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

2. Direct and mean correlated response to selection

H. Huang, J. Harding, T. Byrne and N. Huang

Department of Environmental Horticulture, University of California, Davis, CA 95616, USA

Summary. A Mean Correlation Response (MCR) model was developed to estimate the relative effectiveness of direct selection when other traits also respond to the selection. A measure of the relative effects of mean correlated response and direct response (R) and a measure of the relative efficiency of direct selection (IE) were applied to a genetic correlation matrix of 38 traits. These were measurements of inflorescence, receptacle and involucre, scape, disk florets, ray florets, and trans florets in the Davis population of *Gerbera hybrida*, Compositae. Generally, traits with high heritability had high direct and mean correlated response; these were often traits measuring disk and trans florets. Traits with low heritability had low direct and mean correlated response; these were often traits measuring the inflorescence. Traits of the inflorescence had the lowest efficiency of direct to mean correlated response.

Key words: Direct response – Correlated response – Genetic correlation – Mean genetic correlation – Index of efficiency

Introduction

Estimates of phenotypic, genetic, and environmental correlation for 38 flower traits in generation 5 of the Davis population of *Gerbera hybrida*, Compositae, were reported in paper 1 of this series (Harding et al. 1990). These traits are morphological characteristics of the inflorescence, involucre, receptacle, scape, and corolla and calyx of disk, trans, and ray florets. The combination of moderate to high heritability and positive or negative genetic correlations among these traits (Drennan et al. 1986; Harding et al. 1990) suggests that direct selection for

these traits will result in correlated response. Evidence for correlated response has been reported for several crops (e.g., Miller and Rawlings 1967; Hallauer and Miranda 1981; Gallais 1983; Troyer 1986).

The simple correlation response model is well known (e.g., Falconer 1981; Wricke and Weber 1986). The purpose of this paper is to develop a model that will predict the Mean Correlated Response (MCR) of a large number of traits when direct selection is practiced on a single trait. The analysis is derived from the 38×38 genetic correlation matrix and heritability vector from paper 1 of this series. Mean correlated response and direct response will be predicted for each of the 38 traits. Estimates of (1) direct response to selection, (2) mean correlated response to selection, (3) frequency of statistically significant correlated response, (4) ratio of mean correlated response to direct response, and (5) an index of efficiency are used to predict direct and correlated response to selection on the 38 flower traits.

Mean correlation response model

The model used in this study makes the following assumptions: (1) all genetic variance and covariance is additive, (2) residuals about the additive model are uncorrelated and normally distributed, (3) selection occurs before crossing, and (4) selection is based on individual phenotype. The direct response to selection, DR_0, for a trait X_0, is given by

$$DR_0 = h_0^2 (i_0) (\sigma_0),$$ (1)

where i_0 is the selection intensity, h_0^2 is the heritability, and σ_0 is the phenotypic standard deviation for trait X_0 (e.g., Falconer 1981). Observations for each trait were divided by their respective phenotypic standard deviations because the traits were found to have different standard deviations (Drennan et al. 1986). Thus, traits are expressed in standard deviation units, and an index of direct response can be computed from

$$(DR_0)/i_0 = h_0^2$$ (2)

for any selection intensity i_0. This response to direct selection can be placed on axis 0 in k-dimensional space. Correlated responses are changes that occur in the dimensions associated with the other $k-1$ traits. In dimension j, an index of correlated response for trait X_j is given by

$$(CR_{0j})/i_0 = (h_j)(h_0)(r_{0j}), \tag{3}$$

where r_{0j} is the additive genetic correlation between traits X_0 and X_j, and h_j is the square root of heritability for trait X_j (see Janssens 1979 for concept of coheritability). Since the parameters in Eq. (3) were estimated from parent-offspring regression, it can be shown that

$$(CR_{0j})/i_0 \approx \sqrt{2/f} \, [r(P_0, O_j) + r(P_j, O_0)]/2 \tag{4}$$

where the correlation of traits X_0 and X_j in parent and offspring are estimated from $r(P_0, O_j)$ and $r(P_j, O_0)$ and averaged; $f = 2$, the family size. Since f is a constant, statistical significance for $(CR_{0j})/i_0$ was determined by testing the quantity $[r(P_0, O_j) + r(P_j, O_0)]$.

The total correlated response in the $k-1$ traits to selection for trait X_0 is

$$CR_0 = i_0 h_0 \sum_{j=1}^{k-1} h_j r_{0j}. \tag{5}$$

Mean correlated response of the $k-1$ traits could be obtained by dividing Eq. (5) by $k-1$. However, correlations can vary from -1 to $+1$ with positive and negative estimates canceling each other. This was corrected by the use of absolute values ($a_{ij} = |r_{ij}|$), giving a mean absolute genetic correlation (MGC) of

$$MGC_0 = \frac{1}{(k-1)\bar{h}_0} \sum_{j=1}^{k-1} h_j a_{0j}, \tag{6}$$

where

$$\bar{h}_0 = \frac{1}{(k-1)} \sum_{j=1}^{k-1} h_j \tag{7}$$

and $\bar{h}_0$ is the mean of the square roots of all heritabilities except h_0. Therefore, MGC_0 is proportional to the sum of absolute genetic correlations weighted to square roots of heritabilities. An index of mean correlated response for trait X_0 (MCR_0) is obtained by dividing Eq. (5) by $k-1$, and replacing r_{0j} with a_{0j},

$$(MCR_0)/i_0 = h_0 \bar{h}_0 (MGC_0). \tag{8}$$

The frequency of statistically significant correlated responses for trait X_0 is

$$Q_0 = \frac{C_0}{(k-1)}, \tag{9}$$

where C_0 is the number of $(CR_{0j})/i_0$ ($j \neq 0$) that are statistically significant using Eq. (4). Q_0 will be underestimated because standard errors do not permit detection of all differences. Nonetheless, comparisons of Q for different traits are useful.

The relationship of direct to correlated response can be investigated by two approaches: Indirect Selection, in which the purpose is to improve a trait by selecting for one or several other traits, and Correlated Response, in which the purpose of selection is to obtain direct response in the selected trait while realizing a minimum of correlated response in other traits.

The ratio of correlated/direct response has been used to measure the relative efficiency of indirect selection for the two-trait case (Falconer 1981; Searle 1965). Large values indicate that indirect selection will be more effective. This approach can also be applied to the mean correlated response model with

$$R_0 = \frac{MCR_0}{DR_0}, \tag{10}$$

where R_0 is the ratio of mean correlated response to direct response to selection on trait X_0. Higher values for R_0 indicate that selection will be accompanied by greater correlated response. MCR_0 was chosen instead of total correlated response because the latter is dependent on the arbitrary number of traits studied. This model could also be used to measure the effectiveness of selection on several traits to produce an indirect response in a particular trait.

The Index of Efficiency defines the proportion

$$IE_0 = \frac{DR_0}{(DR_0 + MCR_0)}. \tag{11}$$

Larger values indicate that a higher proportion of total response is direct response for the selected trait; lower values indicate that a higher proportion is correlated response. Since IE_0 and R_0 are related by

$$IE_0 = \frac{1}{(1+R_0)}$$

they only represent different ways of viewing the same information.

Results

DR/i, MGC, and MCR/i, estimated from Eqs. (2), (6), and (8), respectively, are presented in Table 1 for traits 1-16 and in Table 2 for traits 17-38. Each trait is placed in one of the following categories: inflorescence, receptacle/involucre, scape, disk floret, ray floret, or trans floret (for

Table 1. Index of Direct Response (DR/i), Mean Genetic Correlation (MGC), Index of Mean Correlated Response (MCR/i), and Frequency of Significant Correlated Response (Q) for traits 1-16

Trait	DR/i	MGC	MCR/i	Q
Inflorescence				
1	0.26	0.29	0.10	0.08
2	0.55	0.44	0.22	0.35
3	0.12	0.35	0.08	0.00
4	0.21	0.38	0.12	0.03
5	0.16	0.55	0.15	0.11
6	0.16	0.41	0.11	0.05
Mean	0.24	0.40	0.13	0.10
Receptacle/involucre				
7	0.17	0.45	0.12	0.11
8	0.37	0.40	0.16	0.19
9	0.25	0.37	0.12	0.24
10	0.49	0.33	0.15	0.22
11	0.50	0.37	0.17	0.27
12	0.42	0.41	0.18	0.30
13	0.33	0.45	0.17	0.24
Mean	0.36	0.40	0.15	0.22
Scape				
14	0.43	0.37	0.16	0.22
15	0.39	0.40	0.17	0.24
16	0.39	0.37	0.15	0.24
Mean	0.40	0.38	0.16	0.23

Table 2. Index of Direct Response (DR/i), Mean Genetic Correlation (MGC), Index of Mean Correlated Response (MCR/i), and Frequency of Significant Correlated Response (Q) for traits 17–38

Trait	DR/i	MGC	MCR/i	Q
Disk floret				
17	0.21	0.41	0.12	0.11
18	0.63	0.32	0.17	0.27
19	0.44	0.36	0.16	0.11
20	0.46	0.38	0.17	0.22
21	0.86	0.44	0.27	0.49
22	0.46	0.28	0.13	0.11
23	0.76	0.40	0.23	0.35
24	1.06	0.40	0.27	0.27
25	1.15	0.40	0.28	0.30
Mean	0.67	0.38	0.20	0.25
Ray floret				
26	0.28	0.37	0.13	0.11
27	0.37	0.30	0.20	0.05
28	0.80	0.36	0.21	0.35
29	0.24	0.36	0.12	0.08
30	0.40	0.30	0.13	0.16
31	0.28	0.30	0.11	0.11
32	0.70	0.31	0.17	0.22
Mean	0.44	0.33	0.14	0.15
Transitional floret				
33	0.22	0.39	0.12	0.11
34	0.81	0.37	0.22	0.32
35	0.22	0.51	0.16	0.14
36	0.73	0.43	0.24	0.49
37	0.87	0.45	0.27	0.35
38	0.86	0.44	0.27	0.30
Mean	0.62	0.43	0.21	0.28

Table 3. Estimates of the Relative Effect of Indirect Selection (R) and Index of Efficiency (IE), for each of the 38 flower traits

Trait	R	IE
Inflorescence		
1	0.38	0.73
2	0.39	0.72
3	0.68	0.60
4	0.55	0.65
5	0.91	0.52
6	0.70	0.59
Mean	0.60	0.63
Receptacle/involucre		
7	0.73	0.58
8	0.43	0.70
9	0.49	0.67
10	0.31	0.76
11	0.34	0.75
12	0.42	0.71
13	0.53	0.66
Mean	0.47	0.69
Scape		
14	0.37	0.73
15	0.43	0.70
16	0.39	0.72
Mean	0.39	0.72
Disk floret		
17	0.61	0.62
18	0.27	0.79
19	0.36	0.74
20	0.37	0.73
21	0.31	0.76
22	0.27	0.79
23	0.30	0.77
24	0.25	0.80
25	0.25	0.80
Mean	0.33	0.76
Ray floret		
26	0.46	0.68
27	0.32	0.76
28	0.27	0.79
29	0.49	0.67
30	0.31	0.76
31	0.38	0.73
32	0.25	0.80
Mean	0.35	0.74
Trans floret		
33	0.56	0.64
34	0.27	0.79
35	0.72	0.58
36	0.33	0.75
37	0.32	0.76
38	0.31	0.76
Mean	0.42	0.72

descriptions of traits, see Appendix of paper 1). DR/i is greater than MCR/i for each of these traits; mean DR/i and mean MCR/i for the 38 traits are 0.47 and 0.17, respectively. The mean heritability for the 38 traits was 0.47; the mean of the square roots of heritabilities ($\bar{h}_o$) for each of these traits varies from 0.65 to 0.67.

DR/i varies from less than 0.20 for traits 3, 5, 6, and 7 to more than 0.80 for traits 21, 24, 25, 34, 37, and 38; MCR/i varies from less than 0.10 for traits 1 and 3 to more than 0.25 for traits 21, 24, 25, 37, and 38 (Tables 1 and 2). Mean DR/i and MCR/i are highest for disk and trans floret traits, and lowest for inflorescence traits. Mean MGC is also high for trans floret traits, but is not low for inflorescence traits.

The frequency of statistically significant correlated responses (Q) for each trait is also presented in Tables 1 and 2. Trait 3 has no significant correlated response; six traits (1, 3, 4, 6, 27, and 29) have less than 0.10. Two traits (21 and 36) have frequencies of correlated response greater than 0.40. Mean Q is highest for trans floret traits and lowest for traits measuring the inflorescence. Mean frequency of correlated response for the 38 traits is 0.21,

i.e., about 1 trait in 5 is expected to have a statistically significant correlated response.

Estimates of R and IE for each trait are presented in Table 3. The ratio R of mean correlated/direct response varies from less than 0.25 for traits 25 and 32, to more
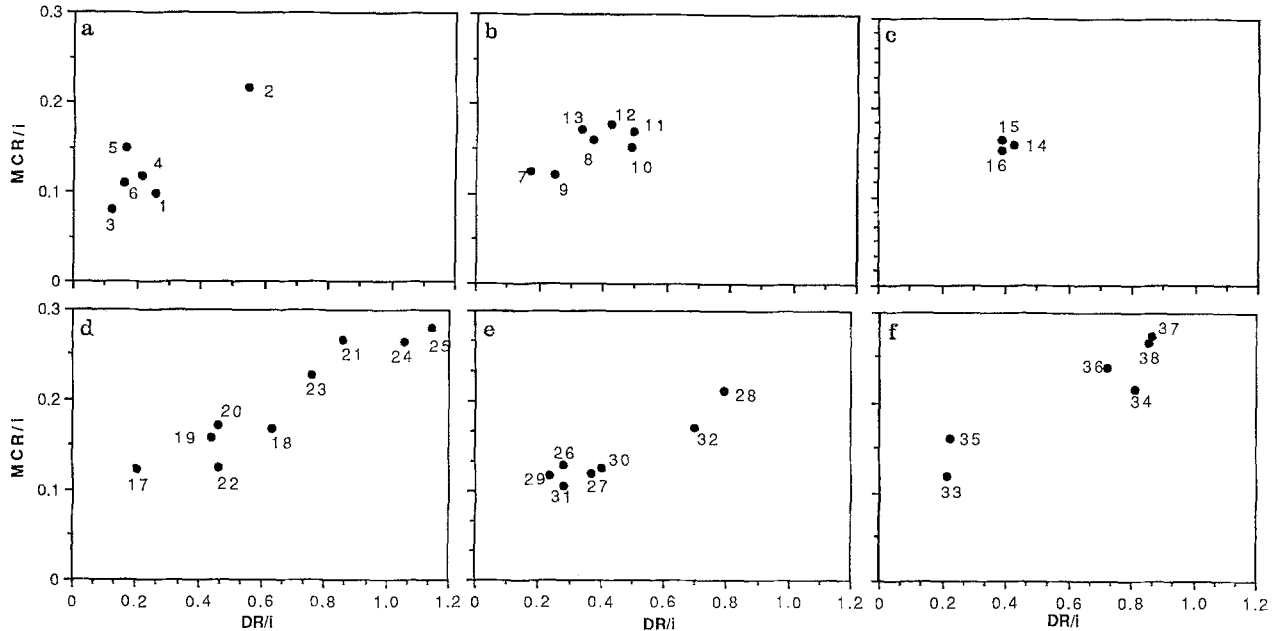
Fig. 1 a–f. Scatter diagrams for DR/i and MCR/i for the 38 traits in the morphological categories: **a** inflorescence, **b** receptacle and involucre, **c** scape, **d** disk floret, **e** ray floret, and **f** trans floret traits. For descriptions of traits, see Appendix in paper 1 of this series

than 0.70 for traits 5, 7, and 35. IE, the ratio of direct response to direct plus mean correlated response, varies from less than 0.60 for traits 3, 5, 6, 7, and 35, to more than 0.80 for traits 25 and 32. Mean R and mean IE for the 38 traits are 0.42 and 0.71, respectively.

Discussion

The relationship between DR/i and MCR/i for all traits in the six morphological categories is illustrated in Fig. 1. The apparent regression in these graphs is expected because DR/i and MCR/i are functions of heritability [Eqs. (2) and (8)]. Hence, higher heritability is expected to produce greater DR/i and MCR/i; this relationship varies with changes in MGC.

MCR/i is a function of heritability and mean genetic correlation; differences in $\bar{h}_0$ can be ignored. Consequently, a high level of correlated response will result from high heritability and high MGC, but moderate levels of correlated response can result from different combinations of these factors. Heritability and MGC can be seen in Tables 1 and 2; heritability is equivalent to DR/i. There is no correlation between MGC and heritability.

Trait 2 is the only trait measuring the inflorescence (Fig. 1 a) that has relatively large estimates of direct and mean correlated response; the frequency of significant genetic correlation is 0.35. This trait, measuring the distance from the center of the flower to the outer edges of the corolla lobes of trans florets, is expected to respond to direct selection with moderate correlated response. Traits

1, 3, 4, 5, and 6 are not expected to have large direct or correlated responses to selection. Trait 5, the number of ligules per flower, has MCR/i nearly as large as DR/i, resulting in $R > 0.9$ and IE near one-half. The combination of low heritability (0.16) and large mean genetic correlation (0.55) indicates that any selection required to produce a given response for this trait will also result in approximately equivalent responses for other traits.

Receptacle and involucre traits have moderate to low direct and mean correlated response (Fig. 1 b), moderate mean genetic correlation (0.40), and frequency of significant correlation between 0.11 and 0.30. Highest values for DR/i and MCR/i are for traits 10, 11, and 12, which measure diameters of receptacle, and base and top of involucre, respectively; lowest are for traits 7 and 9, which measure heights from base of involucre to disk surface and height of receptacle, respectively. The reason for higher estimates of DR/i and MCR/i for diameter than height traits for the receptacle and involucre is not known.

The three traits measuring the scape have nearly equal estimates of direct and correlated response, very near the mean for all traits (Fig. 1 c). Each has a frequency of significant genetic correlation near 0.23; they are expected to give moderate direct and correlated responses to selection.

Disk floret traits (Fig. 1 d) present an array of responses: very little response for trait 17, moderate responses for traits 18, 19, 20, and 22, and high responses for traits 21, 23, 24, and 25. Direct selection will be most successful for length of pappus bristles (trait 21) which are

modified sepals, for width (trait 23) and length (trait 24) of outer corolla lobe, and for length of inner corolla lobe (trait 25); very large correlated responses are also expected. The frequency of these responses is expected to be in the range of 0.3 to 0.5. Number of pappus bristles (traits 17 and 20) and length of corolla tube (traits 19 and 22) are not expected to respond strongly to selection. Although disk floret traits may not have received as much attention from ornamental breeders as some other traits, they appear to have great potential for direct and correlated response.

Ray florets, on the other hand, have 5 of 7 traits with below average estimates of direct and correlated response (Fig. 1 e). Only traits 28, length of pappus bristles, and 32, length of inner corolla lobe, have high values for DR/i and MCR/i; trait 28 also has a high estimate of Q (0.35). Length of inner corolla lobes of ray florets has a marked effect on the appearance of the center of the gerbera flower. These results also indicate that intense selection will be required to produce either direct or correlated response in traits 30 and 31, the width and length of ligules, although each has received much attention from breeders. As a group, ray floret traits have low values for mean genetic correlation, with mean MGC of 0.33. However, in paper 1 the length and width of corolla lobes of ray florets were found to have important negative genetic correlations with traits of trans florets.

The trans floret traits (Fig. 1f) are divided into two distinct groups; traits 33 and 35 with low estimates, and traits 3, 36, 37, and 38 with high estimates of direct and correlated response. Traits 33 and 35 measure the number of pappus bristles and length of corolla tube), respectively; the latter has very high mean genetic correlation (0.51), but low MCR/i because its heritability is only 0.22. Traits 34, 36, 37, and 38 measure length of pappus bristles, width and length of outer corolla lobes, and length of inner corolla lobes, respectively. Traits 36 and 37 also have high estimates of $Q = 0.49$ and 0.35, respectively. Although length and width of outer corolla lobes of trans florets have been selected in the development of semi-double and double flower types, it appears there is potential for further response. However, these results also indicate that a high frequency of correlated responses is expected.

Estimates of the index of efficiency (Table 3) range from 0.52 to 0.80, with mean of 0.71. However, it is important to note that this index defines the total selection response as the sum of direct response and mean correlated response, not the total of responses for all traits. We avoid total correlated response because it is dependent on number of traits, which is arbitrary. The mean of all estimates of IE in this study of 0.71 does not mean that 71% of response to selection of 38 traits is direct, but that a 71% direct selection response will result per trait.

The unusually high heritability responsible for high direct and mean correlated response for some traits (e.g., 24, 25, 28, 34, 37, 38) suggests the possibility of major genes for those traits. Although family patterns have occasionally suggested such a possibility, there is as yet no firm evidence for single major genes for these traits.

References

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

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

Gallais A (1983) Use of indirect selection in plant breeding. In: Proc 10th Congr Eucarpia, Pudoc, Wageningen, The Netherlands, pp 45–60

Hallauer A, Miranda JB (1981) Quantitative genetics in maize breeding. Iowa State University Press, Ames/IO

Harding J, Huang H, Byrne T, Huang N (1990) Quantitative analysis of correlation among flower traits in Gerbera hybrida, Compositae. 1. Genetic and environmental correlations. Theor Appl Genetics 80:552–558

Janssenns MJJ (1979) Co-heritability: its relation to correlated response, linkage, and pleiotropy in cases of polygenic inheritance. Euphytica 28:601–608

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

Searle SR (1965) The value of indirect selection. I. Mass selection. Biometrics 21:682–707

Troyer AF (1986) Selection for early flowering in corn: 18 adapted F$_2$ populations. Crop Sci 26:283–285

Wricke G, Weber WE (1986) Quantitative genetics and selection in plant breeding. De Gruyter, Berlin