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LIFE HISTORY VARIATION WITHIN POPULATIONS OF AN ASEXUAL PLANT, ERIGERON ANNUUS (ASTERACEAE)[1]

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Genetic variation was measured for several morphological and life history characters in *Erigeron annuus,* a triploid and obligately apomictic species. There was significant genetic variation for nearly all characters measured, including plant size, growth rate, time of flowering, biomass allocation to roots and shoots, seed weight, and germination response to temperature. Variance among genotypes accounted for up to 55% of the total phenotypic variance, well within the range of heritabilities observed for sexual species. These estimates of broad-sense heritability predict substantial short-term response to selection on life history characters in this asexual species.

In obligately asexual species it is often assumed that lack of genetic variation is the primary limiting factor for evolution. Apomicts have been classically regarded as unable to adapt to a changing environment (Williams, 1975) and hence considered evolutionary "blind alleys" (Darlington, 1939). Selection quickly erodes genetic variation in asexual populations as superior genotypes are rapidly fixed (Crow and Kimura, 1965). Because the genome is effectively a single linkage group, genetic variation at unselected loci will also decline at the same rate. However, this same efficiency of selection may allow rapid and precise matching of genotypes to particular microsites, provided that sufficient standing genetic variation exists within the population.

It has recently become clear that most populations of apomictic (= agamospermous) plants are polymorphic with respect to variation at enzyme loci (reviewed by Ellstrand and Roose, 1987). In *Erigeron annuus,* Hancock and Wilson (1976) found a total of 17 genotypes in three populations using three electrophoretic loci. *Taraxacum* species (which are also triploid and apomictic) have been well studied and have similarly high numbers of coexisting genotypes within populations (Lyman and Ellstrand, 1984; Ford and Richards, 1985; Mogie, 1985; reviewed by Richards, 1986). Thus, available data show that multiclonal populations are the rule rather than the exception in obligately asexual species.

Less is known about the quantitative genetics of morphological and life history characters in apomictic species (but see Solbrig and Simpson, 1974; Ford, 1981) and the potential response to selection on these traits. Questions of whether asexual species consist of widespread, general purpose genotypes or consist of a variety of locally adapted clones (Lynch, 1984; Bierzychudek, 1985, 1989; Michaels and Bazzaz, 1990) implicitly assume sufficient genetic variation exists to allow life history evolution.

Erigeron annuus is a common early-successional weed in old fields and other disturbed habitats throughout eastern North America. It is native to North America but is now cosmopolitan in distribution (Cronquist, 1947). *E. annuus* is a winter annual, germinating in August and flowering during the summer of the following year. Occasional individuals will reproduce as biennials or short-lived perennials. It is triploid ($3n = 27$) and apomictic, forming embryos through meiotic diplospory (McDonald, 1927; Gustafsson, 1946; Fagerlind, 1947). *E. annuus* reproduces only by seed; each plant may produce 10,000 to 100,000 genetically identical seeds in a season.

MATERIALS AND METHODS

Seedling size and biomass allocation — Twenty-two families of genetically identical seeds were collected from a single population near Stony Brook, New York. These were assigned to ten multi-locus genotypes, based on variation at four polymorphic enzyme loci

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(Stratton, 1988). Four common genotypes were represented by three replicate families, three genotypes were represented twice, and there was only a single family for three rare genotypes. Plants were grown in the greenhouse in standard soil (soil, peat, "promix" mixture; pH 6.5) and fertilized monthly. Ten replicates of each family were arranged in a randomized blocks design, and plants were not rotated during the experiment.

Seeds were planted in November 1985 and thinned after emergence to three seedlings per 10-cm pot. After 2 wk, seedling size (measured as the number of true leaves) was recorded and all seedlings except the largest were removed. At 2 and 3 mo I recorded the rosette diameter, number of leaves, and the length, width, and petiole length of the largest leaf. The date of bolting was recorded weekly from March to May, and the basal stem diameter was measured on mature individuals in midsummer.

The above- and below-ground biomass of seedlings was measured in a separate experiment using a subset of six genotypes. In this and all other experiments, the three replicate families of each genotype were all genetically identical by descent from a common, electrophoretically distinct grandparent. Seedlings were grown in the greenhouse in an artificial soil ("Turface") and harvested after 60 d. Leaves and roots were rinsed free of soil and dried at 60 C for 48 hr before weighing.

Mean seed mass was determined for ten genotypes by weighing lots of 50–300 seeds to the nearest 0.1 mg. Genotypes were represented by 2–12 independent seed families, again identical by descent from a common grandparent.

Seed germination—The germination response to temperature was measured for six genotypes using four replicate lines of each. Plants were grown in a common environment for one generation prior to testing the germination response. Fifty seeds (all from disk florets) of each family were placed on moist sand and incubated in constant-temperature, illuminated growth chambers at 10, 15, 19, and 30 C. Seeds were censused daily for 21 d. Germination was defined as the appearance of cotyledons.

Data analysis—Maximum likelihood estimates of variance components were calculated using SAS Institute (1985) procedure VARCOMP. Significance of the variance components was determined by a random effects model analysis of variance (SAS Institute, 1985, procedure GLM). Percent germination was arcsine-transformed prior to analysis. Rosette diameter, leaf length and width, and petiole length were log-transformed, which yielded a normal distribution of residuals. Broad-sense heritabilities are defined as the proportion of total phenotypic variation attributable to genotype (Vg/Vp). For comparison with field data, the genetic coefficient of variation (CV_g) was defined as the square root of the genetic variance divided by the mean.

RESULTS

Seedling size and biomass allocation—There was significant variation among genotypes in the expression of nearly all seedling characters (Table 1). Genetic variation in plant size was present at 2 wk and persisted throughout the experiment. For plants that flowered, there were significant differences among genotypes for the average date bolting was initiated, but not for adult stem diameter. There were also highly significant genetic effects on the probability of flowering during the first season ($\chi^2 = 136.8$, $P < 0.001$). The variance among clones (broad-sense heritability) accounts for 33% of the variance in size at 2 wk, 36%–50% at 2 mo, and 0%–18% at 3 mo (Table 1). Variance among families within genotypes was generally much lower (mean = 7%) but still significant.

Genotypes differed significantly in dry weight at 2 mo and in the relative biomass allocation to roots and shoots (Table 2). Differences among families within genotypes (maternal environmental effects) were significant for root and shoot mass but not for the relative biomass allocation. The genetic component of variance for root and shoot biomass ranged from 20% to 40% and was always stronger than the effects of the maternal environment.

Mean seed mass varied significantly among the ten genotypes tested ($F = 9.29$; df = 9,49; $P < 0.001$). There was a 60% difference in mean seed mass between the smallest-seeded genotype and the largest (24 μg vs. 37 μg; Fig. 1), which corresponded to a broad-sense heritability of 0.55.

Germination—The average germination of *E. annuus* achenes was highest in the 19 C treatment (64%; Fig. 2). Mean germination was 35% at 30 C and was less than 10% at 10 and 15 C. There was no main effect of genotype on percent germination, nor were there significant differences among maternal families within genotypes (Table 3). However, the genotype × temperature interaction was highly significant, indicating that genotypes responded differently to the temperature treatments. The genotype

TABLE 1. *Maximum likelihood estimates of variance components (×100) for life history characters in the greenhouse. The broad-sense heritability (h^2) and genetic coefficient of variation (CV_g) are defined in the text. Significance levels are for the corresponding terms in a random effects ANOVA*[a]

		Variance components (×100)					
Character	df =	Blocks 9	Genotype 9	Family (genotype) 12	Error 172	h^2	CV_g
2 wk:							
Leaf number		0.45*	5.13***	0.57	9.19	0.33	22.26
2 mo:							
Leaf number		40.65***	165.76**	0	259.58	0.36	12.96
Rosette diameter		0.08	7.55**	2.34***	8.79	0.40	6.55
Leaf length		2.86	8.16***	1.25***	8.22	0.40	7.72
Leaf width		0.06*	4.89***	0.41*	4.39	0.50	7.78
Petiole length		0.79	12.43***	1.62*	13.13	0.44	13.03
3 mo:							
Leaf number		482**	1,345	1,070*	6,264	0.15	15.39
Rosette diameter		0.28*	0	0.90**	4.38	0	0
Leaf length		0.45**	0.64	0.48*	4.56	0.10	3.46
Leaf width		1.14***	0.95*	0.39*	4.84	0.13	7.51
Petiole length		1.59***	3.06**	0.74	11.18	0.18	15.12
Adults	df =	9	8	11	84		
Bolting date		0	365.3*	123.2	806.3	0.28	13.80
Stem diameter		0	0	0.35*	2.87	0	0

[a] *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$.

× temperature interaction accounted for 36% of the total variance in percent germination. Much of this effect was due to the inclusion of genotype 4, which had the lowest percent germination below 30 C and had the highest percent germination at 30 C (Fig. 2). If that genotype is omitted, the genetic main effect becomes highly significant ($h^2 = 0.21$) in addition to a significant but small genotype × temperature interaction (Table 3).

The mean time to germination decreased linearly with temperature, from 11.8 (± 1.6) days at 10 C to 5.4 (± 3.1) days at 30 C. Again, genotypes differed significantly in the mean time to germination (Table 3). The genotype × temperature interaction was significant but small, explaining only 3% of the variation in germination time, and there was no effect of maternal environment (families within genotype).

DISCUSSION

Significant variation among genotypes was observed for most morphological and life history characters. The estimates of broad-sense heritability ranged as high as 0.55 and are well within the range of heritabilities observed for sexual plants and animals (e.g., Venable, 1984; Mousseau and Roff, 1987). The low heritabilities for plant size at 3 mo were unexpected, given the large variation among genotypes at 2 mo. This may partly result from limitations in growth imposed by the 4″ pots, allowing small plants to "catch up" with larger ones. Alternatively, if genotypes had been grown in competition, the initial differences in growth may have persisted longer (Stratton, 1989). Stem diameter is highly correlated with seed production ($r = 0.80$; unpublished data), and low levels of genetic variation are often found in characters closely related to fitness (Mousseau and Roff, 1987).

These estimates of broad-sense heritability are free of maternal environmental effects, but they include an unknown combination of additive, dominance, and maternal genetic components. Nevertheless, broad sense heritabil-

TABLE 2. *Biomass allocation to roots and shoots of 2-mo-old seedlings. Shown are variance components with significance levels from the corresponding ANOVA*[a]

	Blocks df = 6	Genotype df = 5	Family (genotype) df = 12	Error df = 90	h^2	Mean
Leaf mass	0	3,292.0**	1,698.8***	3,231.5	0.40	155.03
Root mass	18.19	170.82*	138.60***	295.00	0.27	42.94
Root/shoot ratio (×1,000)	1.056***	1.064**	0	2.664	0.22	282.3

[a] * = $P < 0.05$; ** = $P < 0.001$; *** = $P < 0.0001$.

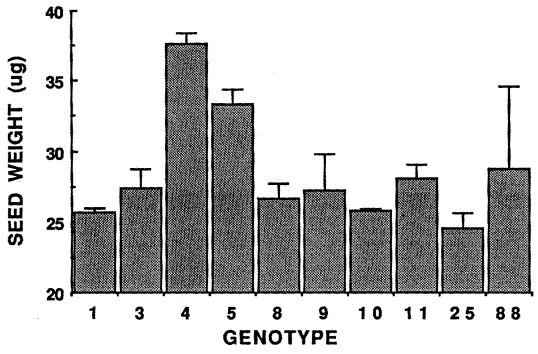

Fig. 1. Mean seed weight (μg) for ten genotypes of *Erigeron annuus*. Error bars show one standard error. Only two replicate seed families were measured for genotype 88.

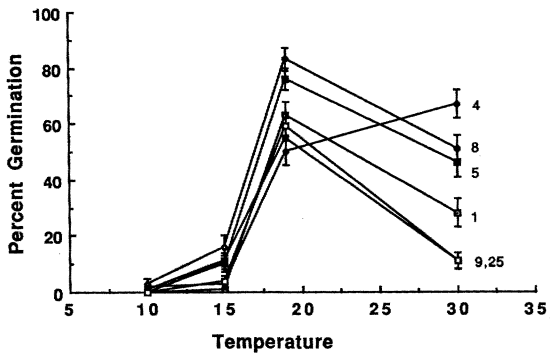

Fig. 2. Percent germination (± 1 SE) as a function of temperature. The genotype × temperature interaction is highly significant (see text).

ities are the appropriate measures for predicting the evolutionary response to selection in obligate apomicts, because genotypes are faithfully transmitted across generations.

More serious problems arise when one tries to apply greenhouse heritability estimates to field data. The greenhouse heritabilities for seedling size are an order of magnitude larger than field estimates of heritability for the same characters (< 0.1; unpublished data), a result of the much reduced environmental variation in the greenhouse. However, if the genetic variance is scaled by the mean instead of by the environmental variance, to produce a genetic coefficient of variation, the estimates of genetic variance are congruent in both environments. For example, the genetic coefficient of variation for rosette diameter at 2 mo was 6.55, compared to 5.2 within natural field sites (unpublished data). Thus the actual means and variance components are more useful than the heritabilities when comparing genetic variation in widely different environments.

The variation among replicate families in the first experiment represents a combination of maternal environmental effects and cryptic genetic variation undetected by electrophoresis. In contrast, the significant effect of families within genotypes for biomass, where replicate lines were identical by descent, can be unambiguously attributed to maternal environmental effects. Maternal effects on biomass were significant even when the parents had been grown under "uniform" greenhouse conditions. The presence of cryptic genetic variation among families would cause the true genetic differences to be underestimated. Thus, estimates of genetic variance components and associated statistical tests are conservative with respect to this source of error.

Sources of variation—Rare sexual reproduction may help maintain variation in some "apomictic" species, as has been observed in several species of *Taraxacum* (Richards, 1970). However, sexual reproduction has never been documented in *E. annuus*. Microsporogenesis in *Erigeron annuus* produces gametes of varying chromosome numbers (Oka, 1935; Bergman, 1944; Mehra et al., 1965), some of which may be fertile. Enzymatic tests for isocitrate dehydrogenase (IDH) activity show 10%–15% viable pollen (personal observation). Diploid and tetraploid variants have been observed in the closely related apomict, *E. strigosus* (Nesom, 1978), and genetic variation may be augmented by rare hybridization events. Even a very low frequency of sexual reproduction (on the order of mutation rate) may have a profound effect on the maintenance of genetic variation (Lynch and Gabriel, 1983).

The mechanism of apomixis in *Erigeron annuus* (meiotic diplospory) may allow limited intragenomic recombination. In general this will not affect the zygotic genotype, but it can generate variation when there is intralocus crossing over or if cis-acting position effects are important. Nevertheless, the potential for recombination is limited in *E. annuus* since chromosomal pairing during meiosis is only partial and no chiasmata are present (Gustafsson, 1946; Fagerlind, 1947).

Potential for life history evolution—Morphological variation among clones in asexual species has long been observed (e.g., Babcock and Stebbins, 1938; Turesson, 1943). The recognition of more than 2,000 *Taraxacum* microspecies (Richards, 1972) is evidence of the degree of morphological variation possible in asexual species. Greenhouse heritabilities for morphological traits in *E. annuus* (0.1–0.5) are similar to those of sexual species. The observed

TABLE 3. *Percent germination and days to germination of* Erigeron annuus *genotypes at four temperatures. Percent germination was arcsine-transformed. Seeds within petri dishes were treated as independent observations of germination time (results are qualitatively similar when petri dish means are used). Seeds that did not germinate during the course of this study were not included. Temperature was considered a fixed effect and all others were random effects*[a]

	Temperature	Genotype	Family (genotype)	Temperature × genotype	Error
Percent germination					
df	3	5	18	15	54
Mean square	4.033***	0.147	0.018	0.090**	0.026
Variance	—	0.004	0	0.016	0.026
Variance (without #4)	—	0.008**	0	0.006	0.025
Days to germination					
df	3	5	18	15	623
Mean square	306.04***	51.05**	10.23	16.76*	8.77
Variance	—	1.385	0.055	0.377	8.766

[a] * = $P < 0.05$; ** = $P < 0.001$; *** = $P < 0.0001$.

levels of variation indicate that populations of this apomict are genetically diverse and that the short-term response to selection is not likely to be limited relative to sexual species. While obligate apomixis may be an evolutionary "blind alley" to the extent that higher taxa have not evolved from apomictic lineages (Grant, 1981), microevolution is comparatively unhindered. Thus, it is reasonable to expect genetic differentiation among *Erigeron* populations and adaptations to local conditions.

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