

Predicted responses to recurrent selection in maize (*Zea mays* L.)

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Abstract

Previous studies with computer simulation models have shown that standardised correlated response in one trait, y , to selection for another trait, x , should be the same in one generation regardless of whether selection is for x or for y . In the study reported herein, we tested the hypothesis that direct response to selection for trait x should be the same as standardised correlated response in trait x when selection is based on trait y . Additionally, we compared, observed and predicted correlated responses to seven cycles of reciprocal recurrent selection for grain yield in two maize populations.

Results obtained indicated that predictions of direct and standardised-correlated responses showed poor agreement. Direct response to mass selection, however, agreed more closely with standardised correlated responses than did half-sib selection and S_1 testing, whereas direct response to S_1 testing agreed more closely with conventional correlated response than did the other two selection methods. Also, observed and predicted correlated response to reciprocal recurrent selection for grain yield showed poor agreement. However, predictions based on parameters obtained in the fourth cycle of selection agreed more closely with observed changes than similar estimates obtained from the original populations. Implications of these results in determining indirect selection criteria are discussed.

Introduction

Polygenic inheritance is dependent upon many genes that have similar, small effects in comparison with the nonheritable variation of the phenotype. For this reason, selection applied to one polygenic trait almost always leads to changes in others. When selection is applied to one trait, x , associated changes in another (unselected) trait, y , are known as correlated responses. The genotypic correlation between the two traits largely determines the predicted pattern of the correlated response (Bohren, Hill, and Robertson, 1966).

Recurrent selection is a breeding method involving evaluation of a large number of genotypes from a population, identification and selection of a certain percentage of desirable genotypes, and recombination of the selected genotypes to form a new population from which further selections can be made. Recurrent selection is an effective method for increasing the frequency of favourable alleles for a quantitatively inherited trait without the rapid approach to homozygosity that often limits the progress from selection with systems involving inbreeding.

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Theoretical considerations

It has been shown (Falconer, 1960a) that the correlated response (CR) in y to selection for x would be

$$CR_{y \cdot x} = i_x h_x h_y r_G \sigma_y \quad [1]$$

where i is the standardised selection intensity for trait x; h_x and h_y are the square roots of heritabilities for x and y, respectively; r_G is the genotypic correlation between the two traits, and σ_y is the phenotypic standard deviation in trait y. Dividing both sides of equation [1] by $i_x \sigma_y$ results in a standardised correlated response ($CR'_{y \cdot x}$) or correlated response in standard deviations in y for each standard deviation of selection in x (Bohren et al., 1966). Thus,

$$\begin{aligned} CR'_{y \cdot x} &= \frac{CR_{y \cdot x}}{i_x \sigma_y} = CR'_{x \cdot y} \\ &= \frac{h_x h_y r_G}{h_x h_y r_G} \end{aligned} \quad [2]$$

Since G. represents genetic effects and $h_x = \sigma_{Gx} / \sigma_x$, $h_y = \sigma_{Gy} / \sigma_y$.

$r_G = \sigma_{GxGy} / \sigma_{Gx} \sigma_{Gy}$, equation [2] becomes

$$CR'_{y \cdot x} = CR'_{x \cdot y} = \frac{\sigma_{GxGy}}{\sigma_x \sigma_y} \quad [3]$$

The standardised correlated response, therefore, should be the same in one generation of selection whether selection is based on x or on y, or whether selection is upward or downward. When correlated response is measured over several generations, however, selection may change the values of the parameters in equation [3] in such a way that the standardised responses are different from those predicted on the basis of the original values of the parameters (Falconer, 1960b; Bohren et al. 1966). Therefore, changes that occur in the three parameters σ_{GxGy} , σ_x , and σ_y as a result of selection will determine the magnitudes of correlated responses, and whether or not correlated responses will be symmetrical or asymmetrical (Bohren et al., 1966).

One important common feature for all recurrent-selection schemes is the use of mathematical formulae to predict gain from selection. Lush (1945) suggested that the expected gain from selection could be predicted by multiplying the selection differential by narrow-sense heritability. Because the selection differential can be expressed as $k \cdot \sigma_p$ with a normal distribution,

$$\Delta G = (k \cdot \sigma_a^2) / \sigma_p = HD \quad [4]$$

Thus,

$$\Delta G = \frac{c \cdot k \cdot \sigma_a^2}{\sqrt{\frac{\sigma_e^2}{m} + \frac{\sigma_g^2}{m} + \sigma_g^2}} \quad [5]$$

and

$$\sigma_c^2 = \frac{2}{n} \left(\sigma_u^2 + (\sigma_G - \sigma_g) + \sigma^2 \right) \quad [6]$$

where

ΔG = expected gain, H = heritability, D = selection differential,
 c = parental control, k = standardised selection differential,
 σ_a^2 = additive genetic variance among individual families,
 σ_p = phenotypic standard deviation among individuals or families,
 σ_e^2 = experimental error, σ_{ge} = genotype x environment interaction,
 σ_g^2 = genetic variance among families, σ_c^2 = total genetic variance
among and within individuals, σ_u^2 = within-plot environmental
variance, σ_b^2 = between-plot environmental variance, and n , r , and m
are numbers of plants per plot, replications, and locations, respectively.

As shown in equation [3], standardised correlated response is the same whether selection is based on trait x or on trait y . It follows, therefore, that direct response to selection for trait x (ΔG_x) should be equal to correlated response in trait x when selection is based on trait y , and vice versa. Thus,

$$\Delta G_x = \frac{\text{c.k.} \cdot \sigma_a^2}{\sqrt{\frac{\sigma_e^2}{rm} + \frac{\sigma_{ge}^2}{r} + \sigma_g^2}} = CR'_{y,x} = \frac{\sigma_{GxGy}}{\sigma_x \cdot \sigma_y} \quad [7]$$

The primary objective of the research summarised herein was to test the validity of equation [7] with use of genetic parameters obtained in a maize population. A secondary objective of our study was to compare the observed and predicted correlated responses to seven cycles of reciprocal recurrent selection (Comstock, Robinson, and Harvey, 1949) in maize. This programme was initiated with two maize populations, "Iowa Stiff Stalk Synthetic" (BSSS) and "Iowa Corn Borer Synthetic #1" (BSCB1). Grain yield was the primary selection criterion and significant progress from seven cycles of selection has been reported (Eberhart *et al.*, 1973; Fakorede, 1977; Fakorede and Mock, 1978) for this programme.

Materials and methods

The data analysed in this study were collected on grain yield components of 247 random S_6 lines developed by single-seed descent frp, "Iowa Stiff Stalk Synthetic" (BSSS) maize population. The lines were grown along with 9 unrelated inbred lines as checks in 3 experiments in 1970 and 1972, using a 16 x 16 simple lattice design for each experiment. Details of experimental procedure were reported by Obilana and Hallauer (1974). For the present study, we used the data for grain yield (qha), kernel-row number, ear length (cm), ear diameter (cm), cob diameter (cm), kernel depth (cm), and silking date; i.e., number of days from planting to silk emergence by 50% of the plants in a plot. Data for silking date were collected from 2 experiments only.

Using the variance-component and heritability estimates obtained by Obilana and Hallauer (1974), expected correlated responses (CR) and standardised correlated responses (CR') were computed from equations 1' and 3', respectively. Additionally, the expected responses to three types of recurrent selection were computed with use of appropriate modifications of equation 5'. These were half-sib selection, S testing, and mass selection (one parent selected). In each case, a selection intensity of 5% (i.e., $k = 2.06$) was used.

In another study, the observed responses were compared with the expected correlated responses for seven cycles of reciprocal recurrent selection for grain yield in BSSS and BSCB1. BSSSCO x BSCB1CO and BSSSC7 x BSCB1C7 were grown along with 2 other hybrids in one location for 2 years (1975 and 1976) at 2 plant densities; 59,300 (low density) plants/ha. Each experiment was replicated thrice. Details of experimental procedure were described by Fakorede and Mock (1978). For the study reported herein, we obtained data on grain yield, plant and ear heights, and four yield components (ear length, ear diameter, cob diameter, and kernel depth). Observed correlated response was calculated as the difference between the performance of BSSSC7 x BSCB1C7 and BSSSCO x BSCB1CO. Predicted correlated response to selection for yield was calculated for each trait (other than yield) with use of equation 1'. Hallauer (1971) obtained variance component, heritability, and genetic correlation estimates for BSSSCO x BSCB1CO and BSSSC4 x BSCB1C4, and these were used in the calculations. Selection intensity in the reciprocal recurrent selection programme was 10%.

Results and discussion

Genotypic correlations between grain yield and most yield components, and between yield and silking date were moderately high (Table 1). Except in a few instances, correlations among the yield components were low. Furthermore, correlations of silking date with yield and yield components were negative, indicating that delayed silking affected these traits adversely. Several studies (Mock and Buren, 1972; Buren et al., 1974; Fakorede and Mock, 1978) have shown consistently that delayed silking reduced grain yield in maize.

TABLE 1. GENOTYPIC CORRELATIONS AMONG YIELD AND YIELD COMPONENTS OF 247 S₁ LINES OF MAIZE.

	Kernel row No.	Ear Length	Ear diameter	Cob diameter	Kern depth	Silking date
Yield (q/ha)	.56	.58	.62	.24	.76	.49
Kernel row no.		.33	.74	.44	.61	-.33
Ear length (cm)			.36	.34	.24	-.20
Ear diameter (cm)				.81	.76	-.14
Cob diameter (cm)					.24	-.28
Kernel depth (cm)						-.35

TABLE 2. VARIANCE-COMPONENT AND HERITABILITY ESTIMATES FOR YIELD AND YIELD COMPONENTS OF 247 S_6 LINES OF MAIZE.

Component*	Yield	Kernel					
		row no.	Ear length	Ear diameter	Cob diameter	Kernel depth	Silking date
$\hat{\sigma}_p^2$	345.0	3.4	3.4	12.7	5.5	4.4	18.9
$\hat{\sigma}_p^2$	18.57	1.84	1.84	3.56	2.35	2.10	4.35
$\hat{\sigma}_{G^2}$	147.0	1.5	1.3	4.1	1.8	1.4	8.65
$\hat{\sigma}_{GE}^2$	294.6	3.0	2.6	8.1	3.6	2.8	17.3
$\hat{\sigma}_{GE}^2$	86.7	0.8	1.2	7.8	2.8	1.9	0.8
$\hat{\sigma}_e^2$	129.0	1.4	2.4	11.5	6.0	5.6	4.8
\hat{h}^2	.854	.855	.766	.642	.652	.643	.914
$\sqrt{\hat{h}^2}$.924	.925	.875	.801	.807	.802	.956

* $\hat{\sigma}_G^2$ is the variation among the S_6 lines and is approximately $2\hat{\sigma}_a^2$, the additive genetic variance; $\hat{\sigma}_p^2$ is the phenotypic variance and is calculated as $\hat{\sigma}_G^2 + \hat{\sigma}_{GE}^2/m + \hat{\sigma}_e^2$ where $r = 2$ and $m = 2$ or 3 [no. of environments]; $\hat{\sigma}_{GE}^2$ is genotype x environment interaction; $\hat{\sigma}_e^2$ is pooled experimental error; and \hat{h}^2 is narrow-sense heritability [line-mean basis].

Variance-component and narrow-sense heritability [line-mean basis] estimates indicated that most of the variation among the 247 S_6 lines for each trait studied was additive genetic variance (Table 2). This was expected (Obilana and Hallauer, 1977) because the lines were nearly homozygous at all loci, with inbreeding coefficient of approximately 0.995. Considering the variance-component and heritability estimates, and the range in the means of these traits (Obilana and Hallauer, 1974), it would seem that recurrent selection would be effective in the desired direction in BSSS. Infact, BSSS has been the base population for several recurrent selection schemes in Iowa, U.S.A., and considerable grain-yield improvements have been reported (Eberhart et al., 1973; Russel et al., 1973; Fakorede and Mock, 1978).

Predicted advance from recurrent selection (Table 3) indicated that largest grains would occur with S_4 testing, and the least from mass selection. Predicted gains in grain yield were large, even for mass selection; a consequence of the high heritability value and high selection intensity for yield in this study. Significant yield improvements from half-sib selection with a broad-base tester (Eberhart et al., 1973) and from a reciprocal tester (Eberhart et al., 1973; Fakorede and Mock, 1978) have been reported for BSSS. Grain yield was the selection criterion in these programmes; consequently, comparison of predicted and observed gains from recurrent selection for other traits could not be made.

Predictions of correlated responses (CR) and standardised correlated responses (CR') are presented in Table 4. As expected, both CR and

CR' were negative for silking date because the genotypic correlations between this and other traits were negative (Table 1). Generally, correlated responses and direct responses to selection showed poor agreement. For example, correlated response to selection for grain yield was 1.814 for kernel row number, whereas direct responses to selection for kernel row number were 0.834, 1.520, and 0.418 for half-sib selection, S_4 testing was mass selection, respectively. Our study tested the hypothesis that direct response to selection for a trait, x, would be equal to CR in that trait when selection is based on another trait, y. Results obtained for the predicted responses (Tables 3 and 4) did not substantiate this hypothesis.

TABLE 3. PREDICTED GENETIC GAIN PER CYCLE FROM THREE METHODS OF RECURRENT SELECTION IN BSSS.

Selection criterion	Half-sib Selection	S_4 testing	Mass Selection
Grain yield [q/ha]	9.693	15.129	4.076
Kernel row no.	0.834	1.520	0.418
Ear length (cm)	0.630	1.262	0.363
Ear diameter (cm)	1.183	1.982	0.593
Cob diameter (cm)	0.748	1.287	0.396
Kernel depth (cm)	0.622	1.090	0.344
Silking date	2.485	-3.917	-0.024

TABLE 4. PREDICTED CORRELATED RESPONSES (CR) AND STANDARDISED CORRELATED RESPONSES (CR') TO RECURRENT SELECTION IN BSSS

Selection criterion	Kernel row no.	Ear length	Ear diameter	Cob diameter	Kernel depth	Silking date
Yield CR	1.814	1.777	3.360	0.866	2.436	-3.875
CR'	0.479	0.469	0.459	0.179	0.563	-0.433
Kernel row no. CR		1.012	4.021	1.590	1.958	-2.613
CR'		0.267	0.548	0.328	0.453	-0.292
Ear length CR			1.850	1.162	0.729	-1.498
CR			0.252	0.240	0.168	-0.167
Ear diameter CR				2.535	2.112	-0.960
CR'				0.524	0.488	-0.107
Cob diameter CR					0.672	-1.994
CR'					0.155	-0.216
Kernel depth CR						-0.403
CR'						-0.268

A closer look at Tables 3 and 4, however, revealed a rather consistent pattern. Predicted CR in trait x with selection for trait y, and direct response to S_1 testing for trait x agreed closely. Similarly, predicted CR' in trait x with selection for trait y, and direct response to mass selection for trait x showed a fairly close agreement. To illustrate, suppose selection is for grain yield (i.e., trait y is yield); CR values are 1.814, 1.777cm, and -3.875 for kernel row number, ear length, and silking date, respectively. Direct responses to S_1 testing for these traits were 1.520, 1.262, and -3.917, respectively. Similarly, CR' values are 0.479, 0.469cm, and -0.433 for the three traits, respectively; whereas direct responses to mass selection were 0.418, 0.363, and -1.024. Similar trends were observed for other traits.

Observed and predicted CR to seven cycles of reciprocal-recurrent selection in BSSS and BSCB1 are presented in Table 5. Predictions based on estimates of heritability and genotypic correlations between yield and several traits obtained from $C_A \times C_A$ agreed more closely with observed changes than similar estimates obtained from $C_O \times C_O$ of these populations. Usually, observed and predicted values differed significantly (i.e., predicted values fell outside the ranges that resulted from

TABLE 5. OBSERVED AND PREDICTED CORRELATED RESPONSES TO SEVEN CYCLES OF RECIPROCAL RECURRENT SELECTION FOR GRAIN YIELD IN BSSS x BSCB1.

Traits	Total change after seven cycles		
	Observed (\pm S.E.)	Predicted	
		A	B
Plant height (cm)	7.6 \pm 2.83	-24.19	-14.18
Ear height (cm)	2.42 \pm 1.67	11.36	-0.57
Ear length (cm)	0.94 \pm 0.26	10.57	0.47
Ear diameter (cm)	0.10 \pm 0.04	0.67	0.33
Cob diameter (cm)	0.09 \pm 0.02	0.62	0.02
Kernel depth (cm)	0.00 \pm 0.02	0.52	0.11

¹ Predicted values using estimates of heritability and genotypic correlations from A) $C_O \times C_O$ and B) $C_A \times C_A$ [Hallauer, 1971].

observed values \pm twice their standard errors). Predicted changes based on the parameters from $C_A \times C_A$, however, did not differ significantly from observed changes in ear height and ear length (Table 5). Bohren et al. (1966) concluded from computer simulations that predictions of CR across several generations were not as accurate as predictions made from one generation. Also, Moll and Robinson (1966) obtained poor agreement between observed and predicted CR to selection for grain yield in four maize populations. Results presented herein

agree with findings obtained by these workers.

According to Fakorede (1977), studies of correlated responses are of interest for several reasons. They provide information on 1) the genetic relationship between traits, 2) the type of simultaneous change (negative or positive) that selection for one trait could promote in another (unselected) trait, and 3) the relationship between a quantitative trait and fitness under natural selection. The first two reasons are important in the choice of traits that could be used to construct indices for simultaneous improvement of two or more traits in a selection programme. Furthermore, results obtained in studies of correlated traits, often, can be related to cytogenetic studies to determine whether two traits are associated through linkage or pleiotropism.

In recent years, plant breeders and crop physiologists have been interested in identifying indirect selection criteria for yield improvement in grain and seed crops. Some favourable results have been obtained; for example, grain yield in a maize population increased at the rate of 6.3% per cycle through selection for increased number of ears per plant (Lonnquist, 1967). Direct selection for grain yield in this population (Gardner, 1961) showed a gain of only 3.8% per cycle. In most cases, however, indirect selection for yield through selection for a correlated trait has been unsuccessful. Several researchers (Falconer, 1960b; Bohren et al. 1966) have shown that when correlated response is predicted over several generations, selection may change the values of the three parameters in equation /3/ in such a way that standardised responses are different from those predicted on the basis of the original values of the parameters. Therefore, changes that occur in the three parameters σ_{axcy} , σ_x , and σ_y as a result of selection will determine the magnitude of correlated responses, and whether or not correlated responses will be symmetrical or asymmetrical.

Evidently, correlated responses to selection for a particular trait cannot be generalised for populations of a crop species nor for all recurrent selection methods. Therefore, it may not be advisable for a researcher to decide on indirect selection criteria for his programme on the basis of research findings elsewhere. It may be more profitable for the researcher to determine the pattern or correlation between yield and other traits in the population being improved before deciding on what traits to use either as indirect selection criteria, or in an index for enhanced grain yield.

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