



**Quantitative Genetics of Size, Shape, Life-History, and Fruit Characteristics
of the Seed Heteromorphic Composite *Heterosperma pinnatum*. II.
Correlation Structure**

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QUANTITATIVE GENETICS OF SIZE, SHAPE, LIFE-HISTORY, AND
FRUIT CHARACTERISTICS OF THE SEED HETEROMORPHIC
COMPOSITE *HETEROSPERMA PINNATUM*.
II. CORRELATION STRUCTURE

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Abstract.—We have investigated phenotypic, environmental, within-population broad-sense genetic correlations and among-population genetic correlations for 17 traits in six populations of *Heterosperma pinnatum* Cav. (Compositae) grown in the greenhouse. The within-population genetic, environmental, and phenotypic correlations were somewhat similar while the among-population genetic correlations showed little correspondence to these. The different correlation matrices were compared to a hypothesis matrix, which predicted higher correlations for groups of functionally and developmentally related traits. The groups were seed and head traits, size and shape traits, and life history traits, with subgroups predicted to have still higher correlations. The phenotypic and environmental matrices corresponded well to the hypothesis matrix, the within-population broad-sense genetic matrix showed weaker, though still significant, correspondence, and the among-population genetic correlations showed no correspondence. Genetic correlations did not differ significantly among populations, though the power of these comparisons was low. Some particular genetic correlations are discussed as possible examples of adaptive correlations (e.g., a negative correlation between dispersal and dormancy) and as examples of developmental or physiological constraints including life-history tradeoffs.

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It is widely recognized that traits do not necessarily evolve independently (Lande, 1979, 1980; Falconer, 1981 Ch. 19). The values of other traits may provide an important ecological or selective context determining the fitness of a trait of interest. Likewise, the occurrence of a trait in the developmental or genetic context of others may constrain or enhance evolutionary change. Thus nonrandom shifts in the distribution of a given trait could be the result of selection on a correlated trait rather than of selection on the trait in question (i.e., selection *of* rather than selection *for* a trait, sensu Sober, 1984). Even if selection is operating on a trait, correlations can speed or slow the pace of evolution depending upon the correspondence between the direction of selection pressures and the sign of the correlation. Thus the importance of possible networks of character correlations, or what Mayr called the “unity of the genotype,” is considerable (Mayr, 1975). Yet most studies of adaptation and natural se-

lection have considered only single traits (Endler, 1986).

To understand trait correlations in the context of life history tradeoffs or other developmental constraints on evolution, people have often studied the phenotypic correlation structure of quantitative traits (Olson and Miller, 1958; McNaughton, 1975; Grant et al., 1976). Since such an approach is useful only if phenotypic correlations approximate underlying genetic correlations, it is important to investigate the similarity of phenotypic life history correlations to their genetic counterparts (Cheverud, 1982; Boag, 1983).

If many correlations can be studied, it becomes meaningful to ask which ones we expect to be higher. Olson and Miller (1958) suggested that developmentally or functionally related traits should have higher than average phenotypic integration and thus statistical association. Cheverud (1982) has extended this reasoning by hypothesizing that developmentally and functionally re-

lated traits might be highly integrated genotypically as well. The work of both Olson and Miller and of Cheverud indicates that related traits show higher than average phenotypic correlations, though genetic correlations of related traits were not higher than average in Cheverud's study.

The present study was motivated by an interest in understanding natural selection on the proportions of different seed morphs expressed in the seed-heteromorphic species *Heterosperma pinnatum*. Seed ratios vary within and among populations, the different seed morphs differ in ecological function (notably in germination and dispersal), and seed morph has measurable effects on fitness in the field (Venable et al., 1987). We have found genetic variation for seed ratios both within and among populations (Venable and Búrquez, 1989). Yet for the reasons cited above, we want to know how seed and head traits are embedded in a broader matrix of correlations and to what extent these correlations are genetically controlled. We measured a large number of seed and head, life history, and plant size and shape traits and calculated the phenotypic, environmental, and genetic correlation structure for 17 of them using six populations of *Heterosperma pinnatum*.

The large number of traits permits us to investigate the pattern of the correlation structure. We have examined the average magnitude of correlations for different subsets of functionally or developmentally related traits: life history traits, achene and head traits, and plant size and shape traits. Life history traits may be more cohesive because of life history tradeoffs, or because they are integrated into adaptive syndromes. Plant size and shape are likely to be correlated by virtue of developmental and functional relationships. Tighter integration should occur within certain subgroups of these traits as well. Within achene and head traits, we expect higher correlations for traits corresponding to central achenes, peripheral achenes, or numbers of each achene type per head. For example, there could be tradeoffs in the numbers of different achene types produced within an individual fruiting head. Developmental integration of a single achene type might result in higher than average correlations. Thus

we hypothesize that tighter integration may occur within these general groups of traits than for trait pairs on average and that certain subgroups would have still higher correlations.

MATERIALS AND METHODS

For a description of the experimental organism and the experimental design see Venable and Búrquez (1989). The traits utilized in the correlation analysis were a subset of those studied for variance (Table 1; see also Venable and Búrquez, 1989; variation in achene morphology is illustrated in Venable et al., 1987). Only traits with substantial within-population genetic variance were used. Seventeen variables were chosen, avoiding redundancy and insuring that no variable was a linear combination of others. Thus, the number of achenes of each type were analyzed, but not their relative proportions. An attempt was made to include as many different kinds of variables as possible, so we eliminated seedling height from the linearly dependent group seedling height, width, and shape (height over width) thus retaining a size and a shape variable. Five traits were excluded from the among-population analysis because they had no among-population variance, or had a number of cases with missing data (see Venable and Búrquez, 1989 for details).

Analyses of covariance were performed using the NESTED program of SAS (SAS Institute, 1985). This program uses least squares to calculate variance-component correlations at the within- and among-family and population levels and mean square correlations (which we will subsequently call "product-moment correlations") for individual values, family means, and population means. For individuals, the mean square correlation is the ordinary product-moment correlation. At the family and population levels it is a weighted product-moment correlation that takes into account different sample sizes in the different families or populations.

To test the significance of covariance components or variance component correlations, some investigators have utilized resampling methods (Mitchell-Olds, 1986). Because of the very large number of correlations, these calculation-intensive tech-

TABLE 1. List of characters utilized in the correlation analyses.

Trait	Abbreviation
1) Length of awns on the longest central achene*	LOAWN
2) Length of longest central achene*	LOC
3) Number of central achenes per head	NOC
4) Number of awned achenes per head	NOAWN
5) Number of achenes per head	NACH
6) Number of peripheral achenes per head	NOP
7) Length of widest peripheral achene	LOP
8) Width of widest peripheral achene	WOP
9) Date that first flowering head opened	DFLR
10) Number of heads per plant*	NHEADS
11) Date that first fruiting head opened*	1FRUIT
12) Seedling width at 3 weeks of age	W3WK
13) Seedling shape—H3WK/W3WK*	H/W3WK
14) Adult height	HADULT
15) Height above soil level of the first branch	H1BR
16) Number of branches	NOBR
17) Adult shape—L1BR/HADULT	BR/H

* These traits were omitted from the among-population genetic analysis.

niques were deemed impractical for the present study. Currently available software implementations of maximum-likelihood techniques (Shaw, 1988) are also prohibitively time consuming to be run on normal mainframe computers for designs of the magnitude investigated here (months of CPU time would be required). Fortunately, maximum likelihood programs do not appear to give any better *estimates* of correlations; least square solutions often had higher likelihoods than the solutions obtained with some few variable runs using Shaw's recursive search algorithms on single populations. Because we ran into serious logistical difficulties with implementing currently available maximum-likelihood methods, we estimated correlations using least squares and have followed Arnold (1981) and Via (1984) in opting for a simple approximation to test the significance of these correlations. The covariance and variance of family means contain a fraction of the within-family covariance or variance. As family size increases, the product-moment correlation of family means approaches the variance-component correlation. The weighted correlations of family or population means corresponding to the appropriate within- or among-population genetic correlations are readily tested for difference from zero with *t*-tests.

In addition to test-wise significance levels, we report Bonferroni experiment-wise

significance levels. While the former are appropriate for considering whether a particular correlation is significant, the latter are appropriate for making aggregate statements about correlations. Experiment-wise significance levels represent the proportion of repetitions of the whole experiment in which *any* correlations would be scored as significant by chance alone. Since in this study this usually means any of 66–136 correlations, this is a strict criterion for significance and, usually, many fewer correlations are significant by experiment-wise than by test-wise criteria.

We have assumed complete inbreeding to calculate genetic correlations (see Venable and Búrquez, 1989 for the evidence for inbreeding). Under inbreeding, the variance-component correlations estimate the broad-sense genetic correlations (plus any correlations due to maternal effects) at the within-population level. To the extent that the assumption of complete inbreeding is violated, the estimates of correlations should actually be higher. The error variance-component correlations estimate the environmental correlations, and the product-moment correlations for individual values estimate the phenotypic correlations.

As with all clonal studies and all studies not utilizing paternal half sibs or father-offspring regressions, our design does not distinguish possible maternal-effect correlations from genetic correlations. Emascu-

TABLE 2. Hypothesis matrix used for calculating the correspondence of observed correlations with the predicted hierarchy of integration of functionally and developmentally related traits for size, shape, life history, achene, and head characteristics of *Heterosperma pinnatum*. 0's, 1's, and 2's identify groups of traits with successively higher predicted levels of integration.

Trait	Trait															
	LOAWN	LOC	NOC	NOAWN	NACH	NOP	LOP	WOP	DFLR	NHEADS	IFRUIT	W3WK	H/ W3WK	HADULT	HIBR	NOBR
LOC	2															
NOC	2	2														
NOAWN	1	1	2													
NACH	1	1	2	2												
NOP	1	1	2	2	2											
LOP	1	1	1	1	1	2										
WOP	1	1	1	1	1	2	2									
DFLR	0	0	0	0	0	0	0	0								
NHEADS	0	0	0	0	0	0	0	0	1							
IFRUIT	0	0	0	0	0	0	0	0	1	1						
W3WK	0	0	0	0	0	0	0	0	0	0	0					
H/W3WK	0	0	0	0	0	0	0	0	0	0	0	2				
HADULT	0	0	0	0	0	0	0	0	0	0	0	1	1			
HIBR	0	0	0	0	0	0	0	0	0	0	0	1	1	2		
NOBR	0	0	0	0	0	0	0	0	0	0	0	1	1	2	2	
BR/H	0	0	0	0	0	0	0	0	0	0	0	1	1	2	2	2

TABLE 3. Phenotypic correlations for size, shape, life history, achene, and head characteristics of *Heterosperma pinnatum*.

Trait	Trait						
	LOAWN	LOC	NOC	NOAWN	NACH	NOP	LOP
LOC	0.23b						
NOC	0.49d*	0.57d*					
NOAWN	0.33d	0.52d*	0.36d*				
NACH	0.11	0.02	0.29d*	0.39d*			
NOP	-0.22a	-0.24b	-0.23d*	0.08	0.73d*		
LOP	0.19a	0.52d*	0.23d*	0.41d*	0.18d*	-0.01	
WOP	-0.06	0.03	-0.02	0.15c	0.40d*	0.36d*	0.34d*
DFLR	0.62d*	0.09	0.31d*	0.26d*	0.09	-0.14c	0.05
NHEADS	-0.32d	-0.38d*	-0.25b	-0.24b	-0.20a	0.01	-0.15
1FRUIT	0.58d*	0.17	0.46d*	0.19	0.04	-0.22a	0.10
W3WK	0.06	0.11	-0.09	-0.02	0.10a	0.17d*	0.04
H/W3WK	-0.04	0.03	-0.05	0.23d*	0.02	-0.03	-0.07
HADULT	0.07	0.08	-0.11a	0.14c	0.37d*	0.38d*	0.18d*
H1BR	-0.01	0.21a	-0.05	0.23d*	0.21d*	0.19d*	0.16d
NOBR	-0.11	0.02	0.06	-0.07	0.01	-0.01	-0.02
BR/H	-0.26c	0.02	-0.11a	-0.09	-0.23d*	-0.07	-0.08

a, $P < 0.05$; b, $P < 0.02$; c, $P < 0.01$; d, $P < 0.001$ (probabilities for test-wise significances); *, $P < 0.05$ (probability for experiment-wise significances using the Bonferroni test).

lating and crossing the small, self-compatible florets and heads of *Heterosperma pinnatum* is impractical on a large scale. The more complex designs that would permit the partitioning of additive variance and maternal effects would necessitate much larger sample sizes, further reducing the feasibility of controlled crosses with *H. pinnatum*.

Various matrices were compared using permutation tests for association (Dietz, 1983; programs supplied by E. Jaquelin Dietz and David E. Cowley). Conventional correlation tests are not appropriate for comparing two matrices because, by definition, the entries of a correlation matrix are not independent. The correlations of corresponding entries in each pair of matrices were calculated with Mantel's Z , R , and Kc (Dietz, 1983), then permutations that preserve the dependencies among the elements of each matrix were performed and each statistic was recalculated 4,000 times to generate a null distribution against which the observed statistics were tested. When these test statistics are normalized they give the more standard correlation coefficients, respectively, the Pearson product-moment correlation between two matrices, Spearman's ρ , and a modified Kendall's τ .

To evaluate the hierarchical structure of the correlation matrices we tested their cor-

respondence to a hypothesis matrix (Table 2) consisting of 0's (unrelated trait pairs), 1's (life history, achene and head, and plant size and shape trait pairs), and 2's (subgroups of the trait pairs that were assigned 1's which we hypothesize to be the most tightly integrated). We use the absolute value of the observed correlations as an indication of cohesiveness or integration since the sign of a correlation might be positive or negative, depending on the nature of the traits and their relationship. Correspondence of observed correlation structures to the hypothesis matrix was measured with matrix correlations whose significance was tested with Dietz's permutation test.

RESULTS

Large proportions of the within-population genetic, environmental, and phenotypic correlations were significant, though few of the among-population genetic correlations were (Tables 3–6). Though the among-population genetic correlations may be accurate, the power of the statistical tests is low because only six populations were measured. Yet, interestingly, these among-population genetic correlations measured in the greenhouse are very similar to among-population correlations in the field, suggesting that the greenhouse correlations may be accurate (and perhaps suggesting a partial ge-

TABLE 3. Extended.

WOP	Trait							
	DFLR	NHEADS	1FRUIT	W3WK	H/W3WK	HADULT	H1BR	NOBR
0.02								
-0.10	-0.35d							
-0.11	0.83d*	-0.35d						
-0.12b	-0.19d*	-0.14	-0.03					
0.08	-0.08	-0.02	-0.01	-0.29d*				
0.24d*	-0.25d*	-0.13	-0.06	0.43d*	0.17d*			
0.12b	-0.07	-0.28c	0.02	0.23d*	0.22d*	0.60d*		
0.05	-0.09	0.32d	-0.14	-0.04	-0.02	-0.21d*	-0.41d*	
-0.04	-0.10a	-0.17	-0.24b	-0.20d*	-0.05	-0.31d*	-0.37d*	0.48d*

netic basis for the field correlations). Six of the seed and head traits from Table 1 (number of central, peripheral, awned achenes per head, the total number of achenes per head, length of awns on central achenes, and length of central achenes) were measured on 40 individuals in each of 35 populations for a separate study (Venable et al., 1987) and the correlations among their population means were calculated (33% were significant at $P < 0.05$). The among-population matrix obtained from these field-grown plants has a Pearson correlation of $r = 0.70$, $P < 0.01$, with the among-population genetic correlation matrix obtained from greenhouse-grown plants in the present study. While these two independently derived matrices clearly differ in what they attempt to measure, the probability is very low that their similarity is due to chance alone, rather than due to correspondence in some shared underlying biological property. The only property common to both matrices is among-population genetic correlation.

The among-population genetic correlation matrix has a low and statistically insignificant correspondence to the other matrices in the present study (except the phenotypic matrix, which includes among-population genetic correlations and thus cannot be compared statistically; Table 7). The within-population broad-sense genetic correlation matrix (which also correlates by

definition with the phenotypic matrix) is significantly correlated with the environmental matrix (Table 7). Thus the within-population genetic, environmental, and phenotypic matrices are the most similar while the among-population genetic correlation matrix shows the least correspondence to the others.

We predicted a priori that the following related traits would have higher than average integration: life-history traits, achene and head traits, and size and shape traits. Tighter integration should occur within certain subgroups of these traits as well, such as traits pertaining to central achenes, peripheral achenes, or numbers of each achene type per head (see the introduction for our rationale as to why these groups and subgroups should be more cohesive). The environmental and phenotypic correlation matrices showed highly significant correspondence to the hierarchical hypothesis matrix (Table 8). The mean magnitude of correlations is usually higher for successive subgroupings of traits (Table 8). The within-population broad-sense genetic correlations do not fit the predicted hierarchy of integration as well, though the correspondence was still significant and related traits do tend to have higher correlations than the average correlation of all trait pairs (Table 8). The predicted pattern of integration does not hold at all for the among-population genetic

TABLE 4. Environmental correlations for size, shape, life history, achene, and head characteristics of *Heterosperma pinnatum*.

Trait	Trait						
	LOAWN	LOC	NOC	NOAWN	NACH	NOP	LOP
LOC	0.16						
NOC	-0.04	0.33c					
NOAWN	-0.10	0.22c	0.57d*				
NACH	0.02	0.28c	0.54d*	0.53d*			
NOP	0.11	0.12	0.11b	0.25d*	0.75d*		
LOP	0.22a	0.36d	0.04	0.15c	0.14c	0.01	
WOP	0.10	0.17	0.11a	0.12b	0.32d*	0.29d*	0.04
DFLR	0.22a	-0.12	-0.07	-0.11a	-0.16d	-0.14c	0.04
NHEADS	-0.14	-0.16	0.12	-0.04	0.12	0.13	-0.11
1FRUIT	0.14	-0.15	-0.01	0.02	-0.25b	-0.23a	-0.21
W3WK	0.13	0.21a	-0.05	-0.01	0.12b	0.16c	0.08
H/W3WK	-0.11	0.03	0.02	0.05	0.03	0.02	-0.04
HADULT	0.18	0.34c	0.08	0.08	0.30d*	0.29d*	0.17d
H1BR	0.05	0.10	0.02	0.00	0.01	0.00	0.21d*
NOBR	-0.05	0.18	0.05	0.11a	0.05	0.15c	0.05
BR/H	-0.07	-0.05	-0.03	0.03	0.00	0.02	-0.11a

a, $P < 0.05$; b, $P < 0.02$; c, $P < 0.01$; d, $P < 0.001$ (probabilities for test-wise significances); *, $P < 0.05$ (probability for experiment-wise significances using the Bonferroni test).

correlations. Some subgroups of traits had higher and some lower than average among-population genetic correlations, apparently at random (Table 8). Within- and among-population genetic correlations were generally higher than phenotypic and environmental correlations though this may be in large part due to the higher sampling variances of the former. Individual correlations of particular interest are considered in the discussion. We have decided not to present the correlations for individual populations here, since the results are copious, and there was not much statistical power for genetic correlations of individual populations. Correlations could be high but not significant and none of the genetic correlations differed among populations using the Bonferroni experiment-wise test.

DISCUSSION

Many evolutionary investigations have considered traits one at a time (Endler, 1986). It is clear from our results that to do so for seed and head traits of *H. pinnatum* would be a mistake since there are a number of strong correlations among seed and head traits and of seed and head traits with other less related traits.

To understand life history tradeoffs or other developmental constraints on evolution, people have often studied the corre-

lation structure of phenotypic traits (Olson and Miller, 1958; Grant et al., 1976; Alberch, 1980). Yet we have seen that in *H. pinnatum*, though the phenotypic correlations are often similar to the broad-sense genetic correlations, the matrix correlation, r , between them is only 0.67 (statistics not applicable) and the environmental correlations are not very similar to the genetic correlations ($r = 0.37$, $P < 0.001$). Furthermore, large correlations between unrelated traits are more frequent for broad-sense genetic than for phenotypic correlations. As has been reported in other studies (e.g., Searle, 1961; Cheverud, 1982), the genetic correlations tend to have higher magnitudes than the corresponding phenotypic correlations, though this may be a statistical artifact of smaller error covariance for the latter. The results emphasize the need for genetic studies in evolutionary ecological investigations if the true nature of evolutionary tradeoffs and correlations is to be understood.

When the magnitudes of the correlations in different groups and subgroups of functionally or developmentally related traits were compared, the phenotypic and environmental matrices were found to be the most structured. Related traits such as plant size and shape or life-history traits had higher than average phenotypic and environ-

TABLE 4. Extended.

WOP	Trait							
	DFLR	NHEADS	IFRUIT	W3WK	H/W3WK	HADULT	H1BR	NOBR
-0.09								
-0.06	-0.17							
-0.07	0.37d	-0.09						
0.07	-0.06	-0.22a	-0.10					
0.07	-0.06	0.17	-0.04	-0.30d*				
0.26d*	-0.17d	-0.11	-0.15	0.41d*	0.00			
0.05	-0.08	-0.19	0.12	0.18d	0.04	0.31d*		
0.09	-0.07	0.08	-0.06	-0.05	0.15c	-0.01	-0.17d	
-0.02	0.03	0.25b	0.04	-0.17d	0.09	-0.24d*	-0.19d	0.31d*

mental correlations, as did seed and head traits. Related subgroupings of these traits such as traits involving numbers of achenes had still higher correlations. This hierarchical correlation structure of related traits was not as strongly expressed for the within-population broad-sense genetic correlations (though this matrix did correlate significantly with the hierarchical hypothesis matrix) and was not apparent at all for among-population correlations. The results parallel those of Cheverud (1982) for rhesus monkeys, which showed good correspondence of functionally and developmentally related traits with phenotypic correlation structure, but not with genetic correlation structure. This pattern may imply some sort of physiological cohesiveness of related traits at the modular or organismic level that does not represent an inherent genetic limitation to new character combinations. Since this structuring of correlations of related traits is not at all apparent among populations, under this interpretation, it clearly would not represent a "bauplan" constraining intraspecific evolution. An alternative possibility is that the hierarchical pattern actually does exist for within- and among-population genetic correlations, but is obscured by their greater error covariance. While we think the evidence favors the former interpretation, only larger designs with many more populations could definitively distin-

guish between them. Cowley and Atchley (1990) used a similar approach to ours to see if phenotypic and genetic correlations were higher in *Drosophila melanogaster* for body parts arising from the same imaginal disk than for traits arising from different disks. Both genetic and phenotypic correlations were higher for traits arising from the same disks. While imaginal disks may be meaningful units of integration for holometabolous insects, plants might be expected to have hierarchies of integration reflecting their modular construction. It has long been known that whole plants exhibit high degrees of plasticity in size and shape based on differential repetition of repeated units of structure (leaves, flowers, branch systems), while the individual repeated units are less variable and more highly integrated (Watson and Casper, 1984; White, 1984). It would be interesting to expand the kind of analysis we have done here to more explicitly address the phenotypic and genotypic levels of integration implied by modular construction.

It does not appear that the genetic correlations measured in this study have seriously constrained character combinations during population differentiation. If they had, one would expect the among-population genetic correlations to more closely reflect the within-population genetic constraints, since population divergence in one

TABLE 5. Within-population genetic correlations for size, shape, life history, achene, and head characteristics of *Heterosperma pinnatum*. The upper number is the broad-sense genetic correlation (variance component correlation) and the lower number is the weighted product-moment correlation of family means from which statistics were calculated.

Trait	Trait						
	LOAWN	LOC	NOC	NOAWN	NACH	NOP	LOP
LOC	0.53 0.47						
NOC	0.89 0.72b	0.85 0.79c					
NOAWN	0.93 0.82c	0.76 0.74c	0.11 0.14				
NACH	0.71 0.61a	0.57 0.54	0.30 0.32b	0.43 0.43d			
NOP	0.55 0.46	0.40 0.35	-0.21 -0.17	0.21 0.21	0.73 0.73d*		
LOP	0.09 0.11	0.76 0.72c	0.20 0.20	0.50 0.48d*	0.35 0.32b	0.06 0.06	
WOP	0.06 0.07	0.56 0.50	0.07 0.07	0.26 0.25	0.51 0.48d*	0.47 0.44d*	0.69 0.62d*
DFLR	0.26 0.25	0.53 0.43	0.37 0.33c	-0.02 -0.02	0.03 0.01	-0.09 -0.10	0.01 0.02
NHEADS	-0.72 -0.61a	-0.94 -0.85d	-1.09 -0.89d*	-0.78 -0.71b	-0.68 -0.58	-0.37 -0.27	-0.46 -0.41
1FRUIT	0.32 0.30	0.65 0.59	0.33 0.28	0.58 0.56	0.27 0.23	0.39 0.30	0.70 0.61a
W3WK	0.27 0.24	0.10 0.11	-0.20 -0.19	0.14 0.18	0.27 0.25	0.31 0.29a	0.14 0.13
H/W3WK	0.85 0.66a	0.16 0.14	-0.11 -0.09	0.17 0.15	-0.10 -0.08	-0.16 -0.13	-0.05 -0.05
HADULT	0.73 0.66a	0.57 0.56	0.00 0.06	0.58 0.55d*	0.58 0.54d*	0.35 0.34c	0.36 0.35c
H1BR	0.91 0.79c*	0.59 0.56	0.10 0.10	0.58 0.54d*	0.35 0.30a	0.08 0.07	0.44 0.40c
NOBR	-0.63 -0.53	-0.51 -0.43	0.00 0.01	-0.28 -0.23	0.00 0.03	0.10 0.11	-0.21 -0.17
BR/H	-1.29 -0.77c	-0.38 -0.25	-0.27 -0.23	-0.25 -0.21	-0.32 0.25	-0.02 -0.01	-0.22 -0.20

a, $P < 0.05$; b, $P < 0.02$; c, $P < 0.01$; d, $P < 0.001$ (probabilities for test-wise significances); *, $P < 0.05$ (probability for experiment-wise significances using the Bonferroni test).

trait would result in divergence in a correlated trait [most traits measured have diverged among populations (Venable and Búrquez, 1989)]. Yet we found that the within- and among-population genetic matrices have a very low, non-significant correlation (but see below concerning some specific groups of conservative traits). Again, it is possible that the error covariance of the among-population genetic correlations is so high that it has swamped the true correspondence of the within- and among-population matrices. However, this seems unlikely to us, especially given the close correspondence of the among-population

genetic correlations to an independent measure of among-population correlations.

One caveat should be emphasized. To interpret our correlations as potential constraints on evolution we must assume that additive covariance predominates in our within-population correlations, since only additive covariance constrains traits to co-evolve. It is theoretically possible that epistatic or maternal covariance predominates since these cannot be distinguished from additive covariance with our design. To distinguish additive covariance from any non-additive genetic covariance and maternal-effect covariance in naturally inbred species

TABLE 5. Extended.

Trait								
WOP	DFLR	NHEADS	IFRUIT	W3WK	H/W3WK	HADULT	H1BR	NOBR
-0.06								
-0.07								
-0.45	-0.16							
-0.38	-0.16							
0.22	0.85	-0.20						
0.18	0.75c	-0.18						
-0.08	-0.01	-0.15	0.20					
-0.06	-0.01	-0.16	0.17					
0.14	-0.08	-0.14	0.59	-0.44				
0.12	-0.08	-0.08	0.50	-0.41c				
0.29	0.10	-0.56	0.74	0.45	0.31			
0.29a	0.07	-0.51	0.68a	0.44d*	0.27a			
0.34	0.09	-0.54	0.60	0.19	0.46	0.80		
0.31b	0.08	-0.50	0.57	0.19	0.40c	0.76d*		
-0.11	-0.10	0.70	-0.24	0.05	-0.37	-0.48	-0.59	
-0.07	0.09	0.60	-0.22	0.04	-0.25	-0.40c	-0.52d*	
-0.20	0.01	0.61	-0.42	-0.26	-0.34	0.56	-0.54	0.73
-0.16	0.01	0.44	-0.25	-0.24	-0.24	-0.49d*	-0.47d*	0.62d*

that are more amenable to controlled crosses than *Heterosperma*, we recommend using electrophoresis to determine the level of inbreeding in the population from which the experimental parents are sampled (e.g., Currie-Cohen, 1982). Then a standard crossing design, such as a factorial design, could be applied to generate the progeny generation (see Namkoong, 1979; Hallauer and Miranda, Fo., 1981; or Becker, 1984). The inbreeding coefficient of the parental generation can be used as a correction factor in the calculations of the different biological sources of variation and covariation (e.g., Mitchell-Olds, 1986).

Pollen is located on the inside of each tiny

floral tube of the disk florets of composite heads, and the stigma acts as a piston to present pollen at, or before, the time the stigma is receptive to pollination. Thus it is very difficult, if not impossible, to emasculate the individual disk florets of *H. pinnatum* before they self-pollinate. It is technically possible to remove all disk florets from each head prior to anthesis and utilize only the two to four ray florets per head for outcrossing [as we did to determine compatibility (Venable and Búrquez, 1989)]. However, this rather painstaking procedure (each floret yields one achene, at most) is not very practical for large-scale experiments. This difficulty of performing controlled crosses

TABLE 6. Among-population genetic correlations for size, shape, life history, achene, and head characteristics of *Heterosperma pinnatum*. The upper number is the among-population genetic correlation (variance component correlation) and the lower number is the weighted product-moment correlation of population means from which statistics were calculated.

Trait	Trait										
	NOC	NOAWN	NACH	NOP	LOP	WOP	DFLR	W3WK	HADULT	H1BR	NOBR
NOAWN	0.72										
	0.61										
NACH	-0.52	0.15									
	-0.30	0.22									
NOP	-0.94	-0.43	0.76								
	-0.81a	-0.32	0.73								
LOP	0.59	0.83	-1.03	0.89							
	0.40	0.63	-0.36	-0.49							
WOP	-0.68	-0.11	0.34	0.31	0.00						
	-0.51	-0.02	0.39	0.33	-0.02						
DFLR	0.59	0.81	0.67	-0.21	0.12	0.27					
	0.56	0.71	0.52	-0.19	0.08	0.21					
W3WK	0.15	-0.76	-0.75	-0.18	-0.79	-1.16	-0.69				
	0.08	-0.53	-0.42	-0.08	-0.36	-0.84b	-0.57				
HADULT	-1.03	-1.34	-0.24	0.70	-1.16	-0.06	-0.93	0.47			
	-0.77a	-0.87b	0.02	0.61	-0.45	0.04	-0.75	0.46			
H1BR	-0.63	-0.57	0.68	1.01	-1.35	-0.53	-0.31	0.54	0.52		
	-0.47	-0.31	0.56	0.80a	-0.54	-0.29	-0.25	0.44	0.59		
NOBR	0.21	0.06	-1.09	-0.87	0.98	0.38	-0.20	-0.35	-0.23	-1.03	
	0.17	0.00	-0.75	-0.68	0.47	0.26	-0.18	-0.25	-0.28	-0.90c	
BR/H	-0.04	-0.04	-0.97	-0.59	1.10	0.41	-0.51	-0.18	0.08	-0.81	1.03
	-0.07	-0.07	-0.74	-0.47	0.51	0.25	-0.43	-0.19	-0.08	-0.72	0.93c

a, $P < 0.05$; b, $P < 0.02$; c, $P < 0.01$ (probabilities for test-wise significances; no correlations were significant using the experiment-wise Bonferroni test).

TABLE 7. Correlations among the phenotypic, environmental, within-population genetic, and among-population genetic matrices for size, shape, life history, achene, and head characteristics of *Heterosperma pinnatum*. Pearson product-moment correlations, r ; Spearman's rank correlation, ρ and a modified Kendall's correlation, τ are presented. Probabilities were calculated by comparing observed correlations with a null distribution generated by a permutation procedure (Dietz, 1983).

Type of correlation	Type of correlation			
	Measure of association	Among-population genetic	Within-population genetic	Environmental
Within-population genetic	r	0.16		
	ρ	0.13		
	τ	0.10		
Environmental	r	0.17	0.37*	
	ρ	0.07	0.38*	
	τ	0.04	0.23*	
Phenotypic	r	0.48NA	0.67NA	0.64NA
	ρ	0.47NA	0.69NA	0.59NA
	τ	0.37NA	0.48NA	0.41NA

* $P < 0.001$; NA, statistical test not applicable.

represents a shortcoming of *H. pinnatum* for genetic studies. Indeed, we chose to work with *H. pinnatum* despite these difficulties because of its very interesting variation in seed morphology and behavior.

Some subsets of traits have high within-population broad-sense genetic correlations and among-population correlations. This suggests that the correlations are conservative, since the traits are genetically correlated within populations and, during population differentiation, they have increased or decreased in unison, giving rise to among-population correlations. The number of awned achenes is genetically correlated with the length of peripheral achenes both within and among populations. The length of peripheral achenes was the only achene length trait analyzed for among-population correlations. Yet judging from the high within-population genetic correlations among length of central achenes, length of peripheral achenes, length of awns on central achenes, and number of achenes with awns, there may be some general conservative achene length factor which also results in the production of more and longer awns.

Another set of seed and head correlations that correspond at within- and among-population levels are those between the number of peripheral achenes per head, the width of peripheral achenes, and the total number of achenes per head. This suggests that selection for more peripheral achenes will result in (and has resulted in) wider peripheral

achenes on bigger (more-seeded) heads, or vice versa under selection for more seeds per head. Such genetic correlations may either speed or delay the response to selection depending on the relationship of the traits to fitness and the signs of the correlations. The present example could be argued either way. It has been suggested elsewhere that packaging more achenes into fewer heads may increase the impact of predispersal seed predation (Levin and Turner, 1977; cf. Mitchell, 1977). If this were true in *H. pinnatum*, then selection for more peripheral achenes per head (perhaps due to selection for more dormancy) would result in a correlated predation cost. An alternative scenario is that it might be physiologically less demanding of resources for a plant to supply nutrients or photosynthate to a few many-seeded heads, but the biomechanics of adhesive dispersal by animals makes it desirable to have many small, well-spaced packets of seeds waiting for dispersal agents. If dormancy has a negative selective correlation with dispersal (Venable and Brown, 1988), then the genetic correlation between the total number of achenes per head and the number of peripheral achenes per head should speed the response to selection (i.e., selection for less dormancy would incidentally select for a seed arrangement facilitating dispersal).

Some plant architectural traits are genetically correlated with seed and head traits and with each other both within and among

TABLE 8. Hierarchical correlation structure for size, shape, life history, achene, and head characteristics of *Heterosperma pinnatum*. Mean absolute values of correlations of functionally or developmentally related groups and subgroups of traits are calculated for phenotypic, environmental, within-population genetic, and among-population genetic matrices. The numbers 0, 1, and 2 correspond to the hierarchical level assigned to groups of traits in the hypothesis matrix (Table 2). Correlations of observed matrices to the hypothesis matrix and corresponding probabilities are given for Pearson's product-moment correlation, r ; Spearman's rank correlation, r_{ho} ; and a modified Kendall's correlation, τ_{au} .

Trait group	Group and subgroup means											
	Phenotypic			Environmental			Within-population genetic			Among-population genetic		
	0	1	2	0	1	2	0	1	2	0	1	2
0. All traits	0.19			0.14			0.38			0.42		
1. Achene and head traits	0.28			0.22			0.46			0.65		
2. Numbers of achenes (NOC, NOAWN, NACH, NOP)	0.35			0.46			0.33			0.59		
2. Central achenes (LOAWN, LOC, NOC)	0.43			0.18			0.76			0.59		
2. Peripheral achenes (NOP, LOP, WOP)	0.24			0.11			0.41			0.40		
1. Size and shape												
2. Seedling (H/W3WK, W3WK)	0.27			0.17			0.44			0.35		
2. Adult (HADULT, L1BR, NOBR, BR/H)	0.40			0.21			0.62			0.62		
1. Life history (DFLR, NHEADS, 1FRUIT, NACH)	0.31			0.19			0.38			0.28		
Measure of association	Correlation of observed and hypothesis matrices											
	Phenotypic			Environmental			Within-population genetic			Among-population genetic		
	r	0.46c		0.47c			0.20a			-0.07		
	r_{ho}	0.40c		0.37c			0.21a			-0.06		
τ_{au}	0.26c		0.21c			0.13b			-0.06			

a, $P < 0.02$; b, $P < 0.01$; c, $P < 0.0003$.

populations. Adult height is consistently correlated with the number of peripheral achenes per head and the height above soil level of the first branch. The latter, in turn, is genetically correlated with the total number of achenes per head. The number of branches is uniformly negatively correlated with the height above soil level of the first branch. Adult shape (branch length/adult height) is positively correlated with the number of branches and negatively correlated with the height above soil level of the first branch. These correlations suggest that there is a genetic allocational tradeoff according to which vegetative soma is allocated to vertical growth (the main axis) or lateral growth (more and longer branches).

Several strong within-population correlations that were not analyzed at the among-population level supplement those mentioned above to provide an interpretation of constraints on architecture and reproduction. The number of heads per plant is genetically correlated with the number of branches (because heads terminate branches). This is a genetically based morphological constraint, i.e., selection for more branches should result in more heads and vice versa. The number of heads per plant is negatively correlated with the number of achenes per head (a genetically based life history tradeoff) and, from the previous paragraph, allocation to vertical growth is negatively correlated to the number and length of branches. Thus, short, wide plants with many branches produce many heads with few seeds each. Selection on any part of this pattern should tend to bring along the other parts. These plant shape correlations may be important with respect to the conflicting selective pressures of competition and grazing. Whereas tall plants may be favored in situations of competition for light, grazing is likely to favor shorter plants with a lower height of first branch and more lateral growth (cf. Warwick and Briggs, 1978; Solbrig and Simpson, 1974).

Some trait pairs have strong within-population genetic correlations and were either not analyzed at the among-population level, or had weak among-population correlations. For example, the achene and head correlations suggest a negative genetic cor-

relation between dormancy and dispersal. Central achenes are less dormant than peripheral achenes (Venable et al., 1987), thus selection for less dormancy may favor more central achenes per head. Likewise, the number of awned achenes, and longer awns promote greater dispersibility (Venable et al., 1987). Since these traits are all genetically correlated, selection for more dispersal should favor less dormancy and vice versa. Various theoretical arguments (reviewed in Venable, 1989) and some empirical data (Venable and Lawlor, 1980) suggest that natural selection may favor a negative correlation between dispersal and dormancy. If this is so, then the correlations reported here should speed the response to selection for correlated changes in dormancy and dispersal. Furthermore, this may be an example of a genetic correlation shaped and favored by natural selection (cf. Cheverud, 1984).

The numbers of achenes of each type have high genetic variances (Venable and Búrquez, 1989) and seed morph proportions vary considerably within and among populations (Venable et al., 1987). Yet the numbers of different achene types have relatively low and non-significant genetic correlations with each other, with the exception of the high correlation of the number of peripheral achenes per head with the total number of achenes per head. The average genetic correlation of traits involving numbers of different achene types was lower than the overall average genetic correlation (Table 8). The high genetic variances with comparatively low covariances should permit relatively independent evolution of the numbers of each achene type. This genetic system may account for the large variation in seed ratios among populations.

While a number of these correlations appear to be adaptive or at least to facilitate adaptation, others represent constraints of physiology or development. For example, while there might sometimes be selective reasons to decouple flowering date from fruiting date, these are strongly correlated genetically and environmentally (for obvious developmental reasons). The correlations mentioned above between branch number and number of heads or between

number of achenes per head and number of heads per plant are other examples of constraints of physiology and development.

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