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Evolution, Vol. 48, No. 3 (Jun., 1994), 828-841.

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QUANTITATIVE GENETICS OF SEQUENTIAL LIFE-HISTORY AND JUVENILE TRAITS IN THE PARTIALLY SELFING PERENNIAL, *AQUILEGIA CAERULEA*

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Abstract.—We determined the genetic basis of several traits related to overall fitness of *Aquilegia caerulea*, a perennial herb of the Rocky Mountains in western North America. To obtain measures of heritability relevant to the evolutionary potential of wild populations, we performed full and partial diallel crosses and studied progeny performance in the field. Based on a joint analysis of two designs with a total of 18 parents and 102 crosses, we detected significant maternal variance for seed mass and emergence time, but this component was negligible for later-expressed traits. Low heritability and evidence that maternal effects on seed mass are largely environmental suggest that in this population there is little evolutionary potential for change in seed mass under conditions experienced during the study. Seed mass varied depending on particular combinations of parents and cross direction. Such an interaction can have several different biological interpretations, including that particular maternal parents selectively provision embryos sired by particular pollen genotypes. Width of the first true leaf after 4 wk of growth and leaf size of juvenile plants at years one and two were significantly heritable and positively genetically correlated. Juvenile survival exhibited significant dominance variance, as expected from evidence of inbreeding depression in this trait. In contrast, for other traits that exhibit inbreeding depression in this population (seed mass and third-year leaf size), dominance variance was negligible.

Key words.—*Aquilegia caerulea*, diallel, inbreeding depression, juvenile traits, maternal effects, quantitative genetics, seed mass.

Received November 2, 1992. Accepted September 7, 1993.

Evolutionary change depends on genetic variability, on selection, and on the mating system (Fisher 1941; Falconer 1989). Inference of the potential for evolutionary response in natural populations, therefore, depends on information concerning each of these aspects, but methodological and practical difficulties challenge efforts to characterize them. Whereas recent field studies and theoretical advances have greatly enhanced our understanding of selection (e.g., Campbell 1989; Simms and Rausher 1989; Weis and Gorman 1990; for review, see Endler 1986) and mating systems (e.g., Ritland and Ganders 1987; Schoen and Brown 1991; Willis 1995), field studies concerning the genetic basis of quantitative traits in natural populations (e.g., Roach 1986; Mazer 1987; Simms and Rausher 1989; Biere, 1991a; Schwaegerle and Levin 1991) have accumulated more slowly.

As part of a larger investigation of the evolu-

tionary potential of a natural population of *Aquilegia caerulea* James, we here estimate the components of phenotypic variance for several traits of probable ecological importance. Populations of this species in western Colorado exhibit much phenotypic variation in both vegetative and reproductive traits. For example, Miller (1978, 1981) found phenotypic variation in flower color that correlates with pollinator distributions and seed production. Brunet (1990, pers. comm. 1991–1992) observed substantial variation in the degree of protandry, pistil, ovule, and stamen numbers that may influence variation in outcrossing rate. Seed mass and emergence time are also variable (Montalvo 1991, 1992), and many studies of other species have found fitness consequences to variation in these traits (for reviews, see Winn 1988; Mazer 1989; Stamp 1990; Schmitt et al. 1992). Estimating the evolutionary potential of such variation requires quantitative genetic analysis. Here, we evaluate the heritability and genetic correlations of seed and early life-history traits, including seed mass, germination success, emergence time, initial leaf width, yearly leaf size, and survival. Estimates of additional components of variance are also ob-

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tained, and their implications for phenotypic evolution are presented.

A second objective of this study is to examine the variance components thought to be involved in inbreeding depression. Each of the traits investigated influences lifetime fitness, and most show inbreeding depression (Montalvo 1994). Although it is well-known that many wild plants routinely undergo inbreeding and express inbreeding depression (Charlesworth and Charlesworth 1987; Holtsford and Ellstrand 1990), very few studies have related empirical estimates of genetic variance of specific traits to information concerning the mating system and observations of inbreeding depression (e.g., Mitchell-Olds and Bergelson 1990; Biere 1991a,b). Theoretical work suggests that inbreeding depression is attributable largely to the occurrence of selectively disadvantageous homozygotes at frequencies higher than expected under random mating (Crow and Kimura 1970; Falconer 1989; Lande and Schemske 1985; Charlesworth et al. 1990). It follows that dominance variance is expected for traits that exhibit inbreeding depression. In principle, epistasis involving dominance effects can also contribute (Bulmer 1980; Lynch 1991); however, empirical work on wild (Willis 1993) and crop species (reviewed in Hallauer and Miranda 1981; Jinks and Lawrence 1983; Charlesworth and Charlesworth 1987) suggested that the contribution of epistasis is minor. To further elucidate the genetic basis of inbreeding depression in the study population, we examine the hypothetical link between dominance variance and previously documented inbreeding depression.

Our objectives demand realistic estimates of variance components. Experiments conducted under natural conditions avoid potentially substantial biases in estimates of variance components that are known to be environmentally dependent (Falconer 1989; Roach and Wulff 1987). They therefore provide estimates of components of variance that are realistic and hence most relevant to inference of potential for evolution in the reference population. In the study reported here, we measured progeny traits on individuals raised in their natural habitat. A second feature of our experiment that has not been incorporated in previous designs is the natural maternal environment. This can strongly influence seed traits and emergence patterns (Roach and Wulff 1987). By making all crosses on plants in the wild, seed maturation occurred under natural conditions. This practice is especially important in realisti-

cally partitioning variation of seed traits. In addition, we used diallel designs to avoid confounding maternal variance with either dominance or additive genetic variance (as occurs in nested sib analyses). This feature is especially valuable in quantifying dominance variance in relation to inbreeding depression and also in any study of traits expressed early in the life cycle in which maternal effects are likely to be large.

Data analysis is often problematic in field studies, particularly those involving complex designs, because of missing data resulting from cross failure or mortality. Standard methods of analysis do not readily accommodate the usually unbalanced data (Searle 1971; Shaw 1987). We use a restricted maximum-likelihood (REML) approach (Shaw 1987) to analyze our data. One advantage of this approach is that it readily permits the use of all available data, even when the design is not balanced. With this combination of diallel design, natural environment, and REML analysis, we consider our partitioning of the genetic basis of quantitative traits in nature unusually accurate.

MATERIALS AND METHODS

Study System

Aquilegia caerulea is a self-fertile, perennial herb that grows throughout the southern and central Rocky Mountains between elevations of 2100–3700 m (Miller 1981). Our study population is near the Rocky Mountain Biological Laboratory (RMBL) in western Colorado. Within the large protandrous flowers, five white to bluish-purple sepals alternate with five white, long-spurred petals. Many spirally arranged stamens mature sequentially over 3–4 d, followed by receptivity of the usually six to eight separate pistils, each of which is distinct from the tip of the stigma to the base of the ovary. Stigmas are receptive for 3 d, and each pistil produces an average of 37 ovules. Plants at our study site average 6.4 inflorescences and 3.4 flowers per inflorescence (Montalvo 1992). Selfing can occur by transfer of pollen to stigmas of simultaneously open flowers (Miller 1978) and occasionally by transfer within the same flower when self-pollen survives through to stigma receptivity (Montalvo pers. obs.). An intermediate outcrossing rate ($t = 0.403 \pm 0.048$ SE) in a nearby population in 1987 (J. Brunet pers. comm. 1993), is evidence of mixed mating. Montalvo (1992) estimated an

inbreeding coefficient (F) of 0.153 ± 0.077 (mean, SE) for the study population.

Breeding Designs

A natural population 6.5 km north of the RMBL in Colorado was chosen as the source of parental plants. Twenty individuals within an $18 \text{ m} \times 20 \text{ m}$ area were caged to exclude floral visitors. These plants were randomly chosen from the subset of the population having at least six inflorescences, flowering synchronously, and for the purpose of another study (Montalvo 1992), consisting of distinguishable allozyme genotypes. We used 18 of these plants in two reciprocal breeding designs (D1 and D4, fig 1). Other experiments, D2 and D3, were used to measure inbreeding depression and pollen-tube growth and are presented elsewhere (Montalvo 1992, 1994). We used reciprocal mating designs because they allow unusually thorough partitioning of phenotypic variance (see below).

Pollination procedures were identical for both designs. We protected stigmas from self pollen by covering the gynoecium with 3-cm lengths of plastic straws folded at the distal end and by removing anthers prior to pollination. Before pollinating flowers, we marked each individual ovary of the multiple pistils with color codes representing pollen-donor treatment and separated stigmas in the same flower with strips of paper placed between pistils. Multiple pistils permitted six different pollination treatments to occur in each experimental flower, a practice that reduces the number of flowers and variation caused by flower position. We harvested fruits 5–6 wk after pollination.

Design 1 (Six Parents).—On July 2, 1987, we performed a complete 6×6 diallel in which each individual served both as a pollen donor and ovule parent (fig. 1). For each individual, six pistils within each of four to five flowers received pollen from one each of the six possible donors. On July 7, we pollinated an additional two to five flowers in the same manner. This design produced progeny from both self- and outcross pollination, allowing both an inbreeding depression analysis (Montalvo 1992, 1994) and a quantitative genetic analysis (this study) on the same outcrossed progeny. However, we do not include progeny resulting from selfing (self-sibs) in quantitative genetic analyses of the present study because analytical models accommodating inbreeding include components that are not estimable from our design.

Design 4 (12 Parents without Selves).—Twelve individuals, all different from those in D1, were crossed in a reciprocal factorial (partial diallel) design in which every individual served as both a pollen and ovule parent (fig. 1). This modification of the full diallel provides as complete a partitioning of phenotypic variance and has the additional advantage of permitting increased sampling of parents from the reference population for a given number of crosses planned (Cockerham 1963). On July 3, individuals 1–6 served as ovule parents, receiving pollen from individuals 7–12, and on July 7, individuals 7–12 served as ovule parents, receiving pollen from individuals 1–6. Usually, five flowers per ovule parent received all six pollen treatments, each on a different pistil.

Planting Designs and Traits for Progeny Performance

We planted seeds from D1 and D4 (108 crosses combined) in both the field and greenhouse. Seeds from each maternal parent were taken from flowers pollinated on a single day to minimize seed mass differences among flowers. Offspring were measured from emergence (June–September) in 1988 through late August 1990 (Montalvo 1991). Measures included seed mass, germination success (represented conservatively by emergence of cotyledons), emergence time, leaf width of largest true leaf (not cotyledons) after the first 4 wk (greenhouse) or 6 wk (field) of growth (herein initial leaf width) as an index of initial leaf expansion rate, width of largest leaf at the end of each summer, and survival to August 1990. In 4-yr-old field-grown plants, leaf width is correlated with whole plant dry weight ($r = 0.80$; $P < 0.01$; Montalvo 1994), and is used as an indicator of plant size.

Field-Sown Seeds.—We randomly selected 24 seeds from each of the 108 crosses and assigned one seed for each cross to random positions in each of 24 grids. Each grid had 12×12 cells with all crosses reported here—plus an additional 36 crosses from related studies (Montalvo 1991)—represented once. We planted seeds in September 1987 in a natural meadow at RMBL about 6.5 km from the parental population. Before planting, we clipped the natural vegetation to facilitate placement of planting templates. Each seed was planted 2–3 mm deep in the center of a cell, leaving 5 cm between seeds. We fenced the plot to exclude gophers and grazers. No wild columbine seedlings occurred within the plot,

DESIGN 1		♀						DESIGN 4		♀											
		13	14	15	16	17	18			1	2	3	4	5	6	7	8	9	10	11	12
♂	13	O	X	X	X	X	X	1							X	X	X	X	X	X	
	14	X	O	X	X	X	X	2							X	X	X	X	X	X	
	15	X	X	O	X	X	X	3							X	X	X	X	X	X	
	16	X	X	X	O	X	X	4							X	X	X	X	X	X	
	17	X	X	X	X	O	X	5							X	X	X	X	X	X	
	18	X	X	X	X	X	O	6							X	X	X	X	X	X	
								7	X	X	X	X	X	X							
								8	X	X	X	X	X	X							
								9	X	X	X	X	X	X							
								10	X	X	X	X	X	X							
								11	X	X	X	X	X	X							
								12	X	X	X	X	X	X							

FIG. 1. Breeding designs used for quantitative genetic analyses. Parents were renumbered from original identification numbers (Montalvo 1991, 1992) to 1–18 for convenience. Outcrossed matings, X; selfed matings, O. Genetic analyses used only X matings.

and flowers from adults within 5 m were removed to prevent seed dispersal into the plot. Seeds overwintered under natural conditions before germinating the following summer. For data analysis, we grouped the 24 field grids into four blocks, each containing six original, contiguous grids and an average of 157 outcrossed seedlings (range 138–173; D1 and D4 combined).

Greenhouse-Sown Seeds.—We stratified seeds remaining after field plantings in an airtight container at 4°C for 4 mo. We then randomly selected a total of 10 seeds from two flowers for each of the 108 crosses represented in the field sowings. Seeds were individually weighed and randomly assigned to 10 planting grids consisting of partitioned flats, with each cross represented once per grid. On March 19, 1988, in a greenhouse at the University of California, Riverside (UCR), we planted seeds about 2 mm deep into the partitioned flats, one seed per cell, in a mixture of “UC soil mix #3” (peatmoss and plaster sand in 3:4 ratio plus nutrients), vermiculite, and perlite (1:2:2).

We placed five grids of flats on each of two greenhouse benches and rotated flats within benches every other day. The two greenhouse benches were used as blocks in the analyses of traits measured in the greenhouse. Plants were watered as needed. We recorded emergence daily and fertilized with half strength Hoagland’s on the fifth and thirty-third d following emergence.

One week after the last greenhouse emergence, we transported flats to RMBL (June 10–12, 1988) and maintained them in a greenhouse there at ambient temperatures for 11 wk. On August 28, we transplanted progeny into the gopher-exclu-

sion plot at 1-dm intervals in a grid pattern forming 10, 1-m-wide blocks. We watered plants to decrease transplant shock and censused them 10 d after transplanting and at the end of the subsequent two summers (1989 and 1990).

The Model

Cockerham and Weir (1977) developed the “bio” model for reciprocal breeding designs in which the total phenotypic variance, V_P , is partitioned into six components. Using an equivalent parameterization in terms of “causal” components (Falconer 1989; table 1), we estimated the following components of V_P , where

$$V_P = V_a + V_d + V_{pat} + V_{mat} + V_k + V_e.$$

V_a is the additive genetic variance, V_d is dominance variance, V_{pat} and V_{mat} , respectively, are the variances caused by paternal and maternal effects apart from the nuclear contributions to progeny phenotype, V_k is variance caused by interactions between parental contributions to progeny phenotype apart from the interaction of nuclear genetic effects (V_d), and V_e is environmental variance. With this partitioning, the relative importance of all major variance components, excluding epistasis and genotype × environment interaction, can be determined.

Although the components V_k and V_{pat} have received little attention in the past, they may be of considerable biological importance. Following the definition above, V_k can arise, for example, from an interaction between nuclear genes of one parent and cytoplasmic genes of the other, or between cytoplasmic genes contributed from each parent (Cockerham and Weir 1977). In principle,

TABLE 1. Translation between observed components of variance and causal components of variance for the bio model of Cockerham and Weir (1977). Subscript codes: k, higher order interaction (see text); m, maternal; n, nuclear; p, paternal; t, nuclear specific interaction; w, within full sibs. Abbreviations: CA, combining ability. Reciprocal general combining ability involves a difference between σ_m^2 and σ_p^2 .

Source	Observational variance components	Causal variance components
General CA	σ_n^2	$\frac{1}{4} V_a$
Paternal effect	σ_p^2	V_{pat}
Maternal effect	σ_m^2	V_{mat}
Specific CA	σ_t^2	$\frac{1}{4} V_d$
Reciprocal Specific CA	σ_k^2	V_k
Error	σ_w^2	$\frac{1}{2} V_a + \frac{3}{4} V_d + V_e$

this component could also arise by interaction between environmentally induced maternal effects and pollen genotype, but because it is difficult to adduce mechanisms for such a phenomenon, it may be unlikely (Shaw and Waser 1994). For seed traits, V_k can also arise from a maternal-offspring interaction in which either the individual maternal plants differentially provision seeds sired by particular paternal parents, or progeny of paternal plants vary in ability to sequester nutrients from different maternal plants (Schwaegerle and Levin 1990; Bieri 1991b). By analogy with maternal effects, the presence of paternal effects, V_{pat} , in seed and seedling traits may indicate that environmental effects on pollen donors can affect vigor and character expression in progeny. In those species capable of inheriting plastids from microgametophytes, extranuclear genetic effects are also possible (Chiu and Sears 1993 and references therein).

Data Analysis

For completely balanced designs, estimation of the components of the bio model can be accomplished using modified quadratic ANOVA (Cockerham and Weir 1977). For unbalanced data, a restricted maximum-likelihood (REML) approach for estimation and testing of the six components of variance and their covariances has been developed (Shaw 1987; Shaw and Shaw 1992). We ran all analyses on a Cray Y-MP8/864.

Greenhouse and field-sown progeny were analyzed separately. We examined data for normality and transformed variates as required. Transformations were seed mass², log(emergence week + 0.05) for field emergence time, and log(emergence day) for greenhouse emergence time. To test for block effects, we used the likelihood-ratio test (Shaw 1987) comparing likeli-

hoods from models with and without blocks. Because block effects were significant in exploratory runs, we included blocks in all other models.

For each trait, we first obtained estimates for the full model involving six components of variance. Components estimated as negative were constrained to zero in subsequent analyses. Constrained analyses are conservative, in the sense that they reduce the expected estimates of heritability (h^2) and the power of the test of V_a when h^2 is low (Shaw 1987). We used likelihood-ratio tests to test whether each positive variance component differed significantly from zero, and whether the unconstrained model differed significantly from the constrained model (Shaw 1987). In these tests, twice the difference between the likelihoods of two models under comparison is asymptotically distributed as χ^2 with n degrees of freedom, where n is the difference in number of parameters between the two models being compared.

We analyzed D1 and D4 together to increase the number of parents ($N = 18$) and progeny sample size ($N = 1010$, table 2). Combined data represent a single reference population because all plants grew within 18 m of one another, and crosses were done using the same methods under the same conditions. Separate analyses of D4 were required in the log-linear and covariance analyses described below. For comparative purposes, we also ran REML analyses on the two breeding designs separately.

We also estimated components of covariance between those metric traits having nonzero components of variance using REML and likelihood-ratio tests. We calculated component correlations, including additive genetic correlations (r_a), as $\text{Cov}_{xy}/(\text{var}_x \text{var}_y)^{1/2}$ (Falconer 1989). Because Cray CPU time was too limited to do a joint analysis of D1 and D4, we conducted our co-

TABLE 2. Sample sizes for models reported in table 3. Number of progeny decreased over time primarily because of mortality. Missing observations account for the difference in sample size between initial leaf width and leaf width at year 1 for field-sown progeny.

Trait	Greenhouse sown			Field sown		
	D1	D4	D1 + 4	D1	D4	D1 + 4
Seed mass	300	710	1010	—	—	—
Emergence time	199	502	703	192	436	628
Initial leaf width	199	500	697	139	320	459
Leaf width at year 1	199	496	695	155	353	507
Leaf width at year 2	193	463	653	84	208	292
Leaf width at year 3	186	437	623	52	127	179
No. of seeds planted	300	710	1010	720	1728	2448

variance analysis on D4, the largest of the two designs.

Our measures of survival and germination success are categorical (discrete) measures that are not appropriate for the usual quantitative genetic analysis. We analyzed these traits using multiway log-linear models for categorical data with BMDP procedure 4F (Dixon 1983) and a program by L. Nunney. Tests of partial association were used. Small sample sizes for separate designs and field-sown seedlings surviving to August 1990 precluded separate analysis of germination and survival. Instead, we analyzed a composite variable representing whether a seed resulted in a live seedling after 3 yr. This fitness component is a multiplicative function of the proportion of seeds that produced seedlings and the proportion of emerged seedlings that survived to year 3. Only D4 had the factorial design structure necessary for analysis with a log-linear model.

In the log-linear models, class variables included two sets of parents in which set A refers to individuals 1–6, and set B refers to individuals 7–12 (fig. 1). A third class variable (*D*) was the direction of each cross in which set A parents served as sires and set B as dams in one direction, and set B as sires and A as dams in the other direction. The resulting model effects are closely related to the observational variance components of the bio model listed in table 1. Differences among set A or B parents reflect variation in general combining ability (i.e., differences among parents in their contribution to progeny phenotype, regardless of its basis). The effect of cross direction (*D*) corresponds to differences in overall survival between the two cross directions. The set A × set B interaction reflects the specific combining ability, that is, variation caused by specific combinations of parents (i.e., dominance

variance). Finally, A × D and B × D interactions reflect variation among parents (within set A or set B, respectively) in their effects on progeny survival dependent on whether they serve as maternal or paternal parent (reciprocal general combining ability), and the three-way interaction (A × B × D) reflects variation in the effects of particular combinations of parents depending on cross direction (analogous to V_k or reciprocal specific combining ability) and/or other unexplained variation. When significant interactions involving cross direction occurred, we performed the analysis on each cross direction singly to explore whether maternal or paternal effects, or both, were responsible. This analysis provides tests of these effects for discrete traits but does not yield a partitioning of variance as is available with continuous traits.

RESULTS

Variances of Quantitative Traits

Seed Mass.—Variance in seed mass was largely attributable to environmental and maternal effects. In the joint analysis of D1 and D4 (fig. 2), V_{mat} explained a large and highly significant percentage (37%) of V_p , with lesser contributions of V_a (3.6%, $P > 0.1$) and V_k (2.8%, $P < 0.025$). In the separate analysis of D4, V_{mat} was significant at 44% of the total phenotypic variance, whereas V_k was significant at 4.1% (fig. 3, table 3). V_e was large for both analyses, approaching 50% of V_p . Results from the joint analysis of D1 and D4 (fig. 2) were largely consistent with those from D4 along (fig. 3) possibly because of the larger sample size of D4 (table 2). Results for seed mass and other traits from D1 (fig. 3) frequently differed from results of both the joint analysis with D4 and the separate analysis of D4, presumably because of the few parents in D1.

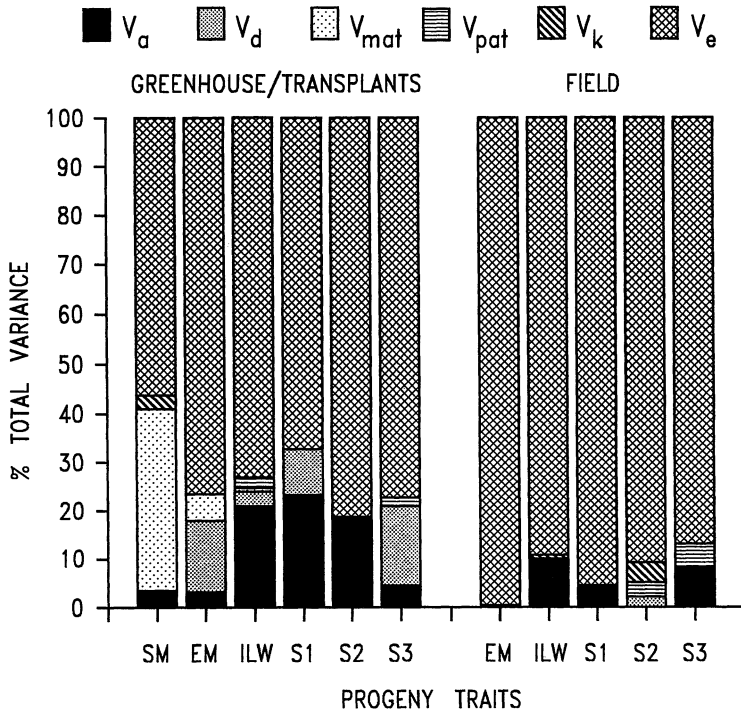


FIG. 2. Relative proportion of six causal components of variance out of total phenotypic variance comparing traits measured on greenhouse-sown progeny and transplants versus field-sown progeny. Results are for the joint analysis of D1 and D4. Abbreviations: SM = seed mass; EM, emergence time; ILW, initial leaf width; and S1–S3, year 1 to year 3 leaf size, respectively.

Given the low statistical power of D1, separate analysis of D1 will not be discussed further.

Postgermination Traits and Greenhouse-Sown Progeny.—Considering D1 and D4 jointly (fig. 2), the variance components of greatest relative magnitude (apart from V_e) were V_a for initial leaf width and leaf width at years 1 and 2 ($h^2 = 21\%$, 23%, 19%, respectively). These substantial estimates of h^2 imply evolutionary potential for these traits. In addition, V_{mat} for emergence time contributed a highly significant 5.5% of V_p , but V_{mat} did not contribute significantly to any later expressed trait. Results were similar for individual analysis of D4 (table 3, fig. 3).

Leaf width at year 3 was the only metric trait with consistently large V_a . In the joint analysis of D1 and D4, V_d was large and marginally significant at 16% of V_p .

Postgermination Traits and Field-Sown Progeny.—Similar numbers of progeny emerged in the greenhouse and field, but greenhouse transplants enjoyed high survivorship ($\geq 93\%$ per year) relative to field-sown progeny ($< 59\%$ per year). As a result, statistical power for analysis of field-

sown progeny was severely diminished, especially for separate analyses of D1 and D4 (table 2). Initial leaf width had appreciable and significant V_a in combined D1 and D4 data. For remaining traits, V_e tended to dominate, often accounting for more than 80% of the total phenotype variance. In separate analysis of D4, heritability in the broad sense (tested by simultaneously constraining V_a and V_d) was 18.7% ($\chi^2 = 5.14$, $P < 0.025$) for initial leaf width, 11.7% ($\chi^2 = 3.69$, $P < 0.1$) for leaf width at year 1, and 12.1% and 6.0% for leaf width at years 2 and 3, respectively (both nonsignificant).

Variance Component Correlations

Only greenhouse-sown progeny from D4 provided nonzero variance terms required for calculation of genetic correlations. Four pairs of metric traits presented above were analyzed (table 4).

The genetic correlation (r_a) and maternal correlation (r_m) between seed mass and emergence time differed in sign, but neither correlation was significant. Initial leaf width showed large posi-

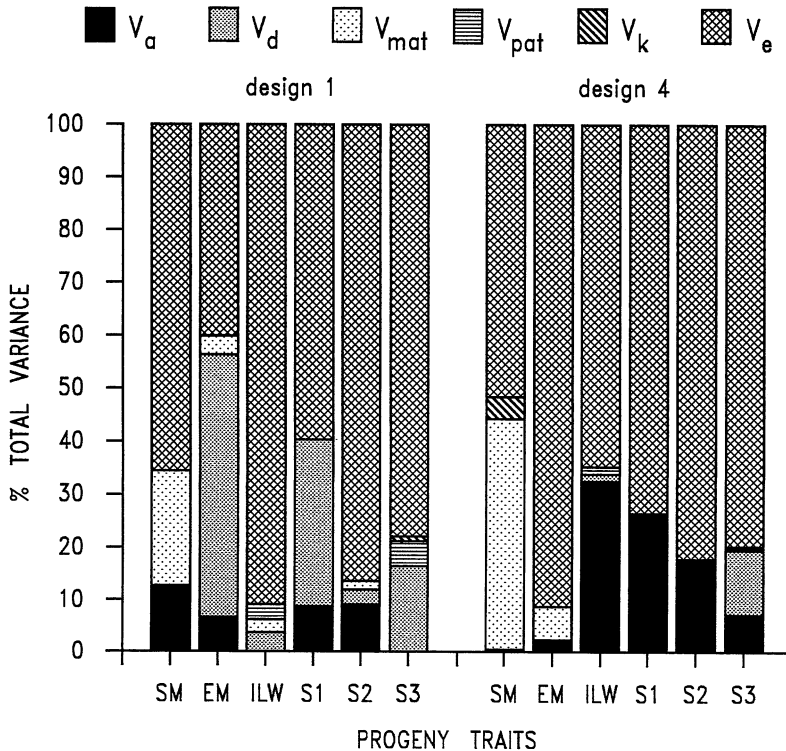


FIG. 3. Relative proportion of six causal components of variance out of total phenotypic variance for traits measured on greenhouse-sown progeny and their transplants. Results are for separate analyses of D1 and D4. Abbreviations are as in figure 2.

tive r_a with leaf width at years 1 ($P < 0.005$), 2 ($P < 0.01$), and 3 ($P < 0.025$). Conversely, the environmental covariance between initial leaf width and these successive leaf size characters was small, nonsignificant, and varied in sign. The dominance correlations (r_d) for initial leaf width and year-1 leaf width, and for initial leaf width and year-3 leaf width were also nonsignificant. Phenotypic correlations were significant and similar to r_a for initial leaf width with leaf width at years 1 and 2 (table 4).

Germination Success and Survivorship

Log-linear analyses of D4 progeny germination/survival showed evidence for significant levels of dominance genetic variance as well as extranuclear parental effects (table 5). The set A \times set B interaction was marginally significant ($P = 0.055$) for field-sown progeny and significant ($P = 0.030$) for transplants, implying the presence of V_d . The remaining two-way interactions (A \times D, B \times D) were significant for transplants only, indicating that, under these conditions, the effect of certain parents on progeny performance

depended on whether they were used as sires or dams (reciprocal general combining ability). Moreover, the three-way interaction (A \times B \times D) was close to significant for transplants suggesting variation in reciprocal specific combining ability (analogous to V_k). Because significant interactions cloud interpretation of lower-order effects, we conducted separate analyses of the two cross directions. These showed greater variation among maternal parents in group B than in group A ($P < 0.005$; $0.1 > P > 0.05$, respectively), whereas effects of sire were not significant in either case. These results indicate that variation among parents in their individual effects on progeny survival is caused primarily by maternal extranuclear effects.

DISCUSSION

We examined the quantitative genetics of life-history and juvenile traits in a natural population using methods capable of producing estimates of additive genetic variance unconfounded with dominance or parental variance components. Others have also used diallel breeding designs

TABLE 3. Variance components for life-history and juvenile traits calculated using Restricted Maximum Likelihood (REML) (Shaw 1987). Zeros indicate components constrained to preserve nonnegative estimates. V_e is not tested for significance. See table 2 for sample sizes.

Trait	Variance components					
	V_e	V_a	V_d	V_{mat}	V_{pat}	V_k
Greenhouse-sown progeny and their transplants						
Design 4						
Seed mass	822.01	7.42	0	696.59***	0	64.94***
Emergence time	7.22	0.18	0	0.51***	0	0
Initial leaf width	5.91	2.98***	0.12	0	0.12	0
Leaf width year 1	23.84	8.52***	0.07	0	0	0
Leaf width year 2	82.16	17.77***	0	0	0	0
Leaf width year 3	33.31	2.99	5.28	0	0.08	0
Designs 1 and 4 joint analysis						
Seed mass	866.16	54.99	0	577.21***	0	43.23*
Emergence time	6.11	0.27	1.17+	0.44***	0	0-
Initial leaf width	6.31	1.81***	0.27	0.04	0.19	0
Leaf width year 1	19.32	6.65***	2.72	0	0	0
Leaf width year 2	85.33	19.56***	0.09	0	0	0
Leaf width year 3	31.44	1.82	6.61+	0	0.74	0

* $P < 0.05$; *** $P < 0.001$.

and analytical models of Cockerham and Weir (1977) in studies of wild plants (Antonovics and Schmitt 1986; Simms and Rausher 1989; Schwaegerle and Levin 1990; Wolff 1990; Biere 1991a,b; Shaw and Platenkamp 1993), but few grew progeny in the field (Schmitt and Antonovics 1986; Simms and Rausher 1989; Biere 1991a; Schwaegerle and Levin 1991), and all performed crosses under artificial conditions.

It is exceedingly difficult to perform large reciprocal crossing designs in the field. Our results

underscore the benefit of using Restricted Maximum Likelihood (REML) to perform joint analyses of relatively small experiments from natural populations. By performing a joint analysis of D1 and D4, which together had 18 parents and 102 parental crosses, we increased the precision of statistics representing the source population.

Variation of Quantitative Traits

We found that most variation in seed mass was caused by large and significant V_{mat} . Our

TABLE 4. Significance tests for covariances (Cov_{xy}) of variance components for pairs of traits (x and y) and their correlations (r) from design 4 (12 parents). Only pairs of traits with nonzero variances could be considered. The P values for χ^2 with 1 df denote whether the covariance terms are significantly different from zero. Correlations larger than 1 or less than -1 are reported as 1 and -1, respectively. Phenotypic correlations for each pair of traits are reported following component correlations for each pair.

Component	Trait x	Trait y	χ^2	P	r
V_a	seed mass	emergence time	0.20	>0.5	-1
V_{mat}	seed mass	emergence time	0.07	>0.1	0.32
Pearson's $r = -0.01$; $P = 0.842$; $N = 502$					
V_a	initial leaf width	leaf width year 1	20.861	<0.005	1
V_d	initial leaf width	leaf width year 1	1.008	>0.1	1
V_e	initial leaf width	leaf width year 1	0.074	>0.5	0.04
Pearson's $r = 0.44$; $P = 0.000$; $N = 496$					
V_a	initial leaf width	leaf width year 2	7.848	<0.01	0.89
V_e	initial leaf width	leaf width year 2	3.311	$0.05 < P < 0.1$	-0.16
Pearson's $r = 0.13$; $P = 0.006$; $N = 463$					
V_a	initial leaf width	leaf width year 3	6.36	<0.025	2
V_d	initial leaf width	leaf width year 3	2.17	>0.1	-1
V_e	initial leaf width	leaf width year 3	0.82	>0.1	0.12
Pearson's $r = 0.06$; $P = 0.178$; $N = 435$					

TABLE 5. Tests of partial association from a hierarchical log-linear analysis on the emergence and survival of seedlings in D4. This fitness component is a multiplicative function of the proportion of seeds producing seedlings, and the proportion of seedlings surviving to year 3. Model effects are sometimes written as an interaction with the response variable, here the composite fitness component (S). For example, the set A effect would be indicated as set A \times S. Set A, parents 1–6; set B, parents 7–12; D, cross direction.

Effects	Field sown			Greenhouse sown		
	df	G	P	df	G	P
Set A	5	10.59	0.060	5	3.37	0.643
Set B	5	7.19	0.207	5	41.76	0.000
D	1	0.20	0.656	1	22.77	0.000
Set A \times set B	27	39.67	0.055	25	39.93	0.030
Set A \times D	5	2.34	0.800	5	12.51	0.028
Set B \times D	5	4.81	0.439	5	12.85	0.025
Set A \times set B \times D	23	17.92	0.762	24	33.60	0.092

results on quantitative variation in seed mass can be compared with three other studies on wild species that used the bio model of Cockerham and Weir (1977). The same pattern of high V_{mat} and low V_{a} was observed for *Anthoxanthum odoratum* (Antonovics and Schmitt 1986), *Phlox drummondii* (Schwaegerle and Levin 1990), and *Lychnis flos-cuculi* (Biere 1991b). In addition to strong maternal effects, we also found significant V_{k} for seed mass in D4 and combined D1 and D4 (4% and 3% of V_{p} , respectively). Likewise, in *P. drummondii* and *L. flos-cuculi*, a small but significant proportion of total phenotypic variance was caused by V_{k} (reported as reciprocal specific effects in *Phlox*).

It is not possible here to distinguish among the different causes of V_{k} , but its frequent finding warrants further study of its biological implications. Among the most interesting of its possible causes is maternal-offspring interaction (Schwaegerle and Levin 1990; Biere 1991b). Such interaction indicates the potential for sexual selection via either maternal choice or competition among embryos sired by particular pollen genotypes. Regardless of the mechanisms underlying these parental interactions, they, like dominance effects, could provide the basis for inbreeding depression, if the reciprocal specific effects correlate with relatedness among parents.

We detected no V_{a} in seed mass, even though the trait had been shown to have significant inbreeding depression (Montalvo 1991, 1992). Similarly, neither *P. drummondii* nor *L. flos-cuculi*, species that respectively suffer higher abortion rates for selfed relative to outcrossed seeds (Levin 1984) and inbreeding depression in seed mass (Biere 1991b), showed significant V_{a} . The pattern for self-compatible species of no V_{a} , high V_{mat} , and significant V_{k} also occurs in *Nemophila*

menziesii (R. G. Shaw and G. A. J. Platenkamp, unpubl data). However, the self-incompatible *A. odoratum* did have large and significant V_{a} (Antonovics and Schmitt 1986).

The influence of maternal effects on seed-size evolution depends on whether the effects are predominantly genetic or environmental (Roach and Wulff 1987; Kirkpatrick and Lande 1989). In analyses of seed mass, incorporating flower replicate as a nested effect within maternal parent resulted in greatly reduced V_{mat} . This result indicates that variance among flowers explains a large proportion of V_{mat} , implying a large environmental component. This finding is consistent with the documented effect of flower position and age on energy allocation to seeds (Brunet 1990). If V_{mat} is mostly environmental, then it could slow response of seed mass to selection.

For traits expressed subsequent to seed germination, the generally larger sample size of greenhouse-sown progeny and their transplants provided more powerful hypothesis testing than with field-sown plants (table 2). Emergence time showed a small significant V_{mat} in D4 and a highly significant V_{mat} in the joint analysis of D1 and D4. The observation of V_{mat} in emergence time is consistent with several studies showing that factors such as flower position and environmental conditions during seed development can influence seed germination (Roach and Wulff 1987), although data of Biere (1991b) suggest that maternal environment can have less influence than maternal genotype on germination rate.

Although joint analysis of emergence time in D1 and D4 showed a marginally significant V_{a} , emergence time shows no inbreeding depression. Though V_{a} is generally expected for traits that show inbreeding depression (here seed mass, leaf width, and survival), the reverse is not neces-

sarily the case. Inbreeding depression occurs when, on average, dominance deviations are in the direction of increased fitness (Falconer 1989).

The significant heritability ($> 20\%$) for initial leaf width of seedlings and leaf width of transplants at years 1 and 2 (D4 and D1 + D4) indicates potential for evolutionary response to selection on these traits. Because initial leaf width represents the amount that the first leaf expanded over the first 4 wk of growth, the significant positive additive genetic covariance between initial leaf width and leaf width in all years, indicates that selection affecting size will likely affect expansion rate (or vice versa). For both environments, Montalvo (1991, 1994) showed that emergence time affected initial leaf width which in turn was phenotypically correlated with year-3 leaf size. In the field, emergence time was also significantly correlated with year-3 leaf size. Conversely, in the greenhouse emergence time did not affect size, perhaps because of the lack of competitive interactions.

Many previous studies have shown that maternal effects decrease with age of progeny (for review see Roach and Wulff 1987). In a study capable of distinguishing nuclear genetic and maternal effects, Biere (1991b) found strong maternal effects for seed mass through to postgermination size of seedlings, but not for size at 4 wk. Similarly, our data show diminishing importance of maternal effects from seed size through year-3 leaf size, a correlate of plant size. Together, these findings suggest that the frequently observed differences in emergence patterns and juvenile traits among maternal sibships are often caused primarily by maternal rather than additive or dominance effects. If maternal effects in such instances are determined largely by environment rather than genotype, then an evolutionary response to selection on juvenile traits is expected to be slow. Furthermore, the lack of significant r_m for seed mass and emergence time suggests that selection of maternal families for one trait would have little influence on the other, even if maternal effects were largely genetic.

Germination Success and Survival

The presence of significant dominance variance for the successful emergence and survival of seedlings to year 3 is consistent with the large inbreeding depression measured in both field-sown progeny and greenhouse-sown transplants. In work reported elsewhere (Montalvo 1994), average inbreeding depression measured for this

component was substantial for D1 and another experiment (D2) not reported here (D1: 0.252 and 0.395; D2: 0.625 and 0.353, field-sown progeny and transplants, respectively). The significant maternal effects (corroborated by significant dam effects in the log-linear analyses of data from one of the two cross directions) indicate the potential for selection among maternal lines if this V_{mat} is genetically based.

Dominance and Inbreeding Depression

As noted earlier, theory suggests that most inbreeding depression depends on directional dominance (Crow and Kimura 1970; Falconer 1989). Significant V_d was expected for the traits previously shown to exhibit significant inbreeding depression (Montalvo 1991), including seed mass, germination success, survival, and leaf size. This expectation is consistent only with results of the log-linear analysis of germination/survival (table 5). Weaker support was obtained for leaf width at year 3 (table 3).

Several factors may have caused weak V_d for most traits measured in this study. First, germination success and survival accounted for nearly 90% of the total inbreeding depression detected by Montalvo (1994). Consequently, detecting dominance variance may be more difficult in traits of survivors. Moreover, the power of statistical tests used to compare means of traits is higher than that for tests of nonzero variance components. Similarly, Mitchell-Olds and Bergelson (1990) failed to detect significant broad-sense heritabilities for several traits showing inbreeding depression, presumably because of low statistical power. Second, if the inbreeding depression is caused by elevated homozygosity of rare deleterious alleles, the probability of creating homozygotes for such alleles in the outcrossed progeny of D1 and D4 is very small. Self-sibs used in the inbreeding-depression analysis would be much more likely to be homozygous for such alleles. Third, if the assumptions of the quantitative genetic models are violated (see Cockerham and Weir 1977; Hinkelmann 1977; Mitchell-Olds and Rutledge 1986; Mitchell-Olds and Bergelson 1990), then detection of significant V_d in metric traits can be compromised. However, most violations of the "bio model" would inflate rather than underestimate V_d . For example, failure to account for inbreeding or epistasis would inflate estimates of V_d . However, inbreeding depression resulting from possible

relatedness among some parents could bias genetic variances in unpredictable directions.

Although inbreeding depression is expected to be small in populations of self-compatible, regularly inbreeding species such as *Aquilegia caerulea* (Lande and Schemske 1985; Mitchell-Olds and Rutledge 1986; but see Charlesworth and Charlesworth 1987), it is commonly found in such populations (Kohn and Barrett 1991; Johnston 1992; Ågren and Schemske 1993). This finding complicates predictions about the evolution of affected traits (Wright and Cockerham 1985), particularly those that influence mating systems. For example, simulation studies by de Boer and van Arendonk (1992) showed that when inbreeding was ignored, significantly biased estimates of additive and dominance effects occurred after selection. In sum, although V_d and inbreeding depression are theoretically linked, empirical estimates of these parameters may not, in practice, be concordant until use of models that incorporate inbreeding depression and different levels of relatedness (e.g., Wright and Cockerham 1985) is practical.

Despite these caveats, our quantitative genetic study of life-history and juvenile traits in *A. caerulea* is among the most relevant to a natural population to date. Our results of maternal variation in seed mass and emergence time, together with the large environmental component for all traits examined, underscore the importance of doing crosses under natural conditions and growing progeny in their native environment when the focus is to determine the potential for traits to undergo natural selection.

ACKNOWLEDGMENTS

D. Campbell, N. Ellstrand, C. Galen, L. Nunney, D. Reznick, N. Waser, and A. Weir provided valuable discussion, encouragement, and comments on the manuscript. We thank J. Ackerman, D. Noble, and L. Meer for field assistance, anonymous reviewers for comments on the manuscript, G. Platenkamp for suggesting the log-linear analysis, and F. Shaw for Restricted Maximum Likelihood (REML) program development funded by the National Science Foundation (BSR-8905808) to N. Waser, M. Price, and R. Shaw. CPU time on the Cray Y-MP8/864 was granted by the San Diego Supercomputer Center. This study was funded by a National Science Foundation Dissertation Improvement grant (BSR-8700870), the University of California, Riverside (U.C.R.) Chancellor's

Patent Fund, a U.C.R. I. M. Newell Graduate Research Award, a Sigma Xi Grant-in-Aid, and H. Barclay and L. Synder Memorial grants from the RMBL awarded to the senior author who was supported by a Ford Foundation Dissertation Fellowship and U.C.R. Graduate Council Pre-doctoral Research Fellowship.

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