Estimates of heritability and correlations of morphometric traits in *Clarkia* (Onagraceae)

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**Summary.** Interspecific heritability values were estimated using parent-offspring regression analyses for 11 morphological traits differentiating *Clarkia nitens* and *C. speciosa* subsp. *polyantha*. Estimates ranged from near 0 for anther color and germination percentage, to 0.8 for calyx length and petal tip color. Phenotypic, genetic, and environmental correlation matrices were computed to determine the extent of interspecific correlations of traits. Cluster analyses of the genetic and environmental correlation matrices each resulted in three clusters of correlated traits; however, the clusters derived from the two matrices were different. The clusters produced by analysis of the environmental correlation matrix were similar to the factors obtained from principal component analysis of the phenotypic correlation matrix. Genetic correlations may result from strong linkage due to interspecific chromosomal differences.

**Key words:** Parent-offspring regression – Multivariate analysis – Cluster analysis – Principal component analysis – *Clarkia*

**Introduction**

Closely-related species are often differentiated by several morphological traits, which may form suites of characters having functional or developmental significance. Studies of intra- and interspecific variation in plants have demonstrated such interrelationships among morphological characters, using phenotypic correlations and multivariate techniques such as principal component analysis (Clausen and Hiesey 1960; Hiesey et al. 1971; Grant 1979; Grant and Grant 1979; Gil-martin 1980; Holsinger 1985). However, more information could be obtained by partitioning the phenotypic correlations into their genetic and environmental components, as has been accomplished in several studies of character coherence in animals (Leamy 1977; Arnold 1981; Boag 1983). Investigations of genetic and environmental correlations have elucidated the genetic relationships among the traits and have revealed functional assemblages of characters. This study examines the genetic relationships among 11 interspecific morphological differences in two *Clarkia* species by estimating the heritability of each trait and the genetic and environmental correlations among pairs of traits.

Heritability values reflect the proportion of additive genetic variance for a trait and indicate the degree to which the trait is genetically determined. High heritability values indicate a large additive genetic component, relative to dominance, epistatic, and environmental components, in the expression of a trait. Heritability estimates also suggest the degree to which selection acts on a trait. Generally, those traits with lower heritabilities are closely connected with reproductive fitness (Fisher 1958). In contrast, traits with higher heritability values usually are less important as components of fitness. Therefore, heritability estimates may be useful in evaluating the role of selection in populations and species (Arnold 1981; Boag 1983; Stearns 1983).

Correlations of traits have both genetic and environmental sources. The genetic correlation ($r_A$) is the correlation of breeding values, whereas the environmental correlation ($r_E$) includes environmental deviations and non-additive genetic factors (Falconer 1981). Correlations of traits are of evolutionary interest for two primary reasons. First, the genetic mechanisms of correlation, such as linkage and pleiotropy, may be elucidated. Although pleiotropy is typically regarded as a more potent cause of genetic correlation (Nagylaki and Crow 1974; Falconer 1981), linkage may also contribute to temporary character associations. Secondly,
correlations of traits may be useful in predicting response to selection. Selection on one trait may cause a correlated response in another. Therefore, understanding the genetic basis of the character association may provide insights as to the direction evolution may take in a population or species.

**Taxa**

Investigation of a species complex in *Clarkia* (Onagraceae) suggested that examination of the morphological differences between *C. niens* and *C. speciosa* subsp. *polyantha* might provide insights into the genetics and evolution of interspecific character assemblages. These taxa are closely-related members of Section *Godetia* (Lewis and Lewis 1955), and although superficially very similar morphologically (Lewis and Lewis 1955), *C. niens* and *C. speciosa* subsp. *polyantha* show significant differences (*P* < 0.05) for 20 of 32 morphological and developmental traits examined (Soltis 1985). Most notable are differences in floral color and floral size. These interspecific differences were evaluated by estimation of heritabilities to determine the degree of genetic control of these traits and by examination and clustering of genetic and environmental correlations to reveal assemblages of traits.

**Materials and methods**

**Plants**

Samples from two populations of *Clarkia niens* and two populations of *C. speciosa* subsp. *polyantha* were grown in a greenhouse located at the University of Kansas, Lawrence, Kansas. All plants were scored for the following 11 traits:

- **ANTC** Anther color
- **STYL** Style length
- **SAD** Stigma-anther distance
- **FLA** Filament length (large stamens)
- **CALL** Calyx length
- **HYPW** Hypanthium width
- **PETW** Petal width
- **PETB** Petal base color
- **GERP** Germination percentage
- **TIPC** Petal tip color
- **STIC** Stigma color

These traits showed highly significant differences (*P* < 0.001) between the two taxa (Soltis 1985).

Twenty individuals from each of the four populations served as parents and were crossed in nearly 400 interspecific combinations to produce *F*₁ offspring. The *F*₁ progeny were grown the following spring and summer.

**Estimation of heritability**

Interspecific heritability values for each trait were estimated by regression analyses of offspring on male parent, female parent, and mid-parent values (Falconer 1981). The slope of the regression of offspring on male or female parent values equals one half the narrow-sense heritability for that trait. The regression coefficient of offspring on mid-parent values directly estimates narrow-sense heritability. The regression of offspring on mid-parent values is most reliable, because it reduces bias in the form of maternal effects (Falconer 1981). However, it can only be used accurately when the parental variances for a trait are equal (Falconer 1981). *F*ₘₐₓ tests for homogeneity of variances indicated that all traits had equal parental variances except anther color, petal base color, and stigma color (Soltis 1985). Standard errors (se) for all heritability (*h*²) estimates were calculated using the standard errors of the regression coefficients (Sokal and Rohlf 1981). For estimates based on the regression of offspring on one parent,

\[
\text{se} (h^2) = 2 \left( \text{se} (b) \right),
\]

where \( b = \) the regression coefficient. The standard error for estimates derived from the regression of offspring on mid-parent is

\[
\text{se} (h^2) = \text{se} (b).
\]

Sixty pairs of parent-offspring data were used to estimate heritability values. Because no segregating generations were involved in the analyses, linkage due to interspecific chromosomal differentiation should have no effect on the results.

**Calculation of phenotypic, genetic, and environmental correlations**

Phenotypic correlations among pairs of the 11 traits were generated using all individuals in the parental samples. The matrices of genetic and environmental correlations were calculated as outlined by Falconer (1981), using the heritability values estimated by the regression of offspring on mid-parent values. The additive genetic correlations for each pair of traits were calculated by the following formula:

\[
r_A = \frac{\text{COV}_{xy}}{\sqrt{\text{COV}_{xx} \text{COV}_{yy}}},
\]

where \( x \) and \( y \) are the two traits under consideration, \( \text{COV}_{xy} \) is the covariance of the two traits in the parents and offspring, and \( \text{COV}_{xx} \) and \( \text{COV}_{yy} \) are the offspring-parent covariances of each trait. Standard errors of the genetic correlations were calculated as follows (Reeve 1955; Robertson 1959; Falconer 1981):

\[
\text{se} (r_A) = \frac{1 - r_A^2}{\sqrt{2}} \sqrt{\frac{\text{se} (h_1^2) \text{se} (h_2^2)}{h_1^2 h_2^2}},
\]

where \( h_1^2 \) and \( h_2^2 \) equal the heritability estimates of traits \( x \) and \( y \), respectively, and \( \text{se} (h_1^2) \) and \( \text{se} (h_2^2) \) equal the standard errors of these heritability estimates.

Environmental correlations for each pair of characters were calculated from Falconer (1981) by the following:

\[
r_E = h_1 h_2 r_A + c_1 c_2 r_F,
\]

where \( r_E \) equals the phenotypic correlation of traits \( x \) and \( y \), \( h_1 \) and \( h_2 \) are square roots of the heritabilities of traits \( x \) and \( y \), and \( c_1 \) and \( c_2 \) are correlation coefficients between the two traits in the parents and offspring.

**Clustering**

A powerful multivariate technique for describing the internal structure of a set of variables is principal component analysis. A PCA was conducted on the phenotypic correlation matrix to