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COMPETITION PROLONGS EXPRESSION OF MATERNAL EFFECTS IN SEEDLINGS OF ERIGERON ANNUUS (ASTERACEAE)[1]

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ABSTRACT

The timing of expression of environmental maternal effects on seedling growth was investigated in greenhouse-grown populations of *Erigeron annuus* (Asteraceae). Maternal differences were generated in genetically identical lines grown under high and low nutrient conditions. There were significant differences among maternal families within genotypes for seed size, cotyledon size, number of leaves, and rosette diameter. When seedlings were grown individually, effects of the maternal fertilizer treatment on leaf number and rosette diameter were present early but could not be detected after eight weeks. When seedlings from HIGH and LOW lines were grown in competition, the maternal effects and the relative size advantage of seedlings from HIGH parents increased throughout the experiment. Most of the variation among nutrient treatments for seedling size characters could be explained by variation in initial seed size. In the competition experiment, the increasing magnitude of maternal environmental differences over time masked genetic variation for seedling characters; without competition, the relative contribution of genetic variation increased through time. Under competitive conditions that generate persistent maternal effects on fitness, maternal environmental effects may retard natural selection.

THE RESEMBLANCE between parents and offspring can result from a number of causes in addition to additive genetic variance (heritability). Maternal effects, the uniparental influence of maternal phenotype on offspring, are one important source of this resemblance (Falconer, 1981). Seeds are connected to the maternal plant through a large portion of their development so there are many ways the maternal phenotype can influence the phenotype of the offspring. Maternal effects may arise from genetic differences among plants in the ability to provision seeds, genetic differences expressed in maternally derived structures such as the seed coat or seed dispersal structures, cytoplasmic factors, or from effects of the maternal environment (Roach and Wulff, 1987). Here I restrict "maternal effects" to mean specifically maternal environmental effects.

Maternal effects are usually considered only as a potential bias that must be eliminated prior to estimating genetic variances, because maternal effects generate spurious correlations among relatives. However, maternal effects themselves can be biologically important. The presence of nongenetic effects due to maternal environmental variation will decrease the heritability of a trait and thus decrease the response to natural selection. Large maternal environmental effects may therefore place important constraints on evolution.

A number of environmental factors have been shown to affect offspring phenotypes in plants, including nutrient levels (Parrish and Bazzaz, 1985; Marshall, 1986; Fenner, 1986), photoperiod (Gutterman, 1982), light quality (Cresswell and Grime, 1981), temperature (Alexander and Wulff, 1985), and plant hormones (Gray and Thomas, 1982). These effects are especially large for juvenile characters such as seed size (Stanton, 1984, 1985; Mazer, 1987; Dolan, 1984), germination behavior (Cresswell and Grime, 1981; Quinn and Colosi, 1977), and seedling establishment (Schmitt and Antonovics, 1986).

The large number of studies documenting maternal effects in plants (see Roach and Wulff, 1987, for a recent review) leaves no question of their existence. However, their importance as a constraint to evolution is less certain. In particular, it is essential to know how long effects of the maternal environment persist in order to understand their effect on natural selection. If maternal effects disappear early in the life cycle, then they may decrease the rate of response to natural selection on juvenile characters but still allow evolution of adult

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characters. On the other hand, persistent maternal effects on fitness will limit selection on all characters, throughout the life cycle.

Competition among plants, and the hierarchies of plant size that often result (Harper, 1977; Rabinowitz, 1979; Weiner, 1985), may affect the persistence of maternal effects. Under competitive conditions, size hierarchies (skewed distributions of plant size, with a few large individuals) develop early and become more pronounced with time (Schmitt, Eccleston, and Erhardt, 1987). Small differences in seedling growth rate (perhaps due to maternal effects) may become amplified over time, and the few largest individuals will contribute a disproportionate number of offspring to the next generation (Cook and Lyons, 1983).

Here I report data from greenhouse experiments on the effects of maternal fertilizer treatments on seedling performance of *Erigeron annuus* (L.) Pers. (Asteraceae). I then examined the persistence of maternal effects in the offspring generation under controlled conditions (competitive and noncompetitive) to maximize my ability to detect effects of the maternal nutrient treatments. In addition, I followed replicate genotypes to measure temporal changes in the relative importance of genetic and maternal environmental contributions to seedling size.

Erigeron annuus is a native winter annual, common in early-successional environments throughout the eastern United States. It is a triploid species ($2n = 27$) and apomictic, reproducing solely by tiny (25 μg) wind-dispersed seeds. Each plant may produce 10,000–50,000 genetically identical seeds. Apomictic reproduction is useful for this study, since it allows the collection of identical seed families and testing for maternal environmental effects in the absence of genetic differences.

METHODS—*Parental generation*—Replicates of four genotypes of *Erigeron annuus* were grown in the greenhouse under high and low nutrient conditions. The four genotypes are electrophoretically distinct at one or more loci (Stratton, 1988) and were collected from a single population near Stony Brook, New York. The HIGH nutrient lines were grown in standard greenhouse soil (soil, peat, "Promix" mixture, pH 6.5) and fertilized monthly with 20 ml fertilizer ("Peter's Professional, High Nitro Special," 30-10-10 NPK, [N] = 530 ppm). Plants in the LOW nutrient treatment were grown in a 2:1 mixture of sterile sand and greenhouse soil and received fertilizer at half-strength. Genotypes and nutrient treatments were randomized within blocks (positions on the greenhouse bench) and plant positions were not rotated during the parental generation. Environmental variation within the greenhouse resulted in significant phenotypic variation among blocks. Plants nearest the south-facing windows were less shaded and wilted more often than plants in other blocks. I weighed a sample of 100–200 seeds from each maternal plant to determine the mean seed mass. Seeds were too small (21–35 μg) to weigh individually.

Offspring generation—Seeds and seedlings from both nutrient treatments were treated identically in the offspring generation. All seedlings were grown in standard greenhouse soil and fertilized biweekly as in the high nutrient treatment, above.

Experiment 1, no competition: In July 1986, seedlings from HIGH and LOW lines of the four genotypes were grown individually in 5 cm pots to measure maternal effects under noncompetitive conditions. I planted five seeds in each of the 112 pots in standard soil and recorded the time to emergence and percent germination of each. Two weeks after planting, I measured the cotyledon length and width and counted the number of true leaves on the two largest individuals in each pot. Fractional counts were used for partially expanded leaves. At this time I thinned the seedlings to one per pot, always leaving the largest seedling. I transplanted a seedling from an appropriate line into the sixteen pots that had no germination. At four weeks and eight weeks I again counted the number of leaves and measured the rosette diameter (average of two perpendicular measurements). After eight weeks I harvested the seedlings at ground level, dried them for 48 hr at 60 C and determined the aboveground biomass.

Experiment 2, with competition: In July 1987 I conducted a similar experiment using two genotypes (5, 8), each with five HIGH and five LOW maternal families and 21 replicates of each. Each 5-cm pot had one HIGH plant (i.e., one offspring from a HIGH parent) growing in competition with one LOW plant of the same genotype. Because significant greenhouse position effects were observed in the parental generation (Stratton, 1988), these lines were paired according to the greenhouse position of the parent plant (the paired HIGH and LOW parents were in the same block). The arrangement of the HIGH and LOW seedlings was randomized within pots and the pots were arranged on a greenhouse bench in a randomized block design. In this experiment differences in germination among genotypes and parental nutrient treatments were not tested: the seeds were germinated on moist filter paper and transplanted to pots at the cotyledon stage. All seedlings were at approximately equal stages of development at the start of the experiment. Two weeks after germination I measured the cotyledon length. Rosette diameter and number of leaves were recorded after two and five weeks. At eleven weeks I harvested the plants and measured the aboveground biomass as in experiment 1. Although the experiments were conducted in different years, they were both performed in the same greenhouse bay at the same time of year (July–September). Thus, the plants are likely to have experienced very similar light and temperature conditions and year effects are likely to be small relative to treatment effects.

Statistical analyses—Data from experiment 1 were analyzed by a two-way ANOVA with both genotype and nutrient treatment considered fixed effects. Percent germination was arcsine transformed prior to analysis. For experiment 2, genotype and maternal nutrient treatment were fixed effects in the ANOVA while maternal families within genotype and the associated interaction terms were considered random. I treated genotypes as fixed, thus precluding the estimation of genetic variation for these traits, because such population parameters cannot be accurately estimated from a sample of two genotypes. Genotype (the blocking factor) was tested over the families within genotype mean square. Families within genotype, treatment, and treatment × genotype were tested over the treatment × family within genotype interaction. I used SAS procedures GLM, REG, and UNIVARIATE for the statistical tests (SAS Institute, 1985).

RESULTS—Highly significant phenotypic differences among parental pants were generated by the fertilizer treatments. The mean seed mass was 24.6 μg in the low nutrient lines compared to 28.6 μg in the HIGH treatment (paired t test; $t = 2.51$; $P = 0.022$). The basal stem diameter of parent plants (a measure of plant size) also differed among treatments (3.12 mm in the LOW treatment vs. 4.04 mm in the HIGH treatment; paired t test; $t = 3.03$; $P = 0.008$). The phenotypic differences among parents resulted in differences in size among offspring, but the persistence of these maternal effects differed in the two experiments.

Experiment 1, no competition—Maternal effects attributable to fertilizer treatment were present early in the experiment, but disappeared by two months. Seedlings from the high nutrient families emerged earlier than seedlings from low nutrient families and had a higher percent germination (Table 1). In high nutrient families, cotyledons were significantly longer and after four weeks seedlings had significantly larger rosette diameters than those from low nutrient families of the identical genotype. At eight weeks, however, the difference in rosette diameter among nutrient treatments was no longer significant. The number of leaves followed a similar pattern: significant differences among nutrient treatments were present at two and four weeks but the treatments were indistinguishable at eight weeks. In contrast, genetic differences became more significant with time (Table 1). The significant maternal fertilizer effects masked any genetic differences at two and four weeks. By eight weeks the the fertilizer treatments were indistinguishable and the four genotypes differed in rosette diameter and number of leaves (but not for aboveground biomass). There was no genotype × treatment interaction for any character measured.

While holding genotype constant, maternal effects resulted in a highly significant correlation between parent size (basal stem diameter) and early seedling size (cotyledon length: $r = 0.29$, $P < 0.01$; diameter at two weeks: $r = 0.33$, $P < 0.01$). The maternal environmental correlations were not significant at later dates.

Experiment 2, with competition—When seedlings from HIGH and LOW treatments were grown in competition, maternal effects persisted throughout the experiment. Seedlings from high nutrient families had larger cotyledons, larger rosette diameters at two and five weeks, and greater aboveground biomass at eleven weeks (Fig. 1). Genetic differences were present early (cotyledon size, rosette diameter at two weeks) but disappeared as the differences between high and low nutrient lines became progressively greater (Table 2). There was again no evidence of a treatment × genotype interaction, indicating that the two treatments resulted in similar maternal effects among both genotypes.

The differences among replicate family-pairs within genotypes (Table 2) indicate persistent effects of parental position on the greenhouse bench, or some other unmeasured difference in the maternal environment, carried over into the offspring generation. Genotype 5 (Fig. 1, left) was particularly sensitive to this source of variation. The range of family means for genotype 5 was approximately twice that for genotype 8. This suggests genetic differences in the magnitude of maternal effects with respect

TABLE 1. *Mean seedling size characteristics of* Erigeron annuus *for offspring of four genotypes grown at two nutrient levels. The nutrient treatments were imposed on the parents; offspring were grown without competition and under high nutrient conditions. F statistics and error mean squares (MSE) are shown for the main effects in a two-way analysis of variance. The nutrient × genotype interaction was not significant for any character*

	Nutrient treatment		Genotype			
Character	High	Low	2	4	5	8
Percent germination	0.77	0.65	0.55	0.71	0.71	0.86
	$F_{[1,102]} = 4.66$*		$F_{[3,102]} = 2.22$		MSE = 0.149	
Days to germination	8.53	11.77	10.93	14.67	9.20	8.46
	$F_{[1,102]} = 8.59$**		$F_{[3,102]} = 4.35$**		MSE = 33.661	
Two weeks						
Cotyledon length	4.61	4.19	4.39	4.55	4.42	4.35
	$F_{[1,88]} = 7.28$**		$F_{[3,88]} = 0.12$		MSE = 0.574	
No. of leaves	1.15	0.76	0.91	0.82	0.97	1.17
	$F_{[1,88]} = 12.72$***		$F_{[3,88]} = 1.56$		MSE = 0.187	
Four weeks						
Rosette diameter	31.13	21.04	24.1	28.0	25.6	28.3
	$F_{[1,102]} = 15.66$***		$F_{[3,102]} = 0.36$		MSE = 208.14	
No. of leaves	1.48	0.76	0.89	1.21	1.19	0.98
	$F_{[1,102]} = 15.90$***		$F_{[3,102]} = 0.65$		MSE = 0.829	
Eight weeks						
Rosette diameter	69.11	65.37	79.3	70.0	61.3	76.3
	$F_{[1,102]} = 1.61$		$F_{[3,102]} = 3.49$*		MSE = 575.85	
No. of leaves	8.34	7.96	9.06	8.06	8.11	7.50
	$F_{[1,102]} = 0.09$		$F_{[3,102]} = 2.36$(*)		MSE = 2.870	
Dry mass	0.145	0.135	0.15	0.15	0.14	0.13
	$F_{[1,102]} = 0.10$		$F_{[3,102]} = 0.21$		MSE = 0.0118	

*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; (*) $P < 0.075$.

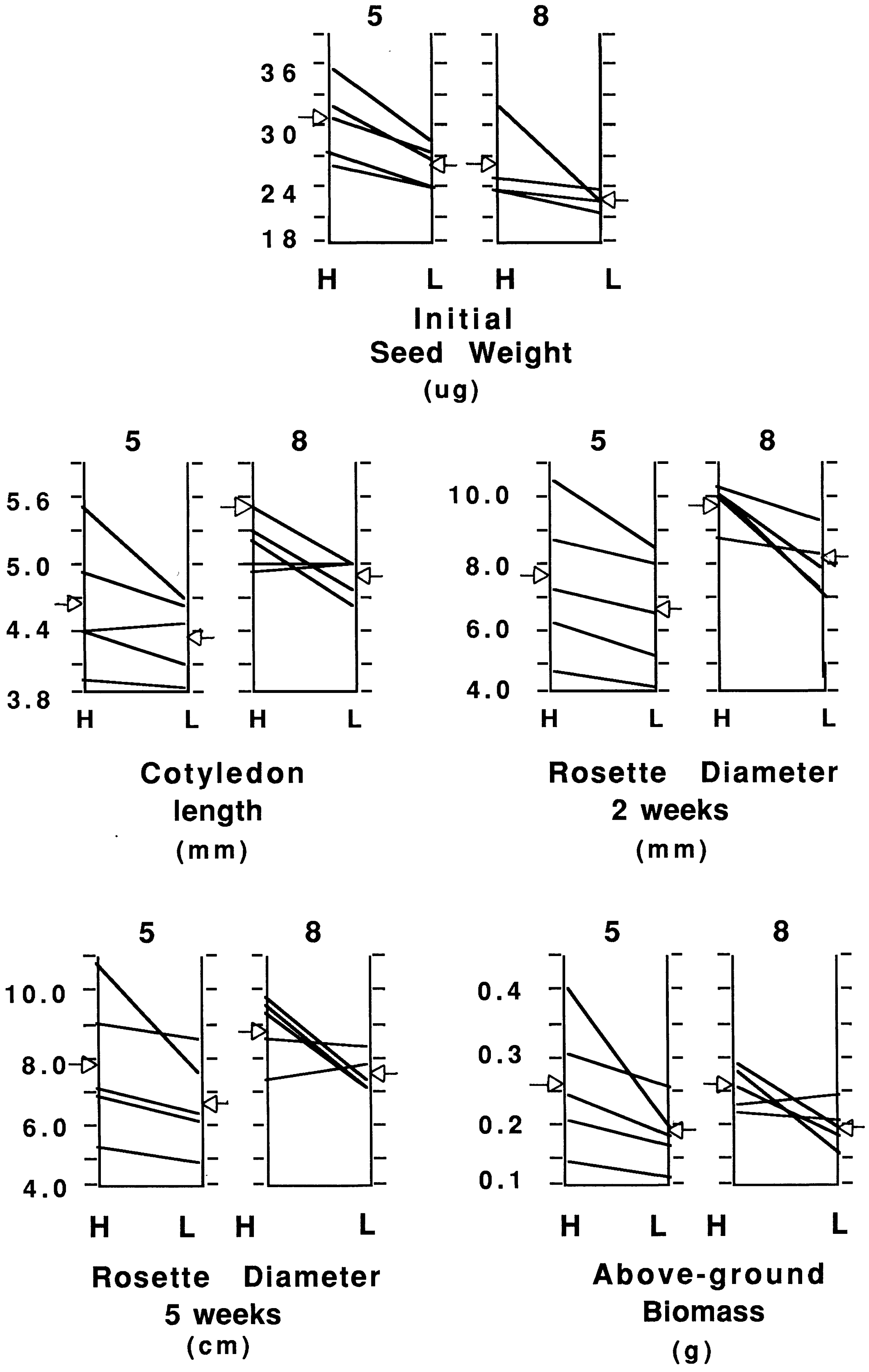
to environmental factors such as light and temperature that are likely to vary spatially within the greenhouse. Both light and temperature have been shown to affect offspring phenotypes in other species (Alexander and Wulff, 1985).

The replicate families responded differently to the parental nutrient treatments, shown by the significant treatment × family within genotype interactions (Table 2). The magnitude of the difference between high and low nutrient effects varied among families, creating a significant interaction, but the sign of the difference was relatively constant. Seedlings from the high nutrient treatment were consistently larger (Fig. 1). A *t* test for paired comparisons confirmed this, indicating that the HIGH seedlings were significantly larger ($P < 0.0001$) for all characters measured.

Figure 2 shows the changes in the relative magnitude of maternal effects over time. In experiment 1 (circles) the difference in seedling size measurements between HIGH and LOW plants decreased from 0.62 standard deviations in cotyledon size to less than 0.1 standard deviation difference in biomass after eight weeks. Under competitive conditions in experiment 2 (squares), the relative size advantage of seedlings from HIGH lines increased from 0.39 standard deviation in cotyledon length to a 0.55 standard deviation difference in final biomass.

Effects of seed mass—Within each genotype, mean seed mass differed among nutrient treatments and was strongly positively related to the seedling size characters. The effects of differences in seed mass within each genotype were statistically controlled by regressions of seedling characters on the mean initial seed mass. The regression residuals were then used in ANOVAs to test for residual effects of nutrient treatments independent of variation in seed size. In the ANOVA on regression residuals (analysis not shown) no residual effects of maternal nutrient treatment could be detected in any character, with or without competition ($P > 0.2$ in all tests). Thus, variation in seed mass may explain most of the observed differences between nutrient treatments for seedling size characters.

DISCUSSION—Increased maternal nutrition can result in a competitive advantage for seedlings. The differences in seedling size caused by maternal environmental effects quickly dis-


Initial Seed Weight (ug)

Cotyledon length (mm)

Rosette Diameter 2 weeks (mm)

Rosette Diameter 5 weeks (cm)

Above-ground Biomass (g)

TABLE 2. *Analysis of variance for seedling size characters when seedlings from HIGH and LOW nutrient parents are grown in competition. Levels of the ANOVA correspond to genotype (G), family (F) within genotype, parental nutrient treatment (T), and the associated interactions. Means for genotypes and nutrient treatments are shown in Fig. 1*

		Two weeks					
		Cotyledon size		Rosette diameter		No. of leaves	
Source	df	MS	F	MS	F	MS	F
G	1	31.47	5.59*	327.61	4.04(*)	4.00	0.57
F(G)	8	5.63	3.93*	81.01	7.55**	7.04	13.23***
T	1	11.58	8.10*	169.03	15.74**	8.92	17.07**
T × G	1	0.02	0.02	8.28	0.77	0.08	0.15
T × F(G)	8	1.43	3.07**	10.73	1.66	0.52	0.91
Error	414	0.46		6.46		0.58	

		Five weeks				Eleven weeks	
		Rosette diameter		No. of leaves		Aboveground dry weight[a]	
Source	df	MS	F	MS	F	MS	F
G	1	11,422	2.11	4.89	1.70	0.0120	0.12
F(G)	8	5,409	3.76*	2.87	2.44	0.1000	2.09
T	1	11,448	7.97*	4.14	3.53*	0.4124	8.63*
T × G	1	0.3	0.00	0.30	0.26	0.0001	0.00
T × F(G)	8	1,436	2.31*	1.17	1.66	0.0478	3.39***
Error	392	622		0.71		0.0141	

*** = $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; (*) $P < 0.075$.

[a] Error df = 386.

appear under noncompetitive conditions; however, when seeds from HIGH and LOW treatments are grown together, the initial size advantage of HIGH plants is maintained and even increases. In nature, establishment of *E. annuus* occurs under a wide range of seedling densities, but dense mats of seedlings are common in large populations during the early years of succession (personal observation). Thus the importance of maternal effects for lifetime fitness probably varies spatially and temporally within populations.

The smaller initial difference in seedling size in experiment 2 probably results from my controlling differences in germination time. By not allowing maternal differences in germination among treatments, I decreased the probability of observing persistent maternal effects. This is conservative with respect to conclusions regarding the effect of competition, since in experiment 1 the time to germination covaried positively with seed mass.

Parrish and Bazzaz (1985) found a significant effect of parental fertilizer treatment on seedling size in *Abutilon theophrasti* within large and small seed size classes, suggesting a direct effect of nutrient content on seedling growth rates independent of total seed mass. Measured differences in the nutrient content of the seeds supported their conclusion. I did not measure the nutrient content of *Erigeron annuus* seeds, but the large contribution of seed mass to the seedling size differences suggests that most of the effect can be attributed to seed size variation. Maternal environmental effects mediated through seed size variation are probably quite common.

Several studies of seed size variation have found similar effects of competition on the persistence of seed size effects. Black (1958) reported a competitive advantage of plants from large seeds, but only when large and small seeds were planted in mixture. Similarly, Dolan (1984), Gross (1984), and Stanton (1984) found no relationship between seed size and seedling size when plants were grown individually, but a positive correlation when grown at higher density or under competitive conditions. In the absence of competition, effects of seed size usually disappear after a few weeks (Schaal, 1984;

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Fig. 1. Norms of reaction for maternal environmental effects of parental nutrition on seedling size characters in *Erigeron annuus*. Each line connects the mean values for the paired high (H) and low (L) nutrient families within each genotype. Genotype 5 is on the left; genotype 8, on the right. The genotype and nutrient treatment means are indicated by arrows.

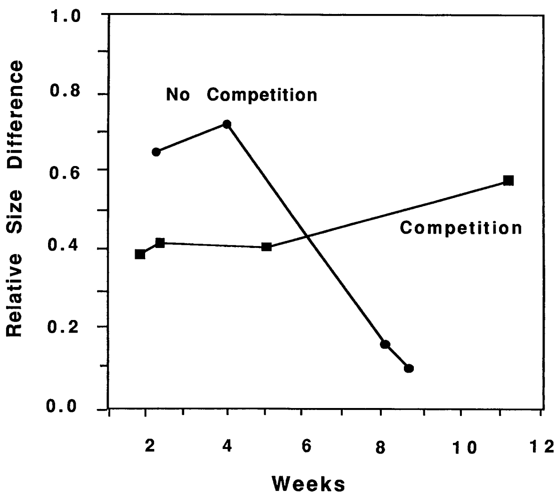

Fig. 2. Relative difference in seedling size [(HIGH − LOW)/std] of high and low nutrient families as a function of time since germination. The difference in size has been scaled in SD units so error bars are omitted. The circles show the relative size difference when seedlings are grown individually in pots; the squares, the difference in seedling size when HIGH and LOW seedlings are grown in competition.

Marshall, 1986; Kromer and Gross, 1987). Thus, the competitive environment seems to be uniformly important for the continued expression of maternal effects at later life stages.

In all of the above studies, genetic and maternal sources of seed size variation were partially confounded. Variation in seed size within families may in part be caused by genetic variation among siblings, such that offspring with advantageous gene combinations have both large seed size and large seedling size. If these phenotypes are the result of heterosis or epistatic interactions, the correlation between seed and seedling size could be genetically based, even in the absence of detectable heritability. Apomixis in *Erigeron annuus* allows me to use offspring with identical genotypes. Therefore, the observed differences among treatments reflect only environmental maternal effects.

Some ambiguity exists concerning the term maternal effects when applied to asexual plants. In apomicts, many sources of variation usually considered types of maternal effects, such as cytoplasmic factors or genetic differences in mothering ability, are completely confounded with nuclear genetic variation and hence unmeasureable. However, nongenetic effects of the maternal environment will operate exactly as they do in sexual species. Thus, it is still useful to identify this type of environmental effect as maternal, even in species where paternal effects are undefined.

Ultimately, the importance of maternal effects must be evaluated under field conditions using natural levels of variation in the maternal environment. In these experiments I tried to create large differences in the maternal environment through the fertilizer treatments. Nevertheless, the range of plant sizes was much smaller than that observed for these same genotypes under field conditions. The range of basal stem diameters was 2.7–5.0 mm in this experiment vs. 1.1–8.2 mm in the field (personal observation). If plant size is correlated with the ability to provision seeds, then the natural variation in maternal effects may be much greater than these experiments indicate. Significant maternal effects on seedling size were present among progeny of field-collected plants of *E. annuus* (Stratton, 1988).

The relative importance of genetic and maternal environmental contributions to the offspring phenotype changes over time, yielding changes in the potential response to natural selection. Any increase in the environmental variance resulting from maternal effects will decrease the correspondence between genotype and phenotype and thus reduce the expected response to selection. Under noncompetitive conditions, maternal effects are of primary importance in the earliest stages of the life cycle (i.e., seedling establishment). Influences of the maternal environment (coupled with large random variation in the microenvironment of seedlings) may significantly retard the evolution of seedling characters. However, the genetic control of later characters may be uninfluenced by maternal effects. Under competitive conditions when early size advantages persist as differences in lifetime fitness, maternal effects may reduce the response to selection in all characters. Finally, maternal effects can bias heritability estimates in several ways. The observed positive correlation between parent and offspring size within genetically identical families is one example of nongenetic correlations among relatives generated by maternal effects. In addition, these experiments imply that heritability estimates from noncompetitive greenhouse experiments or common gardens may be artificially inflated by the decreased importance of maternal effects (in addition to the lower variance in the physical environment). These results underscore the importance of evaluating the genetic variation for plant characters under a natural competitive regime.

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