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Estimation of long-term genetic improvement for gerbera using the best linear unbiased prediction (BLUP) procedure

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Abstract Long-term genetic improvement is measured by the selection response predicted from estimates of narrow-sense heritability. Accurate estimates of selection response require partitioning the change of population mean into genetic and environmental components. A selection experiment for cut-flower yield was conducted for 16 generations in the Davis population of gerbera (*Gerbera hybrida*, Compositae). Breeding values were estimated for individual plants in the population using the best linear unbiased prediction (BLUP) procedure. Genetic change in each generation was calculated from the breeding values of individual plants. The results of this study indicate that long-term selection was successful and necessary for the genetic improvement in cut-flower yield. Genetic improvement in mean breeding value over 16 generations was 33 flowers. Mean breeding values increased monotonically with an S-shape pattern while environmental effects fluctuated from generation to generation. Results predict that cut-flower yield in the Davis population of gerbera will continue to respond to selection.

Key words Selection response · Breeding value · Mixed model · Maximum likelihood · Realized heritability

Introduction

The genetic improvement of yield traits by selection usually requires many generations because (1) these traits typically have relatively low heritabilities, and (2) there are many genes controlling these traits. The success of long-term genetic improvement is measured by the selection response, i.e., the genetic change caused by selection. For one generation of selection, this response can be predicted by the product of the narrow-sense heritability and the selection differential (Falconer 1989). However, the change of population mean from one generation to the next is not equal to the selection response because environmental effects are not constant. Since environmental effects are subject to change from generation to generation, a partitioning of the changes of population mean into genetic and environmental components is required to accurately estimate selection response. Unselected control populations or divergent selection can be used to adjust for environmental effects (Hohenboken 1985); both approaches are expensive. An alternative method is to estimate breeding values which are free from environmental effects.

Henderson's mixed model (Henderson 1984) provides an approach in which a breeding value can be estimated for each individual in a population. The genetic trend is subsequently estimated from the mean breeding value for each generation (Gall et al. 1993; Blair and Pollak 1984; Sorensen and Kennedy 1984).

Estimates of narrow-sense heritability for cut-flower yield in the Davis population of gerbera have varied from 0.30 to 0.60 (Huang 1993). These estimates are relatively high for yield traits, e.g., mean heritability for grain yield was 0.19 in maize (Hallauer et al. 1981). This suggests that genetic improvement in cut-flower yield will be successful as predicted by Harding et al. (1981). The purpose of the present study was to measure the response of cut-flower yield to long-term selection in the Davis population of gerbera using the best linear unbiased prediction (BLUP) procedure.

Materials and methods

A long-term selection experiment for improved cut-flower yield was conducted for 16 generations in the Davis population of gerbera (Harding et al. 1981; 1991). This study includes 6200 plants from

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Table 1 Selection phase of the Davis population of gerbera

Selection phase	Generation	Method of selection	Traits selected
1	1–4	Direct mass	Yield
2	4–8	Independent	Yield Consumer-preference
3	8–10	Optimum index	Yield Consumer-rating Vase-longevity
4	10–13	Optimum index	Yield Scape length Flower diameter
5	13–15	Desired gains	Yield Scape dry weight Flower dry weight

Table 2 Generation mean (Y), mean of selected parents(Y_s), selection differential (D) and cumulated selection differential (cD)

Gen.	Y	Y_s	D	cD
0	10.33	10.33	0.00	0.00
1	15.29	21.50	6.21	6.21
2	17.33	25.12	7.79	14.00
3	17.08	21.67	4.60	18.59
4	18.37	22.34	3.97	22.56
5	20.00	24.79	4.78	27.35
6	18.59	25.43	6.85	34.19
7	30.82	37.23	6.41	40.60
8	13.49	22.85	9.36	49.97
9	20.37	35.18	14.81	64.77
10	28.92	36.79	7.88	72.65
11	24.23	31.13	6.91	79.55
12	24.54	37.47	12.93	92.48
13	30.17	47.41	17.24	109.72
14	23.88	35.12	11.24	120.96
15	26.31	34.69	8.38	129.34
16	28.29	–	–	–

generation 1 to 16 plus the original parents. Cut-flower yield of gerbera in this study is defined as the number of flowers harvested from a plant in the period of 6 months from September to February.

Selection over the 16 generations can be divided into the five phases shown in Table 1 (for more detail see Harding et al. 1991). In every phase, selection was focused on cut-flower yield. The selection differential is defined as the deviation of the mean of selected parents from the population mean. The slope of the regression of population mean on the cumulated selection differential provides an estimate of realized heritability (Falconer 1989).

Mixed model and best linear unbiased prediction

The following additive genetic mixed model (Henderson 1984) is used to predict the additive genetic effect for each individual,

$$y=Xb+Za+e$$

where

y is an N × 1 vector of observations for cut-flower yield, N=6200,
b is a p × 1 vector of fixed year effects, p=17,
a is an N × 1 vector of additive genetic effects,
e is an N × 1 vector of residuals, and
X and Z are incidence matrices.

The expectations before selection, and the variance-covariance matrix, are

$$E\begin{pmatrix} a \\ e \\ y \end{pmatrix}=\begin{pmatrix} 0 \\ 0 \\ Xb \end{pmatrix}$$

and

$$Var\begin{pmatrix} a \\ e \\ y \end{pmatrix}=\begin{pmatrix} A\sigma_a^2 & 0 & AZ'\sigma_a^2 \\ 0 & R & R \\ ZA\sigma_a^2 & R & V\sigma_e^2 \end{pmatrix}$$

where A is the numerator relationship matrix, σ_a^2 and σ_e^2 are the additive genetic and residual variances respectively, and

$R=I\,\sigma_e^2$ (I is an identity matrix), and
$V=(I+ZAZ'r)$ for $r=\sigma_a^2/\sigma_e^2$ or $r=h^2/(1-h^2)$,

where r is the ratio of variance components that can be estimated by derivative free restricted maximum likelihood (DFREML) (Graser et al. 1987) based on the mixed model.

There are 6200+17=6217 unknowns in the model. Solutions for a and b can be obtained from the following Henderson's mixed model equations (MME),

$$\begin{pmatrix} X'X & X'Z \\ Z'X & Z'Z+\frac{1}{r}A^{-1} \end{pmatrix}\begin{pmatrix} a \\ b \end{pmatrix}=\begin{pmatrix} X'y \\ Z'y \end{pmatrix}$$

which provide the best linear unbiased predictions (BLUP) of additive effects (a) and year effects (b) for a given r (the ratio of variance components).

Numerically, solving such a large number of MMEs requires setting up a system of questions followed by iteration. These approaches are computationally complicated and time consuming. A more efficient indirect approach to solve MMEs was introduced by Misztal and Gianola (1987) where solutions can be obtained by successive averaging without constructing the MMEs directly.

The data analysis for this study was carried out on a VAX computer. Variance components were estimated using a DFREML program (Meyer 1988); MMEs were solved by a program from Finley (1991) based on the indirect approach.

Breeding value and genetic trends

Predicted breeding value is calculated relative to generation 0, i.e.,

$$Bv_i=a_i+h^2Y_0$$

where Bv_i is the breeding value for plant i, a_i is the additive genetic effect of plant i, and Y_0 is the mean cut-flower yield in generation 0. The change of mean breeding value between generations provides a genetic trend (Gall et al. 1993) free from environmental effects. Realized heritability then can be calculated by the change of mean breeding value divided by the selection differential.

Results

For each generation, mean cut-flower yield, the mean of selected parents, selection differential and cumulated selection differential are listed in Table 2. The total cumulated selection differential is 129.34, or about 8.08 flowers per generation. Mean yield increased from 10.33 in generation 0 to 28.29 in generation 16 (Fig. 1). Realized heritability based on the regression of generation means on

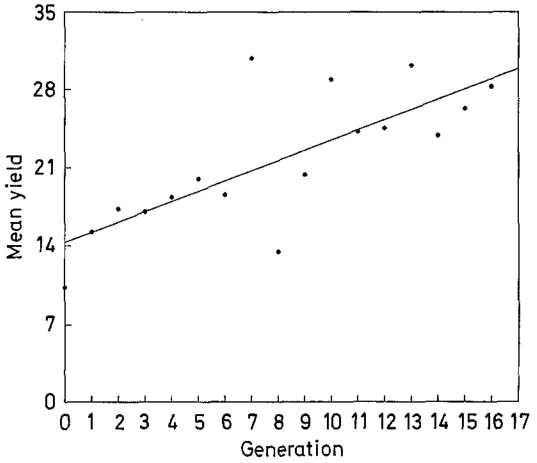

Fig. 1 Mean cut-flower yield in the Davis population of gerbera

Table 3 Mean yield (Y), year effect (b), mean additive genetic effect (a), mean breeding value (BV) and genetic trend (GT)

Gen	Y	b	a	BV	GT
0	10.33	10.28	0.05	3.20	–0.04
1	15.29	15.29	0.01	3.16	0.94
2	17.33	16.38	0.95	4.10	0.74
3	17.08	15.39	1.69	4.84	–0.08
4	18.37	16.75	1.61	4.76	1.38
5	20.00	17.01	2.99	6.14	1.78
6	18.58	13.81	4.77	7.92	2.55
7	30.82	23.50	7.33	10.47	2.47
8	13.49	3.70	9.79	12.94	2.44
9	20.37	8.14	12.23	15.38	3.44
10	28.92	13.25	15.67	18.92	1.56
11	24.23	7.00	17.23	20.38	2.92
12	24.54	4.39	20.15	23.30	4.49
13	30.17	5.54	24.63	27.78	4.18
14	23.88	–4.94	28.82	31.97	2.57
15	26.31	–5.07	31.38	34.53	2.13
16	28.29	–5.22	33.51	36.66	–

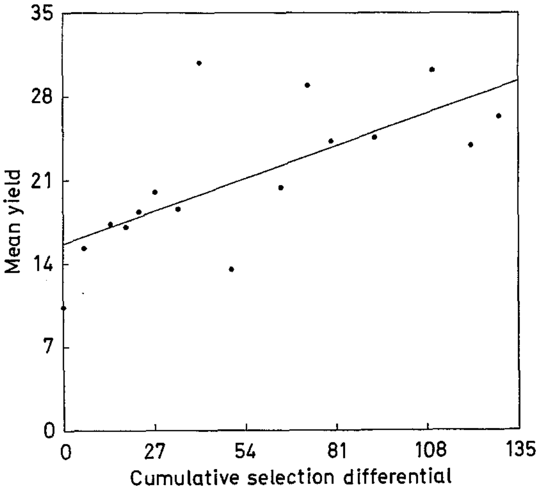

Fig. 2 Regression of phenotypic mean on cumulative selection differential

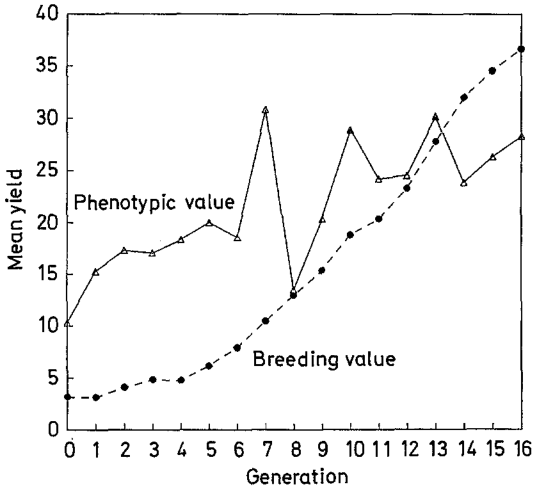

Fig. 3 Mean breeding value and phenotypic mean over generations

cumulated selection differentials was 0.10. Figure 2 shows the trend of generation means against cumulated selection differentials.

DFREML estimates of variance components were: additive genetic variance σ_a^2=28.54, residual variance σ_e^2=65.13, and phenotypic variance σ_y^2=93.66. Therefore, the narrow-sense heritability is 0.31. This value was used to estimate breeding values with the BLUP procedure. The indirect computational procedure converged in 9000 rounds of iteration at an accuracy of 10^{-10}. Predicted additive genetic effects were obtained for each individual. Year effects and mean additive effects for each generation together with generation means are listed in Table 3. Year effects varied from –5.22 to 23.50, while the mean additive effect was 0 in the parent generation and increased to 33.51 in generation 16. Mean environmental (non-additive) effects for each generation, however, were all equal to 0.

Breeding values were calculated for each individual plant. Mean breeding values and genetic trends for each generation are tabulated in Table 3, and breeding values are illustrated in Fig. 3. Genetic trends ranged from –0.08 to 4.49.

Regression of mean breeding value on generation number was 2.24, estimated from the rate of genetic change per generation. On the other hand, regression of mean breeding values on cumulated selection differentials was 0.25. Ratios of genetic change divided by selection differential, i.e., realized heritability, for each generation were also calculated (Table 4). Genetic change, cumulated selection differential, and their ratio within each phase, were calculated and are listed in Table 5.

Table 4 Ratio of genetic change over selection differential

GEN	GT	D	GT/D
0	-0.04	0	–
1	0.94	6.21	0.15
2	0.74	7.79	0.10
3	-0.08	4.60	-0.02
4	1.38	3.97	0.35
5	1.78	4.78	0.37
6	2.55	6.85	0.23
7	2.47	6.41	0.39
8	2.44	9.36	0.26
9	3.44	14.81	0.23
10	1.56	7.88	0.20
11	2.92	6.90	0.42
12	4.49	12.93	0.35
13	4.18	17.24	0.24
14	2.57	11.24	0.23
15	2.13	8.38	0.25

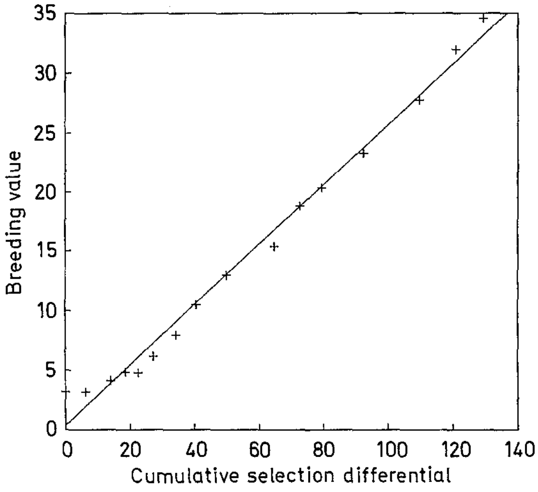

Fig. 4 Regression of breeding value on cumulative selection differential

Table 5 Genetic change (GT), cumulated selection differential (cD) and their ratio within each selection phase

Phase	GT	cD	GT/cD
1	1.57	18.59	0.08
2	8.18	22.10	0.37
3	5.88	24.17	0.24
4	8.96	27.71	0.32
5	8.88	36.86	0.24

Discussion

The mean breeding value of cut-flower yield in the Davis population of gerbera changed from 3 to 36 flowers over 16 generations, i.e., selection response was 33 flowers. This indicates that ,as predicted, long-term additive genetic improvement was successful. However, there was only a two-and-one-quarter flower per generation increase, suggesting that, with the selection intensities practiced in the Davis population, many generations of selection are necessary for a significant genetic improvement.

Although the phenotypic population mean increases with fluctuations, mean breeding values increase monotonously. The plot of mean breeding value vs generation suggests an S curve (Fig. 3).

The phenotypic mean changed from 10.33 in the original parents to 15.29 in the first generation without selection. However, the mean breeding value did not change (Table 3). Therefore, this phenotypic change must be caused by non-additive effects, possibly heterosis. The original parents were derived from different cultivars that may have possessed some level of inbreeding. Mating between these diverged inbred parents could have resulted in heterosis (Reimann-Philip 1983). In selection phase one (generation one to four), both selection response and selection efficiency were low. Heterosis in the early generations would cause this. In the subsequent selection phases, multiple traits were selected. Selection was most efficient in phase two (0.37, Table 5), and only two traits were selected. Three traits were selected in phases three through five. Among index selections, phase four (optimum index) was most efficient (0.32) and phase five (desired gains index) was least efficient (0.24).

The BLUP procedure provides an opportunity to separate additive and year effects from residual effects. Year effects were stable before generation 7, but fluctuated thereafter. This may be related to changes in weather during the last decade. However, in the year of generation 7, the management of the greenhouses was different. In addition, year effects from generation 14 through 16 had negative effects that depressed the expression of breeding values.

Realized heritability can be quite different from estimates. Sheridan (1988) made comparisons among 198 selection lines of animals and found that estimated heritability overestimated the realized heritability in 57%, and underestimated it in 38%, of all the comparisons. In the present study, the realized heritability calculated from the regression of generation mean on the cumulated selection differential (0.10, Fig. 2) is much lower than the DFREML estimate (0.31) because the actual change of generation mean depends on changes in both genetic and environmental effects. For this reason, realized heritability can only measure selection efficiency if environmental effects are unchanged. However, the overall realized heritability calculated from the regression of mean breeding value on the cumulated selection response (0.25, Fig. 4) was close to the prior DFREML estimate.

The declining selection efficiency in the last phase may signify a reduction in genetic variation. In fact, estimates of heritabilities in the later generations also show a declining tendency but remain at a 0.27 level (Huang 1993). This suggests that there is still potential in the Davis population of gerbera for continued selection and that cut-flower yield will continue to respond to selection, though the rate of increase may diminish.

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