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THE GENETIC AND ENVIRONMENTAL CONTROL OF
REPRODUCTIVE TIMING IN A SHORT-LIVED
MONOCARPIC SPECIES *DAUCUS CAROTA*
(UMBELLIFERAE)

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SUMMARY

(1) Offspring of annual, biennial and triennial *Daucus carota* were grown under three nutrient regimes in a growth chamber to measure the effects of nutrient supply and maternal age of flowering on offspring size and growth rate and the effects of all four variables on year of flowering.

(2) Offspring rosette size and recent growth rate were both good predictors of year of flowering. An increase in size but a decrease in relative growth at the end of the summer were associated with an increased probability of flowering in the next season. The results are consistent with the Wilbur–Collins model, which suggests that both size and recent growth rate influence reproductive timing and that individuals track resources by delaying the year of reproduction if resources abound or by accelerating reproduction if resources become limiting. This model, although proposed for amphibians, may describe the general relationship between growth and reproductive timing in monocarpic plants.

(3) Maternal age and nutrient supply influenced rosette size, relative growth rate, and flowering time. Annual maternal plants and high nutrients produced both the largest offspring and the greatest number of annuals. Also, the maternal contribution acted directly upon the year of flowering as well as indirectly through size and recent growth. Both genetic variability and habitat heterogeneity explain the variation in year of flowering in natural populations.

(4) The results provide evidence that the early-rosette growth rate and the length of the pre-reproductive period are negatively correlated, as predicted by theories about the evolution of life-history patterns. Rapid growth may help annuals to persist in habitats which generally favour biennials.

(5) Response to nutrient supply did not vary among maternal age groups as might be expected in colonizing species. This suggests that phenotypic plasticity in response to nutrient supply evolves independently of year of reproduction.

INTRODUCTION

The contribution of age of first reproduction to individual fitness (Cole 1954; Lewontin 1965) has been the subject of many studies of short-lived monocarpic plant species. These studies have examined the natural variation in age of reproduction both to identify the mechanisms controlling time of reproduction (e.g. Werner 1975, 1977; Harper 1977; Baskin & Baskin 1979; van der Meijden & van der Waals Kooi 1979; Reinartz 1981) and to understand the conditions that would, selectively, favour delayed reproduction (Harper & White 1974; Schaffer & Gadgil 1975; Hart 1977; Reinartz 1981; Klinkhamer & de Jong 1983; Lacey *et al.* 1983). Most empirical studies have been focused on plant size and the environmental factors that limit size. Waterschoot (1957) and Werner (1975) proposed that a plant had to reach some minimum, or 'critical', size before it would flower, and Baskin & Baskin (1979) suggested that this critical size had to be achieved by autumn for

flowering to occur in the next growing season. Empirical studies (e.g. Doing, Biddiscombe & Kredlhans 1969; Holt 1972; Gross 1981; Klemow & Raynal 1981) show that resource limitation and plant density determine when this critical size is reached.

Because flowering does not always follow the attainment of the critical size, other factors may also be operating. In a life-history sense, the switch from vegetative to reproductive growth in monocarpic plants is not unlike the switch from the juvenile to the adult stage in amphibians. Wilbur & Collins (1973) proposed that in a resource-limited environment both size and recent growth rate are good predictors of the time of amphibian metamorphosis. Metamorphosis occurs only over a limited range of body sizes and, within this range, increasing size increases the probability of metamorphosis. Wilbur & Collins (1973) argued that, within this range, a rapid growth rate delays metamorphosis 'to capitalize on the growth opportunities', whereas a slow growth rate accelerates metamorphosis. The choice is between early reproduction at low fecundity and delayed reproduction at higher fecundity. Like amphibian metamorphosis, year of flowering in short-lived monocarpic plants may be influenced by both size and recent growth.

Year of flowering may also have a genetic component. Reinartz (1981) showed that *Verbascum thapsis* populations from different regions vary in their year of flowering even when grown in a common garden. Studies (e.g. Correns 1904; Munerati 1931; Whittaker 1944) suggest that a single locus controls flowering year in a few species, and Clausen & Hiesey (1958) argued that several loci control flowering year in *Melilotus alba*.

To elucidate the genetic and environmental components of reproductive timing in short-lived monocarpic plants, an experiment was conducted to examine the relationships between maternal age, nutrient supply, offspring size and growth rate, and year of reproduction in *Daucus carota* ssp. *carota*. Four alternative models of interaction were proposed and evaluated. In the first (Fig. 1a) offspring growth alone determines time of flowering. In the second (Fig. 1b) nutrients and maternal age influence growth, which then directly determines flowering time. In the third model (Fig. 1c) nutrients, maternal age and growth all directly and independently influence flowering, and in the last model (Fig. 1d) maternal age and nutrients influence flowering both directly and indirectly through growth.

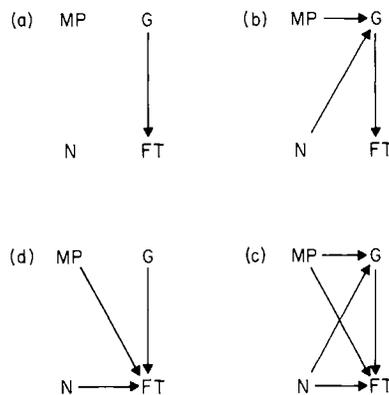


FIG. 1. Four models of interaction among maternal age (MP), nutrient supply (N), growth (G) and flowering time (FT). (a) Only G influences FT; (b) MP and N influence FT indirectly via G; (c) MP, N, and G all directly influence FT; (d) MP and N influence FT directly and via G.

BIOLOGY OF THE SPECIES AND METHODS

Daucus carota ssp. *carota* E.B. (Small 1978) (wild carrot, Queen Anne's lace) is a north-temperate weed of old fields and disturbed habitats (see Lacey 1982). It can be an annual, biennial or longer lived monocarpic plant, though in south-eastern Michigan where seeds were collected for the experiment, biennial plants predominate. Individuals grow vegetatively as a rosette until they produce a flowering stalk (bolt), flower and set seed. Plants die after bolting regardless of whether or not they set seed.

Each year from 1975 to 1977 outdoor experimental plots were established at the Matthaei Botanical Gardens, Ann Arbor, Michigan. Seeds collected from several natural populations near Ann Arbor were sown on these plots. From September 1977 to 1979 seeds (offspring) from the terminal (uppermost) umbel of annual, biennial and triennial plants grown in these plots were collected, keeping each family of offspring distinct. On 5 December 1980, these seeds were sown and maintained under three nutrient regimes in a growth chamber at the Duke University Phytotron. Ten offspring from nine families of each maternal age group were grown under each nutrient treatment, with a total of ninety plants per maternal age group per treatment. The same families provided seeds for each treatment. Initially four seeds were scattered onto each 0.5-l pot filled with a 1:1 gravel:vermiculite mixture. Two weeks later the seedlings were thinned to one per pot.

The fertilizer was half-strength Hoagland's solution. The growth chamber held twenty-four carts, eight carts for each nutrient treatment: high = fertilizer once a day, demineralized water once a day; medium = fertilizer once every two weeks, water twice a day except once only on a day when fertilizer was given; low = fertilizer once every six weeks, water twice a day except once only on a day when fertilizer was given. Each cart could hold a maximum of thirty-six plants. Because of the dimensions of the carts and growth chamber a modified Latin square design (Snedecar & Cochran 1967) was used to arrange the offspring within the carts and the carts (nutrient treatments) within the growth chamber (Fig. 2). Each cart held at least one offspring from each family (Fig. 2, cart 1). Six of the eight carts per nutrient regime held only one offspring from each of six families, but two offspring from the other three families (Fig. 2, cart 2). Adding these offspring increased the offspring sample size per family. Each cart was divided into twelve partitions (Fig. 2, cart 3) to investigate the effect of position on the cart. Each maternal group was represented once in each partition. Because each family occupied the same position on all carts, position and family effects are confounded. Therefore, differences among families nested within maternal groups were not analysed, although family was included as an independent variable in the analysis of variance model so that the appropriate error sums of squares could be calculated to test for the significance of other effects.

Plants were grown under temperature and photoperiod regimes resembling those found in Ann Arbor: eighteen weeks of summer (day: 14 h, 26 °C; night: 10 h, 20 °C), one week of early autumn and late spring (day: 12 h, 17 °C; night: 12 h, 11 °C), one week of late autumn and early spring (day: 10 h, 10 °C; night: 14 h, 5 °C; no fertilizer for any cart), and ten weeks of winter (day: 8 h, 5 °C; night: 16 h, 0 °C; no fertilizer, water once a day for all carts). In a preliminary experiment eight weeks of winter was sufficient to induce bolting.

Plant size, relative growth and year of flowering were recorded for all plants. Seven weeks after the experiment began, the root-crown diameter (RCD) of each rosette was measured with calipers. Thereafter, each rosette was measured every 4 weeks during the summer until the rosette either bolted or died or until the experiment was terminated in

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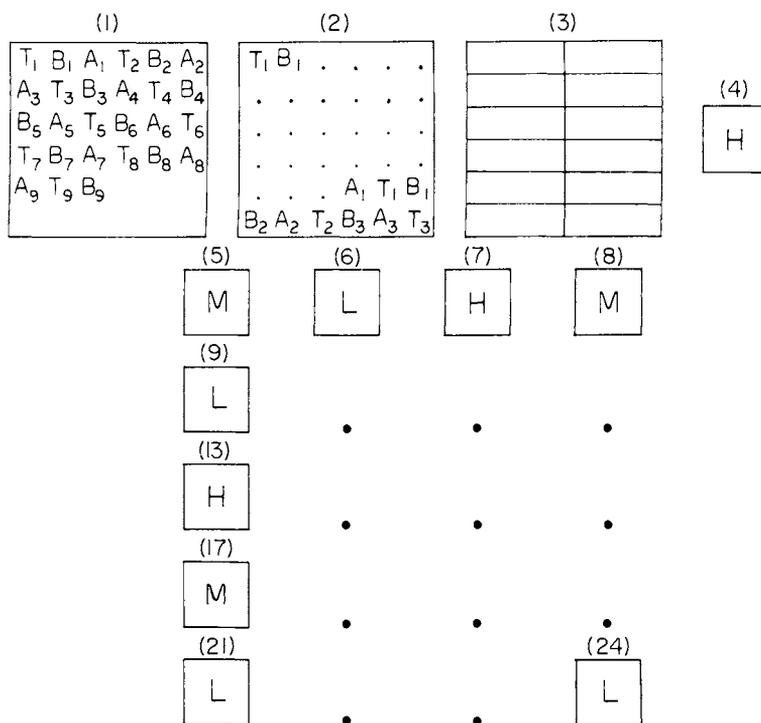


FIG. 2. Experimental design showing the arrangement of carts (numbered) within the growth chamber and for the first three carts, which are enlarged, the position of the maternal age groups and families within carts. Two carts per nutrient treatment held twenty-seven plants (e.g., cart 1) while six held thirty-six plants (e.g., cart 2). Cart 3 shows the partitions used to test for position effects within the carts. Nutrient treatment: H, high; M, medium; L, low; cart number in parentheses; maternal age: A, annual; B, biennial; T, triennial; family number indicated by subscript.

October 1981. Because RCD is strongly correlated with rosette biomass (Gross 1981), RCD was used to estimate rosette size. The relative growth per individual for each time interval was determined by calculating the absolute change in RCD between each set of successive measurements and dividing these values by the RCD at the earlier observation time.

Analysis of variance was used on log-transformed data to analyse the impact of maternal age and nutrient supply on both components of growth. The analysis included the variables, nutrients, maternal age, carts nested within nutrients, families nested within maternal age group and the interaction between nutrients and maternal age. The many levels of carts and families, twenty-four and twenty-seven, respectively, prevented the inclusion of the cart \times family interaction.

A multivariate G^2 test was used to assess the effects of maternal age, nutrients, size and immediate change in size on flowering time. The multivariate G^2 test is based on a hierarchical model for categorical data (Bishop, Fienberg & Holland 1975). In this test a saturated log-linear model includes the main effects and all possible combinations of interactions among the variables. Tests for interactions are accomplished by deleting interaction terms from the saturated model and obtaining expected cell counts by iterative proportional fitting (iteration stop limit = 0.001), working down from the highest order

interaction as described by Fienberg (1970). The procedure produces a likelihood statistic for each interaction term and, in this way, permits the testing of hypotheses about the importance of various interactions. When necessary the degrees of freedom were adjusted to account for cells with expected values of zero (Bishop, Fienberg & Holland 1975).

The effects of cart and position within a cart on flowering time were also examined using the G^2 test. Position within the cart did not contribute significantly to year of flowering for any nutrient treatment ($P > 0.05$). The particular cart did not significantly influence year of flowering in the high- or low-nutrient treatments ($P > 0.05$), but did in the medium-nutrient treatment ($P < 0.005$). A G^2 test examining the effects of maternal age, size and cart on flowering time within the medium nutrient treatment alone produced the same results for the maternal age and size effects as when all carts were lumped within nutrient treatment. Therefore, only the results for all carts grouped within treatments are presented in the results.

RESULTS

Growth

In the first summer both nutrients and maternal age significantly influenced growth; also, nutrient supply influenced the relative change in growth (Table 1). Root-crown diameter increased most dramatically in the high-nutrient group and among the offspring of annual plants (Fig. 3). Both maternal age and nutrients continued to influence growth early in the second summer. By August all but the smallest plants in the high-nutrient group, about half of those in the medium group, and a few in the low-nutrient group had flowered, which explains the dramatic change in mean RCD values from July to August (Fig. 3). At no time was the maternal age–nutrient interaction significant. All maternal groups responded similarly to change in nutrient availability.

TABLE 1. Analysis of variance results for effect of maternal age (MP) and nutrient supply (N) on root-crown diameter (RCD) in *Daucus carota* and recent absolute change in RCD (G) for different observation times. All data are log-transformed.

Observation	Variable	Number of plants	N	F for effect of	
				MP	N × MP
30 January	RCD	804	5440***	9.9***	0.4 ^{N.S.}
28 February	RCD	804	4604***	11.2***	0.5 ^{N.S.}
	G		55***	2.8 ^{N.S.}	0.9 ^{N.S.}
27 March	RCD	780	4276***	11.9***	2.0 ^{N.S.}
	G		23***	2.6 ^{N.S.}	1.9 ^{N.S.}
15 July	RCD	754	3293***	13.8***	0.7 ^{N.S.}
	G		15***	3.4*	0.4 ^{N.S.}

Significance symbols: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; N.S., $P > 0.05$.

Year of flowering

When maternal and nutrient groups were pooled, both size and recent relative growth predicted the summer of flowering. Large rosettes in late January (about five weeks after germination) flowered significantly earlier than small rosettes (Fig. 4; $G^2 = 436$, d.f. = 8, $P < 0.005$). The largest rosettes at the end of the first summer (late March) were most likely to flower the second summer (Fig. 5; $G^2 = 375$, d.f. = 16, $P < 0.005$). Additionally, the less the rosette grew during late summer (March), the higher the probability of flowering

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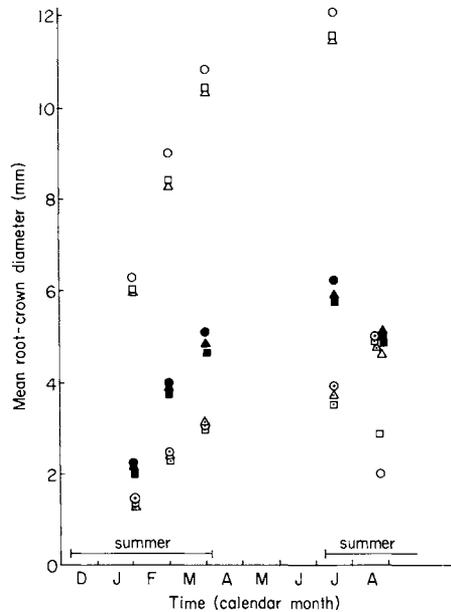


FIG. 3. Mean root-crown diameter of *Daucus carota* plants grown under low (symbols with dot), medium (solid symbols) and high (open symbols) nutrient treatments, and from annual (circle), biennial (square) and triennial (triangle) maternal plants.

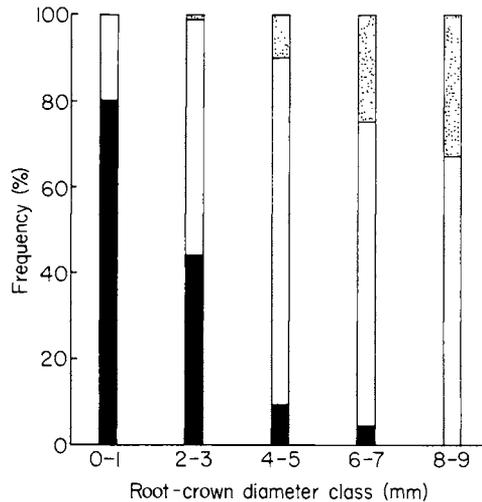


FIG. 4. Percentage frequency of annual (□), biennial (□) and perennial (■) plants of *Daucus carota* for January root-crown diameter classes.

the next summer ($G^2 = 49$, d.f. = 15, $P < 0.005$). This correlation is best seen in the medium RCD classes, which constitute the medium-nutrient group, and is independent of size (Fig. 5). The three-way interaction among RCD, recent relative change in RCD, and flowering year was insignificant ($G^2 = 20$, d.f. = 12, $P > 0.05$).

Maternal age and nutrient regime also affected flowering year (Fig. 6). Increasing nutrient supply accelerated flowering time (only the high-nutrient group produced any

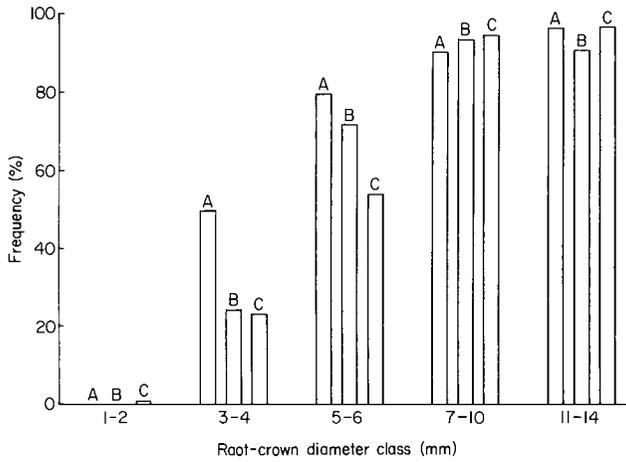


FIG. 5. Percentage frequency of biennial plants for different values of root-crown diameter and recent relative change in root-crown diameter in *Daucus carota* at the end of the first summer. Relative change: A, 0–19%; B, 20–39%; C, 40–100%.

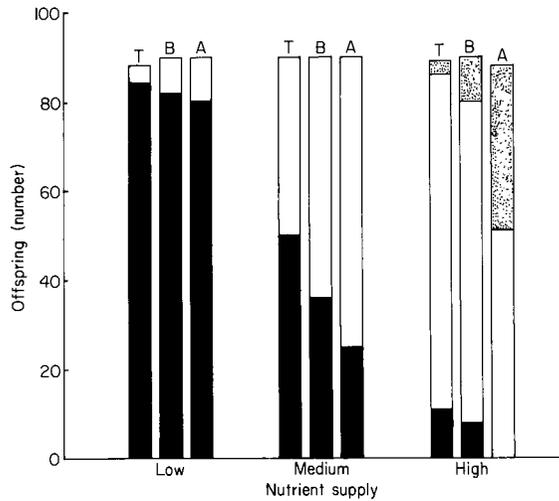


FIG. 6. Number of annual (▣), biennial (□) and perennial plants (■) of *Daucus carota* produced by each maternal phenotype (A, annual; B, biennial; T, triennial) and nutrient-supply group.

annual plants), and the annual-maternal group produced the greatest number of annual offspring. These effects were highly significant when all offspring were considered and when biennial and perennial offspring alone were considered (Table 2). Thus the impact of the maternal age and nutrients was felt in the second growing season as well as over all seasons. All the maternal groups responded similarly to changes in nutrient supply.

Next, the influence of nutrient supply and maternal age on year of flowering independently of growth was considered. Because the size classes for each nutrient treatment were largely disjunct for any observation time (Fig. 7), the independent nutrient effects could not be explored. However, the independent maternal effects could be investigated. A G^2 test of the interactions among January size, maternal age and year of flowering showed a significant maternal age–flowering interaction ($G^2 = 71$, adjusted d.f.

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TABLE 2. Three-way G^2 test results showing the effect of maternal age (MP) and offspring nutrient availability (N) on offspring year of flowering (F) in *Daucus carota*. The G^2 statistic represents the consequence of leaving the indicated interaction or the indicated interaction plus the three-way interaction out of the model.

	Interaction	Adjusted d.f.	G^2 statistic
All maternal and offspring groups	MP \times N \times F	4	6 ^{N.S.}
	N \times F	12	548 ^{***}
	MP \times F	8	77 ^{***}
Biennial and triennial offspring only	MP \times N \times F	4	6 ^{N.S.}
	N \times F	6	423 ^{***}
	MP \times F	6	28 ^{***}

Significance symbols: ^{***}, $P < 0.001$; N.S., $P > 0.05$.

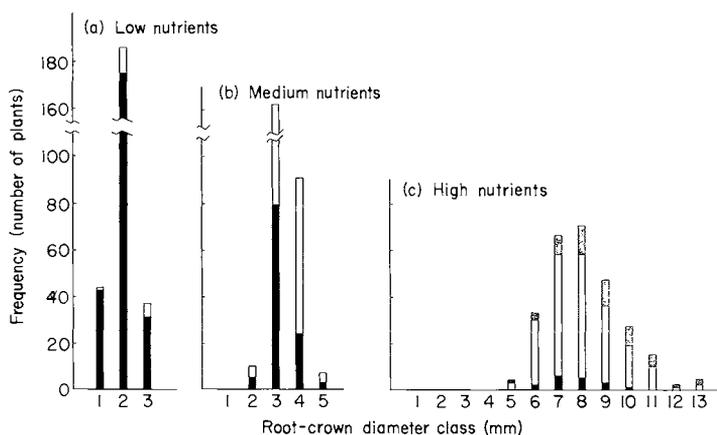


FIG. 7. Plant-size distribution of *Daucus carota* by nutrient treatments (a, low; b, medium; c, high) on 27 February 1981 (week 11). Symbols for plant species: (▨), annual; (□), biennial; (■), perennial.

TABLE 3. Fraction of annual (A), biennial (B), and longer lived (LL) offspring of *Daucus carota* for each maternal-age group within the January size (root-crown diameter) classes. Sample sizes in parentheses.

Maternal age	Offspring	Root-crown diameter (mm)				
		0-1	2-3	4-5	6-7	8-9
Annual	A	—	0	0.26 (9)	0.49 (24)	0.80 (4)
	B	0.22 (23)	0.65 (53)	0.70 (23)	0.51 (25)	0.20 (1)
	LL	0.78 (79)	0.35 (28)	0.04 (1)	0	—
Biennial	A	—	0.01 (1)	0.05 (2)	0.14 (7)	0
	B	0.28 (31)	0.51 (36)	0.84 (31)	0.80 (39)	1.00 (4)
	LL	0.72 (79)	0.48 (33)	0.11 (4)	0.06 (3)	—
Triennial	A	—	0	0	0.08 (3)	0
	B	0.15 (18)	0.47 (28)	0.86 (38)	0.85 (33)	1.00 (3)
	LL	0.85 (100)	0.53 (32)	0.14 (6)	0.07 (3)	—

= 16, $P < 0.005$). Annual mothers produced the most annual plants, and triennial mothers produced the most longer-lived offspring regardless of size (Table 3). A G^2 test of maternal age, size at the end of first summer, recent relative growth and future flowering also

showed a significant maternal age-flowering interaction that was independent of size and recent growth ($G^2 = 70$, d.f. = 42, $P < 0.005$). Annual mothers produced the highest proportion of biennial plants and the triennial mothers the lowest (Table 4). All other three- and four-way interactions involving maternal age and flowering time were non-significant.

TABLE 4. Fraction of non-annual rosettes of *Daucus carota* that flowered during the second summer for each maternal-age group, size class in late March (end of first summer), and recent relative growth class. Total number of biennial and longer lived offspring shown in parentheses.

Maternal age	Relative change in RCD in March (%)	March root-crown diameter (mm)				Over size classes
		0-3	4-5	6-9	10-16	
Annual	0-19	0.18 (38)	0.91 (22)	0.92 (12)	1.00 (8)	0.58
	20-39	0.04 (22)	0.76 (33)	0.89 (9)	1.00 (19)	0.64
	40-100	0.13 (30)	0.52 (27)	1.00 (5)	1.00 (6)	0.43
	Over growth increments	0.12	0.72	0.92	1.00	
Biennial	0-19	0.38 (24)	0.65 (20)	0.85 (20)	1.00 (14)	0.68
	20-39	0.08 (37)	0.35 (34)	0.89 (19)	0.88 (17)	0.44
	40-100	0.06 (35)	0.71 (21)	1.00 (6)	0.92 (12)	0.46
	Over growth increments	0.14	0.53	0.89	0.93	
Triennial	0-19	0.22 (40)	0.57 (30)	0.89 (28)	0.94 (16)	0.59
	20-39	0 (28)	0.40 (30)	0.83 (6)	0.90 (20)	0.42
	40-100	0.03 (34)	0.38 (13)	0.75 (8)	0.93 (14)	0.36
	Over growth increments	0.10	0.46	0.86	0.92	

Critical size

Because a number of studies have investigated the 'critical size' for flowering, the annual and biennial plants with the smallest RCD within treatments were sought to examine what minimum RCD must be reached for flowering in the first and second summer. For annual plants, the smallest values from the January data were examined because, at this time, year of flowering was correlated with RCD and no annual plants had begun to flower. For biennial plants, the smallest RCD at the end of the first summer was chosen. Because the medium- and low-nutrient treatments produced no annual plants, minimum biennial-RCD values were selected from only these two treatments. The presence of annual plants would have biased the sample.

Biennial mothers produced offspring which flowered at the smallest RCD regardless of nutrient treatment (Table 5). The probability of any one of the maternal groups producing

TABLE 5. Smallest root-crown diameter (mm) for annual and biennial plants of *Daucus carota* in the three maternal-age and three nutrient groups. The root-crown diameter for the annual plants were selected from January measurements and for biennial plants from the measurements at the end of the first summer (late March). Sample size in parentheses.

Maternal age	Offspring		
	Low nutrients	Biennial Medium nutrients	Annual High nutrients
Annual	2.8 (90)	3.7 (90)	4.6 (88)
Biennial	2.4 (90)	3.1 (90)	3.4 (90)
Triennial	2.7 (89)	3.6 (90)	6.7 (89)

the smallest offspring in all three treatments was 0.11. Within the biennial offspring, the smaller root-crown diameters were all in the low-nutrient treatment. The probability of this happening for all three maternal groups is 0.125. This value is higher than the 0.05 significance level, but it is the lowest probability value possible given the small sample size of three maternal treatments.

DISCUSSION

Previous studies of *Daucus carota* (Rempel 1970; Holt 1972; Dale 1974; Gross & Werner 1982) have attributed natural variation in the pre-reproductive period within and among populations to environmental differences. The results of this experiment are consistent with these studies and show that nutrient supply can determine flowering year. In natural populations, either abiotic or biotic factors could limit nutrients and strongly influence the year of reproduction.

Experimental results show an additional effect of maternal phenotype. The offspring of annual plants exhibited the greatest propensity for flowering during the first year, and the offspring of triennial plants the greatest propensity for delaying flowering beyond the second year. These results probably reflect underlying genetic differences among the maternal groups. All the maternal plants, and most likely also the paternal plants, were grown under similar conditions (albeit different from those in the growth chamber). The experiment indicates that populations in south-eastern Michigan maintain genetic variation in tendency to flower in a particular year. Further, the results suggest that this genetic variation should manifest itself most clearly in nutrient-rich areas (e.g. recently-abandoned high-quality agricultural land) and should be least obvious in nutrient-poor areas (e.g. marginal agricultural land or fields in mid-succession rather than in the early stages). To the extent that annual plants have been reported only from the most recently disturbed sites, observations of natural populations are consistent with this prediction.

Previously-cited studies of short-lived monocarpic plants have demonstrated a good correlation between RCD and flowering year, and this is confirmed here. The correlation between recent relative growth and flowering year has not been shown before, however, and shows that the Wilbur–Collins (1973) model describes reproductive timing among years in *D. carota*. Additional studies should be conducted to see if the model applies to monocarpic plants in general.

The premises of the model may explain why it could apply to both amphibians and monocarpic plants. Wilbur & Collins (1973) based their model on observations that resource availability influences juvenile growth and that juvenile mortality decreases with increasing size. These trends are seen in short-lived monocarpic plants as well as amphibians. Wilbur & Collins also assumed that increasing size at metamorphosis increases adult fecundity. Many studies show this to be true for monocarpic plants (e.g. Werner 1975; van der Meijden & van der Waals Kooi 1979; Gross 1981; Reinartz 1981). From these premises Wilbur & Collins (1973) argued that if resources become plentiful, the probability of dying as a juvenile should fall while potential fecundity should increase. If resources become limited, however, the probability of dying should remain high while potential fecundity should increase little. Therefore, natural selection should favour those individuals which can delay metamorphosis when resources abound and accelerate metamorphosis when resources become limited. Whether or not natural selection has acted upon *D. carota* in this manner remains to be tested. The cause of the correlation between

relative growth in late summer and probability of subsequent flowering in this experiment could be that flower induction had already occurred in the plants which were going to flower the next summer. Thus, energy in late summer was being shunted not into growth but into flower initiation. Experiments on biennial plants argue against this, however, and in particular, in *D. carota*, it is the cold temperatures of winter that induce flowering (Lang 1957).

The fact that both relative growth rate and size influence flowering time suggests that the critical (minimum) size for flowering may be, to some extent, environmentally determined. This is further suggested by the observation that for biennial plants, the critical size for flowering differed with nutrient treatment (Table 5). The *P*-values for both environmental and maternal age effects were derived from *a posteriori* data inspection, and so must be viewed cautiously. They do suggest, however, that further studies examining the environmental as well as genetic control of 'critical size' are warranted. Flowering in biennial plants occurs over a wide range of sizes in natural populations. Baskin & Baskin (1979) explained this variation in terms of differential growth beyond the critical size during the growing season preceding the cold period that induces bolting (e.g. Lang 1957; Doing, Biddiscombe & Knedlhans 1969; Glier & Caruso 1974). This mechanism would explain why many plants bolt at sizes much larger than the critical size. The results presented here suggest that microenvironmental heterogeneity within a habitat may produce within-population variation in the critical size and that increasing nutrient supply may increase the critical size. This mechanism would explain why some plants will not bolt even after passing the minimum size observed for the population as a whole.

Although nutrients, size and recent growth were all good predictors of flowering year, it was impossible to determine whether nutrients affect flowering directly or indirectly through growth. The results do show that maternal phenotype influences year of flowering both directly and indirectly through growth. Thus, model d (Fig. 1) most appropriately describes the maternal phenotype-flowering year relationship. Annual mothers produce larger offspring and, because increasing size increases the probability of flowering, more offspring of annual plants flower early. Additionally, the probability of flowering is highest for the annual-maternal group and lowest for the triennial group independent of size.

Models addressing the evolution of life-history patterns have predicted a negative correlation between growth rate and length of the pre-reproductive period (see Stearns 1976). Comparisons of closely-related plant species growing in different habitats have provided circumstantial evidence for this correlation (Salisbury 1942; Baker 1965; Harper 1977). This experiment provides supporting evidence from within a single species. Annual mothers produce both the fastest growing offspring and the most annual offspring while the triennial mothers produce the slowest growing and latest flowering offspring. In general, ecologists studying the evolution of life-history patterns have argued that a habitat will favour either rapid growth and a short pre-reproductive period or slower growth and delayed reproduction. In *D. carota* populations in Michigan, both patterns occur together. The low net fitness (population growth rate averaged over years and sites) of annual plants may explain why annuals are not very abundant in these populations (Lacey *et al.* 1983); a negative genetic correlation between growth rate and length of the pre-reproductive period would help to explain their persistence. If annual plants do grow more quickly than longer lived plants, they will set more seeds than they would if they grew at the same rate as longer lived plants. Thus, although biennial fitness may surpass annual fitness when viewed over habitats and years, in particular years and in particular sites, annuals will be favoured. Spatial and temporal

variation may maintain the polymorphism or may favour individuals which produce genetically variable offspring.

Because *D. carota* colonizes disturbed sites fairly rapidly and, in Michigan, persists for many years after an initial disturbance (Gross & Werner 1982; Lacey 1982), one would predict that its growth and reproductive timing would be plastic (Bradshaw 1965, 1973; Levins 1968). The experimental results agree with this prediction. One might also hypothesize that year of flowering would be negatively correlated with the degree of phenotypic plasticity. This is based on the assumption that selection for phenotypic plasticity would be strongest in individuals which have the least amount of time to accumulate resources before flowering. According to a prediction made by the Wilbur–Collins model, flowering should begin at large sizes and show little phenotypic plasticity in long-lived monocarpic plants, but should start at small sizes and show high plasticity in short-lived monocarpic plants. The experimental results provide no support for this hypothesis. All maternal groups showed similar flowering responses to change in size and relative growth. Additionally, the absence of a significant maternal age–nutrient effect on either growth or year of flowering showed that all the maternal groups responded similarly to changes in nutrient supply. The results suggest that flexibility in nutrient response is controlled independently of year of reproduction.

Genetic variation in the time of onset of reproduction in *D. carota* may have been produced in several ways. First, natural selection may have acted directly upon the genes that control reproductive timing. Alternatively, the variation may be an artefact of selection for a correlated character; this mechanism presumes that reproductive timing has had no adaptive value and that it has undergone evolutionary change only because selection has acted upon a genetically correlated character (Cole 1954; Lewontin 1965; Hamilton 1966). Thirdly, selection may have acted upon reproductive timing indirectly through a genetically correlated character. For example, natural selection may favour genetic changes which accelerate growth rate because an increased growth rate would increase the number of progeny reaching the critical size in time for flower induction. An alternative model could involve changes which lower the critical size; this would increase the number of progeny reaching the critical size. While these models have yet to be tested, they illustrate how genetically correlated characters might influence the evolution of reproductive timing. Clearly if we are to understand the natural diversity in the time of onset of reproduction and the potential for further evolutionary change, we must determine the genetic basis for the onset of reproduction.

In summary, year of reproduction in *Daucus carota* is determined by both environmental and genetic components, and both size and recent growth are good predictors of year of flowering. The genetic control of year of flowering acts directly on flowering and indirectly through growth. This study provides evidence that year of flowering is strongly correlated with growth and at most only weakly correlated with phenotypic plasticity. Further studies should elucidate further the genetic relationships among these traits.

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REFERENCES

- Baker, H. G. (1965).** Characteristics and modes of origin of weeds. *The Genetics of Colonizing Species* (Ed. by H. G. Baker & G. L. Stebbins, Jr), pp. 147–172. Academic Press, New York.
- Baskin, J. M. & Baskin, C. C. (1979).** Studies on the autecology and population biology of the weedy monocarpic perennial, *Pastinaca sativa*. *Journal of Ecology*, **67**, 601–610.
- Bishop, Y. M., Fienberg, S. E. & Holland, P. W. (1975).** *Discrete Multivariate Analysis: Theory and Practice*. MIT Press, Cambridge, Massachusetts.
- Bradshaw, A. D. (1965).** Evolutionary significance of phenotypic plasticity in plants. *Advances in Genetics*, **13**, 115–155.
- Bradshaw, A. D. (1973).** Environment and phenotypic plasticity. *Basic Mechanisms in Plant Morphogenesis*, pp. 75–94. Brookhaven Symposium No. 25, Brookhaven National Laboratory, Upton, New York.
- Clausen, J. & Hiesey, W. M. (1958).** Experimental studies on the nature of species. IV. Genetic structure of ecological races. *Carnegie Institute of Washington Publication*, **615**, 1–312.
- Cole, L. C. (1954).** The population consequences of life history phenomena. *Quarterly Review of Biology*, **29**, 103–137.
- Correns, C. (1904).** Ein typisch spaltender Bastard zwischen einer einjährigen und einer zweijährigen Sippe des *Hyoscyamus niger*. *Berichte der Deutschen Botanischen Gesellschaft*, **22**, 517–524.
- Dale, H. M. (1974).** The biology of Canadian weeds. 5. *Daucus carota*. *Canadian Journal of Plant Science*, **54**, 673–683.
- Doing, H., Biddiscombe, E. F. & Knedlhans, S. (1969).** Ecology and distribution of the *Carduus nutans* group (nodding thistles) in Australia. *Vegetatio*, **17**, 313–354.
- Fienberg, S. E. (1970).** The analysis of multidimensional contingency tables. *Ecology*, **51**, 419–433.
- Giler, J. H. & Caruso, J. L. (1974).** The influence of low temperature on activities of starch degradative enzymes in a cold-requiring plant. *Biochemical and Biophysical Research Communications*, **58**, 573–578.
- Gross, K. L. (1981).** Prediction of fate from rosette size in four 'biennial' plant species: *Verbascum thapsus*, *Oenothera biennis*, *Daucus carota*, and *Tragopogon dubius*. *Oecologia, Berlin*, **48**, 209–213.
- Gross, K. L. & Werner, P. A. (1982).** Colonizing abilities of "biennial" plant species in relation to ground cover: implications for their distributions in a successional sere. *Ecology*, **63**, 921–931.
- Hamilton, W. D. (1966).** The moulding of senescence by natural selection. *Journal of Theoretical Biology*, **12**, 12–45.
- Harper, J. L. (1977).** *Population Biology of Plants*. Academic Press, London.
- Harper, J. L. & White, J. (1974).** The demography of plants. *Annual Review of Ecology and Systematics*, **5**, 419–463.
- Hart, R. (1977).** Why are biennials so few? *American Naturalist*, **111**, 792–799.
- Holt, B. R. (1972).** Effect of arrival time on recruitment, mortality, and reproduction in successional plant populations. *Ecology*, **53**, 668–673.
- Klemow, K. M. & Raynal, D. J. (1981).** Population ecology of *Melilotus alba* in a limestone quarry. *Journal of Ecology*, **69**, 33–44.
- Klinkhamer, P. G. L. & deJong, T. G. (1983).** Is it profitable for biennials to live longer than two years? *Ecological Modelling*, **20**, 223–232.
- Lacey, E. P. (1982).** The timing of seed dispersal of *Daucus carota* L. (Apiaceae). *Oikos*, **39**, 83–91.
- Lacey, E. P., Real, L., Antonovics, J. & Heckel, D. (1983).** Variance models in the study of life histories. *American Naturalist*, **122**, 114–131.
- Lang, A. (1957).** The effect of gibberellin upon flower formation. *Proceedings of the National Academy of Science*, **43**, 709–717.
- Levins, R. (1968).** *Evolution in Changing Environments*. Princeton University Press, Princeton, New Jersey.
- Lewontin, R. C. (1965).** Selection for colonizing ability. *The Genetics of Colonizing Species* (Ed. by H. G. Baker & G. L. Stebbins, Jr), pp. 79–94. Academic Press, New York.
- Meijden, E. van der & Waals Kooi, R. E. van der (1979).** The population ecology of *Senecio jacobaea* in a sand dune system. *Journal of Ecology*, **67**, 131–153.
- Munerati, O. (1931).** L'eredità della tendenza alla annualità nella comune barbabietola coltivata. *Zeitschrift für Pflanzenzüchtung*, **17**, 84–89.
- Reinartz, J. A. (1981).** *Biomass partitioning, life history and population dynamics of common mullein* (*Verbascum thapsus* L.). Ph.D. thesis, Duke University.
- Rempel, E. (1970).** *Interference studies on Daucus carota (wild carrot)*. Masters thesis, University of Guelph.
- Salisbury, E. J. (1942).** *The Reproductive Capacity of Plants*. Bell, London.

- Schaffer, W. M. & Gadgil, M. V. (1975).** Selection for optimal life history in plants. *Ecology and Evolution of Communities* (Ed. by M. G. Cody & J. M. Diamond), pp. 142–157. Belknap Press, Cambridge, Massachusetts.
- Small, E. (1978).** A numerical taxonomic analysis of the *Daucus carota* complex. *Canadian Journal of Botany*, **56**, 248–276.
- Snedecor, G. W. & Cochran, W. G. (1967).** *Statistical Methods*. Iowa State University Press, Ames.
- Stearns, S. C. (1976).** Life history tactics: a review of the ideas. *Quarterly Review of Biology*, **51**, 3–47.
- Waterschoot, H. F. (1957).** Effects of temperature and daylength on flowering in *Dianthus barbatus* L. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen Series C, Biological and Medical Sciences*, **60**, 318–323.
- Werner, P. A. (1975).** Predictions of fate from rosette size in teasel (*Dipsacus fullonum* L.). *Oecologia, Berlin*, **20**, 197–201.
- Werner, P. A. (1977).** Colonization success of a “biennial” plant species: experimental field studies of species cohabitation and replacement. *Ecology*, **58**, 840–849.
- Whittaker, T. W. (1944).** The inheritance of certain characters in a cross of two American species of *Lactuca*. *Bulletin of the Torrey Botanical Club*, **71**, 547–555.
- Wilbur, H. M. & Collins, J. P. (1973).** Ecological aspects of amphibian metamorphosis. *Science, New York*, **182**, 1305–1314.

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