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Optimum prediction of three-way crosses from single crosses in forage maize (*Zea mays* L.)*

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Summary. Three-way cross means were predicted with formulae involving linear functions of general (GCA) and specific combining ability (SCA) effects estimated from single-cross factorials between genetically divergent populations. Data from an experiment with 66 single-cross and 66 three-way cross forage maize (*Zea mays* L.) hybrids was used for comparing the prediction formulae. The genotypic correlation (r) between observed and predicted three-way crosses increased with increasing $\varkappa$, the weighting factor of SCA effects, for plant height and ear dry matter (DM) content. It displayed slightly convex curves for total and stover DM yield, ear percentage, and metabolizable energy content of stover. For Jenkins' method B, r was considerably less than 1.0 for all traits, indicating the presence of epistasis. The square root of heritability ($h_{\hat{G}}$) of the predicted means decreased with increasing $\varkappa$, the reduction being small with a greater number of test environments. Using the product $r \cdot h_{\hat{G}}$ as a criterion of efficiency, none of the prediction methods was consistently superior and the differences among them were rather small (< 7.5%) for all traits, irrespective of the number of test environments. We recommend evaluating the GCA of a greater number of lines from each parent population in testcrosses with a small number of elite lines from the opposite population. All possible three-way or double crosses between both sets of lines should be predicted by Jenkins' method C. This procedure allows one to select with a higher intensity among the predicted hybrids and thus should increase the genetic gain.

Key words: Epistasis – Genotype × environment interactions – Forage maize breeding

Introduction

The majority of cultivars at present in use for grain and forage maize (*Zea mays* L.) production in north-west Europe are three-way and double crosses. It is common to predict the performance of these types of hybrids from single cross test results.

Jenkins (1934) proposed four methods for predicting the performance of double crosses from single-cross data. In numerous investigations (for review, cf. Hallauer and Miranda 1981) Jenkins' method B, which employs the mean of the nonparental single crosses, proved more suitable and is therefore generally used in hybrid maize breeding for prediction of three-way and double crosses.

Cockerham (1967) presented a unified theory for predicting double crosses from diallel single crosses taking into account both genetic and environmental factors. Assuming that the parent lines are random samples from a population in linkage equilibrium, he developed an "optimum" predictor with minimum mean squared error. Otsuka et al. (1972) showed that the "optimum" predictor corresponds to weighting the estimates of the general (GCA) and specific combining ability (SCA) effects of the nonparental single crosses by appropriate regression factors. In an empirical comparison involving two grain maize experiments with Corn Belt materials, these authors obtained nearly the same efficiency for Jenkins' method B as for Cockerham's optimum predictor. With the exception of this study, however, no further comparisons are available in literature.

In this paper, we present an "optimum" predictor of single, three-way or double cross performance where the single crosses tested originate from factorial matings between lines from two parent populations. This situation is of greater practical importance than the case of diallels within a single population considered

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* Extended version of a paper (Geiger et al. 1986) read at the sixth meeting of the EUCARPIA Section 'Biometrics in Plant Breeding' held at Birmingham, UK, July 28 – August 1, 1986

by Cockerham (1967), since commercial maize hybrids in Europe are usually established between lines from genetically divergent gene pools. Employing data from a forage maize experiment, the "optimum" predictor is compared with Jenkins' methods B and C and with an empirically optimised predictor. Comparisons are made for two and six environment situations.

Materials and methods

Theory

In terms of GCA and SCA the phenotypic mean of the single cross $k \times l$ between lines k and l from populations 1 and 2, respectively, can be partitioned in the following manner:

$$Y_{kl} = \mu + g'_k + g''_l + s_{kl} + e \qquad (1)$$

where

μ	denotes the expected mean of hybrids between lines from populations 1 and 2;
g'_k, g''_l	the GCA effects of lines k and l when tested against populations 2 and 1, respectively;
s_{kl}	the SCA effect of the single cross $k \times l$; and
e	the experimental error.

Ignoring epistasis, the genotypic value of the three-way cross $k \times l \cdot m$ between line k and single cross $l \times m$ from populations 1 and 2, respectively, can be written as follows:

$$G_{k \times l \cdot m} = \mu + g'_k + (g''_l + g''_m)/2 + (s_{kl} + s_{km})/2 \qquad (2)$$

using the same notation as above.

In this section, it is assumed that the single crosses used for prediction originate from a complete factorial mating design between K female and L male parent lines representing random samples from populations 1 and 2, respectively. Furthermore, besides μ all terms on the right hand side of equation (1) are considered as stochastically independent random effects with expectation zero and

$$\begin{aligned} \text{var.}(g'_k) &= \sigma^2_{g'} \quad (k = 1, \ldots, K); \\ \text{var.}(g''_l) &= \sigma^2_{g''} \quad (l = 1, \ldots, L); \\ \text{var.}(s_{kl}) &= \sigma^2_s \quad (k = 1, \ldots, K;\ l = 1, \ldots, L); \\ \text{var.}(e) &= \sigma^2 \end{aligned}$$

Provided the true values of these variances are known and applying the general results of Henderson (1963, 1975) to the problem of estimating the random effects in the two-way random model of equation (1) yields the following solution for the **b**est (minimum mean squared prediction error) **l**inear **u**nbiased **p**redictor (**BLUP**) of $G_{k \times l \cdot m}$:

$$\tilde{G}_{k \times l \cdot m} = \hat{\mu} + \lambda_1 \hat{g}'_k + \lambda_2 (\hat{g}''_l + \hat{g}''_m)/2 + \lambda_3 (\hat{s}_{kl} + \hat{s}_{km})/2 \qquad (3)$$

where

$$\begin{aligned} \hat{\mu} &= Y_{..}; \\ \hat{g}'_k &= Y_{k.} - Y_{..}; \\ \hat{g}''_l &= Y_{.l} - Y_{..}; \\ \hat{s}_{kl} &= Y_{kl} - Y_{k.} - Y_{.l} + Y_{..} \end{aligned} \qquad (4)$$

This adopts the usual dot notation to indicate averages. Analogous definitions hold for $\hat{g}''_m$ and $\hat{s}_{km}$. The weights λ_1, λ_2, and λ_3 are functions of the above variances and can be written as

$$\begin{aligned} \lambda_1 &= \alpha + (1 - \alpha)\gamma; \\ \lambda_2 &= \beta + (1 - \beta)\gamma; \\ \lambda_3 &= \gamma \end{aligned} \qquad (5)$$

where

$$\alpha = \frac{\sigma^2_{g'}}{\sigma^2_{g'} + (\sigma^2_s + \sigma^2)/L}; \quad \beta = \frac{\sigma^2_{g''}}{\sigma^2_{g''} + (\sigma^2_s + \sigma^2)/K};$$

$$\gamma = \frac{\sigma^2_s}{\sigma^2_s + \sigma^2} \qquad (6)$$

In practical applications of the BLUP approach, e.g. in predicting the breeding value of sires in animal breeding, the unknown variances are substituted by some "good" estimates. In our case these estimates can be obtained from the analysis of variance of the single crosses used for prediction. The resulting predictor is referred to as the "optimum" predictor, adopting the terminology of Otsuka et al. (1972). This predictor can be considered an empirical Bayes estimator (Harville 1977). It remains unbiased if the pertinent random effects follow a symmetric distribution (Kackar and Harville 1981).

Equations (4) correspond to the least squares estimates of μ, g'_k, g''_l, and s_{kl} if these effects were treated as fixed rather than random.

Equations (6) show that α, β, and γ can be regarded as the "heritabilities" of the estimated GCA and SCA effects for given K and L. It can, therefore, be assumed that formulae (3), (4) and (5) are valid in the multi-environment situation too, if genotype × environment interactions are included in the definition of α, β, and γ. Furthermore, it can be shown that λ_1, λ_2, and λ_3 are also the weighting factors in the BLUP of single and double crosses analogous to equation (3).

Equations (5) and (6) imply the following inequalities: $0 \leqq \lambda_3 \leqq \lambda_1, \lambda_2 \leqq 1$. These elucidate the "philosophy" behind the BLUP approach showing that the "heritabilities" α and β of the GCA effects are generally greater than γ, the "heritability" of the estimated SCA effects. The reason for this is that $\hat{s}_{kl}$ has a higher standard error than $\hat{g}'_k$ or $\hat{g}''_l$ and hence should receive a smaller weight in an optimum predictor of $G_{k \times l \cdot m}$ (Wricke and Weber 1986).

If σ^2 is small compared to σ^2_s, $\lambda_3 \to 1$ and, consequently, λ_1 and $\lambda_2 \to 1$. Thus, with an increasing number of test environments and replications, the "optimum" predictor converges towards Jenkins' method B. On the other hand, if σ^2_s is small relative to σ^2, then $\lambda_3 \to 0$, i.e., the SCA effects are disregarded for prediction. For $\lambda_3 = 0$ and $L \cdot \sigma^2_{g'} = K \cdot \sigma^2_{g''}$ the "optimum" predictor is identical to Jenkins' method C, which is solely based on the GCA effects of the parental lines. For a given value of λ_3, weights λ_1 and λ_2 increase with the number of lines (K, L) involved in the estimation of the GCA effects, but for $K, L > 5$, the increments decrease rapidly. Thus the relative sizes of $\sigma^2_{g'}$ and $\sigma^2_{g''}$ in comparison to $\sigma^2_s + \sigma^2$ become important only for small values of L and K.

The results given in this section do not require the parent populations to be in gamete phase equilibrium. The parents of the hybrids may therefore consist of selected lines.

Data collection

The data for the empirical comparison of prediction methods were taken from an experiment with forage maize (Geiger et al. 1985; Schmidt 1986). Briefly, 11 flint lines were mated with 11 dent lines according to an incomplete factorial mating design to produce 66 single crosses, each line being involved in six crosses (Melchinger 1984). In addition, 66 three-way crosses were established from the same lines, 33 of the flint × dent · dent type according to the mating scheme given in Fig. 1 and analogously 33 of the dent × flint · flint type. The two sets of three-way crosses were balanced with regard to the corresponding nonparental single crosses, involving 11 of the above 66 single crosses twice and 44 only once. The parent lines are selections for grain yield from early maturing European flint and dent gene pools displaying a distinct heterotic pattern. For the forage traits considered here, however, they can be regarded as random samples from each gene pool.

The 132 hybrids and 12 checks were grown in 12 × 12 simple lattice designs in 1983 and 1984 at three sites in West Germany. The following traits were analysed: plant height (cm), ear dry matter (DM) content (%), total DM yield (kg/ha) of aerial parts, stover DM yield (kg/ha), ear percentage (%) and metabolisable energy (ME) content of stover per kg DM (MJ/kg) as described in detail by Schmidt (1986).

All subsequent computations are based on lattice-adjusted entry means. For each environment, the mean and the GCA and SCA effects employed in the prediction equations were estimated from the single-cross data as outlined by Melchinger (1984). These effects were then used to predict the three-way cross means by the following formula:

$$\hat{G}_{k\times l\cdot m} = \hat{\mu} + \hat{g}'_k + (\hat{g}''_l + \hat{g}''_m)/2 + \varkappa(\hat{s}_{kl} + \hat{s}_{km})/2 . \qquad (7)$$

Weighting coefficient $\varkappa$ for the SCA effects in this prediction equation varied from 0.0 to 1.0. For each value of $\varkappa$, combined analyses of covariance were performed with the observed and predicted three-way cross means and the genotypic correlation between them estimated by established procedures (Mode and Robinson 1959). In addition, heritability (h^2) on an entry mean basis was calculated as the ratio of the genotypic to phenotypic variance of three-way crosses for both the observed and the predicted means.

Combined analyses of variance of the single-cross data were computed to estimate the GCA and SCA variances (for details see Schmidt 1986) and their "heritabilities" α, β and γ. Inserting these estimates into equations (5) yields estimates of the "optimum" weights (λ's). To simplify matters, standardised "optimum" weights (denoted by λ^*) were calculated by dividing the original λ-values by the largest.

Results

Estimates of GCA and SCA variances were highly significant for all traits, with the GCA variances about 2 to 6 times greater than those of the SCA (Table 1). In general, the variances of interactions with environments relative to those of the main effects were more important for SCA than fo GCA. One of the standardised "optimum" weights λ_1^* and λ_2^* of the GCA effects is by definition equal to 1.00; the remaining one exceeded 0.97 for five of the six traits. Estimates of λ_3^* for the SCA effects ranged between 0.34 and 0.64 and between 0.55 and 0.84 for two and six test environments, respectively.

The square root of heritability of the predicted three-way cross means ($h_{\hat{G}}$) slowly decreased with increasing $\varkappa$ for all traits (Figs. 2 and 3). The greatest reduction in $h_{\hat{G}}$ occurred with stover ME content (6.8%), total DM yield (3.8%), and plant height (3.7%) for two test environments. The decrease in $h_{\hat{G}}$ with six test environments was always less than 2%.

♀	Flint lines										
♂ Dent single crosses	1	2	3	4	5	6	7	8	9	10	11
1 × 2			×	×			×				
2 × 3				×	×			×			
3 × 4					×	×			×		
4 × 5						×	×			×	
5 × 6							×	×			×
6 × 7	×							×	×		
7 × 8		×							×	×	
8 × 9			×							×	×
9 × 10	×			×							×
10 × 11	×	×			×						
11 × 1		×	×			×					

Fig. 1. Scheme for producing the 33 flint × dent · dent three-way crosses by mating 11 flint lines with 11 dent × dent single crosses as indicated

The genotypic correlation (r) between the observed and predicted three-way cross means was high (> 0.89) for all traits and all values of $\varkappa$ (Figs. 2 and 3). The curves for r as a function of $\varkappa$ continuously increased for plant height and ear DM content and were slightly convex for the other trais.

The curves for the correlation between the genotypic and predicted values of the three-way crosses ($r_{G\hat{G}} = r \cdot h_{\hat{G}}$) were consistently convex for two and six test environments (Figs. 2 and 3). Like those for $h_{\hat{G}}$ and r, they were rather flat in most instances. The maximum change (7.5%) in $r_{G\hat{G}}$ was found for stover ME content with two test sites. Although the value of $\varkappa$ maximizing $r_{G\hat{G}}$ differed considerably from λ_3^* in certain cases, the corresponding difference in $r_{G\hat{G}}$ was neglible.

There were only minor differences between the values of $r_{G\hat{G}}$ for Jenkins' methods C and B and the "optimum" predictor ($\varkappa = 0$, 1 and λ_3^*, respectively, see Table 2). No method was clearly and consistently superior to all others. The values of $r_{G\hat{G}}$ were in most cases distinctly smaller than those of h_Y, the square root of the heritability of the observed three-way cross means, for six test environments. They were similar for two environments.

Discussion

The most important criterion for a predictor ($\hat{G}$) is its ability to maximise the genetic gain. According to theory, the expected genetic gain from indirect selection using a predictor is proportional to $r_{G\hat{G}}$ (Falconer 1981). Provided the true optimum weights were known

Table 1. Estimates of variance components (σ^2) obtained from the combined analyses of variance of 66 maize single crosses grown in six environments, and standardised "optimum" weights (λ^*) computed for two and six (in parentheses) test environments for six forage traits. DM: ear dry matter; ME: metabolizable energy

Variance component/standardised "optimum" weight		Plant height (cm)	Total DM yield (kg/ha) × 10^4	Stover DM yield (kg/ha) × 10^4	Ear DM content (%)	Ear percentage (%)	Stover ME cont. (MJ/kg)
σ^2_{GCA}	(flint)	46.56**	30.73**	35.93**	9.02**	9.48**	2.69**
σ^2_{GCA}	(dent)	45.33**	51.24**	42.79**	9.03**	6.63**	2.02**
σ^2_{SCA}		8.05**	14.05**	13.65**	1.22**	3.49**	0.91**
$\sigma^2_{\mathrm{E\times GCA}}$	(flint)	8.05**	24.34**	7.25**	2.26**	6.01**	1.59**
$\sigma^2_{\mathrm{E\times GCA}}$	(dent)	12.47**	7.23**	6.38**	1.34**	4.77**	0.91**
$\sigma^2_{\mathrm{E\times SCA}}$		4.03	− 2.52	2.68**	0.58**	2.24**	1.34**
σ^2_e		45.27	121.65	59.82	1.88	9.41	8.18
λ^*_1, λ^*_2	(flint)	1.00 (1.00)	0.84 (0.95)	0.98 (0.99)	0.98 (0.99)	1.00 (1.00)	1.00 (1.00)
	(dent)	0.97 (0.99)	1.00 (1.00)	1.00 (1.00)	1.00 (1.00)	0.97 (0.99)	0.99 (0.99)
λ^*_3		0.41 (0.66)	0.37 (0.62)	0.50 (0.72)	0.64 (0.84)	0.59 (0.78)	0.34 (0.55)

*, ** Significant at the 0.01 level of probability

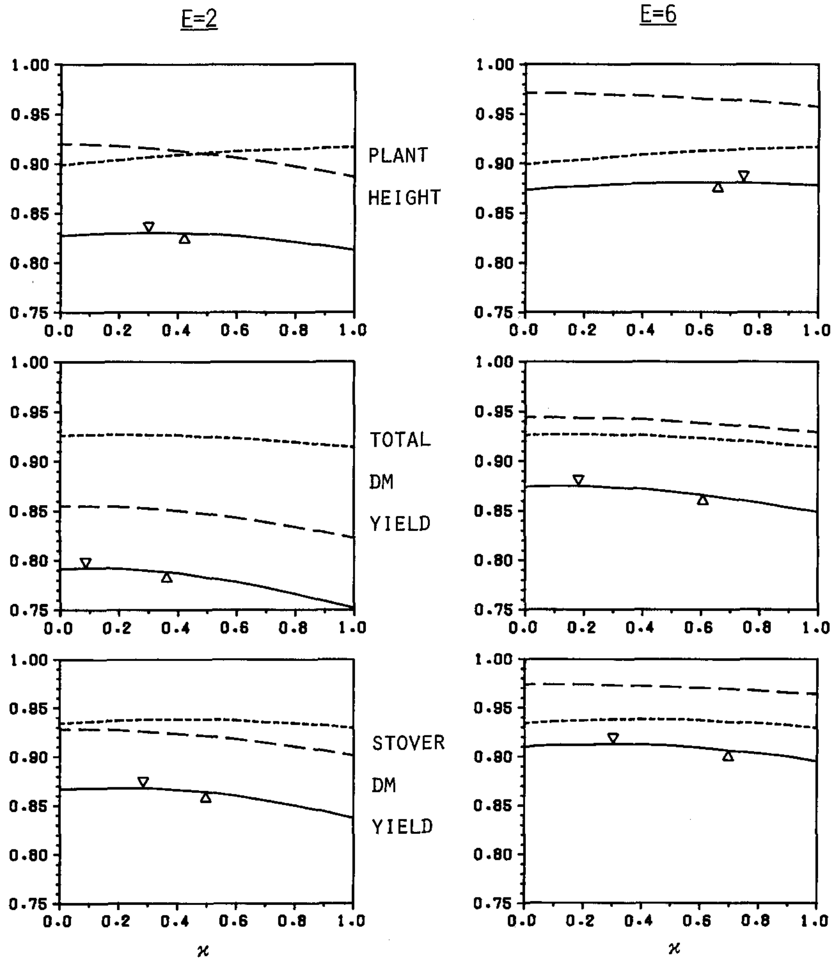

Fig. 2. Square root of heritability ($h_{\hat{G}}$ —) of three-way cross predictors, their genotypic correlation (r ---) with the three-way cross means, and correlation ($r_{G\hat{G}} = r \cdot h_{\hat{G}}$ —) between predicted and genotypic values of the three-way crosses plotted against the weighting factor $\varkappa$ of the SCA effects for E = 2 and E = 6 test environments for three forage maize traits. The maximum of $r_{G\hat{G}}$ and the value corresponding to $\varkappa = \lambda^*_3$ are indicated by ▽ and △, respectively

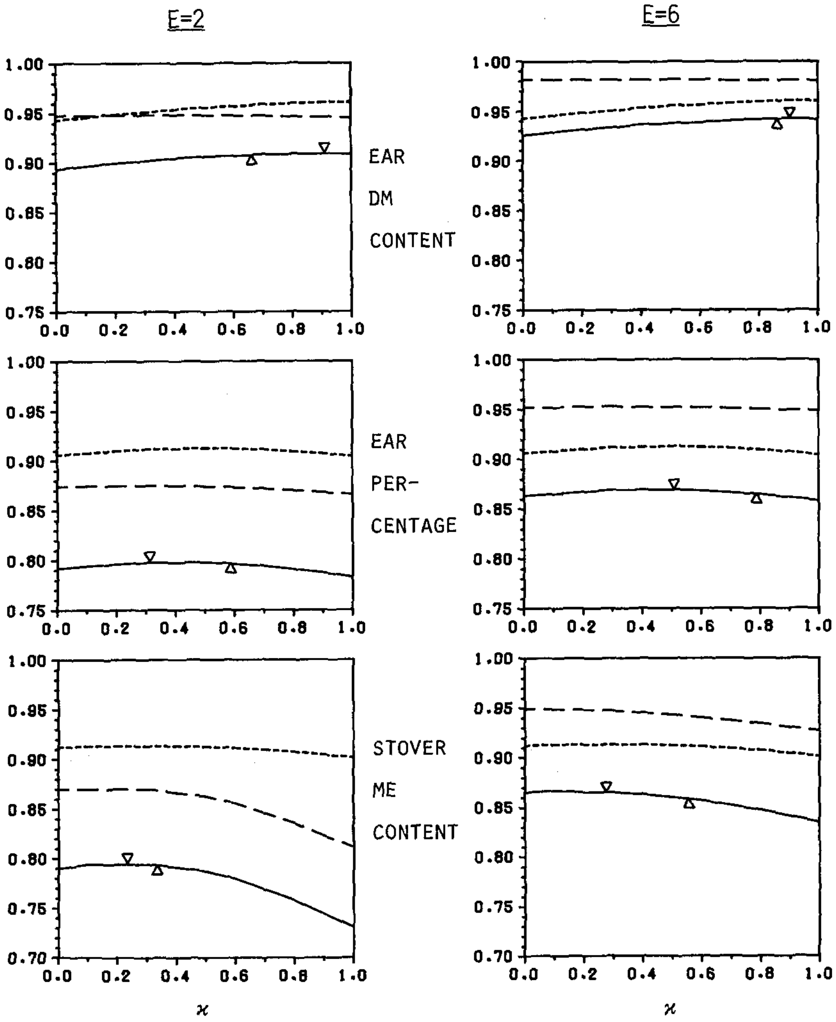

Fig. 3. Square root of heritability ($h_{\hat{G}}$ - -) of three-way cross predictors, their genotypic correlation (r – – –) with the three-way cross means and correlation ($r_{G\hat{G}} = r \cdot h_{\hat{G}}$ —) between predicted and genotypic values of the three-way crosses plotted against the weighting factor $\varkappa$ of the SCA effects for $E = 2$ and $E = 6$ test environments for three forage maize traits. The maximum of $r_{G\hat{G}}$ and the value corresponding to $\varkappa = \lambda_3^*$ are indicated by ▽ and △, respectively

Table 2. Estimates of correlation ($r_{G\hat{G}} = r \cdot h_{\hat{G}}$) between genotypic and predicted values and of heritability (h_Y) of the observed values of 66 maize three-way crosses tested in two and six (in parentheses) environments for six forage traits. $\varkappa$, weight of SCA effects; λ_3^*, "optimum" weight of SCA effects

Trait	$r_{G\hat{G}}$			h_Y
	$\varkappa = 0$	$\varkappa = \lambda_3^*$	$\varkappa = 1$	
Plant height	0.828 (0.873)	0.830 (0.881)	0.813 (0.878)	0.833 (0.934)
Total DM yield	0.792 (0.874)	0.789 (0.866)	0.752 (0.849)	0.743 (0.887)
Stover DM yield	0.867 (0.910)	0.864 (0.906)	0.837 (0.895)	0.855 (0.944)
Ear DM content	0.894 (0.926)	0.908 (0.942)	0.908 (0.942)	0.937 (0.978)
Ear percentage	0.792 (0.863)	0.798 (0.866)	0.786 (0.858)	0.853 (0.943)
Stover ME content	0.790 (0.865)	0.794 (0.858)	0.730 (0.835)	0.766 (0.910)

and the assumptions were valid, the "optimum" predictor would maximise $r_{G\hat{G}}$ among all linear predictors (Henderson 1977).

The curves for $h_{\hat{G}}$ primarily reflect the influence of masking variances (genotype × environment interaction and error variances) on the quality of predictors. Based on theoretical considerations, $h_{\hat{G}}$ is expected to decrease continuously with increasing $\varkappa$, unless γ is large relative to α and β. Furthermore, the total reduction in $h_{\hat{G}}$ from $\varkappa = 0$ to $\varkappa = 1$ becomes greater as γ decreases. The curves obtained for $h_{\hat{G}}$ (Figs. 2 and 3) consistently followed this expected pattern. However, the reduction in $h_{\hat{G}}$ was negligible except in those cases where λ_3 and thus λ_3^* were below 0.5.

In the absence of epistasis, it can be shown that the genotypic correlation (r) between the observed and predicted three-way cross means is an increasing function of $\varkappa$ approaching 1.0 when $\varkappa$ approaches 1.0. However, the estimates of r for Jenkins' method B ($\varkappa = 1$) only approached values of 0.90 to 0.96 (Figs. 2 and 3). Considering their small standard errors (below 0.03), the deviations from $r = 1$ indicate the presence of epistasis except for ear DM content. For parent populations in linkage equilibrium, the shape of the curve for r provides information about the kinds of epistatic effects involved. With purely additive types of epistasis, r continuously increases with $\varkappa$, whereas a convex shape with a local maximum indicates dominance types of epistasis. Besides epistasis and linkage disequilibrium in the parents, nongenetic factors such as competition might also cause reductions in r.

Ignoring epistasis, the product $r \cdot h_{\hat{G}}$ is expected to display a convex curve because of the opposing trends for r and $h_{\hat{G}}$. The maximum of this curve should be located at $\varkappa = \lambda_3^*$, disregarding minor departures due to the fact that λ_1^* or λ_2^* was always slightly smaller than 1.0 (Table 1). The curves for $r_{G\hat{G}} = r \cdot h_{\hat{G}}$ (Figs. 2 and 3) conformed with the convex shape for all traits. The discrepancies between λ_3^* and the value of $\varkappa$ maximising $r_{G\hat{G}}$ might have been caused by errors in the λ^* estimates and/or epistasis.

With the exception of stover ME content for two test environments, the curves for $r_{G\hat{G}}$ were extremely flat in all traits for two and six test environments. This fully concurs with the findings of Otsuka et al. (1972) for the prediction of three-way and double crosses. They studied the correlation between observed and predicted means from different environments (R_d in their notation).

The curves for $r_{G\hat{G}}$ depend upon the number of "tester" lines from the opposite gene pool used for GCA estimation, six in the present study. With a smaller number of tester lines, the efficiency of Jenkins' method C ($\varkappa = 0$) is reduced and the value of $\varkappa$ maximising $r_{G\hat{G}}$ approaches 1.0. For this very reason, $r_{G\hat{G}}$ is also expected to decrease considerably if the GCA is estimated in a topcross test with the opposite population as a tester. Further arguments against GCA estimation in a topcross test were discussed by Geiger et al. (1986).

The minor differences in the efficiency of the "optimum" predictor and Jenkins' methods B and C (Table 2) corroborate the experimental results of Otsuka et al. (1972). Numerical comparisons by Cockerham (1967) with hybrids from one parent population also showed that for a wide range of parameters the efficiencies of all three predictors are similar. Furthermore, Cockerham (1967) found Jenkins' method B more efficient than testing the double crosses per se, when only additive and dominance variances contribute to the genotypic variance. By way of contrast, the present results and those reported by Otsuka et al. (1972) showed that the heritability of the three-way crosses (h_Y) was higher than the correlation between the genotypic and the predicted three-way cross values ($r \cdot h_{\hat{G}}$), probably because of epistasis ($r < 1$).

Our results support Cockerham's (1967) conclusions that the differences among the "optimum" predictor and Jenkins' methods B and C would be unimportant in practice. He suggested choosing either Jenkins' method B or C, depending upon whether λ_3^* is closer to 1 or 0, whereas Otsuka et al. (1972) recommended method B only.

Both Cockerham (1967) and Otsuka et al. (1973) disregarded in their conclusions, however, that Jenkins' method C permits testing schemes other than complete diallels and factorials. Focussing on an optimum allocation of breeding resources, we propose evaluating the GCA of promising lines from each population in test crosses with 4 to 6 lines from the opposite population and predicting all possible three-way or double crosses among both sets of lines by method C. This enables a greater number of lines from each parent population to be tested. Consequently, a greater number of three-way or double crosses can be predicted than with method B. For example, evaluating 20 flint and 20 dent lines in a complete factorial requires testing of 400 single crosses. Alternatively, with the same amount of testing, 40 lines from each pertinent population can be evaluated in test crosses with five lines from the opposite population. The former testing procedure (method B) allows 7,600 possible three-way crosses to be predicted whereas the latter (method C) enables the prediction of 62,400 possible three-way crosses, i.e. about 8 times as many. Hence, with the latter procedure a higher selection intensity among the predicted hybrids can be practised. This increases the selection progress even if Jenkins' method C gives slightly less accurate prediction than method B.

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