seed no.)/actual seed no.). To compare rate of loss among populations and between flowering times, I determined the fraction of umbels that had lost all but 50 seeds or less at each collection time for each sample. I chose the number fifty because a few seeds usually become lodged in the primary rays (Fig. 1) and never leave the plant. I then analyzed the data by the SAS FUNCAT model (Grizzle et al. 1969), a linear model of functions of categorial responses that uses generalized least squares to produce minimum chi-square estimates. To eliminate "0" cells that may produce invalid results, I modified the data set first by adding "1" to the empty cells and second by adding "1" to all cells. I then analyzed both modifications.

Tab. 1. Sampling procedure for observations of temporal dispersal pattern.

Type of observation	Year	Field (age in yr)	Flowering time	No rosettes marked	No plants sampled
1. Relationship between flowering time and onset of dispersal	1976	>30	Mid-Jul	–	68
			Beginning Aug	–	50
			Mid-Aug	–	58
2. Flowering time differences among fields	1977	1	–	30	26
		2	–	200	173
		2	–	100	70
		8–9	–	75	55
		10–12	–	200	81
		>30	–	258	101
3. Rate of seed loss	1976	5	Mid-Jul	–	56
		>30	Mid-Jul	–	126
			Mid-Aug	–	70
	1977	1	Mid–Jul	–	45
		2	"	–	60
		2	"	–	60
		8–9	"	–	60
		10–12	"	–	60
		>30	"	–	60

To study specifically flowering time and dispersal onset differences among populations, in spring 1977 I marked rosettes along transects in six fields (Tab. 1, Lacey 1978). Later I recorded the flowering time of the terminal umbel on flowering plants. When I did not directly observe flowering, I estimated flowering time from flower and fruit development data (Lacey 1978) that I collected in mid-July and early and late August.

To examine the fate of seeds dispersed at different times, I focused on seed viability, germination time, seedling survivorship, and dispersal distance. First, I simulated natural weathering of seeds in umbels by suspending in mosquito net bags approximately one meter above ground (a common height for an umbel) samples of seeds (1000 in 1976 and 500 in 1977) from many sources (Lacey 1978). Approximately monthly I scattered a sample from each source onto a nearby plot (0.5 × 1.0 m in 1976 and 0.5 × 0.5 m in 1977). The plots were set in an area of the Matthaei Botanical Gardens that had been freshly plowed in late August and thus represented a recently disturbed habitat. Plots were arranged in rows chronologically by sowing time in 1976 and randomly in 1977 and were separated by 0.5 m on all sides; several were left as controls to check for natural germination.

From autumn 1976 through spring 1978 I recorded percent germination, growth, and survivorship as a function of dispersal time. To examine germination more closely I occasionally germinated indoors seed samples from the mosquito net bags and natural umbels (Lacey 1978). Also, in July 1978 I sifted the top centimeter of soil from four plots sown in 1976 to collect any remaining dormant seeds. I tested recovered seeds for viability by soaking them in a 1% solution of 2, 3, 5 triphenyl tetrazolium chloride in the dark for two hours. Viable (respiring) seeds turn pink. In 1978 I examined growth differences of autumn- and spring-germinating individuals after their first summer. I measured length of the longest leaf and number of leaves on all autumn-germinating rosettes and an equal number of spring-germinating rosettes per plot and also recorded the number of annuals produced by each group. For a comparison with survivorship in experimental plots, I recorded in natural populations seedling survival in 1975 in the 30 yr old field, in 1976 in fields aged 2, 5, 7-8, 30 yr, and in 1977 in fields aged 2, 8-9, 10-12, and 30 yr. At least two plots per field were set up at ends of transects that sampled available microenvironmental conditions within the field (Lacey 1978). Plots varied in size from 0.25 × 0.25 m to 0.25 × 1.0 m.

In 1977 I used four experimental plots to examine the genetic basis for flowering time. In November and January I sowed seeds from mid-July and mid-August flowering plants from the 30 yr old field, and in late July 1979 I recorded the developmental stage (Lacey 1978) of all biennials to see if the parental flowering time difference was maintained in the offspring.
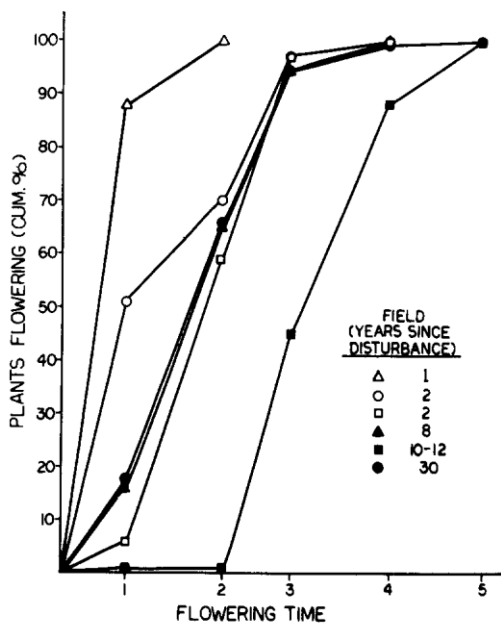

Fig. 2. Temporal change in percent plants initiating flowering in six fields in 1977. Flowering times: 1 = 1–18 Jul, 2 = 19–25 Jul, 3 = 26 Jul – 5 Aug, 4 = 6–19 Aug, 5 = 20–31 Aug.
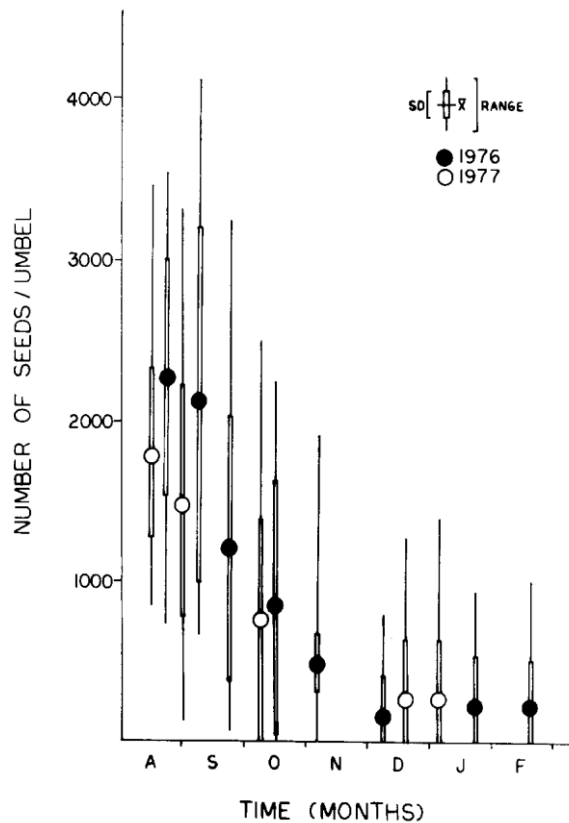
Fig. 3. Number of seeds remaining in terminal umbels over time in two fields in 1976 and six fields in 1977. Sample umbels come from plants initiating flowering in mid-Jul. Sample size per collection time ranged from 11 to 24 umbels in 1976 and from 48 to 81 in 1977.

Effects of dispersal time on distance of dispersal were examined in autumn and winter. Twice in autumn I placed a plant, from which I had removed all seeds, on a lawn and covered the nearby ground with blankets, cheesecloth, or plastic painted with Tanglefoot. I then dropped 300 seeds back onto the terminal umbel to simulate natural detachment from the carpophore (Fig. 1) but retention in the umbel. I let the seeds disperse for one hour, while an anemometer recorded wind speed. Then I counted the undispersed seeds and calculated the distance between each dispersed seed and the plant. While a lawn differs from a topographically diverse old

field in early autumn, it resembles one later in the season when most vegetation (not including carrots) has fallen. Once in winter 1976 and again in 1977 I placed several hundred field-collected seeds on snow and measured how far they moved under different wind and snow conditions. Again an anemometer measured wind speed approximately 1 m above ground. In 1978 I laid cheesecloth (3.89 × 0.97 m) against an upright fence bordering a snow-covered softball field and released 300 seeds sixteen meters upwind. After 45 min, I checked the cheesecloth for seeds and collected and melted the snow at the base of the cheesecloth to re-cover seeds trapped there.
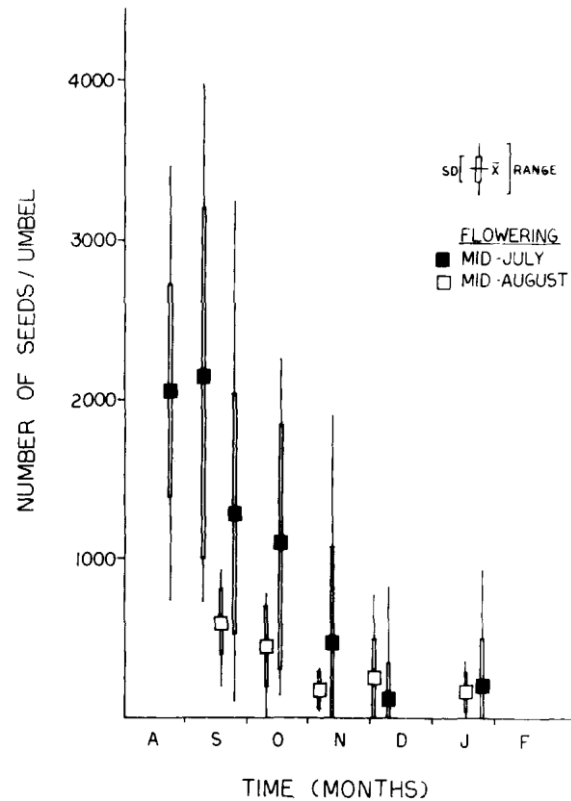

Fig. 4. Temporal change in number of seeds remaining in terminal umbels from plants initiating flowering in mid-Jul and mid-Aug in the > 30 yr old field in 1976. Sample size per collection time ranged from 10 to 18 for mid-Jul plants and from 9 to 10 for mid-Aug plants.

Results

Onset of dispersal was directly related to flowering time. By 5 September 1976, 57% (N = 14) of mid-July flowering plants had begun releasing seeds. By 20 September, 100% (N = 14) of mid-July flowering plants, 50% (N = 14) of early August, and 0% (N = 10) of mid-August flowering plants had begun dispersal. Not until the next collection time, 16 October, did I note seed loss from the latest flowering group (3 of 10 had lost seeds).

Flowering time distributions varied greatly among populations (Fig. 2). Populations in younger fields flowered significantly earlier (see Appendix). Parental differences in flowering time were not maintained by offspring growing in experimental plots (N = 50, χ^2 = 0.97, df = 3, p > 0.50). Over half the biennial offspring of both mid-July and mid-August flowering parents flowered by late July.

In both 1976 and 1977 most seeds from early flowering plants dispersed in autumn (Fig. 3). The FUN-CAT analysis showed no significant differences in rate of seeds loss among populations except for one 2-yr old field (Tab. 2). Also there was no difference in the rate of seed loss between early and late flowering groups in the same population (Fig. 4, Tab. 3). In all fields there was much individual variation in dispersal rate among plants flowering simultaneously. Of 166 umbels flowering in mid-July, 12% finished dispersal by 7 October and 55% by 21 December; 40% still held many seeds on 7 January.

In the outdoor plots total percent germination de-creased as sowing time was delayed (Fig. 5; $r^2 = 0.69$; N = 38, for 1976 plots; $r^2 = 0.78$, N = 17, for 1977). Germination in November and December sown plots was significantly lower than in August, early September and October sown plots in 1976 (Kruskal-Wallis statistic = 19.35, df = 4, p < 0.001). In 1977 germination in November sown plots was significantly less than in September sown plots (Mann-Whitney U statistic = 0.5, N_1/N_2 = 5/6, p <0.005). Germination of January and March sown seeds was so low that in neither year did it differ significantly from that in the "control" plots into which I sowed no seeds (p >0.10). These results are consistent with those of germination and viability tests indoors (Lacey 1978). The low germination in the late September 1976 and early October 1977 outdoor plots may have been caused by weather that induced germination but was not favorable (e.g., warm) enough to maintain growth to the visible seedling stage. Few *D. carota* seeds germinated in the control plots, indicating few residual seeds in the soil and little movement of seeds among plots.

Tab. 2. Fraction of empty umbels in populations flowering at the same time. The disappearance of some of the marked umbels produced the differences in sample size among collection times.

Collection time	Field (age in yr)					
	1	2A	2B	8–9	10–12	>30
Oct	1/8	2/10	1/10	0/10	3/10	0/10
Dec	4/8	7/9	3/9	6/9	5/8	3/8
Jan	3/8	9/10	4/10	7/10	5/8	6/11

All fields*			
Source	DF	Chi-square	Prob
field	5	11	0.05
month	2	37	<0.001

Fields minus 2A			
Source	DF	Chi-square	Prob
field	4	4	0.35
month	2	25	<0.001

* Analyses of both modified data sets yielded similar results; hence only one set of analyses is shown.

Tab. 3. Fraction of empty umbels from two flowering times in the >30 yr old field.

No. days since onset of dispersal	Flowering time	
	Mid-Jul	Mid-Aug
37–45	0/10	1/10
60–67	3/10	2/10
87–95	6/10	3/10
133–141	4/10	3/9

Source	DF	Chi-Square	Prob.
Flowering time ..	1	1	0.40
Month	3	10	0.02

For the August and early September sowings, autumn germination accounted for ca. 10% of all seeds dispersed and ca. 30% of all those that germinated; the rest germinated the next spring. Very few seeds germinated after the first summer, which corroborates Holt's (1972) observation that less than 1% germination occurs the second year after sowing. After almost 2 yr only one inviable seed of 4000 sown was found in the top centimeter of soil.
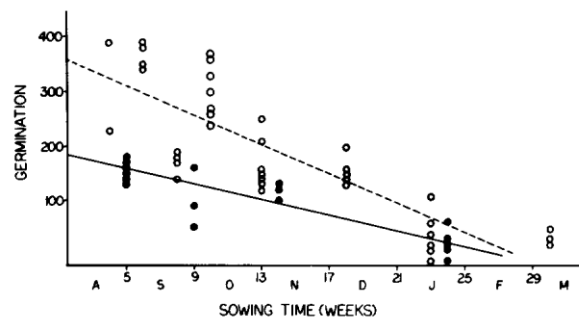

Fig. 5. Number of seeds germinating in experimental plots when seeds sown at different times. In 1976–77 (○) Y = 12.1x + 356 and in 1977–78, (●) Y = 6.6x + 184.

Relative survival of autumn-versus subsequent spring-germinating seeds was highly variable from year to year in both experimental plots and natural populations (Tab. 4). Whereas survival to the second summer (i.e., year of biennial flowering) of 1975 autumn-germinating plants was five times that of spring 1976 plants, 1976 autumn-germination resulted in almost 0% survival. Although survival through the first summer of 1977 autumn-germinating individuals was only one-third that of spring 1978 individuals, autumn-germinating rosettes significantly surpassed spring rosettes in both leaf length (Tab. 4; t = 7.36, df = 52, p <0.001) and

number of leaves (t = 9.07, df = 52, p <0.001). Of the twenty-five annuals in 1978, 23 had germinated in autumn 1977, only 2 in spring 1978.

Seed dispersal distances were 2.11 m ± 1.07 and 2.48 m ± 1.18 ($\bar{x}$ ± s.d.) for autumn dispersal tests, con- ducted while winds gusted to 5 and 7.2 m s^{-1} respectively. No seed was caught more than 6.25 m from the plant, though seed traps extended downwind at least a meter beyond the farthest recovered seed. In 1976 I observed that a wind speed of 5.4 m s^{-1} was necessary to move seeds along crusty snow; however, seeds sank into the snow at this wind speed when the temperature was near freezing. Both strong winds and low temperatures were necessary for dispersal along snow. From 1975 to 1978 such conditions occurred two to three times during December and January each year. On a day of winds gusting to 7.2 m s^{-1}, I found after 10 min not one of several hundred seeds released, even after traversing the snow in a 10 m wide belt up to 125 m downwind of the release point. On another occasion, with winds approximately 6.7-11.2 m s^{-1} and powdery snow, I recovered 37 of 300 seeds in a cheesecloth trap 16 m from the release point. Fluctuating winds probably carried most seeds to either side of the trap.

Tab. 4. Survival and size of autumn- and spring-germinating individuals in field and experimental plots of *D. carota*. Field plots varied in size from 0.25 × 0.25 m to 0.25 × 1.0 m. The number of plots varies with cohort because some fields went back into cultivation, and new plots were begun in new study fields. Experimental plots in autumn 1976 and spring 1977 were 2 × the size of 1977–78 plots (0.25 m²).

Time of germination	Mean no. seeds germinating per plot	Initial seedling density m^{-2}	Percent survival through first summer	Seedling size after 1st summer	
				Longest leaf length (cm)	No. leaves
Field					
Autumn 1975	30±12(3)*	107±45	29±2	–	–
Spring 1976	25±6 (11)	99±24	13±6	–	–
Autumn 1976	5±2 (8)	22±6	0	–	–
Spring 1977	39±11(11)	231±74	40±10	–	–
Experimental					
Autumn 1976	89±7 (6)	178±15	≤0.03**	–	–
Spring 1977	277±34(6)	520±58	53±7	–	–
Autumn 1977	66±7 (6)	264±28	12±5	13.6±1.0(27)	3.6±0.2(27)
Spring 1978	89±4 (6)	358±17	40±11	5.0±0.6(27)	2.4±0.2(27)

*Mean ± S.E. (sample size).
**Winter survival = 0.03%.

Discussion

The fate of a *D. carota* seed is clearly affected by time of departure from its umbel. First, seed viability and germination decline with an increase in the time the seed remains in the umbel. This trend, first suggested by Dale and Harrison (1966), has also been observed in *Larix laricina* (Duncan 1954) and *Plantago major* (Hawthorne 1973). In *D. carota* the later a seed disperses after October, the lower its chances of germinating.

Second, reproductive success of autumn- versus spring-germinating offspring fluctuates greatly from year to year; some years only one or the other cohort survives. Survival is probably correlated with weather (Lacey 1978). For example, autumn 1975 was warm and moist, and plants germinating then withstood the severe drought of summer 1976 better than did plants establishing in spring 1976. In less severe years, the reproductive success of both cohorts should be similar. For example, although survivorship of 1978 spring-germinating individuals was greater than that of 1977 autumn-germinating individuals, the latter formed larger plants and presumably produced more seeds per plant. Probability of flowering increases with rosette size (Lacey unpubl.), and in this study, autumn-germinating individuals in the 1977 plots had a greater propensity to flower as annuals. Fluctuations in relative cohort success affect the mature seeds that can germinate immediately after early autumn dispersal and that are scattered throughout the umbel (Lacey 1978). The data suggest that in some years these seeds will do better to leave the umbel by early September and germinate in autumn, in other years they will do better to remain in the umbel until October.

Third, potential dispersal distances are greater over snow. My data corroborate Dale's (1974) and Dale and Harrison's (1966) reports that *D. carota* seeds are dispersed short distances by wind in autumn, then long distances over winter snow. Although seeds unaccounted for in my autumn experiments may have dispersed farther than six meters, they are a small fraction of those dispersed. In contrast, seeds released in winter, certainly all those recaptured under appropriate wind and temperature conditions, dispersed much farther. Conditions promoting longer-distance dispersal are unpredictable, however, and only in some years will many viable seeds disperse over snow.

The data show that offspring success is not independent of dispersal time. Nor are there several predictably advantageous times for dispersal. Instead, there appears to be a complex relationship between environmental uncertainty and the temporal dispersal pattern. In all populations there is much individual variation in dispersal rate, associated with and possibly maintained by 1) abiotic fluctuations in quality of autumn versus subsequent summer growing seasons and 2) time when dispersal over snow is possible. In some years early dispersers, in other years late dispersers, are favored. The "bet-hedgers" (Stearns 1976) that spread dispersal over a longer time probably have the greatest chance of producing some offspring.

Maintaining some seeds for longer-distance dispersal (i.e., extending dispersal into the winter) per se does not represent an adaptation to environmental uncertainty (Hamilton and May 1977); however, the observed flexibility in onset of dispersal may be uniquely associated with this uncertainty. I found that plants flowered, on average, earlier in younger fields and that early flowering plants began dispersal earlier. This early onset should improve chances for rapid local population expansion by increasing autumn seed germination, which when successful should speed population expansion by shortening the pre-reproductive period (cf. Cole 1954, Lewontin 1965). In *D. carota* local rapid population growth would most increase fitness in recently disturbed sites where open space is available for colonization by the firstcomer. I found further that early and late flowering plants dispersed seeds at the same rate, which means that late flowering plants retained a greater proportion of their seeds for winter dispersal: ca. 30-40% in December in contrast to 6-10% for the early flowering group (Fig. 4). Late flowering plants were found most often in older fields. Delayed onset of dispersal in older fields should improve the chances of colonizing new sites, which is important for *D. carota* since seed set and germination drop and year of flowering is delayed in older populations in southern Michigan (Holt 1969, Lacey 1978 and unpubl. data). Moreover, unlike some weeds *D. carota* does not appear to accumulate large seed reservoirs in the soil. After almost two years I found no viable seeds in the top soil layer of several experimental plots. Some seeds survive longer if deeply buried (Muenscher 1935), but my data suggest that few remain viable until buried (cf. Livingston and Allesio 1968). Although delaying dispersal incurs some risk (e.g., loss of seed viability before dispersal) the relative chance of success for older populations increases by dispersing to new habitats.

The importance of delayed dispersal in older populations rests on the proportion of new site colonizations actually achieved by seeds from these populations. This information would be difficult to obtain. Because of better germination of seeds that are dispersed early and the many years over which this takes place, one could argue that early dispersed seeds contribute much more to new colonizations. While not resolving the issue, one can point out that as distance separating new sites increases, delaying dispersal in senescing populations should become more important. In this study delaying dispersal increased dispersal distance from a few meters to tens and perhaps hundreds of meters. Such increases should improve chances for colonizing abandoned fields, which in SE Michigan have a very patchy distribution. They are scattered among woodlots, pasture-land, cultivated fields and, increasingly, urban sprawl.

In general, few studies have examined temporal polymorphisms or variation in dispersal patterns, and even fewer the genetic basis for such variation (Harrison 1980, Gaines and McClenaghan 1980). Studies of insects indicate that environmental uncertainty may select either for phenotypic plasticity (Shapiro 1976) or for maintenance of several genotypes (Dingle 1972). The temporal dispersal pattern of *D. carota* may reflect both, but clearly more data are needed. At least the absence of parental flowering time differences in their offspring suggests that flowering time and onset of dispersal are plastic characters. In any case, we should expect

flexibility in dispersal patterns such as we see in *D. carota*. Most plants are stationary, at least after germination, and selection for plasticity in growth and reproductive characters is strong (Bradshaw 1965). Flexibility in dispersal patterns should also be selected particularly in weedy species that spend several generations in one place and then disappear. Such flexibility, in general, should be recognized as a critical component of fitness.

Appendix

To show that plants in younger fields *do* tend to flower (and thus to disperse seeds) earlier than those in old fields, I performed 15 (all possible combinations) pair-wise Kolmogorov-Smirnov tests and used the 0.001 significance level for each test so that the overall significance level for all tests was at most 0.015. The fields fell into three clusters (Tab. 5). The fields within each cluster did not differ from one another in flowering time but did differ highly significantly from all fields in other clusters. The ordering of flowering times was that cluster 1 fields flowered earlier than cluster 2 fields, which in turn flowered earlier than the cluster 3 field.

Tab. 5. Ordering of fields by flowering time distribution.

Cluster	Field in cluster (age in yr)
1	1, 2*
2	2, <30, 8
3	10–12

*The fields are not ordered according to flowering time within a cluster.

To see if the ages of fields were random with respect to flowering time given the cluster sizes my data suggested, I asked the following question: If the six fields were randomly divided into three clusters (of sizes 1, 2, and 3 respectively), and the three clusters were then randomly ordered to represent order of flowering time, what would be the probability that at most one pair occurred out of order. A pair of fields is out of order if each field in the pair is in a different cluster and the older field is in a cluster that flowers earlier than the cluster containing the younger field. For example, in the ordering (2, 1, 2) (8, 30) (10) the 30-10 yr old pair is the only pair out of order. Since the observed number of out-of-order flowerings is only one (Tab. 5; the > 30 yr field flowers before the 10-12 yr field, and there are no other fields flowering significantly before a younger one), I am asking what tail probability the observed value (1) represents, if fields were clustered randomly and the clusters then ordered randomly for flowering time. There are $\frac{6!}{3!2!1!} = 60$ possible partitions of the six fields into three clusters of sizes 1, 2, and 3, respectively, and for each such partition there are 3! = 6 possible orderings. So if all partitions and orderings are equiprobable, there are $60 \times 6 = 360$ possible states of this system. For each of these states I tallied the number of out-of-order fields, and for only 23 of the 360 states was this number as small as or smaller than the observed number, one. So the actual arrangement is in the $\frac{23}{360} = 0.064$ tail of all possible arrangements, and one can reject at that level the null hypothesis that flowering time of a population is independent of age of field.

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