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QUANTITATIVE GENETICS OF SIZE, SHAPE, LIFE-HISTORY, AND
FRUIT CHARACTERISTICS OF THE SEED-HETEROMORPHIC
COMPOSITE *HETEROSPERMA PINNATUM*.
I. VARIATION WITHIN AND AMONG POPULATIONS

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Abstract.—We document phenotypic and genetic variation within and among populations of the seed heteromorphic species *Heterosperma pinnatum* Cav. (Compositae) in the production of seed morphs and in a variety of life-history and morphological characteristics that might be correlated with seed and head traits. Each trait is found to have significant genetic variance in most or, usually, all populations. Significant among-population genetic variation exists for all traits except number of achenes per head and seedling shape, although some traits have much less genetic variation among than within populations. Number and percentage of intermediate achenes per head, total number of achenes per head, and lengths of central and peripheral achenes had little among-population genetic variation compared to within-population variation. Most traits had slightly less genetic variation among than within populations; however, some traits (percentage of central achenes, length of awns, date that the first flowering head opened, date that the first fruiting head opened, and death date) had more among-population genetic variation. The proportions of achene morphs produced had high broad-sense heritabilities and high among-population genetic variance, except in the case of intermediate achenes. All phenological variables had high among-population genetic variation. Within-population heritabilities were high for dates of first flowering head and fruiting head but low for death date and reproductive interval.

Family and population means measured in the greenhouse for traits having high broad-sense heritability or among-population genetic variance were closely correlated with field means for the corresponding families or populations. The amounts of phenotypic variation were similar for traits that were measured in both the field and the greenhouse. These lines of evidence suggest that greenhouse results provide reasonable estimates of genetic variation in the field for this species.

Numerous studies have reported variation in the proportion of seed morphs for different heteromorphic-seeded species and have discussed adaptive scenarios for the evolution of seed proportions; however, our investigation is one of only a few that have documented the amount of phenotypic and genetic variation within and among populations.

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Many of the ecological consequences of seed heteromorphisms are now known, and plausible adaptive scenarios "explaining" the evolution of such heteromorphisms have been constructed. Seed heteromorphism most likely represents a form of bet-hedging in the face of environments that may vary in time (Stebbins, 1974; Harper, 1977; Venable, 1985*b*) or space (Schoen and Lloyd, 1984). Life-history models have confirmed that temporal or spatial environmental variation affecting the relative demographic success of seed morphs can, in theory, maintain seed heteromorphisms (Schoen and Lloyd, 1984; Venable, 1985*b*). Indeed, seed heteromorphisms are frequently found in highly variable environments such as in dis-

turbed habitats (Harper, 1977) and arid and semiarid habitats (van der Pijl, 1972; Ellner and Shmida, 1981, 1984). Functional differences among seed morphs are necessary for the existence of temporal or spatial variation in their relative success. Seed morphs may differ in dispersal (Wilson, 1976; Baker and O'Dowd, 1982; Venable and Levin, 1985*a*), dormancy (McDonough, 1975; Baker and O'Dowd, 1982; Venable and Levin, 1985*a*), competitive performance (Flint and Palmblad, 1978; Weiss, 1980; Venable, 1985*a*), or survival and fecundity schedules (Cheplick and Quinn, 1982; Venable and Levin, 1985*b*).

We have embarked on a project to measure natural selection on seed proportions

and other correlated traits and to quantify their genetic variation within and among natural populations of the seed heteromorphic composite *Heterosperma pinnatum*. In this paper, we document quantitative-genetic variation in the production of seed morphs in *Heterosperma pinnatum*. Since traits do not always evolve independently, we have also documented quantitative-genetic variation in a variety of other characters that might have genetic or phenotypic correlations with seed proportions. The genetic correlations among these traits will be presented elsewhere. The documentation of genetic variation and covariation among traits is an important first step in investigating natural selection and its consequences.

Heterosperma pinnatum is a good species to use in such an investigation because there is considerable within- and among-population phenotypic variation in seed-morph proportions and because the dormancy and dispersal biology have been investigated (Venable et al., 1987). Since achene morphs do not have a one-to-one correspondence to ray and disk florets, as occurs in most other achene-heteromorphic Compositae, evolutionary changes in achene proportions are not necessarily accompanied by changes in floral proportions. This allows us to investigate the evolution of seed biology with less worry that the phenomena under investigation represent correlated responses to selection on floral biology.

MATERIALS AND METHODS

Heterosperma pinnatum is an herbaceous summer annual found from southwest Texas west to Arizona and south to Honduras. It produces achenes (single-seeded, dry-walled fruits), which vary in morphology from the periphery to the center of each head. We have grouped achenes into three types for experimental convenience. Central achenes are long, very narrow, possess a beak, have little or no wing, and are usually 5–15 times as long as they are wide. Peripheral achenes are short, wide-winged, concave, and usually at least half as long as wide. Intermediate achenes include a range of morphologies intermediate between the peripheral and central types. Aspects of its seed ecology, life cycle, and demography are

described and the achenes are illustrated in Venable et al. (1987).

We investigated the breeding system of *Heterosperma pinnatum* using three heads from each of 30 plants from several central Mexican populations grown in the greenhouse. Emasculation of heads was effected by removing the hermaphroditic disc florets before pollen release (it is impractical to remove anthers from the tiny individual disc florets before pollen release). The remaining 2–4 ray florets are male-sterile; thus, the head is “emasculated.” Twenty-seven heads (each from a different plant) were manipulated in this fashion and bagged without further treatment. Twenty-three heads (each from a different plant) with hermaphroditic florets removed were crossed with pollen from two or more other plants, and 30 heads were bagged without manipulation and left to self-pollinate.

One mature fruiting head was collected from each of 40 individuals in each of six populations (Table 1) for a common-environment experiment to estimate within- and among-family and population variances and heritabilities. Each head was scored for the first 13 achene and head traits listed in Table 2. In the following germination season (June), the achenes were sown in petri dishes and, upon germination, were individually transplanted to pots 10 cm in diameter filled to 10 cm with fine sand. For 11 randomly chosen families from each population, 8–14 seedlings were transplanted; for the remaining 29 families two seedlings were transplanted. The former were used for calculating within- and among-family variance components; all 40 families were used for calculating parent-offspring regressions to test whether field-grown parents produce phenotypically similar progeny in the greenhouse, i.e., to determine whether heritable variation in the greenhouse is expressed in the field. The pots were randomized on benches in the greenhouse of the Instituto de Biología, Universidad Autónoma de México, in Mexico City. At three weeks, the size and shape of each seedling were measured (traits 19–21 in Table 2), and at three months adult size, shape, and branching pattern were measured (traits 22–26 in Table 2). The date when the first flowering head opened (DFLR) was recorded, and the

TABLE 1. Study sites in central Mexico. The numbers in parentheses refer to map locations in figure 1 of Venable et al. (1987).

Site	Geographic coordinates	Elevation (m)
San Bartolo, México (5)	19°52'N, 99°04'W	2,500
Tula, Hidalgo (6)	20°03'N, 99°20'W	2,036
Golondrinas, Hidalgo (7)	20°25'N, 99°20'W	2,000
Huichapan, Hidalgo (9)	20°22'N, 99°39'W	2,100
Zitácuaro, Michoacán (15)	19°26'N, 100°23'W	1,990
Mirador, Jalisco (37)	20°41'N, 103°15'W	1,580

first mature fruiting head was scored for the same achene and head traits as were scored on the parental plants (traits 1–13 in Table 2). For a subsample of five families from Huichapan and two families from each of the other populations, the age at which the first fruiting head matured, the age at death, and the total number of fruiting heads were recorded for each of 8–14 individuals per family. These characters were analyzed in the same way as the others to estimate within- and among-family variance.

An analysis of variance was performed for each trait in each population using the SPSS program ONEWAY (Nie et al., 1975) and nested analyses of variance were performed for the six populations together using the NESTED program of SAS (SAS Institute, 1985). The latter program calculated variance components within and between families and populations. Parent-offspring regressions for each population, were calculated for each trait scored on the parents using the REGRESSION program of SPSS (Nie et al., 1975). Those traits measured only on a subset of families (age when the first fruiting head matured, age at death, and total number of fruiting heads) were not analyzed for each population separately, because of inadequate sample size, but these traits were included in the nested analyses.

Heterosperma pinnatum appears to be predominantly inbred. Unmanipulated heads have high seed set (see Results). Stigmas have been observed to curl around and pick up self pollen. Heads have only 2–4 small ray florets, and as expected for predominant selfers (Stebbins, 1974), heads are

TABLE 2. List of characters measured in this investigation and their abbreviations.

Achene and head traits:	
1) Number of central achenes per head (NOC)	
2) Number of intermediate achenes per head (NOI)	
3) Number of peripheral achenes per head (NOP)	
4) Number of awned achenes per head (NOAWN)	
5) Number of achenes per head (NACH)	
6) Percentage of central achenes (%C) = NOC/NACH	
7) Percentage of intermediate achenes (%I) = NOI/NACH	
8) Percentage of peripheral achenes (%P) = NOP/NACH	
9) Percentage of achenes with awns (%AR) = NOAWN/NACH	
10) Length in mm of awns on the longest central achene (LOAWN)	
11) Length in mm of longest central achene (LOC)	
12) Length in mm of widest peripheral achene (LOP)	
13) Width in mm of widest peripheral achene (WOP)	
Life-history traits:	
14) Number of heads per plant (NHEADS)	
15) Age when first flowering head opened (DFLR)	
16) Age when first fruiting head opened (1FRUIT)	
17) Age at death (DEATHDATE)	
18) Reproductive interval (RINT) = DEATHDATE - 1FRUIT	
Size and shape traits:	
19) Seedling height in cm at three weeks of age (H3WK)	
20) Seedling width in cm at three weeks of age (W3WK)	
21) Seedling shape (H/W3WK) = H3WK/W3WK	
22) Adult height in cm (HADULT)	
23) Length of first branch in cm (L1BR)	
24) Adult shape (BR/H) = L1BR/HADULT	
25) Height in cm above soil level of the first branch (H1BR)	
26) Number of branches (NOBR)	

highly reduced and unattractive compared to related outcrossing species. Little nectar or pollen is produced. Given these considerations, we chose to assume complete inbreeding to calculate estimates of heritability. With complete inbreeding, all individuals are homozygous, and thus all selfed offspring are genetically identical. Thus the within-family variance is only environmental, while the among-family variance component is the total genetic variance (plus any maternal effects). Under this assumption, the intraclass correlation coefficient (which is defined as the among-family variance divided by the among- plus within-family variance) approximates the broad-sense heritability. With predominant but not

complete selfing, the broad-sense heritability is actually a little higher than the intraclass correlation coefficient, and it involves a slightly different mix of additive, dominance, and epistatic variance (Crow and Kimura, 1970 p. 138; Falconer, 1981 pp. 151–152). Among-population genetic variance is reported as a proportion of total genetic variance (within and among populations). This was done to permit easy comparison to within-population (i.e., among-family) genetic variance.

As with all clonal studies and all studies not utilizing paternal half sibs or father-offspring regressions, our design does not distinguish possible maternal effects from genetic effects. Thus our estimates of heritabilities and the proportions of genetic variance among populations may be biased by maternal effects. Our decision not to attempt a more complex design was based on the difficulty of emasculating and crossing the small, self-compatible florets and heads as well as on the relatively low statistical power often associated with such designs.

Significances and errors were calculated from the regressions and ANOVAs. We also report standard deviations for the intraclass correlation coefficients. These standard deviations are only approximate, since they were calculated according to the formula provided in Falconer (1981 p. 168), which assumes balanced data and large sample sizes.

RESULTS

Seed set was 75% for the self-pollinated bagged heads, 81% for the emasculated cross-pollinated heads, and 4% for the emasculated heads. Low seed set in emasculated heads was probably due to the inadvertent transfer of some pollen in the process of removing hermaphroditic disk florets (there is only a short time window between the opening of the head and the opening of the first hermaphroditic flowers). Plants in the greenhouse achieved a high seed set from unaided selfing that was not statistically different from the seed set obtained via artificial cross pollination. On the basis of this evidence, combined with the natural-history observations mentioned in the Materials and Methods, we have assumed pre-

dominant inbreeding for our calculations of broad-sense heritability.

Phenotypic means measured in the greenhouse differed among populations for all traits except percentage of intermediate achenes, length of peripheral achenes, and seedling shape (Table 3). Thus, populations differed in plant size, shape, branching patterns, various phenological traits, the number of heads per plant, and achene and head traits. For example, the number of peripheral achenes per head was more than twice as great in Huichapan and Tula as in Mirador, while the number of central achenes was roughly twice as great in Mirador. The number of awned achenes per head was four times as great in Zitácuaro as in Tula. The total number of achenes per head was lower for Mirador than for the other populations. There was also considerable within-population phenotypic variation in most traits (Table 3); such variation was usually as great or greater than that among populations (Table 4). All of the achene and head traits had high within-population heritability estimates. Yet, only seven of these (NOC, NOP, NOAWN, %C, %P, %AR, and LOAWN in Table 2) had proportions of genetic variance among populations greater than 0.25 (Table 5).

The consistency of the among-population variation in our greenhouse experiment with that in natural populations can be tested by comparing our data to an independent data set. Forty field-grown individuals from each of our populations were scored for %C, %I, %P, and NACH in another study (Venable et al., 1987). For the traits with proportions of genetic variance among populations greater than 0.25 the rankings of the population means from this independent field study were very similar to those in the greenhouse in the present study (Kendall rank correlations, $\tau = 0.73\text{--}0.87$, $P < 0.03$ for each trait). For the achene and head traits with proportions of genetic variance among populations less than 0.25, greenhouse and field rankings were not significantly correlated ($\tau = 0.33\text{--}0.41$, $P \gg 0.05$).

Among life-history traits, age at first flowering, age at first fruiting, and the number of heads per plant had high within-population estimates of broad-sense heritability, while age at death and reproductive interval

TABLE 3. Phenotypic means and standard deviations of individual values for each greenhouse-grown population. The significance level for differences among populations in the mean values of traits is given after the data for the last population. See Table 2 for definitions of trait abbreviations.

Trait	San Bartolo		Tula		Golondrinas		Huchapan		Zitácuaro		Mirador		P
	\bar{x}	s	\bar{x}	s	\bar{x}	s	\bar{x}	s	\bar{x}	s	\bar{x}	s	
Achene and head traits:													
NOC	2.43	1.03	2.14	1.14	2.70	1.10	2.67	1.12	4.13	2.34	4.88	1.25	<0.001
NOI	3.28	1.06	3.16	1.39	2.98	1.14	2.79	1.30	3.36	1.57	1.94	1.20	<0.05
NOP	5.39	1.61	7.00	2.72	6.54	2.05	7.09	2.28	5.38	1.92	2.87	1.64	<0.001
NOAWN	4.63	2.86	1.88	1.36	4.38	4.13	6.20	3.51	7.69	2.45	5.37	1.56	<0.001
NACH	11.09	2.20	12.30	2.70	12.21	2.38	12.55	2.48	12.87	2.84	9.69	2.33	<0.001
%C	21.94	8.48	17.75	9.29	22.20	9.37	21.47	9.11	31.77	16.52	51.69	11.40	<0.001
%I	29.79	8.31	26.62	11.42	24.89	9.39	22.42	10.06	26.88	12.73	20.23	11.16	ns
%P	48.27	10.09	55.63	14.57	52.91	11.00	56.12	13.72	41.35	10.81	28.08	13.14	<0.001
%AR	40.63	22.36	16.10	11.84	34.15	29.08	48.81	24.72	59.64	16.33	56.79	14.39	<0.001
LOAWN	2.34	0.22	2.27	0.48	2.09	0.34	2.12	0.33	2.58	0.29	2.38	0.30	<0.001
LOC	10.21	1.46	9.61	2.02	10.46	1.43	11.38	1.74	10.94	1.44	13.57	1.54	<0.001
LOP	4.95	0.39	4.38	0.74	4.83	0.68	4.79	0.65	4.89	0.84	4.98	0.70	ns
WOP	3.34	0.35	3.17	0.56	3.08	0.53	3.00	0.50	3.23	0.31	2.65	0.38	<0.005
Life-history traits:													
NHEADS	8.8	5.0	6.8	3.1	6.3	3.3	10.0	4.1	4.3	2.4	8.6	3.9	<0.001
DFLR	13.59	4.33	15.99	5.12	17.86	5.65	18.40	5.66	42.60	14.78	15.74	5.52	<0.005
IFRUIT	21.6	5.3	28.8	7.1	32.6	5.3	24.5	11.3	67.9	15.7	30.7	6.8	<0.001
DEATHDATE	68.8	12.6	56.9	16.0	73.7	18.7	67.5	13.5	95.4	15.9	63.4	11.4	<0.001
RINT	47.2	11.3	28.1	14.8	41.1	17.1	43.0	15.1	27.5	13.3	32.6	12.3	<0.001
Size and shape traits:													
H3WK	4.38	1.09	5.65	1.25	5.08	1.14	5.17	1.78	4.26	1.28	5.69	1.32	<0.005
W3WK	3.13	0.72	3.61	0.71	3.47	0.73	3.52	0.69	2.96	0.68	4.04	0.87	<0.01
H/W3WK	1.42	0.30	1.60	0.37	1.52	0.41	1.46	0.38	1.46	0.39	1.44	0.33	ns
HADULT	25.13	7.35	29.31	7.39	28.38	7.05	25.33	8.76	19.55	5.84	21.53	7.06	<0.005
L1BR	10.72	4.13	8.10	3.52	8.47	2.89	7.22	3.44	5.74	3.12	7.84	2.70	<0.001
BR/H	0.44	0.16	0.29	0.14	0.31	0.11	0.31	0.14	0.31	0.18	0.39	0.19	<0.005
H1BR	3.50	3.57	11.14	8.56	9.95	6.99	12.22	9.43	5.49	6.31	5.17	3.99	<0.005
NOBR	3.12	1.45	1.97	1.05	1.93	0.99	1.81	0.81	2.28	1.31	2.81	1.52	<0.001

TABLE 4. Phenotypic means and standard deviations (*s*) for greenhouse-grown populations. The grand mean is the average phenotypic value of the six populations investigated. The within-population standard deviation is the square root of the pooled estimate of phenotypic variance within populations. The among-population standard deviation is the square root of the variance attributable to population means. See Table 2 for definitions of trait abbreviations.

Trait	Grand mean (pooled)	<i>s</i> within populations	<i>s</i> among populations
Achene and head traits:			
NOC	3.09	1.44	1.02
NOI	2.97	1.30	0.45
NOP	5.85	2.09	1.42
NOAWN	5.08	2.88	1.99
NACH	11.91	2.51	1.06
%C	26.65	11.14	11.20
%I	25.50	10.61	9.81
%P	47.94	12.25	3.07
%AR	42.46	20.97	15.90
LOAWN	2.30	0.33	0.19
LOC	10.96	1.61	1.26
LOP	4.79	0.68	0.20
WOP	3.11	0.45	0.20
Life-history traits:			
NHEADS	7.39	3.71	1.93
DFLR	21.25	7.94	11.23
1FRUIT	34.79	9.06	17.07
DEATHDATE	72.00	14.36	13.08
RINT	37.21	14.02	8.66
Size and shape traits:			
H3WK	5.00	1.34	0.59
W3WK	3.42	0.73	0.35
H/W3WK	1.48	0.37	0.51
HADULT	25.01	7.33	3.75
L1BR	8.02	3.36	1.64
BR/H	0.34	0.15	0.06
H1BR	8.19	7.03	3.62
NOBR	2.27	1.19	0.49

had low heritability estimates (Table 5). All of the phenological variables had high proportions of genetic variance among populations, while the number of heads per plant did not (Table 5). We have good field data on phenology for the San Bartolo and Zitácuaro populations, which have been extensively investigated for other purposes (Venable et al., 1987). Flowering, fruiting, and death occurred 3–4 weeks later at the Zitácuaro site than at the San Bartolo site. In the greenhouse, the average flowering, fruiting, and death dates were roughly one month apart for these two populations (Table 3). Thus, as with achene and head traits, the genetic differences between populations

encountered in the greenhouse were of the same direction and similar magnitude as the phenotypic differences between populations encountered in the field.

When populations were analyzed individually, estimates of broad-sense heritability were generally large (104 out of the 132 calculated values were greater than 0.25). There was significant genetic variance for all but three traits ($P < 0.05$; Table 6). Some populations had higher heritabilities than others. In both the Huichapan and Tula populations, 20 of the 22 traits had heritability values greater than 0.25, and 15 were greater than 0.50. The samples from San Bartolo had lower heritabilities, with only 11 being greater than 0.25 and three being greater than 0.50.

The within-population genetic variation demonstrated in the greenhouse is also expressed in plants grown in the field. Achene and head traits were measured for the field-grown parents of the greenhouse-grown plants for each of the 11 families used to calculate heritabilities plus 29 other greenhouse-grown families represented by two offspring each. Regressions of mean offspring phenotype in the greenhouse on parental phenotype in the field are actually independent (though very rough) estimates of heritabilities. To use parent-offspring regressions properly as estimates of heritabilities, parents and offspring should be grown in a common environment. We use parent-offspring regressions to verify that families with higher than average values of a given trait in the greenhouse can be expected to have higher than average values of the trait in the field (i.e., that our greenhouse results are relevant to the study of natural selection in the field). Indeed, regressions attempting to explain mean offspring phenotype in the greenhouse by their parental phenotype in the field tended to have high and positive slopes (66 of 72 slopes are positive; only one of the six negative slopes was significantly different from zero, but 49 of the 66 positive slopes differed significantly from zero. [Regressions with $P < 0.05$ were considered to be statistically significant; *d.f.* ranged from 32 to 38].) The traits with high positive regression coefficients tended to be those with high greenhouse-estimated heritabilities (the correla-

TABLE 5. Genetic variation within and among populations of *Heterosperma pinnatum*. Variance components at individual (V_I), family (V_F), and population (V_P) levels are presented. Broad-sense heritabilities (h^2) are calculated from within- and among-family variances pooled across populations. The proportion of genetic variance among populations (PGVAP) is calculated by dividing the among-population variance component by the total genetic variance (among-family plus among-population variance components). Values of PGVAP greater than 0.5 indicate more genetic variation among than within populations. See Table 2 for definitions of trait abbreviations.

Trait	V_I	V_F	h^2	V_P	PGVAP
Achene and head traits:					
NOC	0.89	1.24	0.58	0.70	0.36
NOI	0.95	0.80	0.46	0.09	0.10
NOP	2.48	2.11	0.46	1.33	0.39
NOAWN	2.11	7.22	0.77	3.15	0.30
NACH	3.87	2.48	0.39	0.53	0.18
%C	51.22	70.47	0.58	80.93	0.54
%I	64.34	52.79	0.45	4.38	0.08
%P	82.06	69.41	0.46	63.91	0.48
%AR	112.59	375.86	0.77	199.70	0.35
LOAWN	0.02	0.01	0.37	0.03	0.70
LOC	0.51	1.07	0.68	0.18	0.15
LOP	0.08	0.14	0.63	0.01	0.07
WOP	0.07	0.06	0.47	0.02	0.21
Life-history traits:					
NHEADS	8.72	6.57	0.43	0.00	0.00
DFLR	27.91	34.76	0.56	101.55	0.75
1FRUIT	43.22	66.78	0.61	175.99	0.73
DEATHDATE	178.47	58.09	0.25	89.49	0.61
RINT	198.09	27.82	0.12	27.24	0.50
Size and shape traits:					
H3WK	1.20	0.61	0.34	0.28	0.32
W3WK	0.26	0.28	0.52	0.80	0.22
H/W3WK	0.09	0.50	0.35	0.00	0.00
HADULT	20.49	36.91	0.64	9.27	0.20
L1BR	9.06	2.77	0.23	2.68	0.49
BR/H	0.17	0.01	0.27	0.003	0.29
H1BR	22.01	31.71	0.59	9.30	0.23
NOBR	0.99	0.41	0.29	0.18	0.31

tion of these regression slopes with the heritability estimates was 0.56 ($d.f. = 70, P < 0.001$). While the validity of this last significance test may be questioned due to possible nonindependence of heritability estimates among traits, this correlation would be significant even with a substantial reduction in degrees of freedom. Thus trait values measured in the field correspond to family means in the greenhouse, though only for traits with high heritabilities.

DISCUSSION

Our results indicate that, although most traits should be able to respond to natural selection, some should respond more rapidly than others. For example, both the number and percentage of awned achenes should respond rapidly to selection by vir-

tue of the high estimates of genetic variance for these traits (assuming that a portion of the genetic variance is additive), while length of the reproductive interval should respond slowly. Some populations (e.g., Huichapan) have generally higher estimates of genetic variance and heritability than others (e.g., Golondrinas). This suggests that the ability to respond to selection may differ among populations. Some traits, such as number of heads per plant or seedling shape, have high broad-sense heritability estimates, but their means have not diverged during population differentiation. Other traits, such as length of reproductive interval have low heritabilities, but population means have diverged. This suggests that such traits may have undergone strong natural selection in the past, with adaptive peaks differing

TABLE 6. Among-family variance components (V_F), within-family variance components (V_I), intraclass-correlation coefficients ($i_{intraclass}$) (which estimate heritabilities), and the standard errors of the intraclass-correlation coefficients (in parentheses) for each of the six populations studied. Only those traits measured on all families were analyzed. The statistical significance of the genetic (among-family) variance is indicated by asterisks. See Table 2 for definitions of trait abbreviations.

Trait	Population						
	San Bartolo		Tula		Golondrinas		
	V_F	V_I	V_F	V_I	V_F	V_I	
	$i_{intraclass}$	$i_{intraclass}$	$i_{intraclass}$	$i_{intraclass}$	$i_{intraclass}$	$i_{intraclass}$	
Achene and head traits:							
NOC	0.21**	0.86	0.20 (0.11)	0.63	0.34***	0.91	0.27 (0.12)
NOI	0.23**	0.92	0.20 (0.11)	0.97	0.13*	1.18	0.10 (0.09)
NOP	0.88***	1.79	0.33 (0.13)	3.27	0.88***	3.39	0.21 (0.11)
NOAWN	6.15***	2.56	0.71 (0.10)	0.61	17.56***	1.06	0.94 (0.03)
NACH	1.30***	3.66	0.26 (0.12)	4.75	1.99***	3.86	0.34 (0.13)
%C	7.64*	65.01	0.11 (0.09)	30.53	18.66***	70.77	0.21 (0.11)
%I	15.93***	54.53	0.23 (0.12)	77.76	9.56*	79.50	0.11 (0.09)
%P	35.51***	69.48	0.34 (0.13)	69.58	6.45	115.19	0.05 (0.07)
%AR	364.77***	167.31	0.69 (0.11)	43.41	853.52***	67.67	0.93 (0.03)
LOWVN	0.001	0.03	0.03 (0.08)	0.04	0.04***	0.03	0.56 (0.13)
LOC	0.20*	1.04	0.16 (0.12)	0.53	0.51***	0.70	0.42 (0.13)
LOP	0.02***	0.07	0.23 (0.12)	0.04	0.20***	0.09	0.70 (0.11)
WOP	0.02***	0.05	0.23 (0.12)	0.06	0.07***	0.10	0.40 (0.13)
Life-history traits:							
DFLR	9.13***	10.47	0.47 (0.13)	9.67	17.47***	15.99	0.52 (0.13)
Size and shape traits:							
H3WK	0.31***	0.90	0.26 (0.13)	1.12	0.31***	1.02	0.32 (0.12)
W3WK	0.18***	0.36	0.34 (0.14)	0.19	0.29***	0.27	0.51 (0.13)
H/W3WK	0.01*	0.08	0.15 (0.10)	0.07	0.07***	0.10	0.43 (0.13)
HADULT	36.69***	20.68	0.64 (0.12)	21.76	23.96***	27.97	0.46 (0.13)
L1BR	4.83***	12.67	0.28 (0.14)	7.17	1.26*	7.19	0.15 (0.10)
BR/H	0.00*	0.02	0.12 (0.09)	0.01	0.002**	0.01	0.15 (0.10)
H1BR	0.41	12.41	0.03 (0.07)	27.23	15.79***	34.49	0.31 (0.13)
NOBR	0.69***	1.48	0.32 (0.13)	0.90	0.14*	0.84	0.14 (0.10)

TABLE 6. Continued.

Trait	Huichapan			Zitácuaro			Mirador		
	V_F	V_I	$t_{intraclass}$	V_F	V_I	$t_{intraclass}$	V_F	V_I	$t_{intraclass}$
Achene and head traits:									
NOC	0.86***	0.48	0.64 (0.12)	4.36***	1.50	0.74 (0.09)	0.72***	0.91	0.44 (0.15)
NOI	1.02***	0.77	0.57 (0.13)	1.61***	1.00	0.62 (0.12)	0.51***	0.96	0.35 (0.15)
NOP	3.02***	2.45	0.55 (0.13)	0.78***	2.98	0.21 (0.11)	1.33***	1.46	0.48 (0.14)
NOAWN	11.29***	1.99	0.85 (0.06)	1.88***	4.29	0.31 (0.12)	0.74***	1.76	0.30 (0.14)
NACH	2.91***	3.51	0.45 (0.13)	2.11***	6.12	0.26 (0.12)	3.34***	2.37	0.58 (0.13)
%C	55.84***	32.08	0.64 (0.12)	209.48***	81.16	0.72 (0.10)	66.76***	68.54	0.49 (0.14)
%I	66.51***	40.46	0.62 (0.12)	109.90***	61.32	0.64 (0.12)	33.68**	93.64	0.26 (0.14)
%P	117.90***	80.52	0.59 (0.12)	29.88***	89.44	0.25 (0.12)	53.61***	123.26	0.30 (0.14)
%AR	556.01***	103.62	0.84 (0.06)	94.85***	179.70	0.35 (0.13)	101.62***	113.56	0.47 (0.14)
LOAWN	0.03***	0.03	0.52 (0.13)	0.02***	0.03	0.42 (0.13)	0.02***	0.04	0.29 (0.14)
LOC	1.39***	0.46	0.75 (0.09)	0.58***	0.65	0.47 (0.13)	0.30**	1.09	0.22 (0.13)
LOP	0.18***	0.08	0.69 (0.11)	0.04*	0.37	0.09 (0.08)	0.11***	0.18	0.37 (0.16)
WOP	0.07***	0.08	0.44 (0.13)	0.01**	0.04	0.18 (0.10)	0.04***	0.04	0.50 (0.15)
Life-history traits:									
DFLR	8.66***	24.07	0.26 (0.12)	149.38***	81.79	0.65 (0.11)	11.92***	19.49	0.38 (0.14)
Size and shape traits:									
H3WK	2.40***	0.99	0.71 (0.10)	0.89***	0.82	0.52 (0.13)	1.05***	0.79	0.57 (0.13)
W3WK	0.21***	0.28	0.43 (0.13)	0.21***	0.27	0.43 (0.13)	0.52***	0.27	0.66 (0.12)
H/W3WK	0.08***	0.07	0.56 (0.13)	0.08***	0.08	0.48 (0.13)	0.05***	0.06	0.42 (0.15)
HADULT	66.53***	15.75	0.81 (0.08)	24.28***	11.89	0.67 (0.11)	22.27***	29.56	0.43 (0.16)
L1BR	1.57*	10.41	0.13 (0.09)	1.25*	8.57	0.13 (0.10)	3.19***	4.38	0.41 (0.16)
BR/H	0.00**	0.02	0.17 (0.11)	0.01***	0.02	0.38 (0.13)	0.02***	0.02	0.60 (0.14)
H1BR	73.99***	21.07	0.78 (0.09)	26.16***	15.93	0.62 (0.12)	7.59***	9.01	0.46 (0.16)
NOBR	0.17***	0.49	0.26 (0.12)	0.39***	1.37	0.22 (0.12)	1.10***	1.30	0.46 (0.16)

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

among populations. The numbers and proportions of central and peripheral achenes and of achenes with awns have high estimates of heritability and among-population genetic variation. Thus, population means have diverged, but the potential for continued response to selection favoring changes in achene proportions remains.

The rather high heritability estimates of most characters were somewhat surprising since many of them have fairly obvious effects on fitness (see Venable et al., 1987). One might expect that traits closely related to fitness would have low heritabilities, since selection should consume any additive genetic variance for such traits (Falconer, 1981 pp. 149–150 and Ch. 20). It is possible (though not likely) that our high heritability estimates are entirely the result of epistatic or maternal effects, since these are not distinguished by our design. Aside from this possibility, there are other reasons why additive genetic variance might be found for fitness traits. First, these traits are only components of fitness; they must be combined with other components to yield actual fitness, which might itself have low genetic variance. For example, different combinations of number of seeds per head and number of heads per plant yield the same number of seeds per plant and, thus, may be selectively neutral. Second, the species tends to live in disturbed habitats that vary considerably in space and time. This may result in a variable direction of selection on each character (cf. Istock, 1981). For example, the same flowering date may not be favored every year, because of differences in weather. Spatial variation in grazing pressure, even within a population, could result in simultaneous selection for different optimal plant heights and degrees of branching. The among-population differences in many of these characters suggest that adaptive peaks may differ among populations; perhaps spatial variation in selection occurs locally as well. Third, it is possible that a mutation-selection balance may maintain genetic variance for traits under selection (Lande, 1975; Turelli, 1984). Finally, genetic correlations could retard the erosion of genetic variation (Antonovics, 1976) or in some special cases, even maintain variation at equilibrium (Rose, 1982).

Previous studies of other species have shown significant genetic variation in some of the traits we have studied here, but with a few notable exceptions, these studies did not partition genetic variation within and among populations. Genetic variation is commonly reported in seed size (usually weight; e.g., Linhart, 1974), though not always (e.g., Solbrig 1981; Mazer, 1987). Genetic variation in reproductive components analogous to seeds per head and heads per plant have been reported in several species (Silander and Antonovics, 1979; Burdon, 1980; Clark, 1980; Primack and Antonovics, 1981). Various phenological traits such as days to flowering or reproductive interval have frequently been shown to vary genetically (Imam and Allard, 1965; Kannenberg and Allard, 1967; Jones, 1971; Linhart, 1974; Law et al., 1977). Likewise, various aspects of plant size, shape, and branching patterns have been shown to have genetic variation in a variety of wild species (Antlfinger et al., 1985; reviewed in Venable [1984]).

Most investigations of variation in proportion of seed morphs for heteromorphic species have focused on plastic (as opposed to genetic) variation. Plants with underground cleistogamous and aerial chasmogamous seeds usually have a fairly constant number of subterranean seeds, but the number of aerial seeds varies with plant size (Weiss, 1980; Cheplick and Quinn, 1982). In other species, cleistogamous- and chasmogamous-flower production (with corresponding seed differences) may vary seasonally, on different parts of plants, or with density (Schemske, 1978; Clay, 1982). In a *Danthonia spicata* population from North Carolina, the percentage of cleistogamous-flower production ranges from 12% to 65%, depending on density and plant size. Much of this variation is explained by family and genotype of origin, indicating high heritability for seed-morph proportions (Clay, 1982). Silvertown (1984) summarized data for species (predominantly legumes) that produce a continuous range of seed morphs on single plants. In some of these species, the frequency distribution of the seed morphs varies at different times of the year. In some legume species, there are varietal (genetic) differences in the proportion of

seeds persisting into second and subsequent years and for seed-coat permeability (which mediates intraplant variation in dormancy) (Quinlivan, 1971).

Morph proportions in heteromorphic composites are usually determined by the proportions of ray and disk florets, which have a fairly constant geometric arrangement and therefore are usually much less variable than in *Heterosperma pinnatum*. Morph proportions (and head size) in a Texas population of *Heterotheca latifolia* vary with plant size and season, but proportions seldom change more than 15% (Venable and Levin, 1985a). In *Hypochoeris glabra*, the proportion of ray achenes per head changes from 25.3% at low density to 34.9% at high density (Baker and O'Dowd, 1982). A study of ten inbred and F₁ lines of *Senecio vulgaris* showed stability in the proportion of ray florets in the face of severe changes in the environment; line means for proportions of ray florets varied only from 15.1 to 17.9% (Abbott and Schmitt, 1985). Compared to these species, the variation in morph proportions in *H. pinnatum* (3–44% central achenes, 30–79% peripheral achenes) is high (Venable et al., 1987). The fact that achene morphs are not determined by floret type (ray vs. disk) permits this greater variation in morph proportions which, as we have shown, is partially under genetic control.

Some investigations have suggested that environmental variance may be lower in the greenhouse than in the field, resulting in an overestimate of heritabilities in greenhouse studies (Primack and Antonovics, 1982; Mitchell-Olds and Rutledge, 1986). The phenotypic variance reported for our six greenhouse-grown populations does not differ greatly from that reported by Venable et al. (1987) for 32 populations scored on plants in the field. In fact, for the seven characters for which data are available from both field and greenhouse, within-population phenotypic variance was consistently somewhat larger for greenhouse-grown plants. Among-population phenotypic variance was larger in the greenhouse for three traits and smaller for four.

Not only was the magnitude of phenotypic variance similar among greenhouse-grown and field-collected plants, but our results suggest that the expression of genetic

variation may also be similar in the field and greenhouse. Greenhouse means were correlated with field means for traits with high heritabilities at both family and population levels. Thus, families and populations that varied genetically in the greenhouse varied in the same directions in the field. This similarity of high-heritability traits among field- and greenhouse-grown families and populations suggests that the variance due to the genotype-by-environment interaction may be low enough that the genetic measures from the greenhouse provide reasonable estimates for these field populations.

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