

Latitudinal Variation in Reproductive Timing of a Short-Lived Monocarp, *Daucus Carota* (Apiaceae)

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Abstract:

A reciprocal transplant experiment was conducted to examine several aspects of life-history variation in *Daucus carota* along its latitudinal range in eastern North America. Seeds collected from natural populations at 36°, 42°, and 45° N were sown onto plots at each of the three latitudes. Marked seedlings were followed for 3 yr to examine (1) genetic and environmental components of variation in growth, survival, and year of re-production; (2) size and age at time of reproduction; and (3) the roles that density- and age-dependent selection may play in producing the variation in age of reproduction.

Mean age of reproduction increased clinally from south to north but showed no pattern of variation among different-aged populations within the same latitude. The clinal variation has likely arisen since the introduction of *D. carota* into North America in the 17th century and has developed independently of any role that growth rate plays in determining age of reproduction. Density influences age of reproduction both directly and indirectly by affecting plant size.

Age-specific survival varied strongly over plot latitude but not among populations planted in the same latitude. The ratio of percent germination and survival of 1-yr-olds to percent survival of 2-yr-olds was $\approx 3:1$, $0.2:1$, and $0.15:1$ for plots at 36°, 42°, and 45° N, respectively. The experiment suggests that latitudinal variation in age-specific mortality patterns is helping to maintain clinal variation in age of reproduction. Density-independent factors contribute more strongly to age-specific mortality than do density-dependent factors.

Age classes are based on times of peak flowering rather than on times of growing seasons. Such intervals allow for better evolutionary interpretation of demographic data.

Key words: age-specific selection; *Daucus carota*; density-dependent selection; genetic variation; growth; latitudinal variation; life-history evolution; monocarp; reproductive timing; survival.

Article:

INTRODUCTION

Several studies have shown that the age of first re-production in plants varies latitudinally (Smith 1927, Kocher 1949, Belcher and Larsen 1958, Reinartz 1984). The length of the pre-reproductive period tends to be short at low latitudes but long at high latitudes, and this latitudinal change appears to be genetically based.

Several possible explanations for this apparent clinal variation exist. First, population growth in low-latitude habitats may be limited by high density-independent mortality thereby selecting for early reproduction; whereas population size in high-latitude habitats may increase to the point where density-dependent mortality limits growth, thereby selecting for delayed reproduction (Dobzhansky 1950, MacArthur and Wilson 1967). Second, low-latitude habitats may be less permanent than are high-latitude habitats thereby favoring earlier reproduction at low latitudes. The less permanent the habitat, the lower the potential for density-dependent selection, which favors delayed reproduction (Southwood 1977, Caswell 1982). Third, populations at low latitudes may suffer

high or unpredictable adult mortality relative to juvenile mortality, which should favor precocious reproduction, whereas populations at high latitudes may suffer higher or more un-predictable juvenile mortality, which should favor delayed reproduction (Harper 1967, Istock 1967, Murphy 1968, Charnov and Schaffer 1973). Finally, populations at low latitudes may suffer consistently high density-dependent mortality over all age classes whereas populations at high latitudes may suffer high density-dependent mortality that varies over age classes (Charlesworth 1980). Other possible explanations exist. I mention here only those that address the impact of mortality patterns on reproductive timing. One or all explanations may contribute to the latitudinal pattern in age at first reproduction.

Because we know too little about the biology of any plant species to establish which of the above hypotheses best explains the observed latitudinal pattern, I began studying the life-history variation in *Daucus carota*, a pan-temperate weed. Here I describe the results of a reciprocal transplant experiment on populations from across the species' latitudinal range in North America.

Daucus carota ssp. *carota* (Umbelliferae), commonly called wild carrot or Queen Anne's Lace, is a short-lived monocarpic herb introduced into North America from Europe (Dale 1974, Small 1978). After germination *D. carota* grows vegetatively as a rosette, eventually produces a flowering stalk, produces seeds, and then dies. Few seeds lie dormant in the soil for > 1-2 yr (Lacey 1982). Intrapopulation variation in year of reproduction is high; some individuals flower in the 1st yr and others flower in the 2nd, 3rd, or 4th yr (Holt 1972, Gross 1981, Lacey 1986). Time of flowering is strongly environmentally determined. Large rosettes at the end of a growing season have a higher probability of flowering the next season than do small rosettes (Gross 1981), and nutrient availability strongly influences rosette size (Lacey 1986). Time of flowering is also genetically determined (E. P. Lacey 1986 and *personal observation*).

TABLE 1. Long-term average climatic data and soil characteristics for the three reciprocal transplant sites.

Climatic or soil characteristic*	Greensboro (36° N)	Ann Arbor (42° N)	Ottawa (45° N)
Frost-free period (d)	180-210	150-180	120-140
Daily maximum temperature (°C in June, August)	29-32, 29-32	24-27, 27-29	22-25, 25-28
Annual precipitation (cm)	110-120	70-80	80-90
No. days per year with precipitation	110-120	120-140	120-160
Soil texture (% sand/silt/clay)	60/28/12	59/22/19	32/48/20
Water retention at field capacity (%)	13.06	15.62	24.84
Organic matter (%)	1.8	0.8	1.5
Cation exchange capacity (mmol/100 cm ³)	9.1	9.3	11.4
pH	6.8	5.7	6.1
Phosphorus index†	100	32	66
Potassium index†	44	68	140

* Climatic data from the National Atlas of Canada (CDEM 1973) and the Weather Atlas of the United States (USED 1968). Data on soil characteristics were provided by the North Carolina Department of Agriculture and Dr. Norman Christensen, Duke University.

† Values <100 indicate a need for fertilizer if growing cultivated carrots.

Year of flowering is increasingly delayed as *D. carota* populations age, i.e., as the fields in which populations are found pass through secondary succession (Holt 1972, Gross and Werner 1982). This delay is partially explained by an environmentally induced reduction in growth rate. It is not known whether genetic changes associated with population growth and senescence also contribute to the observed delay in flowering.

The reciprocal transplant experiment had three goals. One was to measure the interpopulation variation in year of reproduction both across and within latitudes. Smith's (1927) study of *Melilotus alba*, also monocarpic, suggested that southern populations of *D. carota* might be annual and northern populations longer-lived. Within a latitude, young and old populations might show genetically based differences in age of reproduction. A second goal was to compare the interpopulation variation in growth and mortality with respect to the variation in reproductive timing. Factors controlling year of reproduction in *D. carota* can act both through their effect on growth rate and independently of growth rate (Lacey 1986). Therefore, if clinal variation in year of reproduction exists, what is its relationship to growth? Do southern populations contain more annuals because of accelerated growth rate, independently of growth, or both? The third goal was to elucidate the roles of age- and density-dependent mortality in the production or maintenance of latitudinal variation in year of reproduction. Do annual populations grow at sites where density-independent mortality is higher than density-dependent mortality? Do

they grow at sites where density-dependent mortality is consistently high at all ages, and/or where 2nd-yr mortality is higher than 1st-yr mortality?

METHODS

I established transplant gardens at three sites that include most of the species' latitudinal range in North America: Greensboro, North Carolina, USA, 36° N; Ann Arbor, Michigan, USA, 42° N; and Ottawa, Ontario, Canada, 45° N. These sites differed climatically, the most obvious difference being the number of frost-free days (Table 1). Seeds were collected from three populations at each latitude. The fields in which the populations were found had been abandoned for different lengths of time. In Greensboro the fields had lain fallow for 1,4-5, and 6-7 yr. I could find no *D. carota* in fields abandoned for >6-7 yr. Ann Arbor fields had been abandoned for 2,9-11, and >30 yr, and Ottawa fields 1-2, ≈ 12-15, and ≈ 20 yr. Because *D. carota* typically colonizes fields within a year or two after abandonment (Lacey 1982) and may persist for a number of years (Holt 1972, Gross and Werner 1982, Lacey 1982), these populations likely represented different stages of population growth and senescence in each geographical region.

At each population, seeds were collected from the terminal umbel of 25 plants. These umbels had all reached anthesis in the first half of the flowering season for that latitude. For each population I constructed 15 replicates of 500 seeds (technically mericarps), which included 20 seeds from each individual. Only 24 umbels were used for the Ottawa 15-yr population, giving 480 seeds per replicate.

In early October 1979 I scattered seeds of five replicates onto outdoor plots (0.5 × 0.5 m) at each latitude. Thus there were three "common gardens" (sites), one at each latitude from which seeds were collected. Each planting site contained 50 plots: 5 rows with 10 plots per row. Each row included one replicate from each population plus one control plot, onto which no seeds were scattered. The nine replicates and control were randomized within rows and were arranged over the 5 × 10 grid of plots in an incomplete Latin Square design. Plots were separated by 0.5 m.

The land on which the plots were placed was plowed once the previous spring and plowed and weeded just before sowing. Plots were placed along one side of the plowed area. In all cases, the plowed area typified a habitat where colonization would naturally occur, a recently disturbed field. The Greensboro and Ottawa land had previously been vegetable gardens. The Ann Arbor land had been covered with dense grass that had been mown 1-2 times a year. The sites differed in soil characteristics (Table 1). The Ottawa soil had a finer texture and consequently retained more water than did the other soils. The Ann Arbor soil held fewer nutrients, as evidenced by the low amount of organic matter, phosphorus, and potassium. After sowing I left the plots undisturbed except to collect data; thus secondary succession was allowed to proceed with minimal intervention.

All of the Greensboro and Ottawa plots were used for the data analysis; however only 36 Ann Arbor plots could be used. Because of a possible sowing error, I eliminated one row of Ann Arbor plots from the experiment soon after germination. Four other plots were eliminated when I discovered in the first summer that they still contained large pieces of grass sod. The grass was extensive enough to make these plots both atypical of an early successional environment and very different from the remaining plots.

Just after the first germination flush I divided each plot into 25 subplots (10 × 10 cm), and for each subplot counted the seedlings and marked the centralmost seedling to follow its fate. After the second germination flush in the Greensboro plots, the only plots to show a second flush, seedlings were counted again and a second seedling in each subplot was marked. Collecting data by subplot allowed me to examine the fate of individuals over a wide range of densities. The density of close neighbors can strongly influence a plant's growth and flowering (e.g., Harper 1977). Data on survival, growth, and year of flowering were then collected for marked plants within subplots for 3 yr. Root crown diameter (RCD) was used to estimate plant size because it correlates well with total biomass in both Michigan (Gross 1981) and North Carolina (E. P. Lacey, *personal observation*).

Analysis of variance was used to determine the effects of experimental site latitude (hereafter abbreviated as "site"), seed source latitude (hereafter abbreviated as "source"), population nested within source, and initial intraspecific seedling density within subplot (hereafter abbreviated as "density") on log-transformed RCD measurements at three times during the first growing season. To use the plot rather than the marked individual as the experimental unit, I first ran the ANOVA model including main and interaction effects of all variables, with density as a covariate. This analysis showed that the response of size to density never differed significantly with seed source or population. In two of three analyses (one for each time that size was measured) it also did not vary with site. There-fore I eliminated these interactions to simplify the model, ran the ANOVA on the simplified model, again using density as a covariate, and then selected the appropriate interaction sums of squares as error terms to calculate *F* statistics. The terms used are shown in the results. For the one analysis that showed a significant density \times site interaction, size data were examined for each site separately.

TABLE 2. Analysis of variance of log-transformed root crown diameter measurements taken in (A) early April, (B) July, and (C) November of the first season.

Site	Source of variation*	ss†	df	Denominator of <i>F</i> statistic	<i>F</i>	<i>P</i>
(A) Greensboro only	Density (D)	10.10	1	error	54.51	<.0001
	Seed source (So)	0.23	2	So \times Row	0.81	>.50
	Population (P)	6.53	6	P \times Row	1.37	>.25
	Row	9.40	4	error	12.69	<.0001
	So \times Row	5.05	8			
	P \times Row	18.99	24			
	error	155.65	840			
(B) All sites	Density (D)	64.71	1	error	274.16	<.0001
	Site (Si)	103.02	2	error	218.28	<.0001
	Seed source (So)	0.31	2	So \times Row	0.34	>.75
	Population (P)	3.49	6	P \times Row	0.87	>.75
	Row	17.04	11	error	6.56	<.0001
	Si \times So	3.20	4			
	Si \times P	8.11	12			
	So \times Row	10.01	22			
	P \times Row	41.30	62			
	error	469.47	1989			
(C) Greensboro	Density (D)	3.70	1	error	13.75	.0003
	Seed source (So)	0.37	2	So \times Row	0.47	>.50
	Population (P)	2.41	6	P \times Row	0.96	>.25
	Row	0.58	4	error	0.54	.7059
	So \times Row	3.21	8			
	P \times Row	9.19	22			
	error	63.14	235			
Ann Arbor	Density (D)	13.74	1	error	56.69	<.0001
	Seed source (So)	0.84	2	So \times Row	1.98	>.10
	Population (P)	2.91	6	P \times Row	1.05	>.25
	Row	0.62	3	error	0.85	.4680
	So \times Row	1.27	6			
	P \times Row	6.47	14			
	error	93.57	386			
Ottawa	Density (D)	15.92	1	error	41.75	<.0001
	Seed source (So)	1.28	2	So \times Row	1.25	>.25
	Population (P)	4.47	6	P \times Row	1.27	>.25
	Row	1.50	4	error	0.98	.42
	So \times Row	4.09	8			
	P \times Row	14.03	24			
	error	154.02	404			

* Populations are nested within source and rows within site.

† I report Type IV sums of squares for all but the April analysis, for which I report Type III sums of squares because there were no empty cells.

The multivariate G^2 (log-likelihood ratio) test (Bishop et al. 1975) was used to analyze the effects of site, source, size, age, and density on the categorical variables, survival and year of flowering. Fienberg (1970) describes the use of this technique for ecological studies, and Schoener (1970) illustrates its application. The relationships among these variables are examined simultaneously when each variable corresponds to a dimension of a multidimensional contingency table. Expected cell counts are generated for such a multiway table by fitting a log-linear model that takes into account the main effects and all possible interaction effects in the analysis (Bishop et al. 1975). Tests for interactions among variables are accomplished by first deleting interaction terms from the saturated model, which includes all possible interactions, working down from the highest order interaction to produce a simpler model. Expected cell counts for the simpler model are obtained by an iterative proportional fitting procedure that involves estimating expected marginal totals for each variable sequentially and iterating over all variables until the expected marginal totals deviate <0.001 from the marginal totals

obtained by the previous iteration. Tests of relative goodness-of-fit of the simpler models and the saturated model are then conducted using the expected and observed cell counts. If the deletion of an interaction term from the saturated model produces a G^2 value that is unlikely to occur by chance alone, then one can conclude that the interaction contributes strongly to the total variation explained by the saturated model and that the variables constituting the interaction are strongly correlated. When necessary I adjusted the degrees of freedom to account for cells with expected values of zero (Bishop et al. 1975). In this paper the source and density effects are shown for all rows lumped within a site because the main source and density effects never differed among rows.

The G^2 test was also used to look at the influence of populations and rows on survivorship and flowering time, but because populations were nested within source and rows within site, I examined the relationships for each site \times source combination separately. Density effects were not included in these analyses because of the small sample sizes.

Finally, to examine age-specific mortality, I used age classes that differ from those traditionally used for plant demographic studies. Traditionally, for monocarps, age class 1 extends from time of germination to end of the first growing season, age class 2 from end of the first season to end of the second, and so on. Here I refer to these divisions as growing season 1, growing season 2, etc. My age class (year) 1, however, begins at germination and ends at peak flowering time the first season; age class 2 extends from peak flowering the first season to peak flowering the second season, etc. For reasons stated in the Discussion, age classes defined this way provided more evolutionarily meaningful insights.

RESULTS

Germination and growth

In the Greensboro site most seeds germinated in October 1979, and the resulting seedlings were those used for the following data analysis. A few additional seeds germinated the following spring, but all that were marked died that summer. In the northern sites all germination occurred in spring 1980. The total (autumn plus spring) germination pattern, including that in the control plots, has been described elsewhere (Lacey 1984). Overall germination per plot declined significantly with increasing latitude of the planting site and with decreasing latitude of the seed source. The mean percent germination per plot of seeds sown in Greensboro was, by source: Greensboro 2.5%, Ann Arbor 44%, Ottawa 46%; of seeds sown in Ann Arbor, by source: Greensboro 13%, Ann Arbor 19%, Ottawa 24%; and of seeds sown in Ottawa, by source: Greensboro 4%, Ann Arbor 14%, Ottawa 12%. The range of seedling densities per subplot typified the range that can be found in natural populations (E. P. Lacey, *personal observation*).

Rosettes in Greensboro grew during the warm spells from midautumn through early spring, and by early April mean RCD values for Greensboro, Ann Arbor, and Ottawa plants were 2.3, 2.1, and 2.0 mm, respectively. No differences in size could be attributed to either source or population (Table 2A), but size did vary negatively with density.

By July size varied significantly among sites (Fig. 1). However, the site effect did not vary monotonically with site latitude as rosettes were largest in the Ottawa plots and smallest in the Ann Arbor plots. Size did not vary with source or population, though it was again negatively correlated with density (Table 2B). Site effects observed in July persisted into November, when nonflowering plants were measured again. The density \times site interaction was significant in November ($df = 2$, $F = 4.69$, $P = .009$), and therefore density, source, and population effects were examined for each site separately. Again only density affected size (Table 2C). The Ottawa garden contained the largest rosettes, and showed the sharpest decline in size with increasing density.

Survival

Rosette survival varied dramatically over sites, densities, and growing seasons (Fig. 2A; see also Appendix). Survival was lowest in the Greensboro plots and at high densities in both growing seasons. Also, survival

during the first growing season (from germination to November of the first season) surpassed survival during the second season (from November of the first season to November of the second season).

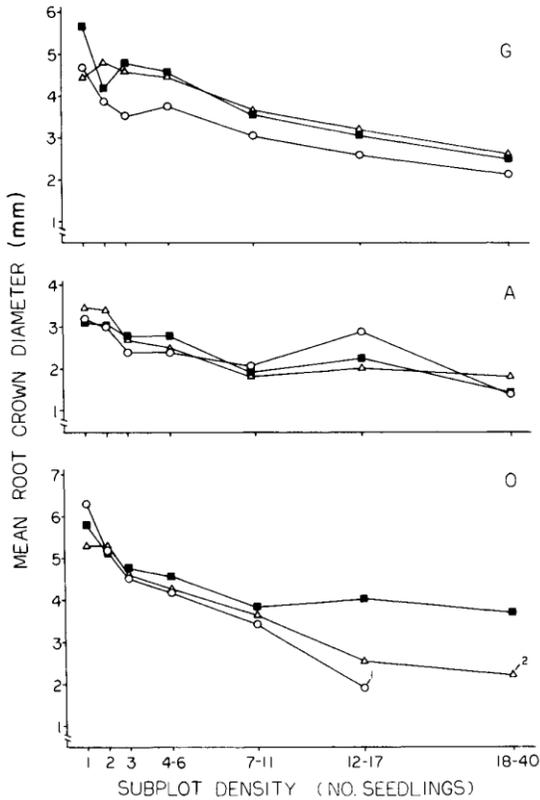


FIG. 1. Mean July root crown diameter for plants growing in subplots with varying initial seedling density, shown by site: Greensboro (G), Ann Arbor (A), Ottawa (O); and seed source: Δ = Greensboro, \blacksquare = Ann Arbor, \circ = Ottawa. (Sample sizes are shown on figure where <5 .)

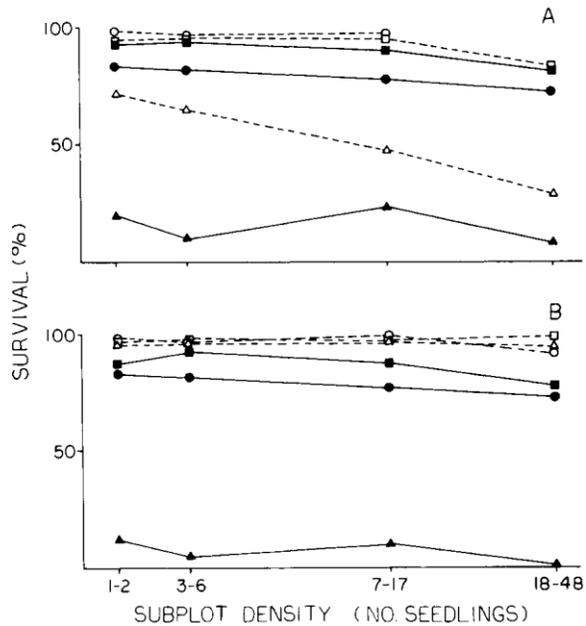


FIG. 2. Percent survival of plants from subplots of varying density, shown by planting site: Greensboro (triangles), Ann Arbor (squares), Ottawa (circles); and (A) season: 1 = open symbols, dotted line; 2 = closed symbols, solid line; or (B) age class: 1 = open symbols, dashed line; 2 = closed symbols, solid line.

The survival pattern examined by age class (Fig. 2B), however, differed from the survival pattern for growing seasons (Fig. 2A). Most of the 1st-yr mortality regardless of site occurred in late summer. Ninety-one percent of the deaths in Greensboro occurred after early July, the peak flowering time. Similarly, 83 and 78% occurred after late July in Ann Arbor and Ottawa, respectively. All plants that died were rosettes. Thus percent survival of rosettes in age class 1 (from germination to peak flowering time in the first summer) did not differ among sites, but sites strongly differed in survival in age class 2 (from peak flowering the first summer to peak flowering the second summer; Fig. 2B). Most rosettes in northern plots survived age class 2, whereas most in Greensboro died irrespective of seed source and density. This site \times age \times survival interaction was highly significant ($G^2 = 58.56$, $df = 8$, $P < .005$) and independent of density.

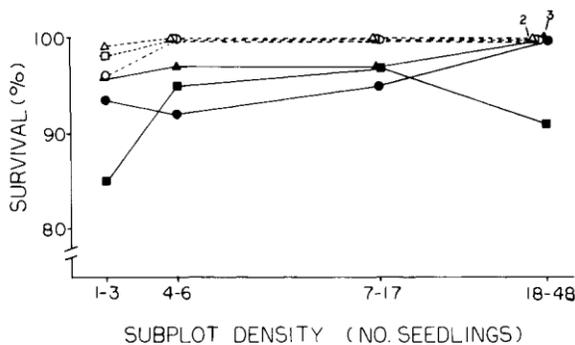


FIG. 3. Percent survival of age class 1 in the Greensboro plots, shown by subplot density and by seed source: Greensboro (triangles), Ann Arbor (squares), and Ottawa (circles); and early April root crown diameter in millimetres: <2.0 = closed symbols, solid lines; $2.0-8.2$ = open symbols, dashed lines. (Sample sizes are shown on figure where <5 .)

TABLE 3. G^2 tests for survival to first flowering (L_1) as a function of: (A) site (S_i), seed source (S_o), and four density (D) levels; (B) seed source, April root crown diameter (R_A), and density (same four levels) in the Greensboro plots.

Interaction(s) deleted†	df	$G^2‡$
(A) All three-way	40	49.09
All three-way; $S_i \times L_1$	42	61.45*
All three-way; $S_o \times L_1$	42	52.04
All three-way; $D \times L_1$	43	51.83
(B) All three-way	23	18.67
All three-way; $S_o \times L_1$	25	22.20
All three-way; $R_A \times L_1$	24	37.30*
All three-way; $D \times L_1$	26	25.47

* $P < .05$.

† The models examined in this and subsequent tables are shown by listing the interaction terms that were deleted from the saturated model to produce the reduced model.

‡ When the reduced model produces a nonsignificant G^2 value (no superscript), the variables constituting the interactions deleted are not correlated with each other at the .05 significance level. If a further reduced model produces a significant G^2 value (with superscript), the variables constituting the stated additional two-way interaction deleted from the model are correlated with each other.

TABLE 4. G^2 tests for survival for age class 2, i.e., to second flowering (L_2), as a function of site (Si), seed source (So), three density (D) levels, and two July root crown diameter (R_j) levels. Degrees of freedom all adjusted for zero cells.

Interaction(s) deleted†	df	$G^2‡$
All three-way	69	85
All three-way; Si \times L_2	71	969***
All three-way; So \times L_2	71	86
All three-way; $R_j \times L_2$	70	93*
All three-way; D \times L_2	72	92

* $P < .05$, *** $P < .005$.

† See footnote † in Table 3.

‡ See footnote ‡ in Table 3.

Though survival of both age classes considered together declined with increasing density ($G^2 = 30.3$, $df = 18$, $P < .05$), density explained little of the total variation in survival. Density did not directly affect survival in either year 1 or year 2. It did, however, always influence survival indirectly through its effect on growth. In the Greensboro plots density strongly influenced April RCD, and rosettes with RCD values < 2 mm in April suffered the highest mortality before peak flowering, while rosettes with RCD > 3 mm suffered no mortality (Fig. 3, Table 3). At all sites density influenced July RCD, and large plants in July survived age class 2 better than did small plants (Table 4). The density effect did not differ among sites or age classes, however.

Seed sources suffered the same percent mortality in all three age classes at each site (e.g., Tables 3 and 4), and populations within source showed similar mortality patterns. Therefore, the observed variation in mortality is best explained by site differences, plant age, plant size, and density, and not by original source of the seeds used for the experiment.

Flowering time

Year of flowering varied strongly with site and density (see Appendix). Flowering in the 1st yr was negatively correlated with density in all plots ($G^2 = 97$, $df = 19$, $P < .005$), and annuals predominated in the Greensboro plots whereas biennials and longer-lived individuals predominated in the more northern plots ($G^2 = 392$, $df = 16$, $P < .005$). In part bienniality was low in the Greensboro plots because very few plants survived past year 1.

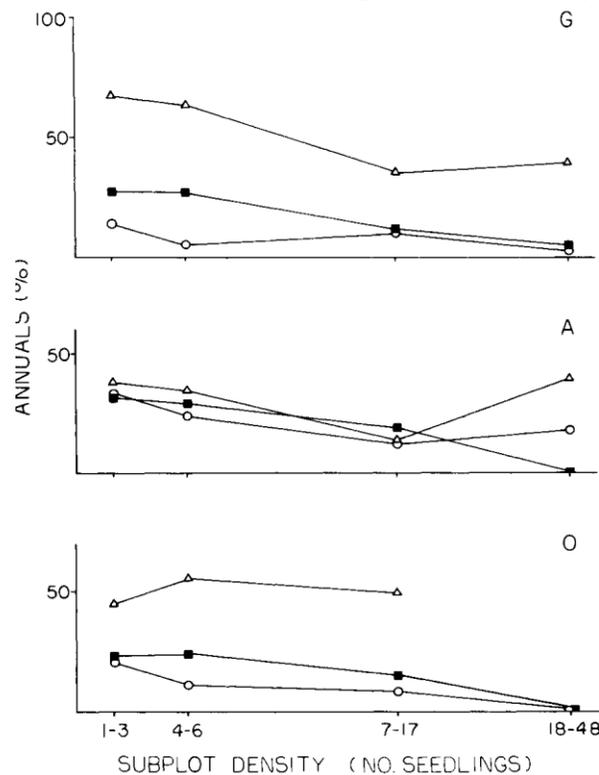


FIG. 4. Percent annuals of those surviving age class 1, shown by subplot density and by planting site: Greensboro (G), Ann Arbor (A), Ottawa (O); and seed source: Greensboro (Δ), Ann Arbor (\blacksquare), Ottawa (O).

TABLE 5. G^2 tests for percent annuals, i.e., those that flowered, of those surviving age class 1 (F_1) as a function of: (A) site (Si), seed source (So), and density (D); (B) seed source, April root crown diameter (R_A), and density for the Greensboro plots alone, and (C) April root crown diameter and density for each source in the Greensboro plots.

Interactions deleted†	df	$G^2‡$
(A) Si × So × D, Si × D × F_1 , So × D × F_1 , Si × So × D, Si × D × F_1 , So × D × F_1 , Si × So × F_1 , Si × So × D, Si × D × F_1 , So × D × F_1 , D × F_1	36	44.63
(B) So × R_A × D × F_1	6	20.04***
(C) For So = Greensboro R_A × D × F_1 R_A × D × F_1 , R_A × F_1 R_A × D × F_1 , D × F_1	3 4 6	6.41 85.39*** 18.47**
For So = Ann Arbor R × D × F_1	3	11.29*
For So = Ottawa R_A × D × F_1 , D × F_1 R_A × D × F_1 , R_A × F_1	6 4	8.87 25.12***

* $P < .05$, ** $P < .01$, *** $P < .005$.

† See footnote † in Table 3.

‡ See footnote ‡ in Table 3.

TABLE 6. Survivors of age class 1 that are annuals for each population at each planting site; G = Greensboro, A = Ann Arbor, O = Ottawa.

Seed source	Relative population age†	Site‡		
		G	A	O
		% (N)	% (N)	% (N)
G	1	55 (92)	29 (56)***	37 (71)**
	2	61 (84)	40 (58)	56 (48) ^b
	3	54 (93)	38 (55)	54 (61) ^b
A	1	13 (100)*	21 (70) ^{e*}	10 (70)
	2	29 (111) ^d	38 (82) ^f	29 (82)
	3	12 (99) ^c	19 (77) ^e	23 (70)
O	1	10 (104)	46 (63)***	26 (72)***
	2	11 (103)	6 (51) ^h	16 (76) ^k
	3	9 (99)	28 (82) ^j	4 (71) ⁱ

† Relative population age is based on number of years the field had lain fallow: 1 = youngest, to 3 = oldest.

‡ Significant differences among populations are shown for each site by source combination:

* $P < .05$, *** $P < .005$; the letter superscripts indicate the source of the differences within each combination. For the Greensboro seed source planted in Ann Arbor there was a significant interaction between populations, rows, and flowering but the source of these differences is not shown here.

Seed sources and populations also differed in year of flowering. In the 1st yr the Greensboro populations produced the most annuals and Ottawa populations the fewest, independent of site and density (Fig. 4, Table 5A). Source differences are most apparent in the Greensboro plots, which produced the most annuals, and least apparent in the Ann Arbor plots, which produced the fewest. Populations within source often differed significantly in the percentage of annuals, though relative differences did not persist over all planting sites, and differences were not related to relative population age (Table 6).

In the Greensboro plots, annuality was significantly correlated with April rosette size and, independently, initial seedling density (Table 5 B and C). Large rosettes in April had a higher probability of flowering that summer than did small rosettes (Fig. 5). Growth rate, however, did not play a role in producing the source differences in flowering time because sources did not differ in April rosette size. Also, decreasing density increased annuality. Because flowering was correlated with density, independently of size, one can conclude that density influenced flowering both indirectly through its effect on early growth and independently of early growth.

Seed source, size, and density effects persisted into the 2nd yr (Fig. 6, Table 7A). The proportion of plants that survived to peak flowering and that flowered in the 2nd yr declined with increasing density. The highest proportion of plants flowering the 2nd yr were from Greensboro sources. Also, large plants at the beginning of age 2 (i.e., in July) were more likely to flower at the end of age 2 than were small plants. Size, however, did not play a role in producing the differences among sources.

Only the Ann Arbor plots contained enough 3-yr-old rosettes also to explore the independent effects of density and size on flowering in the 2nd yr. In these plots the probability of flowering was negatively correlated with density independently of July rosette size (Table 7B). Thus, initial density continued to affect year of flowering over and above its influence on growth in year 1.

Source differences continued into the 3rd yr in the Ann Arbor plots. One hundred percent ($N = 7$) of the remaining rosettes from Ann Arbor sources flowered, but only 46% ($N = 13$) of the remaining Ottawa rosettes flowered ($G^2 = 7.95$, $df = 1$, $P < .005$).

DISCUSSION

This study shows that latitude of the seed source strongly influences age of reproduction. Mean age increases clinally from south to north, which parallels the patterns observed in several other herbaceous plant species (Smith 1927, Böcher 1949, Böcher and Larsen 1958, Reinartz 1984). Unlike other studies, however, this study shows that the pattern can be observed when the plants are grown in common gardens (1) in the northern or

southern part of the species' range, and (2) on nutrient-rich or nutrient-poor soil. In the nutrient-poor soil (Ann Arbor plots) the pattern does not begin to appear until the 2nd yr. This is expected given the strong environmental component to age of flowering (Lacey 1986).

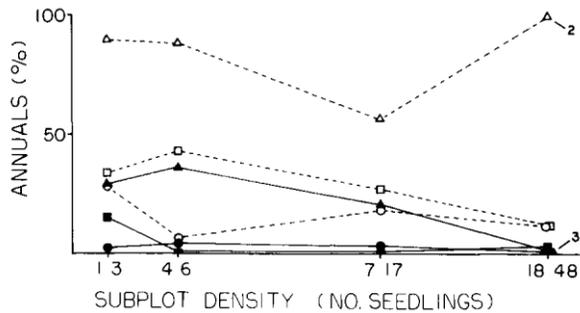


FIG. 5. Percent annuals of those surviving age class 1 in the Greensboro plots, shown by subplot density and by seed source: Greensboro (triangles), Ann Arbor (squares), Ottawa (circles); and April root crown diameter: <2.0 mm = closed symbols, solid line; 2.0–8.2 mm = open symbols, dashed line. (Sample sizes are shown on figure where <5.)

TABLE 7. G^2 tests for percent plants that flowered at age 2 (F_2) of those surviving age class 2 as a function of: (A) site (Si), seed source (So), and four density (D) levels; (B) seed source, density, and two July root crown diameter (R_1) levels in the Ann Arbor plots.

Interaction(s) deleted†	df	$G^2‡$
(A) All three-way	40	46
All three-way; Si \times F_2	42	160***
All three-way; So \times F_2	42	67**
All three-way; D \times F_2	43	77***
(B) All three-way	23	19
All three-way; $R_1 \times F_2$	24	39*
All three-way; D \times F_2	26	45*

* $P < .05$, ** $P < .01$, *** $P < .005$.

† See footnote † in Table 3.

‡ See footnote ‡ in Table 3.

Evidence that the latitudinal variation in *D. carota* is genetically based and is evolutionarily important comes from several sources. First, previous experiments on the growth of selected lines of annuals and biennials have shown that reproductive timing is partially genetically controlled (E. P. Lacey 1986 and *personal observation*). Second, the clinal variation in reproductive timing in this experiment was observed over the species' latitudinal range and in habitats where the species naturally grows. Therefore the genetic variation is expressed in natural populations and can be subject to natural selection (cf. Primack and Antonovics 1982). Third, if environmentally determined maternal effects had been important in this experiment, we would have expected the effects to manifest themselves as latitudinal differences in germination or early growth or both. Maternal effects (including both additive and common environmental) in plants have most often been observed only at the germination or seedling stages, i.e., in the form of germination behavior or early seedling growth (e.g., for natural populations: Gross 1984, Schaal 1984). In *D. carota* seed size effects diminish quickly during seedling growth (Gross 1984). If maternal effects influence life-history traits after the seedling stage, it is most likely a secondary effect of size differences established early after germination (Schaal 1984). In the experiment reported here, seed sources did differ in percent germination and did so because of latitudinal differences in environment that influenced embryo viability (Lacey 1984). However, sources never differed in individual plant size. Thus maternal effects were probably not contributing to the observed variation in year of reproduction. Rather populations at different latitudes comprise different proportions of annual, biennial, and longer-lived genotypes.

Because seed sources never affected size, the genes responsible for the clinal variation in age of reproduction probably differ from those controlling growth rate. Clinal variation could hypothetically arise from changes in genes acting directly on flowering or on genes that accelerate or retard growth to some "critical" size for flowering. A previous study suggests that both pathways may be involved in the production of phenotypic variation in age of reproduction within latitudes (Lacey 1986). Only one pathway, however, appears to contribute to the variation across latitudes.

One possible cause of the clinal variation is latitudinal differences in age-specific survival. Survival of rosettes to peak flowering time in the first growing season varied from 97–99% for all seed sources and sites. If we combine the probability of a seed's germinating with this survival during the vegetative phase, 1st-yr survival drops to 24, 19, and 12% for Greensboro, Ann Arbor, and Ottawa sites, respectively. In contrast, 2nd-yr survival (i.e., for age class 2) was 8, 88, and 80% in Greensboro, Ann Arbor, and Ottawa sites, respectively. Survival patterns within a site were the same for all sources.

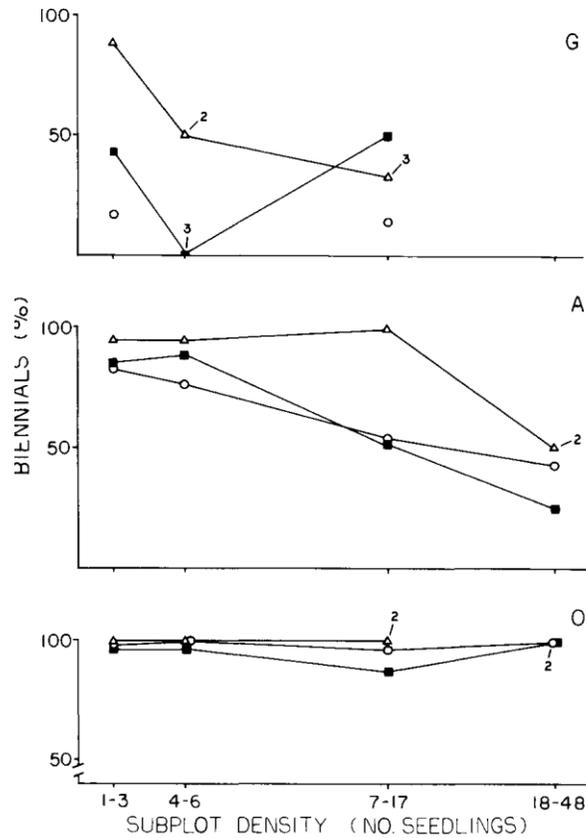


FIG. 6. Percent biennials of those surviving age class 2, shown by subplot density and by planting site: Greensboro (G), Ann Arbor (A), Ottawa (O); and seed source: Greensboro (Δ), Ann Arbor (\blacksquare), Ottawa (O). (Sample sizes are shown on figure where <5 .)

Harper (1967) and Schaffer and Gadgil (1975) first argued that for short-lived monocarps natural selection should favor precocious reproduction when 1st-yr survival surpassed 2nd-yr survival; while in habitats where 2nd-yr surpasses 1st-yr survival, biennials should be favored. My experimental results are quite consistent with this hypothesis. Annuals abound in populations growing near Greensboro where the experimental ratio of germination and 1st-yr survival to 2nd-yr survival is $\approx 3:1$. Biennials and longer-lived individuals are more common in Ann Arbor and Ottawa populations where the ratio is 0.2:1 and 0.15:1, respectively. Also, annuals are slightly more common in Ann Arbor than in Ottawa populations. The results support the view that age-dependent selection is favoring the annual habit in the South and the longer-lived habit in the North.

In contrast, density plays a minor role in explaining the overall latitudinal variation in mortality. It did not directly influence rosette mortality in the 1st or 2nd yr and density-dependent mortality did not vary between age classes at any site. Thus, there is no evidence that variation in age-specific density-dependent mortality (sensu Charlesworth 1980) has produced or is maintaining the clinal variation in age of reproduction. Rather, density-independent mortality varied over age classes and latitudes. Casual observation of plants in both experimental plots and natural populations suggests that the major cause of 2nd yr mortality in Greensboro may have been a root pathogen. Two fungi, *Sclerotium rollsii* and *Rhizoctonia solani*, are particularly serious problems for cultivated carrots in the Southeast, and their presence is primarily determined by climatic and weather conditions and secondarily by host density (e.g., Gurkin and Jenkins 1985).

Many evolutionary ecologists believe that density-dependent natural selection influences the evolution of life-history patterns, even in the absence of much corroborating empirical data (see review by Boyce 1984). In two of the best plant studies, Law et al. (1977) and Solbrig and Simpson (1977) invoke variation in density-dependent population regulation to explain the observed difference in reproductive timing among populations, but they do not measure density-dependent regulation. Few biologists have measured density-dependent regulation of plant populations (Antonovics and Levin 1980, Fowler 1986). Density probably does not strongly

influence the evolution of life-history traits in *D. carota* because the species does not often persist in one location for a long time. In any case this experiment shows that density-dependent and -independent responses need to be examined for each age class separately. For *D. carota*, overall density-independent mortality at low latitudes surpassed that at high latitudes but only during the 2nd yr.

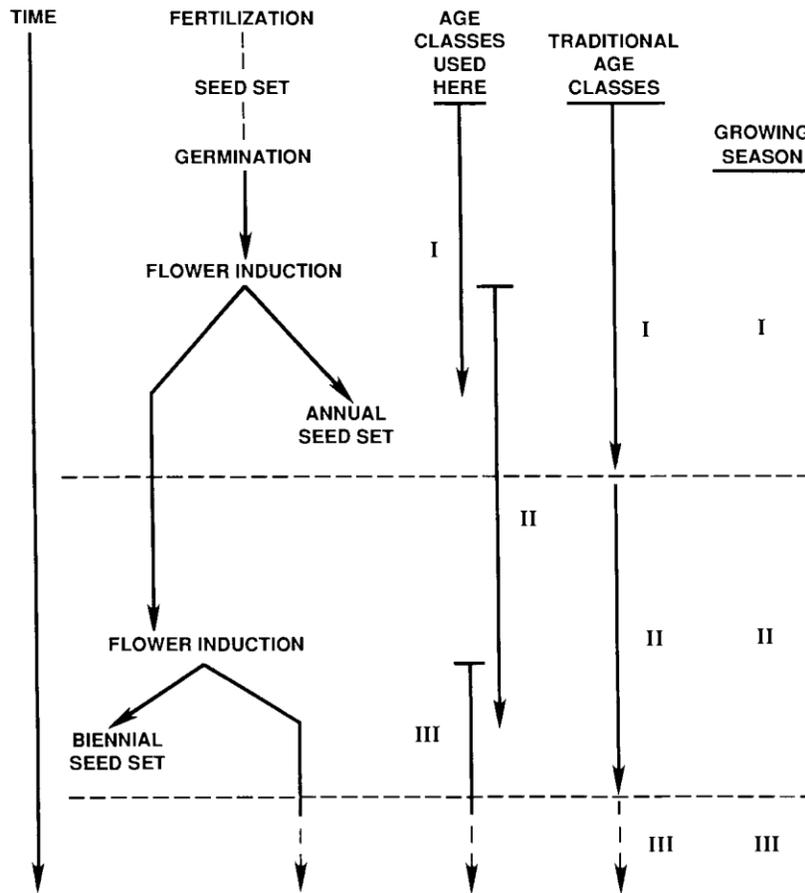


FIG. 7. Schematic drawing showing traditional age classes and those that I have used. The critical differences are: (1) the transition times between age classes, which occur within growing seasons; and (2) the temporal overlap between age classes, during which time age classes may theoretically differ in percent survival.

MacArthur and Wilson (1967) argued that when populations are maintained at small size by high density-independent mortality, selection for rapid population growth will be strong; when populations are allowed to enlarge, density-dependent mortality will increase and selection will favor increased efficiency in use of environmental resources, at the expense of delaying reproduction. Although this experiment per se gives us no information about the sizes of natural populations, it does provide data consistent with MacArthur and Wilson's predictions. Annuality was highest in the populations originating from the site showing the highest density-independent mortality. We must be cautious about drawing too many conclusions from this result, however. For example, in this experiment the density effect was measured by varying seedling density over space. Thus I examined only density effects within the same cohort, not effects among cohorts, which might appear with time. Also, interspecific interactions, which were not measured, likely change over time and may limit the time that a species can persist in one location. Reinartz (1984) suggested that the more rapid rate of succession (i.e., establishment of perennial species) in the South relative to succession in the North may favor a shorter pre-reproductive period in *Verbascum thapsis* in the South.

Daucus carota ssp. *carota* was introduced probably accidentally into eastern North America from Europe sometime in the 17th century (Dale 1974, Small 1978). Thus the present clinal variation in year of reproduction has developed in the past 300 yr. If we assume 2 yr for an average generation, a conservative assumption given the strong environmental control of reproductive timing (Holt 1972, Gross and Werner 1982, Lacey 1986) this variation has established within 150 generations. That such variation would have arisen via genetic drift (or have been maintained through isolation if colonists by chance introduced more annuals in the South than in the North) seems unlikely. *D. carota* abounds along corridors, e.g., train tracks and roads, connecting different parts

of North America, which should prevent the establishment of latitudinally isolated populations. More likely, latitudinal variation in reproductive timing has arisen through and is being maintained by latitudinal differences in selection pressure.

In contrast to the clinal variation in age of reproduction across latitudes, there is no evidence for genetic change in age of reproduction as succession proceeds within a latitude. The observed delay in flowering that is associated with later successional stages and older populations (Holt 1972, Gross and Werner 1982) hypothetically could result from the elimination of early flowering genotypes from the population over time or may represent phenotypic plasticity in the individuals constituting the population. If early flowering genotypes are eliminated, we would expect the reciprocal transplant experiment to show a decline in proportion of annuals from young to old populations. The data clearly do not show this pattern for any seed source and thus do not support the hypothesis that genetic change in reproductive timing occurs during succession. Rather, flowering year is highly plastic and is most likely responding to changing environmental conditions that accompany succession within a particular latitude.

Finally, most plant ecologists have equated age class with growing season. This can create problems when studying age-specific selection of life-cycle traits because equating the two may obscure the evolutionarily important patterns. For example, the age-specific survival patterns based on growing season and age class differed for *D. carota* (compare Figs. 2A and B). If we had examined only the patterns based on growing seasons, we would have erroneously concluded that mortality in the Greensboro plots is high in both age classes and that density explained much of the 1st-yr mortality. In fact, mortality was very low, and there was no evidence of a density effect. If the goal is to understand the evolution of life cycles, then we need to be careful about both choosing the time intervals used to distinguish age classes and reporting what intervals have been chosen. For this study the pertinent evolutionary question is: what is a plant's probability of surviving to flower and set seed next year if it does not flower (i.e., does not respond to the inductive stimulus) this year? Therefore age classes should be based on flowering times not growing seasons.

In practice, determining when age classes > 1 commence may be difficult. Ideally for studies like mine, an age class should begin when a group of individuals either responds or does not respond to the flower induction stimulus, and it should end at the time of completion of seed set for those individuals flowering in that age class (Fig. 7). These age classes are not analogous to age or stage classes used in population projection or demographic studies because they overlap in time. For example, age class 1 can be flowering when age class 2 is growing vegetatively. Hypothetically mortality could vary for these two age classes during this time. I used peak flowering time as both the beginning and end of an age class. Peak flowering time approximated the true commencement of an age class because final flower induction (by short nights), at least for cultivated carrots, occurs in early summer (Atherton and Basher 1984). Peak flowering also approximated the end of an age class because no plant died after bolting but before seed set. Two-year-olds (rosettes) did die while 1-yr-olds were setting seed, and this mortality was included in the overall 2nd-yr mortality. Kachi and Hirose (1985) used similar age classes for their study of *Oenothera glazioviana*, another short-lived monocarp.

Stearns (1980) has argued that intraspecific studies may not permit detection of life-history patterns, and other biologists (e.g., Levins 1966, Quinn and Dunham 1983) argue that the theoretical models designed to explain the evolution of these patterns cannot be tested. This study presents counter-evidence. *D. carota* varies latitudinally in age of reproduction, and latitudinal changes altering age-specific density-independent mortality appear to help maintain that variation. Many extant species contain intra- and interpopulational variation in life-history traits, and with appropriate techniques this genetic variation can be identified and its origins at least partially understood. Transplant experiments have been used since Turesson (1922) to detect ecotypic differentiation in plant species and reciprocal transplant experiments have been used both to detect ecotypic differentiation and to identify the environmental factors contributing to this differentiation (e.g., Clausen and Hiesey 1958). Thus, the reciprocal transplant experiment is a potent tool for studying the evolution of life-history patterns directly (Antonovics and Primack 1982). One transplant experiment is unlikely to identify completely the ecological or selective factors affecting life-history traits, but experiments conducted for even

several species should greatly help us to understand the evolution of life-history patterns and concomitantly assess the relative importance of life-history models.

APPENDIX

TABLE A1. Fate of marked plants in experimental plots shown by planting site, seed source, and initial subplot density. Only the Ann Arbor plots were followed through the 3rd yr. For planting sites and sources: G = Greensboro, A = Ann Arbor, O = Ottawa. Peak flowering times, which mark the transition from one year to the next were: G = late June, A and O = late July.

Site	Seed source	Initial no. seedlings per subplot	No. seedlings marked	1st year (1979-1980)			2nd year (1980-1981)			3rd year (1981-1982)				
				No. rosettes dying	No. plants flowering	No. rosettes remaining	No. rosettes dying	No. plants flowering	No. rosettes remaining	No. plants followed*	No. rosettes dying	No. plants flowering	No. rosettes remaining	
G	G	1-3	130	3	87	40	32	7	1	...	†
		4-6	62	1	39	22	20	1	1
		7-17	67	1	24	42	39	1	2
		18+	5	0	2	3	3	0	0
	A	1-3	109	8	27	74	67	3	4
		4-6	56	1	15	40	37	0	3
		7-17	105	2	12	91	85	3	3
		18+	44	3	2	39	39	0	0
	O	1-3	102	5	14	83	77	1	5
		4-6	57	2	3	52	52	0	0
		7-17	117	3	12	102	88	2	12
		18+	35	0	1	34	33	1	0
A	G	1-3	113	0	43	70	11	56	3	1	0	0	1	1
		4-6	38	1	13	24	3	20	1	1	1	0	0	0
		7-17	14	0	2	12	0	12	0	0
		18+	5	0	2	3	1	1	1	0
	A	1-3	123	2	37	84	12	62	10	4	3	1	0	0
		4-6	55	0	16	39	1	34	4	1	0	1	0	0
		7-17	44	1	8	35	5	16	14	8	5	3	0	0
		18+	10	0	0	10	2	2	6	3	1	2	0	0
	O	1-3	109	2	42	65	5	51	9	5	1	3	1	1
		4-6	42	0	10	32	1	24	7	4	3	1	0	0
		7-17	41	1	5	35	6	16	13	9	3	2	4	4
		18+	11	0	2	9	2	3	4	2	0	0	2	2
O	G	1-3	145	2	65	78	15	63	0
		4-6	33	1	18	14	1	13	0
		7-17	6	0	3	3	1	2	0
		18+	0
	A	1-3	134	2	31	101	14	84	3
		4-6	42	0	10	32	8	23	1
		7-17	39	0	6	33	10	20	3
		18+	10	1	0	9	3	6	0
	O	1-3	142	0	29	113	23	88	2
		4-6	40	2	4	34	6	28	0
		7-17	38	0	3	35	6	28	1
		18+	2	0	0	2	0	2	0

* Some plots were destroyed after the 2nd yr, so the number of plants monitored through the 3rd yr is less than the number of plants remaining at the end of the 2nd yr.

† No data were collected.

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