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Quantitative analysis of correlations among flower traits in *Gerbera hybrida*, Compositae. III. Genetic variability and structure of principal component traits

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Abstract A sample of 36 flower traits consisting of six morphological categories in the Davis population of gerbera was restructured into phenotypic and genetic principal component traits. The first 5 phenotypic principal component traits accounted for 62% of the total phenotypic variance of the 36 traits and have moderate to high heritabilities. The first 5 genetic principal component traits account for 97% of total genetic variance and all have high heritability. Morphological structure of these component traits suggest an underlying process identified by the first genetic principal component involving largely trans and disk floret traits. The results of this study indicate that the quantitative genetic structure of the gerbera flower is controlled by a few independent components and that principal component analysis is a useful tool to reveal variation in this structure. These composite traits are heritable and are expected to respond to selection.

Key words Principal component analysis · Genetic correlation · Heritability · Selection

Introduction

A relatively high degree of phenotypic and genetic correlation among 38 flower traits in the Davis population of *Gerbera* was reported in the first paper of this series (Harding et al. 1990). If selection is applied to this population, these genetic correlations will lead to many correlated responses (Huang et al. 1990). However,

these correlations may result from common underlying developmental processes that determine the structure of the gerbera flower and its component traits. Thus, identifying these processes will increase our understanding of the phenotypic and genetic structures of the gerbera flower. This is critical if we are to understand the complex responses of many traits to selection for flower quality in gerbera.

An underlying process can be represented by a composite trait, usually a linear combination of the original traits. Principal component analysis is used to identify such underlying processes by restructuring the original traits into composite traits (Harding et al. 1991). It has been widely used in biological research (James and McCulloch 1990; Iezzoni and Pritts 1991), and in plant breeding it has been used to cluster parents (Rashal and Mutsenietse 1985) and as a selection index (Godshalk and Timothy 1988).

The purpose of the study reported here was to identify the major underlying processes among the correlated flower traits in the Davis population of gerbera using principal components, to study their genetic variability and heritability, to examine the morphological structure of these composite traits, and to explore the uses of principal components in the genetic improvement of the gerbera flower.

Materials and methods

The data analysis in this study was based on the phenotypic and genetic correlation matrices of the 38 traits presented in the first paper of this series (Harding et al. 1987) and the heritability vector reported by Drennan et al. (1986). These traits include the following six categories: inflorescence, receptacle/involucre, scape, disk floret, ray floret, and transitional floret. Descriptions of these traits are presented in Appendix 1. Because traits 24 and 25 in the disk floret category, i.e., length of outer and inner corolla lobe of the disk floret, had heritability estimates greater than 1, they were deleted from the analysis. Therefore, 36 of the original 38 traits were analyzed in this study.

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In order to eliminate scale effects, we standardized phenotypic values for each trait by dividing by its standard deviation; consequently, the phenotypic covariance matrix (P) for the standardized traits became the correlation matrix, and the genetic covariance matrix (G) became the products of the genetic correlation matrix and the matrices of square roots of heritabilities, i.e.,

$$P = R_p$$

$$G = HR_gH$$

where R_p is the phenotypic correlation matrix, R_g the genetic correlation matrix, and H is a diagonal matrix in which the elements are the square roots of the heritabilities.

Principal component trait (PC)

The first principal component for a set of traits X_1, X_2, \dots , and X_n is the linear combination,

$$PC = a_1X_1 + a_2X_2 + \dots + a_nX_n$$

where coefficients form a unit vector obtained by maximizing the variance of the linear combination. Mathematically, the variances and coefficient vectors of principal components are the eigenvalues and the corresponding eigenvectors of the covariance matrix. The largest eigenvalue is the variance of the first principal component, the second largest eigenvalue is the variance of the second principal component, and so on (Anderson 1958). All principal components are uncorrelated. The total variance of the original traits is equal to the sum of the eigenvalues. The coefficient of a trait in a principal component is the regression coefficient of this trait on the principal component. Thus, the magnitude of a coefficient in the linear function represents the importance of the original trait on this PC. Traits in this study are organized into morphological categories, and we use the square root of mean squares of the coefficients for all of the traits in that category to estimate a category mean. This provides a measure of the average effect of traits in a morphological category on the PC.

If the traits are highly correlated, variances of the first few principal components will account for much of the total variance of the original traits. Principal component analysis can be performed on either the phenotypic covariance matrix ($P = R_p$) or the genetic covariance matrix ($G = HR_gH$). The genetic principal components (PC_g) represent the underlying genetic processes which cause the correlation among the traits and reflect the genetic relationship that will contribute to selection response. The phenotypic principal components (PC_p) include both genetic effects and environmental noise. However, estimates of PC_p have smaller standard errors, so we will estimate principal components in both ways.

Heritabilities of PC_p

Variance components can be obtained from the phenotypic and genetic covariance matrixes. The variance for a phenotypic principal component trait (PC_p) is the corresponding eigenvalue (λ_p) of the phenotypic covariance matrix, i.e.,

$$\text{Var}_p(PC_p) = \lambda_p$$

while the genetic variance corresponding to this PC_p is derived from

$$\text{Var}_g(PC_p) = c'Gc$$

where c is the coefficient vector. Therefore, the heritability for a phenotypic component trait is

$$h_p^2 = (c'Gc)/\lambda_p$$

Heritabilities of PC_g

The genetic variance of a genetic principal component trait (PC_g) is the eigenvalue (λ_g) of genetic covariance matrix,

$$\text{Var}_g(PC_g) = \lambda_g$$

The phenotypic variance corresponding to this PC_g is derived from

$$\text{Var}_p(PC_g) = b'Pb$$

where b is the coefficient vector. Therefore, the heritability for a PC_g is

$$h_g^2 = \lambda_g/(b'Pb)$$

Genetic correlation between a PC_p and the individual traits

The genetic covariance between a PC_p and individual trait i is

$$\text{Cov}_g(PC_p, X_i) = \alpha'_i Gc$$

where $\alpha'_i = (0, 0, \dots, 0, 1, 0, \dots, 0)$ where 1 is the i th element in the vector. Therefore, the genetic correlation is

$$\text{Corr}_g(PC_p, X_i) = \frac{\alpha'_i Gc}{\sqrt{c'Gc\sigma_{g_{x_i}}}}$$

where $\sigma_{g_{x_i}}$ is the genetic standard deviation for trait i .

Genetic correlation between a PC_g and the individual traits

Similarly, the genetic correlation between a PC_g and original trait i is

$$\text{Corr}_g(PC_g, X_i) = \frac{\alpha'_i Gb}{\sqrt{b'Gb\sigma_{g_{x_i}}}} = \frac{\alpha'_i Gb}{\sqrt{\lambda_g\sigma_{g_{x_i}}}}$$

Generalized heritability

The idea of heritability for a single trait can be generalized to a set of traits. A generalized variance for a set of variables can be defined as the trace of the variance-covariance matrix which is also equal to the sum of all the eigenvalues of the matrix (Johnson and Wichern 1988). Therefore, a generalized heritability for a set of traits can be defined as the ratio of the generalized genetic variance over the generalized phenotypic variance or the ratio of total genetic eigenvalues over the total phenotypic eigenvalues. This becomes the average of the heritabilities for the 36 traits in this study because the phenotypic data were standardized.

Results

Eigenvalues of the phenotypic covariance matrix (P) and the genetic covariance matrix (G) are listed in Table 1 from the largest to the smallest. Eigenvalues for matrix P , the phenotypic variances for the PC_p , vary from 9.20 to 0.04. The first eigenvalue is 26% of the total variance, and the sum of first 5 eigenvalues is 22.25, which accounts for 62% of the total variance of the 36 traits. The eigenvalues for the matrix G , the genetic variances for PC_g , vary from 5.26 to -0.87 ; the negative eigenvalues are due to sampling error and are generally small in absolute value. The sum of all genetic

Table 1 Eigenvalues of the phenotypic and the genetic covariance matrixes^a

| Principal component | Phenotypic | Genetic | Principal component | Phenotypic | Genetic |
|---------------------|------------|---------|---------------------|------------|---------|
| 1 | 9.20 | 5.26 | 19 | 0.36 | -0.19 |
| 2 | 4.83 | 4.43 | 20 | 0.35 | 0.16 |
| 3 | 3.95 | 2.50 | 21 | 0.31 | 0.14 |
| 4 | 2.39 | 1.88 | 22 | 0.28 | -0.12 |
| 5 | 1.89 | 1.23 | 23 | 0.24 | -0.12 |
| 6 | 1.69 | -0.87 | 24 | 0.22 | 0.12 |
| 7 | 1.24 | 0.81 | 25 | 0.19 | 0.10 |
| 8 | 1.14 | -0.70 | 26 | 0.17 | -0.09 |
| 9 | 0.97 | 0.67 | 27 | 0.16 | -0.08 |
| 10 | 0.96 | 0.56 | 28 | 0.14 | 0.07 |
| 11 | 0.92 | -0.49 | 29 | 0.13 | 0.05 |
| 12 | 0.74 | 0.45 | 30 | 0.12 | -0.04 |
| 13 | 0.61 | 0.33 | 31 | 0.10 | -0.03 |
| 14 | 0.55 | -0.26 | 32 | 0.09 | -0.03 |
| 15 | 0.53 | 0.25 | 33 | 0.06 | 0.02 |
| 16 | 0.48 | -0.23 | 34 | 0.06 | -0.02 |
| 17 | 0.45 | 0.23 | 35 | 0.05 | 0.01 |
| 18 | 0.40 | -0.20 | 36 | 0.04 | -0.001 |
| | | | Sum | 36.00 | 15.77 |

^aNote that phenotypic and genetic eigenvalues of a given number (e.g., PC_p1 and PC_g1) are not related

eigenvalues is 15.77; the first genetic eigenvalue is 5.26, which is 33% of the total genetic variance, and the sum of the first 5 genetic eigenvalues is 15.28, which accounts for 97% of the total genetic variance. Estimates of variance components and heritabilities for PC_p and PC_g are listed in Table 2. The generalized heritability for the 36 traits is 0.44.

The first 3 phenotypic and genetic principal components are studied in detail. The coefficients for the first 3 PC_p on the original traits are listed in Table 3 along with the genetic correlations between the PC_p and the original traits. Heritabilities for the original traits are also listed in the Table. The coefficients for the first 3 PC_g on the original traits are listed in Table 4 along with the genetic correlations between the PC_g and the original traits.

The category means, i.e., the average coefficients of the PC on the morphological categories, are listed in Table 5. For the phenotypic principal component, PC_p1, category means vary from 0.14 to 0.24; for PC_p2, category means vary from 0.05 to 0.21, and for PC_p3, category means vary from 0.08 to 0.23. For genetic principal components, PC_g1 has category means from 0.03 to 0.26; PC_g2 has category means from 0.10 to 0.26, and PC_g3 has category means from 0.08 to 0.26. The overall category mean for each PC is 0.17 since the coefficient vector is a unit vector.

Discussion

Principal component analysis of 36 flower traits in the Davis population of gerbera explains much of the variation among these correlated traits. The first

Table 2 Estimates of variance component and heritabilities for phenotypic principal component traits (PC_p) and genetic principal component traits (PC_g)

| PC | Phenotypic | | | Genotypic | | |
|----|----------------|----------------|----------------|----------------|----------------|----------------|
| | V _p | V _g | h ² | V _p | V _g | h ² |
| 1 | 9.20 | 3.69 | 0.40 | 6.09 | 5.26 | 0.86 |
| 2 | 4.83 | 2.80 | 0.58 | 5.41 | 4.43 | 0.82 |
| 3 | 3.95 | 3.47 | 0.88 | 3.38 | 2.50 | 0.74 |
| 4 | 2.39 | 1.34 | 0.56 | 2.13 | 1.88 | 0.88 |
| 5 | 1.89 | 1.22 | 0.65 | 1.95 | 1.23 | 0.63 |
| 6 | 1.69 | 0.74 | 0.44 | 2.00 | -0.87 | -0.44 |
| 7 | 1.24 | 0.60 | 0.48 | 1.29 | 0.81 | 0.62 |
| 8 | 1.14 | 0.17 | 0.15 | 1.69 | -0.70 | -0.42 |
| 9 | 0.97 | 0.28 | 0.29 | 0.96 | 0.67 | 0.70 |
| 10 | 0.96 | 0.23 | 0.24 | 1.00 | 0.56 | 0.55 |
| 11 | 0.92 | 0.25 | 0.28 | 0.92 | -0.49 | -0.53 |
| 12 | 0.74 | 0.13 | 0.17 | 0.62 | 0.45 | 0.73 |
| 13 | 0.61 | 0.04 | 0.07 | 0.72 | 0.33 | 0.46 |
| 14 | 0.55 | 0.22 | 0.41 | 0.45 | -0.26 | -0.58 |
| 15 | 0.53 | 0.03 | 0.06 | 0.47 | 0.25 | 0.53 |
| 16 | 0.48 | 0.14 | 0.28 | 0.49 | -0.23 | -0.47 |
| 17 | 0.45 | 0.13 | 0.28 | 0.69 | 0.23 | 0.34 |
| 18 | 0.40 | 0.08 | 0.20 | 0.45 | -0.20 | -0.45 |
| 19 | 0.36 | 0.12 | 0.33 | 0.51 | -0.19 | -0.37 |
| 20 | 0.35 | 0.02 | 0.06 | 0.38 | 0.16 | 0.42 |
| 21 | 0.31 | -0.01 | -0.02 | 0.51 | 0.14 | 0.28 |
| 22 | 0.28 | 0.05 | 0.19 | 0.42 | -0.12 | -0.29 |
| 23 | 0.24 | 0.04 | 0.15 | 0.37 | -0.12 | -0.31 |
| 24 | 0.22 | -0.08 | -0.34 | 0.38 | 0.12 | 0.30 |
| 25 | 0.19 | 0.01 | 0.07 | 0.29 | 0.10 | 0.34 |
| 26 | 0.17 | 0.03 | 0.17 | 0.34 | -0.09 | -0.25 |
| 27 | 0.16 | 0.01 | 0.06 | 0.20 | -0.08 | -0.40 |
| 28 | 0.14 | 0.02 | 0.14 | 0.38 | 0.06 | 0.17 |
| 29 | 0.13 | 0.01 | 0.08 | 0.25 | 0.05 | 0.19 |
| 30 | 0.12 | 0.00 | 0.01 | 0.16 | -0.04 | -0.25 |
| 31 | 0.10 | -0.01 | -0.08 | 0.24 | -0.03 | -0.14 |
| 32 | 0.09 | -0.00 | -0.04 | 0.20 | -0.03 | -0.14 |
| 33 | 0.06 | -0.00 | -0.02 | 0.19 | 0.02 | 0.12 |
| 34 | 0.06 | -0.01 | -0.23 | 0.15 | -0.02 | -0.10 |
| 35 | 0.05 | -0.00 | -0.04 | 0.18 | 0.01 | 0.08 |
| 36 | 0.04 | 0.00 | 0.02 | 0.16 | -0.00 | -0.01 |

Table 3 The coefficients for PC_p on the original traits and the genetic correlation between PC_p and the original traits

| Original trait | h ² | PC _p 1 | | PC _p 2 | | PC _p 3 | |
|----------------|----------------|-------------------|-------------|-------------------|-------------|-------------------|-------------|
| | | Coefficient | Correlation | Coefficient | Correlation | Coefficient | Correlation |
| 1 | 0.26 | 0.19 | 0.50 | 0.19 | 0.28 | -0.19 | -0.05 |
| 2 | 0.55 | 0.18 | 0.42 | 0.25 | 0.77 | 0.19 | 0.70 |
| 3 | 0.12 | 0.20 | 0.02 | -0.11 | -0.44 | -0.05 | -0.27 |
| 4 | 0.21 | 0.01 | -0.04 | -0.28 | -0.83 | 0.01 | -0.21 |
| 5 | 0.16 | 0.14 | 0.09 | 0.14 | 0.16 | -0.05 | 0.91 |
| 6 | 0.16 | 0.17 | 0.54 | 0.18 | -0.23 | -0.19 | -0.58 |
| 7 | 0.17 | 0.17 | 0.44 | -0.10 | -0.86 | 0.10 | 0.48 |
| 8 | 0.37 | 0.13 | 0.86 | -0.21 | -0.29 | 0.04 | 0.06 |
| 9 | 0.25 | 0.20 | 0.68 | 0.10 | 0.04 | -0.18 | -0.23 |
| 10 | 0.49 | 0.21 | 0.60 | 0.08 | 0.05 | -0.21 | -0.29 |
| 11 | 0.50 | 0.26 | 0.77 | 0.08 | 0.14 | -0.16 | -0.28 |
| 12 | 0.42 | 0.22 | 0.73 | 0.23 | 0.45 | -0.08 | 0.21 |
| 13 | 0.33 | 0.07 | 0.67 | 0.06 | 0.76 | 0.05 | 0.39 |
| 14 | 0.43 | 0.25 | 0.55 | -0.05 | -0.49 | -0.20 | -0.54 |
| 15 | 0.39 | 0.23 | 0.79 | -0.06 | -0.46 | -0.17 | -0.48 |
| 16 | 0.39 | 0.23 | 0.59 | -0.04 | -0.36 | -0.20 | -0.60 |
| 17 | 0.21 | -0.00 | -0.22 | -0.07 | -0.18 | -0.10 | -0.70 |
| 18 | 0.63 | 0.12 | 0.59 | -0.19 | -0.39 | 0.24 | 0.58 |
| 19 | 0.44 | 0.14 | 0.16 | -0.15 | -0.35 | 0.27 | 0.77 |
| 20 | 0.46 | 0.00 | -0.29 | -0.07 | -0.35 | -0.18 | -0.81 |
| 21 | 0.86 | 0.23 | 0.94 | -0.13 | -0.15 | 0.17 | 0.40 |
| 22 | 0.46 | 0.13 | 0.13 | -0.20 | -0.53 | 0.20 | 0.32 |
| 23 | 0.76 | 0.12 | 0.30 | 0.17 | 0.53 | 0.23 | 0.72 |
| 26 | 0.28 | 0.19 | 0.31 | -0.06 | 0.01 | -0.08 | -0.31 |
| 27 | 0.37 | 0.19 | 0.33 | -0.11 | -0.37 | -0.06 | -0.21 |
| 28 | 0.80 | 0.22 | 0.92 | -0.21 | -0.40 | 0.05 | -0.10 |
| 29 | 0.24 | 0.08 | 0.08 | -0.27 | -0.50 | 0.12 | 0.14 |
| 30 | 0.40 | 0.13 | 0.34 | 0.04 | -0.22 | -0.06 | 0.02 |
| 31 | 0.28 | 0.16 | -0.09 | -0.20 | -0.51 | -0.05 | -0.46 |
| 32 | 0.70 | 0.13 | 0.15 | 0.19 | 0.55 | 0.13 | 0.43 |
| 33 | 0.22 | 0.01 | -0.04 | -0.01 | -0.49 | -0.15 | -0.67 |
| 34 | 0.81 | 0.23 | 0.91 | -0.18 | -0.41 | 0.07 | 0.05 |
| 35 | 0.22 | 0.13 | 0.63 | -0.18 | 0.38 | 0.20 | 0.69 |
| 36 | 0.73 | 0.11 | 0.34 | 0.26 | 0.75 | 0.30 | 0.84 |
| 37 | 0.87 | 0.13 | 0.33 | 0.27 | 0.85 | 0.29 | 0.77 |
| 38 | 0.86 | 0.16 | 0.46 | 0.24 | 0.79 | 0.25 | 0.72 |

phenotypic PC explain 62% of the total variation, while the first 5 genetic PC explain 97%. The generalized heritability for all of the traits was 44%. Therefore, the first 5 genetic PC account for 43% of the total genetic variation for the 36 traits.

Genetic variability of principal component traits

Estimates of the genetic variances for phenotypic PC increase as their phenotypic variances (the eigenvalues) increase. The correlation coefficient between the genetic variances and the phenotypic variances is 0.93. Estimates of heritabilities for the first 5 phenotypic PC are moderate to high, but the correlation coefficient between estimates of heritabilities and the eigenvalues is only 0.57. The first phenotypic PC has a heritability of only 0.40, the second phenotypic PC has a heritability of 0.58, and the third phenotypic PC has the largest heritability of 0.88.

A similar pattern is obtained for the genetic PC. The correlation between the genetic variances (the eigenvalues) and the phenotypic variances is 0.90, but the correlation coefficient between estimates of heritabilities and the eigenvalues is only 0.69. Estimates of heritabilities for the first 5 genetic PC are all very high. PC_g4 has the largest heritability of 0.88.

Genetic PC maximize the genetic variance and phenotypic PC maximize the phenotypic variance. Therefore, neither genetic nor phenotypic PC would be expected to maximize heritability. However, breeders are interested in both larger heritability and larger genetic variance. In this study, the third phenotypic PC and the first genetic PC satisfy these criteria. Although PC_g4 has the largest heritability, its genetic variance as well as its phenotypic variance are quite small.

Even though the first PC, PC_g1 or PC_p1, has maximum variance, selection may not achieve the maximum response. To obtain maximum response on a PC, we should use an optimum index (Baker 1986) which

Table 4 The coefficients for PC_g on the original traits and the genetic correlation between PC_g and the original traits

| Original trait | h ² | PC _g 1 | | PC _g 2 | | PC _g 3 | |
|----------------|----------------|-------------------|-------------|-------------------|-------------|-------------------|-------------|
| | | Coefficient | Correlation | Coefficient | Correlation | Coefficient | Correlation |
| 1 | 0.26 | 0.09 | 0.39 | 0.05 | 0.19 | 0.17 | 0.33 |
| 2 | 0.55 | 0.27 | 0.82 | -0.15 | -0.43 | 0.06 | 0.12 |
| 3 | 0.12 | -0.04 | -0.26 | 0.05 | 0.28 | -0.04 | -0.19 |
| 4 | 0.21 | -0.09 | -0.43 | 0.09 | 0.40 | -0.14 | -0.48 |
| 5 | 0.16 | 0.10 | 0.55 | -0.07 | -0.39 | -0.19 | -0.73 |
| 6 | 0.16 | 0.01 | 0.07 | 0.12 | 0.65 | 0.11 | 0.43 |
| 7 | 0.17 | 0.08 | 0.43 | 0.12 | 0.63 | -0.20 | -0.78 |
| 8 | 0.37 | 0.14 | 0.52 | 0.19 | 0.66 | -0.05 | -0.14 |
| 9 | 0.25 | 0.10 | 0.45 | 0.14 | 0.59 | 0.15 | 0.47 |
| 10 | 0.49 | 0.11 | 0.36 | 0.19 | 0.56 | 0.25 | 0.57 |
| 11 | 0.50 | 0.14 | 0.45 | 0.18 | 0.53 | 0.26 | 0.58 |
| 12 | 0.42 | 0.21 | 0.74 | 0.05 | 0.15 | 0.15 | 0.37 |
| 13 | 0.33 | 0.18 | 0.72 | -0.16 | -0.24 | 0.13 | 0.35 |
| 14 | 0.43 | 0.01 | 0.03 | 0.27 | 0.86 | 0.07 | 0.17 |
| 15 | 0.39 | 0.05 | 0.18 | 0.26 | 0.89 | 0.10 | 0.25 |
| 16 | 0.39 | 0.02 | 0.06 | 0.25 | 0.85 | 0.13 | 0.33 |
| 17 | 0.21 | -0.10 | -0.48 | 0.08 | 0.35 | 0.06 | 0.21 |
| 18 | 0.63 | 0.20 | 0.58 | 0.13 | 0.33 | -0.36 | -0.71 |
| 19 | 0.44 | 0.10 | 0.36 | -0.03 | -0.10 | -0.39 | -0.94 |
| 20 | 0.46 | -0.17 | -0.57 | 0.14 | 0.43 | 0.12 | 0.27 |
| 21 | 0.86 | 0.32 | 0.80 | 0.24 | 0.54 | -0.18 | -0.30 |
| 22 | 0.46 | 0.01 | 0.05 | 0.05 | 0.14 | -0.38 | -0.88 |
| 23 | 0.76 | 0.28 | 0.74 | -0.13 | -0.31 | -0.00 | -0.00 |
| 26 | 0.28 | 0.04 | 0.19 | 0.12 | 0.46 | 0.21 | 0.63 |
| 27 | 0.37 | 0.02 | 0.06 | 0.15 | 0.50 | 0.05 | 0.12 |
| 28 | 0.80 | 0.19 | 0.50 | 0.36 | 0.85 | -0.03 | -0.06 |
| 29 | 0.24 | -0.00 | -0.02 | 0.06 | 0.26 | -0.26 | -0.84 |
| 30 | 0.40 | 0.07 | 0.25 | 0.12 | 0.39 | 0.06 | 0.14 |
| 31 | 0.28 | -0.10 | -0.43 | 0.08 | 0.33 | -0.03 | -0.08 |
| 32 | 0.70 | 0.16 | 0.43 | -0.17 | -0.44 | 0.14 | 0.27 |
| 33 | 0.22 | -0.09 | -0.45 | 0.11 | 0.49 | -0.02 | -0.05 |
| 34 | 0.81 | 0.22 | 0.57 | 0.34 | 0.79 | -0.10 | -0.17 |
| 35 | 0.22 | 0.18 | 0.88 | -0.01 | -0.02 | -0.10 | -0.33 |
| 36 | 0.73 | 0.30 | 0.82 | -0.21 | -0.52 | 0.02 | 0.03 |
| 37 | 0.87 | 0.33 | 0.81 | -0.24 | -0.55 | 0.08 | 0.14 |
| 38 | 0.86 | 0.34 | 0.85 | -0.18 | -0.41 | 0.11 | 0.18 |

Table 5 Average coefficients of principal components on morphological categories

| Morphological categories for original traits | Principal component traits | | | | | |
|--|----------------------------|-------------------|-------------------|-------------------|-------------------|-------------------|
| | Phenotypic | | | Genetic | | |
| | PC _p 1 | PC _p 2 | PC _p 3 | PC _g 1 | PC _g 2 | PC _g 3 |
| Flower | 0.16 | 0.20 | 0.14 | 0.13 | 0.10 | 0.12 |
| Receptacle/involucre | 0.19 | 0.14 | 0.13 | 0.14 | 0.14 | 0.18 |
| Scape | 0.24 | 0.05 | 0.19 | 0.03 | 0.26 | 0.10 |
| Disk floret | 0.13 | 0.15 | 0.21 | 0.20 | 0.13 | 0.26 |
| Ray floret | 0.16 | 0.17 | 0.08 | 0.11 | 0.17 | 0.14 |
| Trans floret | 0.14 | 0.21 | 0.23 | 0.26 | 0.21 | 0.08 |

maximizes the correlation between the index and the PC. There are two additional concerns. (1) principal components may be different in different generations because phenotypic and genetic covariance matrices may be subject to change from generation to genera-

tion. This could lead to conflicting explanations of underlying genetic processes. (2) Genetic eigenvalues could be negative if the genetic variance-covariance matrix is not positive definite. Hill and Thompson (1978) discussed the probability that a genetic matrix is

non-positive definite. Means to overcome these problems include sampling more generations, increasing data per generation, and using more efficient methods of estimating variance components (e.g., Mixed model methodology; Henderson 1984).

Structure of principal component traits

Phenotypic

The first three PC_p include 50% of the total phenotypic variance of the 36 traits, and PC_{p1} accounts for 26% of the total phenotypic variance. Its heritability is only 0.40, and its structure is indicated by large category means of 0.24 for scape traits and 0.19 for receptacle/involucre traits. These traits include the more vegetative characteristics of the flower with less influence from the floret categories. In spite of high variance, the moderate heritability suggests this PC will respond slowly to selection.

PC_{p2} accounts for 13% of the phenotypic variance, and its heritability is 0.58. The structure of this PC is indicated by category means of 0.21 for trans floret traits, 0.20 for flower traits, and 0.17 for ray floret traits. These traits generally measure the size of the flowers or the size of the larger ray and trans florets that make up the flowers. The substantial variance for PC_{p2} and its high heritability suggest a rapid response to selection.

PC_{p3} accounts for 11% of the phenotypic variance, and its heritability is 0.88. The structure of this PC is indicated by category means of 0.23 for trans floret traits, 0.21 for disk floret traits, and 0.19 for scape traits. It is not surprising that trans and disk floret traits are inter-connected because trans florets are disk florets that have been modified by breeding for more ligule-like outer lobes. The connection of disk and trans floret traits with scape traits is unclear. The high heritability suggests a very rapid response to selection for PC_{p3} .

Although the first phenotypic principal component (PC_{p1}) focuses on scape and receptacle/involucre traits, the mean coefficients on the other four categories are not small. This suggests that all of the six morphological categories should be included in studies of the phenotypic correlation among gerbera flower traits. Furthermore, PC_{p1} has very large coefficients (> 0.22) on traits 21, 28, and 34, which belong to the three categories, disk, ray and trans florets. Because each of these traits measures the length of pappus bristles (sepal), this suggests a pappus bristle structure.

Genetic

The first 3 PC_g account for 77% of the total genetic variance of the 36 traits. The PC_{g1} accounts for 33% of the genetic variance and its heritability is 0.86. Category means suggest this PC is structured on disk and

trans floret traits much like the third phenotypic PC but without the connection to scape traits. This genetic PC is expected to respond rapidly to selection.

PC_{g2} accounts for 28% of the genetic variance, and its heritability is 0.82. The structure of this genetic PC is suggested by category means of 0.26 for scape traits and 0.21 for trans floret traits. Although the relationship between scape and trans floret traits are unclear, selection response for PC_{g2} is expected to be rapid.

PC_{g3} accounts for 16% of the genetic variance and its heritability is 0.74. This genetic PC is dominated by disk floret traits with category mean of 0.26, and to a lesser extent by receptacle/involucre traits with a category mean of 0.18. The number and size of disk floret traits may be connected with measurements of the receptacle that supports them, and the involucre that subtends the receptacle. PC_{g3} is expected to respond rapidly to selection, but less so than the first 2 genetic PC.

Trans and disk floret structure

All PC except PC_{p1} focus on either disk floret or trans floret traits or both. These traits are important in determining the flower quality, and most have very high heritabilities. PC_{g1} and PC_{p3} have very similar emphases on five out of six morphological categories, both focusing on disk and trans floret traits. Furthermore, PC_{g1} and PC_{p3} have high genetic correlations with the traits in these categories. Therefore, the underlying process suggested by this trans and disk floret structure affects the expression of these heritable traits, resulting in correlations among all the traits. As a result, this underlying process plays a dominant role in the source of the variation and the cause of the correlation among the 36 flower traits.

Appendix

Descriptions of the 36 traits used in this study. Traits 24 and 25 have been deleted because their heritabilities are greater than 1. For more detailed descriptions of traits see Drennan et al. 1986 (numbers in parentheses are numbers used in that paper)

| Category/ trait | Description of trait |
|----------------------|--|
| Flower | |
| 1 | Diameter of center disk (1) |
| 2 | Radius to outer edge of trans florets (2) |
| 3 | Radius entire flower (3) |
| 4 | Height from disk to highest ligule surface (5) |
| 5 | Number of ligules per flower (14) |
| 6 | Number of whorls of disk florets across capitulum (21) |
| Receptacle/involucre | |
| 7 | Height from base of involucre to disk surface (6) |
| 8 | Height of involucre (7) |

| Category/ trait | Description of trait |
|--------------------|--|
| 9 | Height of receptacle (8) |
| 10 | Diameter of receptacle (9) |
| 11 | Diameter at base of involucre (10) |
| 12 | Diameter at top of involucre (11) |
| 13 | Distance on transect of capitulum for ray florets (17) |
| Scape | |
| 14 | Fresh weight of top 10 cm of scape (13) |
| 15 | Diameter of restriction at distal end of scape (15) |
| 16 | Diameter of scape 10 cm from distal end (16) |
| Disk floret | |
| 17 | Number of pappus bristles on immature disk floret (23) |
| 18 | Length of pappus bristles on immature disk floret (24) |
| 19 | Length of corolla tube on immature disk floret (25) |
| 20 | Number of pappus bristles on disk floret (40) |
| 21 | Length of pappus bristles on disk floret (41) |
| 22 | Length of corolla tube of disk floret (42) |
| 23 | Width of outer corolla lobe of disk floret (43) |
| Ray floret | |
| 26 | Fresh weight of ray floret (26) |
| 27 | Ligule area of ray floret (27) |
| 28 | Length of pappus bristles on ray floret (29) |
| 29 | Length of corolla tube on ray floret (30) |
| 30 | Width of ligule of ray floret (31) |
| 31 | Length of ligule of ray floret (32) |
| 32 | Length of inner corolla lobe of ray floret (33) |
| Trans floret | |
| 33 | Number of pappus bristles on trans floret (34) |
| 34 | Length of pappus bristles on trans floret (35) |
| 35 | Length of corolla tube on trans floret (36) |
| 36 | Width of outer corolla lobe of trans floret (37) |
| 37 | Length of outer corolla lobe of trans floret (38) |
| 38 | Length of inner corolla lobe of trans floret (39) |

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