

Genotype × Environment Interaction Bias in Heritability Estimates for Cut-flower Yield of Greenhouse Gerberas

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Additional index words. *Gerbera hybrida*, unadjusted heritability, adjusted heritability, index of interaction, genetic variance, response equation

Abstract. Statistics were developed to measure the relative importance of genotype × environmental (GE) interactions. Estimates indicate that as much as half of the genetic variance for cut-flower yield in the Davis Population of *Gerbera* may be attributable to GE interactions. The bias this causes in broad-sense heritability estimates averaged $10.3\% \pm 2.97\%$ for single-factor interactions; $15.6\% \pm 3.52\%$ for 2-factor interactions, and $26.8\% \pm 3.45\%$ for 3-factor interactions. The mean unadjusted broad-sense heritability for cut-flower yield in the same experiments was $37.1\% \pm 6.54\%$. Therefore, response equations that do not take interaction bias into account will overestimate selection potential.

The heritability of a trait is defined as the proportion of the phenotypic variance attributable to the additive effects of genes; it only has meaning for a specific population existing within a specific environment. For this reason, it may be inappropriate to generalize from a single estimate of heritability obtained from a sample of such a population. Nonetheless, selection within a specific population and environment is intended to result in genetic improvement that can be generalized to other environments. Comstock and Moll (3) discuss this problem and conclude that overestimates of genetic improvement will result where genotype × environment (GE) interactions are ignored. Estimates of GE interactions are numerous in the literature (1, 2, 6-8, 13-17, 19), but none estimate the *magnitude* of this interaction bias.

Most studies of GE interaction are based on agronomic or horticultural crops grown in the field. Cut-flower crops, on the other hand, often are grown in greenhouses in which certain environmental variables are controlled (e.g., temperature, growing medium, and nutrients). This control leads to the hypothesis that GE interactions may *not* result in serious biases in heritability estimates for greenhouse cut-flower crops. However, only one study of these crops has provided estimates of GE interaction (12).

A number of genotypes of greenhouse-grown *Gerbera hybrida* have been evaluated for cut-flower yield over the course of several years. The designs of six of the experiments conducted during this period permit the estimation of genotype and genotype × environment interaction components of variance. The effect of these GE interactions on heritability can be assessed with this material. A study was undertaken a) to develop statistics to measure the relative importance of GE interactions, b) to apply these statistics to the six experimental designs, and c) to evaluate the magnitude of the bias these GE interactions may impose on the selection strategies of flower breeders.

Experimental Material

Genetic material used in this study was sampled from the Davis Population of *Gerbera hybrida* (5, 9-11). Each genotype

selected was cloned by vegetative propagation of the crown, grown to flowering, and evaluated for cut-flower yield for ≈6 months. Experiments were conducted in glass greenhouses at Davis, Calif. and in rigid FRP greenhouses in San Jose, Calif. Davis is located in a hot central valley and San Jose in a cool coastal valley. Night temperatures were maintained between 13° and 16°C; day temperatures between 21° and 26°. Plants were grown in separate containers filled with a 1 mineral : 1 organic substrate (v/v) and irrigated as needed with a complete nutrient solution. Flowers were harvested as they matured and the count summarized monthly. Genetic materials in the six experiments were arranged in the following experimental designs.

Experiment A: genotype; years

Nineteen of the original 26 parents of the Davis Population were evaluated for yield in a greenhouse at Davis from 1 Sept. 1972 through 28 Feb. 1973 and from 1 Sept. 1973 through 28 Feb. 1974. Plants were grown in 7.1-liter containers at a density of 10.76 plants/m². Each planting consisted of two replications of each genotype arranged in a completely random design.

Experiments B and C: genotype; months; EW blocks

The data for these experiments were collected at San Jose over a 12-month period. They were divided into consecutive 6-month experiments to place the yield evaluations of all experiments on a 6-month scale. The 28 genotypes were arranged in four randomized complete blocks on an east-west (EW) gradient. Expt. B ran from 1 June 1975 to 30 Nov. 1975; Expt. C from 1 Dec. 1975 to 30 May 1976. In these experiments, 15.2-liter containers were used and spacing was 5.38 plants/m².

Experiment D: genotype; months; houses; EW blocks

Twelve genotypes from the first three generations of the Davis Population were arranged in two randomized complete blocks on an EW gradient in each of two adjacent greenhouses at San Jose. Plants were grown in 7.1-liter containers at a density of 10.76 plants/m². Night temperatures in one house were maintained between 13° and 16°C, but were allowed to fall to 10° in the other house. Flowers were harvested from 1 Sept. 1977 to 30 Apr. 1978.

Experiment E: genotype; months; EW blocks; NS blocks

Eighteen genotypes were taken at random from generation 5 of the Davis Population and evaluated in a greenhouse at Davis.

Received for publication 2 June 1986. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked *advertisement* solely to indicate this fact.

Table 1. Estimates of components of variance from Expts. A, E, and F grown at Davis and Expts. B, C, and D grown at San Jose, Calif.

Components of variance	Experiment					
	A	B	C	D	E	F
Genotype	2.67	2.98	6.05	2.78	3.77	0.54
Error	15.50	3.50	8.06	3.62	2.98	2.14
Interactions, two-way						
Genotype × year	11.95	--- ^z	---	---	---	0.50
Genotype × month	---	0.68	2.34	0.0	0.23	0.13
Genotype × house	---	---	---	0.01	---	---
Genotype × EW blocks	---	0.55	3.22	0.0	0.81	---
Genotype × NS blocks	---	---	---	---	0.74	---
Interactions, three-way						
Genotype × house × EW blocks	---	---	---	1.78	---	---
Genotype × month × EW blocks	---	---	---	0.0	0.64	---
Genotype × month × NS blocks	---	---	---	---	0.05	---
Genotype × EW blocks × NS blocks	---	---	---	---	0.46	---
Genotype × month × house	---	---	---	0.17	---	---

^zComponent not estimable in this experiment.

Table 2. Estimates of the index of interaction from Expts. A, E, and F grown at Davis, Calif. and Expts. B, C, and D grown at San Jose, Calif.

Interacting environmental factors	Index of interaction					
	Expt. (no. genotypes)					
	A (19)	B (28)	C (28)	D (12)	E (18)	F (115)
Single factors						
Years	81.7	--- ^z	---	---	---	48.1
Months	---	19.1	27.9	0.0	5.7	19.4
Houses	---	---	---	0.1	---	---
EW Blocks	---	15.8	34.7	0.0	17.6	---
NS Blocks	---	---	---	---	16.4	---
Two factors						
Months; houses	---	---	---	5.9	---	---
Months; EW blocks	---	29.8	47.9	0.0	30.8	---
Months; NS blocks	---	---	---	---	21.2	---
Houses; EW blocks	---	---	---	39.2	---	---
EW blocks; NS blocks	---	---	---	---	34.7	---
Three factors						
Months; EW blocks; NS blocks	---	---	---	---	50.6	---
Houses; months; EW blocks	---	---	---	41.3	---	---

^zIndex not estimable in this experiment.

Table 3. Estimates of the interaction bias in cut-flower yield from Expts. A, E, and F grown at Davis, Calif.

Expt. (unadjusted H ²)	Interacting environmental factors	Adjusted H ²	Interaction bias (b)
A (14.7)	Years	8.9	39.5
E (55.9)	Months	54.0	3.4
	EW blocks	49.9	10.7
	NS blocks	50.4	9.8
	Months; EW blocks	44.7	20.0
	Months; NS blocks	48.6	13.1
	EW blocks; NS blocks	43.1	22.9
	Months; EW blocks; NS blocks	39.0	30.2
F (20.2)	Months	19.3	4.5
	Years	17.0	15.8

Table 4. Estimates of the interaction bias in cut-flower yield from Expts. B, C, and D grown at San Jose, Calif.

Expt. (unadjusted H ²)	Interacting environmental factors	Adjusted H ²	Interaction bias (b)
B (45.3)	Months	41.0	9.5
	EW blocks	41.8	7.7
	Months; EW blocks	38.0	16.1
C (42.9)	Months	36.8	14.2
	EW blocks	34.9	18.6
	Months; EW blocks	30.8	28.2
D (43.4)	Houses	43.4	0.0
	Months	43.4	0.0
	EW blocks	43.4	0.0
	Houses; months	42.3	2.5
	Houses; EW blocks	33.9	21.9
	Months; EW blocks	43.4	0.0
	Months; houses; EW blocks	33.3	23.3

They were arranged into four randomized complete blocks corresponding to NE, NW, SE, and SW quadrants of the growing area. Plants were grown singly in 7.1-liter containers at a

Table 5. Index of interaction, unadjusted broad-sense heritability, adjusted broad-sense heritability, and interaction bias for a sample of field-grown crops. Roman numerals following soybean refer to maturity groups; numbers following muskmelon refer to different experiments.

Crop, yield character, (ref.)	Index of interaction			Unadjusted heritability	Adjusted heritability			Interaction bias		
	Years (Y)	Location (L)	Y + L		Years	Location	Y + L	Years	Location	Y + L
Wheat, seed, (14)	5.6	35.5	77.2	32.9	32.3	27.9	15.6	1.8	15.2	52.6
Wheat, seed, (2)	2.2	10.7	39.6	47.8	46.1	40.6	28.9	3.6	15.1	39.5
Barley, seed, (14)	30.9	50.5	82.4	50.3	41.1	33.3	17.6	18.3	33.8	65.0
Oats, seed, (14)	18.8	1.7	45.6	39.1	35.9	38.9	29.5	8.2	0.5	24.6
Cotton, lint, (1)	18.3	69.9	75.2	26.1	24.7	16.2	13.1	5.4	37.9	49.8
Cotton, lint, (17)	3.4	6.7	40.4	30.8	30.4	30.1	25.5	1.3	2.3	17.2
Tobacco, leaf, (13)	4.7	0.2	18.3	66.1	64.0	66.0	57.6	3.2	0.2	12.9
Lespedeza, seed, (8)	30.4	9.7	61.9	20.8	19.1	20.3	15.5	8.2	2.4	25.5
Lespedeza, plant, (8)	37.0	18.3	62.3	13.9	12.8	13.5	11.3	7.9	2.9	18.7
Soybean VI, seed, (15)	87.1	82.0	96.2	2.4	2.1	2.2	1.5	12.5	8.3	37.5
Soybean VII, seed, (15)	33.0	0.0	67.6	23.8	21.3	23.8	15.9	10.5	0.0	33.2
Muskmelon 1, fruit, (19)	7.9	---z	---	47.1	43.4	---	---	7.9	---	---
Muskmelon 2, fruit, (19)	24.6	---	---	60.4	45.6	---	---	24.5	---	---
Strawberry, fruit, (7)	16.9	---	---	62.5	55.4	---	---	11.4	---	---
Cherry, fruit, (6)	0.0	---	---	14.5	14.5	---	---	0.0	---	---

^zNot estimable in this experiment.

density of 10.76 per m²; flowers were harvested from 1 Mar. to 31 Aug. 1981.

Experiment F: genotype; months; years

A sample of 115 genotypes from generations 7 and 8 of the Davis Population was grown in Davis in a completely randomized design in 7.1-liter containers at a density of 10.76 per m². Flower yields were recorded from 1 Sept. 1983 to 28 Feb. 1984, and from 1 Sept. 1984 to 28 Feb. 1985.

The parents used in Expt. A were not drawn from any specific reference population but are assumed to be an *a priori* sample of the initial generation of the Davis Population. The genotypes in Expt. E, on the other hand, were a random sample from generation 5. The other experiments used selected, rather than random, genotypes; therefore, estimates of heritability from these experiments are expected to be underestimates for this population. However, the purpose of the study was to compare components of genetic variance with components of interaction variance. It is assumed that sampling method did not influence this comparison.

Statistical Methods

Components of variance. Analyses of variance were performed on the data from each of the six experiments. Variance components were estimated by treating all effects as random variables.

Index of interaction. A measure of the relative contributions of GE interactions can be obtained by expressing them relative to the total genetic variance. If the genotypic component of variance is σ_g^2 and the GE component of variance is σ_{ge}^2 , the index of interaction, expressed as a percentage, is:

$$I^2 = \frac{\sigma_{ge}^2 (100)}{\sigma_{ge}^2 + \sigma_g^2}$$

Note that I^2 is not a function of components of variance associated with environmental main effects. When the experimental design allows two or more GE components to be estimated, the interactions are summed. As more interacting factors are taken into account, I^2 is expected to increase.

Heritability bias. Heritability in the broad sense, H^2 , is defined as total genetic variance divided by the sum of genetic plus environmental variance; as such, it does not take GE interactions into account. Adjusted heritability (H_a^2), expressed as a percentage, and defined as

$$H_a^2 = \frac{\sigma_g^2 (100)}{\sigma_g^2 + \sigma_{ge}^2 + \sigma_e^2}$$

does take these interactions into account. The relative bias, b , expressed as a percentage, is estimated from:

$$b = \frac{(H^2 - H_a^2) 100}{H^2}$$

When two or more environmental factors are included, the various interactions can be summed. As more interacting environmental factors are added, adjusted heritability is diminished.

Results and Discussion

Estimates of the components of variance from Expts. A through F are presented in Table 1. These components were used to estimate I^2 values presented in Table 2. The mean I^2 for single-factor interactions is 22.4%. This value approximates the I^2 of 23.7% that we estimated from the results of Horn et al. (12) for a clone \times greenhouse interaction in gerbera. If this estimate is combined with the present data, the mean single-factor I^2 for gerbera is 22.2%, with a SE of 5.87%. The mean increases to 26.2% \pm 5.78% for 2-factor I^2 , and to 46.0% \pm 4.65% for 3-factor I^2 . These results indicate that genotypes interact with different environments occurring within greenhouses, between greenhouses, between different months of the year, and from one year to another. Estimates indicate that as much as half the genetic variance in this study may be attributable to GE interactions. While these protected greenhouse environments may be less variable than unprotected environments, cut-flower breeders must deal with environmental interactions. Therefore, populations of cut-flower crops should be evaluated over a wide range of greenhouse conditions.

Estimates of the bias in H^2 caused by interaction with the environment for these experiments are given in Tables 3 and 4. The mean bias for single-factor interactions (including all ex-

periments) was 10.3% with a SE of 2.97%; that for two interacting factors was 15.6% \pm 3.52%, and for three factors the mean was 26.8% \pm 3.45%. These means represent reductions from an unadjusted mean broad sense heritability of 37.1% \pm 6.54% for the six experiments. The data suggest that if as few as two or three environmental factors interact with genotype, heritabilities will be reduced by one-half to one-third of their unadjusted values.

Response equations that fail to take heritability bias into account will overestimate the progress expected from selection. Progress through selection will continue at a reasonable rate, as it has in the Davis Population (9, 10), if unadjusted heritabilities are large relative to the interaction bias. Most cut-flower crops appear to have been selected primarily for their aesthetic value, not for flower yield. Additive genetic variance for cut-flower yield still may be relatively large, thus mitigating the negative effect of GE interaction bias on selection efficiency. There may be other quantitative traits of commercial cut-flower importance with exploitable additive genetic variance. Such variance has been reported in gerberas for cut-flower yield (4, 9, 10, 20), vase longevity (11), consumer preference (5), scape length (4), and various inflorescence characters (4, 18). The amount of data available for greenhouse flower crops is too limited to allow precise generalizations. Nonetheless, the need to evaluate genotypes under diverse environments remains important.

Evaluation of genotypes under different years and/or locations is standard testing procedure for field crops. We have estimated components of genetic variance, the index of interaction, and heritability bias due to GE interactions for a number of such crops (Table 5); estimates of b range from 0.0% to 37.9% for single-factor interactions (genotype and year; genotype and location), and from 1.5% to 65.0% for 2-factor interactions (genotype; year; location). It appears that this model can be used to improve predictions of selection response in field crops, as well as in greenhouse cut-flower crops.

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CORRIGENDA

●In the article “Effect of Fertilizer, Paclobutrazol, and Chlormequat on Strawberry”, by D.A.J. McArthur and G.W. Eaton (*J. Amer. Soc. Hort. Sci.* 112:241–246, March 1987), the authors note that the fertilizer ratio that reads “20N–4.3P–8.3K” throughout the text and tables should read “20N–8.7P–16.6K”.