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THEORETICAL AND APPLIED GENETICS

Quantitative analysis of correlations among flower traits in *Gerbera hybrida* Compositae

1. Genetic and environmental correlations

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Summary. Phenotypic (r_p), genetic (r_g), and environmental, (r_e) correlations were estimated for 38 flower traits in the Davis population of gerbera (*Gerbera hybrida*, Compositae). Fifty-two percent of r_p and 38% of r_g were statistically significant at $P<0.05$. Significant negative r_p were infrequent, but significant negative r_g occurred in 10% of cases. There was a negative correlation between estimates of r_g and r_e, resulting in cases where r_g was significant, but r_p was not. Individual traits varied in their tendency to correlate phenotypically or genetically, and positively or negatively, with other traits. Traits within the same morphological category, such as disk florets or transitional florets, were more highly intercorrelated than were traits from different categories.

Key words: Genetic correlation – Heritability – Hidden genetic correlation

Introduction

The purpose of selection usually is to change the mean of one particular trait in a population, with little or no change in other traits. However, genetic correlations can cause correlated responses in crops, e.g., maize (Robinson et al. 1951), soybean (Brim et al. 1959), cotton (Miller and Rawlings 1967), oats (Eagles and Frey 1974), areca nut (Bhagavan et al. 1981), cacao (Kumaran and Prasannakumari 1981), cucumber (Strefler and Wehner 1986), and gerbera (Harding et al. 1987). Thus, it is not uncommon to be confronted with the problem of correlated responses. The magnitude of these responses can be predicted if the genetic correlation of two traits and their heritabilities are known (Falconer 1981).

The selective improvement of *Gerbera hybrida*, Compositae, has resulted from selection for many traits, and it is now one of the more important cut-flower crops in European markets. It is grown under glass as a perennial or annual crop. The gerbera flower, in the horticultural sense, includes scape, involucre, receptacle, and disk, transitional, and ray florets. Estimates of heritability for 68 flower traits in gerbera have been reported by Drennan et al. (1986), but estimates of correlation among these traits have not been reported. Thus, it is not known whether the gerbera flower is composed of highly correlated traits of different flower structures, or if these flower traits are largely independent. The large number of traits that are involved in flower quality may be one of the most difficult challenges for the flower breeder.

The purpose of this series of studies is to estimate the degree to which flower traits are phenotypically, genetically, and environmentally correlated; to define a correlation parameter that quantifies correlation between a trait under direct selection and other traits, and predicts mean correlated response; to explore the use of principal components as selection indices; and to use canonical correlation analysis to select for mean correlated response. The present paper determines the degree to which flower traits are correlated and examines the relationships among phenotypic, genetic, and environmental correlations. Frequencies of positive and negative, phenotypic and genetic correlation will be estimated between and within morphological categories of traits. The results indicate the degree of phenotypic and genetic integration within and between morphological components of the gerbera flower.

Materials and methods

Population and sampling

The Davis population of gerbera was formed in 1971 by crossing 21 diverse stocks; the purpose was to create genetic variability.

The population has been selected by various methods (Harding et al. 1981a, b; Drennan et al. 1983); direct selection has not been practiced on individual flower traits. Selected parents in each generation have been intercrossed at random to minimize inbreeding.

A sample of 55 plants taken from generation 5 was crossed at random to form 43 full-sib families. Since parents of these families were not selected for any of the traits in this study, we will assume the families represent a random sample of generation 5 of this population. Each of the 55 parents, and 2 offspring from each of the 43 crosses, were vegetatively propagated to produce 141 individual plants; these were grown in individual containers. Thus, individual plants were arranged in a Completely Randomized Design on a greenhouse bench, in order to compare parents and offspring in the same reference environment. All traits were measurements of flowers grown in this environment; hence, all results of this study relate to generation 5 of the Davis population and to this reference environment.

Traits

Measurements were made on the following morphological categories of traits: inflorescence, receptacle/involucre, scape, disk floret, ray floret, and transitional floret. Descriptions of traits in each of these six categories are given in Appendix 1. They were chosen from the 68 traits reported by Drennan et al. (1986); none of the 38 traits of the present study are direct functions of each other.

In gerbera, transitional florets occur between the disk and ray florets (Drennan et al. 1986). These trans florets vary greatly from genotype to genotype; some have small corolla lobes similar to lobes of disk florets, others have enlarged outer corolla lobes similar to those of ray florets. Trans and ray florets are functionally pistillate; disk florets are functionally staminate.

Two flowers were sampled from each plant and measurements for traits 1–16 were made on each; means of these two measurements were used in further analysis. Three disk, three trans, and three ray florets were sampled from each flower, and traits 17–38 were measured on each; means of three florets on two flowers (six measurements) were used in further analysis. Means were found to have significant skewness to their distributions for traits 2, 15, 16, 26, 30, and 31. They were transformed by natural logarithm before heritabilities or correlations were estimated. If a measurement was missing, that case was eliminated from the analysis.

Heritability for each trait was estimated by the regression of the mean of two offspring on the mean of two parents. Therefore parent and offspring means were based on a total of four measurements for traits 1–16, and 12 measurements for traits 17–38. The standard error of each estimate of heritability was obtained by standard regression procedures with 41 degrees of freedom from the 43 families.

Correlations

A total of 703 phenotypic correlations was estimated for all pairs of the 38 variables; each was estimated for the generation 5 parents, generation 6 offspring, and for the combined sample. The 703 estimates of phenotypic correlation for the combined sample were tested by a standard t-test. The critical value of 0.17, based on 139 degrees of freedom, was used to test all phenotypic correlations. All statistical tests in this study will be based on $P<0.05$.

Heritabilities for each trait were estimated from the regression of offspring means on means of the parents for the 43 families. Genetic (additive) covariance between traits was also estimated from parent-offspring covariance. $\mathrm{Cov}(P_i, O_j)$ for trait i (mid-parent) with trait j (mean offspring) and $\mathrm{Cov}(P_j, O_i)$ for trait j (mid-parent) with trait i (mean offspring) are each expected to be 1/2 of the additive genetic covariance between traits,

$$\sigma_{g_{ij}} = \mathrm{Cov}(P_i, O_j) + \mathrm{Cov}(P_j, O_i).$$

Therefore, the genetic correlation between traits i and j is

$$r_{g_{ij}} = \frac{\mathrm{Cov}(P_i, O_j) + \mathrm{Cov}(P_j, O_i)}{2\sqrt{\mathrm{Cov}(P_i, O_i)\,\mathrm{Cov}(P_j, O_j)}} \tag{1}$$

(e.g., Van Vleck 1987). These estimates refer only to the single reference environment; inferences to other environments may be biased by covariances caused by environmental effects (e.g., Casler 1982). Effects of dominance and inbreeding will be ignored in this study.

An approximate standard error of the genetic correlation was estimated from

$$\mathrm{SE}(r_{g_{ij}}) = \frac{(1-r_{g_{ij}}^2)}{\sqrt{2}} \sqrt{\frac{\mathrm{SE}(h_i^2)\,\mathrm{SE}(h_j^2)}{h_i^2\, h_j^2}} \tag{2}$$

where h_i^2 and h_j^2 are the heritabilities for traits i and j (Robertson 1959; Jain 1982). This was used to test the null-hypothesis for each of the 703 estimates of genetic correlation.

Estimates of environmental correlation were obtained from

$$r_{e_{ij}} = \frac{r_{p_{ij}} - h_i\, h_j\, r_{g_{ij}}}{\sqrt{(1-h_i^2)\,(1-h_j^2)}} \tag{3}$$

(from Falconer 1981). No statistical tests were made on estimates of environmental correlation. Equation (3) is undefined if either estimate of heritability is equal to or greater than one.

If the number of statistically significant correlations for trait X_j is S_j, then

$$F_j = \frac{S_j}{(k-1)}, \tag{4}$$

where k is the number of traits. This frequency can be estimated either for phenotypic or genetic correlations, or for positive or negative correlations. Estimates of F_j were used to compared the tendencies of flower traits to be correlated with other flower traits.

Phenotypic correlations of ± 0.17 are statistically significant, hence, F_j is the frequency of phenotypic correlations greater than 0.17 in absolute value. The frequency of statistically significant genetic correlations is a function of standard errors that vary from estimate to estimate [Eq. (2)]. In most cases, estimates of genetic correlations greater than 0.30 in absolute value are statistically significant.

Frequencies of statistically significant correlations within and between the categories of traits were estimated to determine if frequency of correlations varies among the categories. If the number of statistically significant correlations among all traits within category n is N_{wn}, and there are k_n traits in category n, then the frequency of significant correlations within category n is

$$W_n = \frac{2\,N_{\mathrm{wn}}}{k_n(k_n-1)}. \tag{5}$$

If the number of statistically significant correlations between traits within category n with all other traits is N_{bn}, then the frequency between categories is

$$B_n = \frac{N_{\mathrm{bn}}}{(k-k_n)\,k_n}, \tag{6}$$

where $k=38$ is the number of traits in all categories.

The frequency of significant correlations within and between categories can be estimated either for phenotypic or genetic correlations; each can be partitioned into frequencies of positive and negative correlation. Therefore, four different estimates were made for W_n and for B_n.

Results

Estimates of heritability for each of the 38 traits are presented in Table 1; 25 estimates are significantly greater than zero. Mean heritability for traits measuring the inflorescence, scape, and receptacle/involucre is less than that for traits measuring disk and trans florets. These estimates were used to estimate $SE(r_{g_{ij}})$ and $r_{e_{ij}}$.

The distribution of the 703 estimates of phenotypic correlation is presented in Fig. 1. The mean phenotypic correlation for the combined sample of parents and offspring is +0.20, with individual estimates of phenotypic correlation ranging from −0.37 to +0.93. Figure 1 also indicates that 565 (80%) fall between −0.375 and +0.375. Of the 703 estimates of phenotypic correlation, 348 are significantly greater than zero; 14 are significantly less than zero.

Estimates of genetic correlation range from −1.53 to +1.37 (Fig. 1), with a mean of +0.15. Standard errors vary from near zero to 0.85, but most are between 0.1 and 0.5. Of the 703 estimates of genetic correlation, 194 are significantly greater than zero; 69 are significantly less than zero.

The distribution of environmental correlations (Fig. 1) is based on 630 estimates, because estimates of heritability for traits 24 and 25 were greater than one. Estimates vary from −0.91 to +1.09; the mean is +0.25. Less than 2% fall below −0.375; more than 35% are greater than +0.375.

The correlation between the 703 phenotypic and genetic correlation coefficients is +0.63. The correlation between the estimates of genetic and environmental correlation is −0.26.

The frequencies of statistically significant positive or negative phenotypic or genetic correlations associated with each of the 38 traits are summarized in Tables 2 and 3. Frequency of positive phenotypic correlations for the 38 traits varies from 0.24 to 0.76. Estimates of the frequency of negative phenotypic correlations for most traits are zero and, except for one estimate, are not greater than 0.08. Frequency of positive genetic correlations for traits varies from 0.05 to 0.65; frequency of negative genetic correlations varies from 0 to 0.30.

Frequencies of statistically significant phenotypic and genetic correlations within and between categories of traits are presented in Table 4. Positive phenotypic correlations occur more frequently within than between categories, except for the trans floret category. The greatest

Table 1. Estimates of heritability and standard error. Estimates vary slightly from those of Drennan et al. (1986) due to transformation of traits 2, 15, 16, 26, 30, and 31. Estimates of h^2 significantly greater than 0 are indicated with an *

Trait	h^2	SE
Inflorescence		
1	0.26*	0.13
2	0.55*	0.13
3	0.12	0.20
4	0.21	0.16
5	0.16	0.22
6	0.16	0.17
Mean	0.24	
Receptacle/involucre		
7	0.17	0.21
8	0.37*	0.16
9	0.25	0.15
10	0.49*	0.20
11	0.50*	0.18
12	0.42*	0.17
13	0.33*	0.14
Mean	0.36	
Scape		
14	0.43*	0.17
15	0.39*	0.14
16	0.39*	0.16
Mean	0.40	
Disk floret		
17	0.21	0.15
18	0.63*	0.14
19	0.44*	0.20
20	0.46*	0.16
21	0.86*	0.16
22	0.46*	0.19
23	0.76*	0.16
24	1.06*	0.15
25	1.15*	0.19
Mean	0.67	
Ray floret		
26	0.28	0.21
27	0.37	0.19
28	0.80*	0.13
29	0.24	0.14
30	0.40*	0.17
31	0.28	0.19
32	0.70*	0.14
Mean	0.44	
Trans floret		
33	0.22	0.15
34	0.81*	0.14
35	0.22	0.16
36	0.73*	0.09
37	0.87*	0.13
38	0.86*	0.18
Mean	0.62	

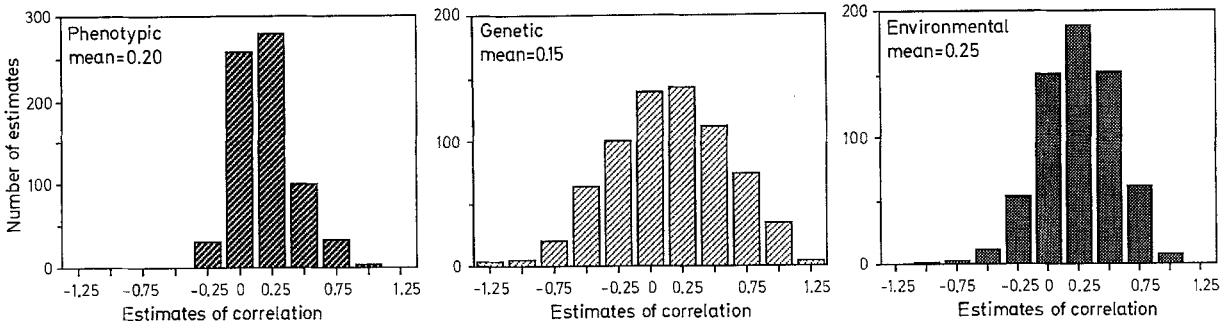

Fig. 1. Distributions of 703 estimates of phenotypic (r_p) and genetic (r_g) correlation, and 630 estimates of environmental (r_e) correlation

Table 2. Estimates of the frequency (F_j) of positive and negative statistically significant phenotypic and genetic correlations ($P<0.05$) for traits 1–16

Trait	Phenotypic		Genetic	
	+	−	+	−
Inflorescence				
1	0.57	0.05	0.24	0.03
2	0.59	0.05	0.35	0.11
3	0.76	0.00	0.05	0.11
4	0.24	0.24	0.11	0.22
5	0.46	0.00	0.32	0.14
6	0.43	0.03	0.24	0.05
Mean	0.51	0.06	0.22	0.11
Receptacle/involucre				
7	0.65	0.00	0.27	0.08
8	0.54	0.00	0.41	0.00
9	0.65	0.00	0.24	0.03
10	0.59	0.00	0.27	0.05
11	0.68	0.00	0.38	0.03
12	0.65	0.03	0.43	0.03
13	0.22	0.00	0.32	0.03
Mean	0.57	0.00	0.33	0.04
Scape				
14	0.62	0.00	0.27	0.08
15	0.65	0.00	0.41	0.03
16	0.59	0.00	0.32	0.03
Mean	0.62	0.00	0.33	0.05

Table 3. Estimates of the frequency (F_j) of positive and negative statistically significant phenotypic and genetic correlations for traits 17–38

Trait	Phenotypic		Genetic	
	+	−	+	−
Disk floret				
17	0.08	0.00	0.14	0.19
18	0.30	0.03	0.32	0.03
19	0.54	0.00	0.22	0.11
20	0.05	0.08	0.11	0.30
21	0.76	0.00	0.65	0.00
22	0.43	0.00	0.19	0.08
23	0.49	0.03	0.27	0.24
24	0.54	0.03	0.32	0.14
25	0.73	0.00	0.35	0.05
Mean	0.44	0.02	0.29	0.13
Ray floret				
26	0.65	0.00	0.16	0.14
27	0.62	0.00	0.14	0.05
28	0.65	0.00	0.43	0.00
29	0.32	0.00	0.14	0.14
30	0.38	0.00	0.19	0.08
31	0.51	0.00	0.11	0.19
32	0.49	0.00	0.19	0.11
Mean	0.52	0.00	0.19	0.10
Trans floret				
33	0.05	0.03	0.14	0.24
34	0.65	0.00	0.43	0.00
35	0.41	0.03	0.35	0.14
36	0.38	0.05	0.35	0.22
37	0.32	0.05	0.32	0.14
38	0.57	0.03	0.32	0.14
Mean	0.40	0.03	0.32	0.15

frequency of negative phenotypic correlations occurs within the category measuring the inflorescence. Genetic correlation tends to occur more frequently within than between categories, but not consistently.

Estimates of phentoypic, genetic, and environmental correlation for traits measuring corolla lobes are presented in Table 5. All correlations are positive, with the exception of ray floret traits 30 and 31. Estimates of genetic correlation for trait 31 with other corolla traits are negative; four are statistically significant. All estimates of environmental correlation among these corolla lobe traits are positive.

Discussion

The analyses of phenotypic, genetic, and environmental correlation of the gerbera flower in the Davis population are summarized in Table 6. Phenotypic correlation analysis indicates that traits are significantly correlated in about 52% of the 703 cases. However, the magnitude of phenotypic correlations is not generally large, with more

Table 4. Estimates of frequency of statistically significant positive or negative phenotypic or genetic correlations within (W_n) and between (B_n) morphological categories of traits

Category	Frequency of significant correlation within categories (W_n)				Frequency of significant correlation with traits from other categories (B_n)			
	Phenotypic		Genetic		Phenotypic		Genetic	
	+	−	+	−	+	−	+	−
Inflorescence	0.73	0.20	0.20	0.13	0.47	0.04	0.22	0.10
Receptacle/ involucre	0.71	0.00	0.57	0.00	0.54	0.00	0.29	0.04
Scape	1.00	0.00	1.00	0.00	0.60	0.00	0.30	0.05
Disk floret	0.47	0.00	0.36	0.22	0.43	0.02	0.26	0.10
Ray floret	0.67	0.00	0.29	0.19	0.49	0.00	0.18	0.08
Trans floret	0.33	0.07	0.47	0.27	0.41	0.03	0.30	0.13
Mean	0.65	0.05	0.48	0.14	0.49	0.02	0.26	0.02

Table 5. Estimates of phenotypic (p), genetic (g), and environmental (e) correlation for ray floret traits 30 and 31 (width and length of outer corolla lobe), and 32 (length of inner corolla lobe); trans floret traits 36 and 37 (width and length of outer corolla lobe), and 38 (length of inner corolla lobe); and disk floret traits 23 and 24 (width and length of outer corolla lobe), and 25 (length of inner corolla lobe)

		Ray floret			Trans floret			Disk floret		
		30	31	32	36	37	38	23	24	25
30	p	1								
	g	1								
	e	1								
31	p	+0.08	1							
	g	−0.10	1							
	e	+0.17	1							
32	p	+0.13	+0.11	1						
	g	−0.37*	−0.03	1						
	e	+0.78	+0.26	1						
36	p	+0.19*	−0.15	+0.49*	1					
	g	+0.09	−0.57*	+0.55*	1					
	e	+0.35	+0.25	+0.32	1					
37	p	+0.06	−0.04	+0.60*	+0.84*	1				
	g	−0.16	−0.56*	+0.62*	+0.94*	1				
	e	+0.53	+0.76	+0.56	+0.51	1				
38	p	+0.14	+0.06	+0.62*	+0.77*	+0.91*	1			
	g	−0.05	−0.53*	+0.60*	+0.89*	+0.98*	1			
	e	+0.55	+0.99	+0.76	+0.36	+0.51	1			
23	p	+0.31*	−0.07	+0.28*	+0.66*	+0.55*	+0.55*	1		
	g	+0.55*	−0.68*	+0.19	+0.82*	+0.66*	+0.68*	1		
	e	+0.03	+0.57	+0.53	+0.18	+0.10	+0.03	1		
24	p	+0.10	+0.12	+0.63*	+0.63*	+0.85*	+0.85*	+0.44*	1	
	g	−0.14	−0.23	+0.67*	+0.73*	+0.88*	+0.93*	+0.54*	1	
25	p	+0.15	+0.21*	+0.54*	+0.56*	+0.76*	+0.83*	+0.48*	+0.93*	1
	g	−0.02	−0.22	+0.53*	+0.71*	+0.80*	+0.89*	+0.65*	+0.95*	1

* Denotes statistically significant at $P<0.05$

Table 6. Summary of means and frequencies of statistical significance for phenotypic, genetic, and environmental correlations

	Correlation		Frequency of statistically significant correlations	
	Mean	Absolute Mean	Positive	Negative
Phenotypic	+0.20	+0.23	0.50	0.02
Genetic	+0.15	+0.39	0.28	0.10
Environmental	+0.25	+0.32	–	–

than 80% falling between −0.375 and +0.375. Less than 5% are greater than +0.70 and none is less than −0.70. Consequently, phenotypic analysis suggests that traits of gerbera flowers in this population are often correlated, although usually not strongly. Phenotypic correlations are almost always positive; there are only 14 significant negative phenotypic correlations.

Analysis of genetic correlations presents a different result (Table 6). Statistically significant negative genetic correlations (69 cases) are more frequent than are significant negative phenotypic correlations (14 cases). Significant negative correlations are not associated with significant phenotypic correlations in 57 cases, i.e., 8% of the 703 estimates. In these cases, analysis at the phenotypic level does not reveal negative associations at the genetic level. These hidden negative genetic correlations result from the tendency of estimates of genetic and environmental correlation to be negatively correlated (−0.26), and for estimates of environmental correlation to be positive, i.e., mean is +0.25 (Table 6).

Flower traits were organized into morphological categories, and statistically significant correlations were partitioned into frequencies within and between categories. In most cases, frequencies of correlation were greater within than between categories (Table 4). This suggests that correlations may result from developmental relationships between traits measuring the same floral structure.

Individual traits vary greatly in frequency of phenotypic or genetic correlation with other traits. Trait 4, e.g., has an unusually large frequency (24%) of significant negative phenotypic correlations (Table 2); it measures the height of the flower from the surface of the disk. Large measurements for trait 4 are associated with flowers that appear cup-shaped; they tend to have a small disk, a narrow involucre, but large flower diameter resulting from long ray ligules.

Corolla lobe traits (Table 5) are moderately correlated phenotypically and strongly correlated genetically, especially for trans and disk florets. However, lengths and widths of ray floret lobes (traits 31 and 30) are often negatively correlated with those of trans and disk florets. Flowers with ray florets having long ligules tend to have trans florets with short, narrow, outer corolla lobes. Hence, flowers classified as doubles or semi-doubles tend to have ray florets with short ligules.

Negative genetic correlation was also found between pappus bristle number (traits 17, 20, and 33) and traits that measure length or width of corolla lobes. Pappus bristles are modified sepals, hence, the inverse relationship between numbers of calyx parts and size of corolla parts is not surprising.

The results of this study indicate that gerbera flowers in the Davis population have a high degree of phenotypic and genetic correlation among traits, particularly those describing the calyx and corolla of disk and trans florets. Selection for these traits is expected to result in substantial correlated response in this population.

Appendix

Descriptions of the 38 traits used in this study. Traits 1–16 are means of two flowers per plant; traits 17–38 are means of three florets on each of two flowers per plant; traits, 2, 15, 16, 26, 30, and 31 were transformed by natural logarithm. 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
Inflorescence	
1	Diameter of center disk (1)
2	Radius to outer edge of trans florets (2)
3	Radius of entire flower (3)
4	Height of flower measured from disk (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)
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 (18)
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)
24	Length of outer corolla lobe of disk floret (44)
25	Length of inner corolla lobe of disk floret (45)

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 ligure 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)

References

Bhagavan S, Bavappa KLV, Ramachander PR, Nair BP, Ratnambal MJ (1981) Impact of seed nut selection on heritability, and genotypic and phenotypic correlations in areca nut. Placrosym IV:207–210

Brim CA, Johnson HW, Cockerham CC (1959) Multiple selection criteria in soybeans. Agron J 51:42–46

Casler MD (1982) Genotype × environment interaction bias to parent-offspring regression heritability estimates. Crop Sci 22:540–542

Drennan D, Harding J, Byrne T (1983) Heritability of consumer preference in gerbera. Euphytica 32:465–474

Drennan D, Harding J, Byrne TG (1986) Heritability of inflorescence and floret traits in gerbera. Euphytica 35:319–330

Eagles HA, Frey KJ (1974) Expected and actual gains in economic value of oat lines from five selection methods. Crop Sci 14:861–864

Falconer DS (1981) Introduction to quantitative genetics, 2nd edn. Longman, London

Harding J, Byrne TG, Nelson R (1981 a) Estimation of heritability and response to selection for cut-flower yield in gerbera. Euphytica 30:313–322

Harding J, Byrne TG, Nelson RL (1981 b) Heritability of cut-flower vase longevity in gerbera. Euphytica 30:653–657

Harding J, Byrne T, Drennan D (1987) The use of a selection index to improve gerbera cut-flowers. Acta Hortic 205:57–64

Jain JP (1982) Statistical techniques in quantitative genetics. Tata McGraw Hill, New Delhi

Kumaran K, Prasannakumari S (1981) Genetic variability and correlation of some pod and bean characters in cocoa 'Forastero'. Placrosym IV:183–190

Miller PA, Rawlings JO (1967) Selection for increased lint yield and correlated responses in upland cotton, *Gossypium hirsutum* L. Crop Sci 7:637–640

Robertson A (1959) The sampling variance of the genetic correlation coefficient. Biometrics 15:469–485

Robinson HF, Comstock RE, Harvey PH (1951) Genotypic and phenotypic correlations in corn and their implications in selection. Agron J 43:283–287

Strefler MS, Wehner TC (1986) Comparison of six methods of multiple-trait selection for fruit yield and quality traits in three fresh-market cucumber populations. J Am Soc Hortic Sci 111:792–798

Van Vleck D (1987) Summary of methods for estimating genetic parameters using simple statistical models. Cornell University, Ithaca/NY