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Maternal, paternal, additive, and dominance components of variance in Gerbera

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Summary. Estimates of additive, dominance, maternal, and paternal components of variance were obtained for a sample of 18 traits, including measurements of yield, scapes, flowers, disk, ray and trans florets, leaves, and branching in the Davis population of *Gerbera hybrida*. The results, based on the covariance of reciprocals, indicate that although heritability averaged 0.52, extranuclear maternal or paternal effects are not important sources of variability. Therefore, reciprocal differences do not seriously affect estimates of additive variance or heritability in this population.

Key words: Heritability – Extranuclear – Inheritance – Reciprocal – Covariance

Introduction

Genetic variances and heritabilities have been estimated in the Davis population of *Gerbera hybrida* for numerous traits (Harding et al. 1981 a, b, 1985; Drennan et al. 1983, 1986). These estimates indicate that most traits are moderately to highly heritable, and selection has been successful for cut-flower yield and consumer preference. However, selected parents from each generation were crossed at random, without regard to which parent was male or female. Thus, the assumption was made that there are no reciprocal differences due to either maternal or paternal effects.

The estimation of genetic components of variance and heritability in plant populations often assumes no reciprocal differences resulting from either maternal or paternal extranuclear contributions of parents to their offspring. The broad range of factors that lead to maternal and paternal effects is reviewed by Roach and Wulff (1987). The evidence for reciprocal differences in crop plants is reviewed by Aksel (1977). This literature suggests that maternal effects are often important in the inheritance of quantitative characteristics of higher plants. Evidence for paternal effects, on the other hand, is less frequent in the literature, but has been reported (e.g., Leng 1949; Bingham 1966; Garwood et al. 1970; Fleming 1975; Burton et al. 1980; Smith et al. 1986). Furthermore, Mazur (1987) found that heritabilities based on maternal and paternal half-sib families were not equal in *Raphanus raphanistrum*.

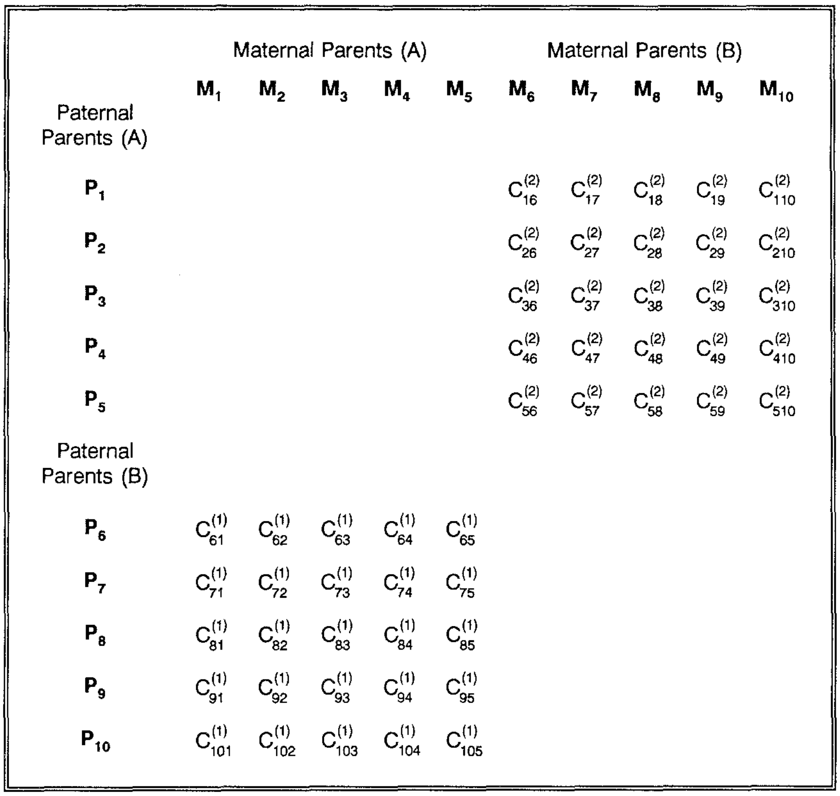
The purpose of this study is to test the assumption of no reciprocal differences for a sample of 18 traits in the Davis population of gerbera. Estimates of components of variance based on maternal and paternal half-sib and full-sib families confound additive and dominance effects with extranuclear maternal and paternal effects. Therefore, the model of Cockerham and Weir (1977), based on a factorial analysis of covariances of reciprocals, is used to estimate unconfounded components of variance for maternal, paternal, additive, and dominance effects.

Materials and methods

The Davis population

Gerbera hybrida is a cross-pollinated species commonly grown as a cut-flower crop in the glasshouse. The cultural practices, selection procedures, and mating designs of this population have been described in several papers (see, e.g., Harding et al. 1985). Generation 13 was chosen for this study; it originated from crosses of 40 parents from generation 12, selected for an index that placed equal weight on cut-flower yield and flower diameter.

The crossing design for this study is illustrated in Fig. 1. The 40 parents were randomly assigned to eight *sets* of five parents each; two sets were randomly placed in each of four *crossing blocks*. Each of these crossing blocks has an NC II design (Comstock and Robinson 1948; Hallauer and Miranda 1981) with a potential for 25 full-sib families. There are two reciprocal crosses



	Maternal Parents (A)					Maternal Parents (B)				
	M_1	**M_2**	**M_3**	**M_4**	**M_5**	**M_6**	**M_7**	**M_8**	**M_9**	**M_{10}**
Paternal Parents (A)										
P_1						$C^{(2)}_{16}$	$C^{(2)}_{17}$	$C^{(2)}_{18}$	$C^{(2)}_{19}$	$C^{(2)}_{110}$
P_2						$C^{(2)}_{26}$	$C^{(2)}_{27}$	$C^{(2)}_{28}$	$C^{(2)}_{29}$	$C^{(2)}_{210}$
P_3						$C^{(2)}_{36}$	$C^{(2)}_{37}$	$C^{(2)}_{38}$	$C^{(2)}_{39}$	$C^{(2)}_{310}$
P_4						$C^{(2)}_{46}$	$C^{(2)}_{47}$	$C^{(2)}_{48}$	$C^{(2)}_{49}$	$C^{(2)}_{410}$
P_5						$C^{(2)}_{56}$	$C^{(2)}_{57}$	$C^{(2)}_{58}$	$C^{(2)}_{59}$	$C^{(2)}_{510}$
Paternal Parents (B)										
P_6	$C^{(1)}_{61}$	$C^{(1)}_{62}$	$C^{(1)}_{63}$	$C^{(1)}_{64}$	$C^{(1)}_{65}$					
P_7	$C^{(1)}_{71}$	$C^{(1)}_{72}$	$C^{(1)}_{73}$	$C^{(1)}_{74}$	$C^{(1)}_{75}$					
P_8	$C^{(1)}_{81}$	$C^{(1)}_{82}$	$C^{(1)}_{83}$	$C^{(1)}_{84}$	$C^{(1)}_{85}$					
P_9	$C^{(1)}_{91}$	$C^{(1)}_{92}$	$C^{(1)}_{93}$	$C^{(1)}_{94}$	$C^{(1)}_{95}$					
P_{10}	$C^{(1)}_{101}$	$C^{(1)}_{102}$	$C^{(1)}_{103}$	$C^{(1)}_{104}$	$C^{(1)}_{105}$					

Fig. 1. Crossing scheme for Crossing Block I; Parent Set A (parents 1–5) with Parent Set B (parents 6–10). Crossing (1) and Crossing (2) are reciprocals obtained by switching Parents Set A from maternal to paternal parent, and switching Parent Set B from paternal to maternal parent. Paternal parents are *i*; maternal parents *j*, $C_{ij}^{(1)}$, and $C_{ij}^{(2)}$ are reciprocals of the same cross. The same scheme holds for Crossing Blocks II, III, and IV

Table 1. Description of the traits; for explanation of trans floret, see Harding et al. (1990)

Trait	Description
1	Length of the scape from base of involucre to sympodium
2	Diameter of circle of disk flowers
3	Diameter of circle to outer edge of trans florets
4	Diameter of entire flower (inflorescence)
5	Length of outer corolla lobe of ray floret (ligule)
6	Width of outer corolla lobe of ray floret
7	Length of inner corolla lobe of ray floret
8	Length of outer corolla lobe of trans floret
9	Width of outer corolla lobe of trans floret
10	Length of inner corolla lobe of trans floret
11	Dry weight of the scape
12	Dry weight of the flower (inflorescence)
13	Flowering time (days from planting to first flower)
14	Cut-flower yield (flowers harvested in 24-week period)
15	Number of leaves at 90 days from planting
16	Length of lamina of mature leaf at 90 days from planting
17	Width of lamina of mature leaf at 90 days from planting
18	Number of growing points (branches) at 90 days from planting

(subfamilies) nested in each full-sib family, producing a total of 50 subfamilies in each crossing block, and 200 subfamilies in the four blocks. Four individual plants from each subfamily were arranged at random in the glasshouse. To obtain a population size of 736 plants (space limit), 16 families were randomly eliminated, subject to the condition that two subfamilies were not eliminated if they had a parent in common.

The sample of 18 traits used in this study consisted of individual plant measurements of yield, scapes, flowers, disk, ray and trans florets, leaves, and branching. Descriptions of these traits are given in Table 1.

The Cockerham-Weir model

This model can be applied to the NC II design (Comstock and Robinson 1948, 1952) for each crossing block; parent set A is female and B is male in crossing direction (1), and parent set A is male and parent set B is female in crossing direction (2). Cockerham and Weir (1977) developed the model

$$Y_{ijk}=\mu+M_i+P_j+(MP)_{ij}+E_{ijk}\,, \tag{1}$$

where

M_i = the effect of maternal parent *i*,
P_j = the effect of paternal parent *j*,
$(MP)_{ij}$ = the interaction effect, and
E_{ijk} = total other effect.

Mean squares and their expectation for maternal and paternal effects, and their interaction are given in Table 2. The components of variance, σ_M^2 and σ_P^2 for maternal and paternal parents, are functions of additive (nuclear), maternal (extranuclear), and paternal (extranuclear) effects; they can be estimated by equating MSM and MSP to their respective expected mean squares. The components of variance, σ_M^2 and σ_P^2, can be estimated for balanced data from the analysis of variance in Table 2. However, family size is not equal in this study, and components of variance were estimated from the mean squares and expected mean squares obtained from the SAS General Linear Model (SAS Institute 1988).

Table 2. Analysis of variance and analysis of covariance of reciprocal crosses for one crossing block with r parents in Sets A and B, and k full-sibs within each cross in each crossing direction. Note that σ_A, σ_B, and $\sigma_{A\times B}$ are covariances of reciprocals

Source	Degrees of freedom	MS or MP	Exp (MS or MP)
Variances			
Maternal			
Sets A and B	$2(r-1)$	MSM	$\sigma_E^2+k\,\sigma_{MP}^2$ $+k\,\mathrm{r}\,\sigma_M^2$
Paternal			
Sets A and B	$2(r-1)$	MSP	$\sigma_E^2+k\,\sigma_{MP}^2$ $+k\,r\,\sigma_P^2$
Maternal × paternal			
Sets A and B	$2(r-1)(r-1)$	MSMP	$\sigma_E^2+k\,\sigma_{MP}^2$
Error			
Sets A and B	$2(k-1)\,r^2$	MSE	σ_E^2
Covariance of Reciprocals			
Set A	$r-1$	MPA	$\sigma_{A\times B}+r\,\sigma_A$
Set B	$r-1$	MPB	$\sigma_{A\times B}+r\,\sigma_A$
Set A × Set B	$(r-1)(r-1)$	MPAB	$\sigma_{A\times B}$

Cockerham and Weir (1977) used covariances of reciprocals to estimate the nuclear components of variances

$$\sigma_n^2=(\sigma_A+\sigma_B)/2$$

$$\sigma_t^2=\sigma_{A\times B}, \tag{2}$$

where σ_n^2 is the nuclear fraction of σ_M^2 or σ_P^2, σ_t^2 the nuclear fraction of $\sigma_{M\times P}^2$, σ_A and σ_B the covariances between reciprocal half-sib family means for parent sets A and B, respectively, and $\sigma_{A\times B}$ the covariance between reciprocal full-sib family means. The mean products and expectations appear in Table 2. Genetic parameters were estimated according to

$$\sigma_a^2=4\,\sigma_n^2$$

$$\sigma_d^2=4\,\sigma_t^2$$

$$\sigma_m^2=\sigma_M^2-\sigma_n^2$$

$$\sigma_p^2=\sigma_P^2-\sigma_n^2$$

$$\sigma_e^2=\sigma_T^2-\sigma_a^2-\sigma_d^2-\sigma_m^2-\sigma_p^2, \tag{3}$$

where σ_a^2 is the additive nuclear variance, σ_d^2 the dominance nuclear variance, σ_m^2 the maternal variance, σ_p^2 the paternal variance, σ_e^2 the environmental variance, which includes interaction effects (e.g., maternal × dominance), and σ_T^2 is the total phenotype variance,

$$\sigma_T^2=\sigma_M^2+\sigma_P^2+\sigma_{MP}^2+\sigma_E^2.$$

This procedure provides estimates of aditive and dominance variance that are not confounded with maternal or paternal extranuclear effects. For details, see Cockerham and Weir (1977).

The nested model

Reciprocal differences were tested using the nested model

$$Y_{ijk}=\mu+A_i+B_j+(AB)_{ij}+R_{ij}(AB)+\varepsilon_{ijk}, \tag{4}$$

where Y_{ijk} denotes any one of the 18 traits; A_i and B_j are effects of parents in set A and B, respectively; $i,j=1, 2, \ldots 5$; $R_{ij}(AB)$ are effects of reciprocal differences (subfamilies) nested within full-sib families, and ε_{ijk} are all effects within the reciprocal crosses.

Table 3. Estimates of the components of variance for the sample of 18 traits. Components for each trait are averaged over the four crossing blocks and divided by the total phenotypic variance of that trait to place values on the same scale. Means over the 18 traits provide an assessment of the relative inportance of these effects in this sample

Trait	σ_a^2	σ_d^2	σ_m^2	σ_p^2	σ_e^2
1	0.54	0.11	0.01	−0.02	0.35
2	0.61	−0.15	−0.04	−0.02	0.59
3	0.39	0.10	−0.01	0.02	0.49
4	0.89	0.06	0.00	−0.03	0.08
5	0.68	0.18	−0.00	−0.02	0.16
6	0.52	0.17	0.04	−0.04	0.32
7	0.35	0.06	−0.02	0.02	0.59
8	0.44	0.19	0.03	0.01	0.33
9	0.53	0.27	0.01	−0.03	0.22
10	0.44	0.17	0.07	0.01	0.32
11	0.65	0.07	−0.02	−0.02	0.31
12	0.59	0.02	−0.02	−0.03	0.44
13	0.58	0.08	0.01	0.02	0.31
14	0.30	0.01	−0.03	−0.02	0.74
15	0.50	0.26	0.02	−0.01	0.23
16	0.40	0.21	0.02	0.03	0.34
17	0.66	0.35	−0.09	−0.09	0.17
18	0.30	0.01	0.03	−0.01	0.67
Mean	0.52	0.12	0.01	−0.01	0.37

The hypothesis we test is whether $R_{ij}(AB)=0$. The analysis was done using the SAS General Linear Model (SAS Institute 1988).

Results

Estimates of additive, dominance, maternal, paternal, and environmental components of variance are presented for each of the 18 traits (Table 3). To express all traits on the same scale, each component is divided by the total phenotypic variance, obtained by summing the components for each trait. Consequently, the additive variance is also the heritability, based on individual plants. The individual components were averaged over the 18 traits to assess general patterns for the different causes of variation in this population. Estimates of maternal and paternal components were always small, never accounting for as much as 10% of the phenotypic variance; means over the 18 traits were actually negative. Estimates of additive components were generally large, with mean 0.52; estimates of environmental variance were also large, with mean 0.37. However, estimates of dominance variance were smaller, with mean 0.12.

The results of the nested analysis for reciprocal differences are presented in Table 4 for each of the 18 traits in each of the four crossing blocks. There were 71 cases where reciprocal effects were not significant at the 0.05 level, and one case where the reciprocal effect was highly significant, in which the actual significance probability was less than 0.006.

Table 4. Analysis of variance for reciprocal differences for each trait in each of the crossing blocks

	Crossing block							
	I		II		III		IV	
Trait	*F*-value	Prob.	*F*-value	Prob.	*F*-value	Prob.	*F*-value	Prob.
1	0.90	0.59	0.97	0.50	1.11	0.35	0.51	0.96
2	1.08	0.38	1.16	0.30	1.10	0.36	0.91	0.58
3	0.39	0.99	0.93	0.55	1.23	0.24	0.47	0.98
4	1.15	0.31	0.51	0.96	1.39	0.13	1.07	0.39
5	1.08	0.38	0.89	0.61	1.01	0.46	1.23	0.24
6	0.59	0.92	1.07	0.39	0.82	0.69	1.00	0.46
7	0.69	0.83	1.30	0.19	0.68	0.85	1.41	0.12
8	0.33	0.99	0.90	0.59	1.49	0.09	0.72	0.81
9	0.37	0.99	1.35	0.16	0.92	0.57	0.70	0.82
10	0.54	0.95	0.81	0.70	1.25	0.22	0.62	0.90
11	1.50	0.09	0.70	0.82	1.08	0.37	0.37	0.99
12	1.17	0.29	0.87	0.62	1.40	0.13	0.74	0.78
13	2.13	0.01	1.36	0.15	1.07	0.39	0.94	0.54
14	1.29	0.19	1.05	0.41	1.49	0.09	0.74	0.79
15	1.62	0.05	0.65	0.88	1.15	0.31	1.59	0.06
16	0.76	0.77	0.86	0.64	0.81	0.70	1.22	0.24
17	1.11	0.35	1.19	0.27	0.63	0.89	1.09	0.37
18	0.86	0.64	0.69	0.84	0.83	0.68	1.13	0.32

The exception occurred for trait 13 in Crossing Block I. To test the significance of traits 13 in the four blocks, the sums of squares were pooled over blocks; the significance probability was increased to 0.012. An additional analysis was performed on this trait in Crossing Block I, in which the parent that produced the greatest reciprocal differences was eliminated, reducing the crossing block to a 5 x 4 set. The analysis was repeated, but the results were unchanged, indicating that the reciprocal difference in flowering time could not be traced to the effects of a single parent in crossing Block I.

Discussion

Estimates of components of variance, using the Cockerham-Weir Model (1977), indicate that maternal and paternal extranuclear effect were not important in this population. The mean additive variance for this sample of 18 traits was 0.52, while the maternal and paternal variances were near zero. Therefore, maternal and paternal effects were generally not expected to be important in this population, and reliable estimates of genetic components of variance were obtained, irrespective of which direction parents were crossed.

The results of this study indicate that reciprocal differences do not generally occur in the Davis population of gerbera. Three crossing blocks of ten parents each produced no statistically significant reciprocal effects for the 18 traits. One crossing block produced a single significant reciprocal difference. Therefore, only 1 of the 72 estimates was statistically significant.

Flowering time (trait 13) may be an exception, since the reciprocal effect was significant in Crossing Block I. However, the maternal component of variance was only 1% of the total variance, and the paternal component of variance was only 2%. Therefore, statistically significant reciprocal differences in flowering time may occur infrequently, but are not expected to contribute substantially to the total variance.

These results point out the importance of experimental design in studies of maternal and paternal effects. When a traditional analysis was carried out on this data by comparing maternal and paternal half-sib family mean squares, the results suggested that maternal and paternal factors were important. This was due to the fact that additive variances were not equal in the two sets of parents. The Cockerham-Weir Model provides an opportunity to obtain unconfounded estimates of maternal, paternal, additive, and dominance components of variance. Therefore, conclusions regarding the importance of maternal or paternal effects cannot be made from comparisons of maternal and paternal half-sib family components of variance, unless the number of parents is sufficiently large to safely assume that the additive variances are identical in the two sets of parents.

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