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Combined S_2 and Crossbred Family Selection in Full-sib Reciprocal Recurrent Selection*

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Summary. A method (CRRS) that combines S_2 and crossbred family selection in full-sib reciprocal recurrent selection (FSRRS) is proposed. The method requires four generations per cycle in single-eared maize populations. Selection is based on performance of S_2 and full-sib families by applying selection index theory. Equations to estimate the coefficients included in the index are given. These estimates are functions of the genetic and phenotypic variances and covariances among and between the two kinds of families. Comparisons of FSRRS and CRRS under equivalent amount of effort show that CRRS has some advantage over FSRRS for low heritability of the trait being selected (e.g., maize yield) and when only one or two locations with two replications are involved in the selection experiment.

Key words: Selection index – Breeding value – *Zea mays* L.

Introduction

Jones et al. (1971) showed that full-sib reciprocal recurrent selection (FSRRS) as proposed by Hallauer and Eberhart (1970) was a more efficient method of selection in some instances than reciprocal recurrent selection (RRS) designed by Comstock et al. (1949). Only half als many families are included for FSRRS as for RRS to obtain nearly the same genetic gain in the improved crossbred populations. For the FSRRS method, individuals in population A and B are selected on the basis of the performance of the crossbred full-sib families. Because individuals in population A are mated at random to individuals in population B in order to generate the full-sib families, selected families will not necessarily include the best individuals from A and B. Selection for a member of one population depends partially on the member of the reciprocal population with which it was crossed. Therefore, additional evaluation (such as S_2 family) of each one of the members that generate the full-sib families will contribute to select more precisely the best breeding individuals in each population.

The objectives of our study are: 1) to combine in a selection index performance of reciprocal full-sib families and selfing families as a method of discriminating more effectively (within each population) among individuals with the best breeding values for the population cross (CRRS); and 2) to compare genetic gain by CRRS with that by FSRRS.

Methods

Field Plans

Reciprocal full-sib selection was described by Hallauer (1967a), Lonnquist and Williams (1967), and Hallauer and Eberhart (1970). This method requires two-eared maize (*Zea mays* L.) plants in at least one of the populations. A modification of FSRRS that can be used in single-eared populations of maize was described by Hallauer (1967b). One cycle of FSRRS can be completed in 2 years if winter nurseries are available. The following steps are proposed for the combined selfing full-sib reciprocal recurrent selection (CRRS) method.

Season 1. Generate 300 to 400 S_1 families in populations A and B.

Season 2. Plant 300 to 400 paired S_1 rows. Each pair includes one S_1 family from population A and another from population B. Self four plants in each A row and cross them to four plants in its paired B row. Similarly, self pollinate four plants in each B row and cross them onto four plants in its respective A row. Full-sib families are obtained by bulking seed from the eight crossed plants in each pair of rows. S_2 selfing families are obtained by bulking seed from selfed plants within each row.

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Table 1. Mating genotypes for the cross between population A and B, their frequencies, breeding values of genotypes in populations A and B for the population cross, and genotypic values of the S_2 and full-sib family means

Mating types		Frequency of mating types	Breeding values of genotypes in population A when crossed to population B	Breeding values of genotypes in population B when crossed to population A	Genotypic value of the S_2 family means in population A	Genotypic value of the S_2 family means in population B	Genotypic value of the full-sib family means
Population A	Population B						
EE	EE	$p_A^2 p_B^2$	$q_A \alpha_B$	$q_B \alpha_A$	a	a	a
EE	Ee	$2p_A^2 p_B q_B$	$q_A \alpha_B$	$1/2\,(q_B - p_B)\,\alpha_A$	a	1/4 d	1/2 (a + d)
EE	ee	$p_A^2 q_B^2$	$q_A \alpha_B$	$-p_B \alpha_A$	a	− a	d
Ee	EE	$2p_A q_A p_B^2$	$1/2\,(q_A - p_A)\,\alpha_B$	$q_B \alpha_A$	1/4 d	a	1/2 (a + d)
Ee	Ee	$4p_A q_A p_B q_B$	$1/2\,(q_A - p_A)\,\alpha_B$	$1/2\,(q_B - p_B)\,\alpha_A$	1/4 d	1/4 d	1/2 d
Ee	ee	$2p_A q_A q_B^2$	$1/2\,(q_A - p_A)\,\alpha_B$	$-p_B \alpha_a$	1/4 d	− a	1/2 (d − a)
ee	EE	$q_A^2 p_B^2$	$-p_A \alpha_B$	$q_B \alpha_A$	− a	a	d
ee	Ee	$2q_A^2 p_B q_B$	$-p_A \alpha_B$	$1/2\,(q_B - p_B)\,\alpha_A$	− a	1/4 d	1/2 (d − a)
ee	ee	$q_A^2 q_B^2$	$-p_A \alpha_B$	$-p_B \alpha_A$	− a	− a	− a
Mean			0	0	$a\,(p_A - q_A) +$ $1/2\,p_A q_A d$	$a\,(p_B - q_B) +$ $1/2\,p_B q_B d$	$a\,(p_A - q_B) +$ $d\,(p_A q_B + q_A p_B)$

Season 3. Evaluate 200 full-sib families. At the same time, evaluate the 200 corresponding S_2 progenies from both populations.

Season 4. Recombine remnant S_1 seed from selected individuals within each population.

In temperature zones, Seasons 1 and 3 would be the summer seasons and Seasons 2 and 4 would be winter seasons grown at lower latitudes. If difficulties arise in growing the Season 2 generation, each cycle will require 3 years, but additional selection for agronomic traits among the S_1 families could be conducted while generating the full-sib families.

Theory

Consider a single locus, with alleles E and e and genotypes EE, Ee, and ee having genotypic values a, d, and − a, respectively. Let p_A and p_B be the frequencies of the favorable allele in A and B, respectively. Let $\alpha_A = a + (1 - 2\,p_A)\,d$ and $\alpha_B = a + (1 - 2\,p_B)\,d$ be the average effect of a gene substitution in populations A and B, respectively. In the same manner that Falconer (1960) defined the breeding value of a genotype within a population, we can define the breeding value of a genotype in one population when crossed to another population as the deviation of the mean of the cross of this genotype by the reciprocal population from the population cross mean. The following breeding values can be obtained according to the previous definition:

$q_A \alpha_B$ = breeding value of EE in population A, when it is crossed to population B;

$1/2\,(q_A - p_A)\,\alpha_B$ = breeding value of Ee in population A, when it is crossed to population B; and

$-p_A \alpha_B$ = breeding value of ee in population A, when it is crossed to population B.

The different mating genotypes for the cross between populations A and B, their frequencies, the breeding values of genotypes in A and B, and the genotypic values of the S_2 and the full-sib family means are shown in Table 1. From Table 1 the following genetic variances and covariances can be derived:

$$\sigma_{FS}^2 = \tag{1}$$
$$\frac{1}{2}\sum_{j=1}^{n} p_{jA}\,q_{jA}\,\alpha_{jB}^2 + \frac{1}{2}\sum_{j=1}^{n} p_{jB}\,q_{jB}\,\alpha_{jA}^2 + \sum_{j=1}^{n} p_{jA}\,q_{jA}\,p_{jB}\,q_{jB}\,d_j^2;$$

$$\sigma_{SA}^2 = 2\sum_{j=1}^{n} p_{jA}\,q_{jA}\left[a_j + \frac{1}{4}\,(q_{jA} - p_{jA})\,d_j\right]^2 + \frac{1}{4}\sum_{j=1}^{n} p_{jA}^2\,q_{jA}^2\,d_j^2; \tag{2}$$

$$\sigma_{SB}^2 = 2\sum_{j=1}^{n} p_{jB}\,q_{jB}\left[a_j + \frac{1}{4}\,(q_{jB} - p_{jB})\,d_j\right]^2 + \frac{1}{4}\sum_{j=1}^{n} p_{jB}^2\,q_{jB}^2\,d_j^2; \tag{3}$$

$$\sigma_{gA}^2 = \mathrm{Cov}_{(gA,FS)} = \frac{1}{2}\sum_{j=1}^{n} p_{jA}\,q_{jA}\,\alpha_{jB}^2; \tag{4}$$

$$\sigma_{gB}^2 = \mathrm{Cov}_{(gB,FS)} = \frac{1}{2}\sum_{j=1}^{n} p_{jB}\,q_{jB}\,\alpha_{jA}^2; \tag{5}$$

$$\mathrm{Cov}_{(gA,SA)} = \mathrm{Cov}_{(FS,SA)}$$
$$= \sum_{j=1}^{n} p_{jA}\,q_{jA}\,\alpha_{jB}\left[a_j + \frac{1}{4}\,(q_{jA} - p_{jA})\,d_j\right]; \tag{6}$$

$$\mathrm{Cov}_{(gB,SB)} = \mathrm{Cov}_{(FS,SB)}$$
$$= \sum_{j=1}^{n} p_{jB}\,q_{jB}\,\alpha_{jA}\left[a_j + \frac{1}{4}\,(q_{jB} - p_{jB})\,d_j\right]; \tag{7}$$

and

$$\mathrm{Cov}_{(gA,SB)} = \mathrm{Cov}_{(gB,SA)} = \mathrm{Cov}_{(SA,SB)} = 0. \tag{8}$$

σ^2 and Cov refer to genetic variances and covariances, respectively, and FS, SA, SB, gA, and gB refer to full-sib families (FS), S_2 families in populations A (SA) and B (SB), and breeding values of populations A (gA) and B (gB) for the population cross, respectively. Subscript j refers to locus j (j = 1 . . . n). $\sum_{j=1}^{n}$ refers to summation over loci j's.

According to Moreno-González and Grossman (1976), the expected genetic gain (ΔG) of a population cross mean is:

$$\Delta G = \frac{1}{2}\,\frac{i}{\sigma_p}\,p_A\,q_A\,\alpha_B^2 + \frac{1}{2}\,\frac{i}{\sigma_p}\,p_B\,q_B\,\alpha_A^2$$
$$- \frac{2\,d\,i^2}{4\,\sigma_p^2}\,p_A\,q_A\,p_B\,q_B\,\alpha_A\,\alpha_B, \tag{9}$$

where σ_p^2 is the phenotypic variance of the reciprocal full-sib families and i is the selection intensity. The term $\frac{2\,d i^2}{4\,\sigma_p^2}\,p_A\,q_A\,p_B\,q_B\,\alpha_A\,\alpha_B$ has been considered negligible by some authors (Empig et al. 1972), and it also will be considered negligible for further discussions in this paper.

Let ΔgA (FS) and ΔgB (FS) be the expected genetic gains of the breeding values of populations A and B for the population cross, respectively. They can be calculated as the regression coefficients of the breeding values on the full-sib family performance multiplied by the selection differential. That is,

$$\Delta gA\,(FS) = \frac{Cov_{(gA,FS)}}{\sigma_p^2}\, i\, \sigma_p = \frac{1}{2}\,\frac{i}{\sigma_p}\sum_{j=1}^{n} p_{jA}\, q_{jA}\, \alpha_{jB}^2; \quad \text{and}$$

$$\Delta gB\,(FS) = \frac{Cov_{(gB,FS)}}{\sigma_p^2}\, i\, \sigma_p = \frac{1}{2}\,\frac{i}{\sigma_p}\sum_{j=1}^{n} p_{jB}\, q_{jB}\, \alpha_{jA}^2 .$$

Substituting in expression (9), the predicted gain for the population cross becomes:

$$\Delta G = \Delta gA\,(FS) + \Delta gB\,(FS).$$

The theory developed in this paper is under the assumption of no epistasis.

Selection Index

Performance of full-sib and S_2 families can be combined in a selection index with the theory developed by Smith (1936), Hazel and Lush (1942), and Hazel (1943). Let I_A be the selection index for individuals from population A, then

$$I_A = b_1\, x_1 + b_2\, x_2 + b_3\, x_3,$$

where x_1 is performance of full-sib families, and x_2 and x_3 are performance of S_2 families in populations A and B, respectively; b_1, b_2, and b_3 are coefficients to be calculated.

In the same manner, the selection index for individuals from population B (I_B) is

$$I_B = c_1\, x_1 + c_2\, x_2 + c_3\, x_3$$

where, c_1, c_2, and c_3 are coefficients to be calculated.

Let $\Delta gA\,(C)$ be the genetic gain of the breeding value of population A when the selection index approach (CRRS method) is applied. Then,

$$\Delta gA\,(C) = \frac{Cov_{(gA,I_A)}}{\sigma_{I_A}^2}\,\sigma_{I_A} \cdot i = [b_1\, Cov_{(gA,x_1)} + b_2\, Cov_{(gA,x_2)} + b_3\, Cov_{(gA,x_3)}]\,\frac{i}{\sigma_{I_A}},$$

where $\sigma_{I_A}^2$ is the variance of the selection index I_A.

Selection index theory determines b_1, b_2, and b_3 by maximizing $\Delta gA\,(C)$.

$$\Delta gA\,(C) = \frac{(b_1 G_1 + b_2 G_2 + b_3 G_3)\, i}{[b_1^2 P_{11} + b_2^2 P_{22} + b_3^2 P_{33} + 2 b_1 b_2 P_{12} + 2 b_1 b_3 P_{13} + 2 b_2 b_3 P_{23}]^{1/2}}, \tag{10}$$

where $G_1 = Cov_{(gA,x_1)} = Cov_{(gA,FS)} = \sigma_{gA}^2$;
$G_2 = Cov_{(gA,x_2)} = Cov_{(gA,SA)} = Cov_{(FS,SA)}$; and
$G_3 = Cov_{(gA,x_3)} = Cov_{(gA,SB)} = 0$ by equation (8).

P refers to the phenotypic variance and covariances, depending on whether the subscripts are equal or different, respectively. Subscripts 1, 2, and 3 refer to full-sib families, S_2 families in population A, and S_2 families in population B, respectively. If environmental × genetic covariances and environmental × environmental covariances are zero, as expected by randomization of the experimental design, then phenotypic covariances are equal to genetic covariances. Hence, $P_{23} = Cov_{(x_2,x_3)} = Cov_{(SA,SB)} = 0$.

Our goal is to find the b_1, b_2, and b_3 that maximize $\Delta gA\,(C)$. This can be found by differentiating (10) with respect to b_1, b_2, and b_3 and equating to zero. The following expressions are then obtained:

$b_1 P_{11} + b_2 P_{12} + b_3 P_{13} = G_1$;
$b_1 P_{12} + b_2 P_{22} + b_3 P_{23} = G_2$; and
$b_1 P_{13} + b_2 P_{23} + b_3 P_{33} = G_3 = 0$.

Arranging these equations in matrix form we can solve these equations for b_1, b_2, and b_3 as follows:

$$\begin{bmatrix} b_1 \\ b_2 \\ b_3 \end{bmatrix} = \begin{bmatrix} P_{11} & P_{12} & P_{13} \\ P_{12} & P_{22} & 0 \\ P_{13} & 0 & P_{33} \end{bmatrix}^{-1} \begin{bmatrix} G_1 \\ G_2 \\ 0 \end{bmatrix}.$$

Then,

$$b_1 = \frac{P_{22} P_{33} G_1 - P_{12} P_{33} G_2}{P_{11} P_{22} P_{33} - P_{13}^2 P_{22} - P_{12}^2 P_{33}};$$

$$b_2 = \frac{-P_{12} P_{33} G_1 + (P_{11} P_{33} - P_{13}^2)\, G_2}{P_{11} P_{22} P_{33} - P_{13}^2 P_{22} - P_{12}^2 P_{33}}; \quad \text{and}$$

$$b_3 = \frac{-P_{22} P_{13} G_1 + P_{12} P_{13} G_2}{P_{11} P_{22} P_{33} - P_{13}^2 P_{22} - P_{12}^2 P_{33}}.$$

Because the b's are relative weights we can set $b_1 = 1$, then

$$b_2 = \frac{-P_{12} P_{33} G_1 + (P_{11} P_{33} - P_{13}^2)\, G_2}{P_{22} P_{33} G_1 - P_{12} P_{33} G_2} \quad \text{and}$$

$$b_3 = \frac{-P_{13}}{P_{33}}.$$

The coefficients of the selection index for selecting individuals in population B can be obtained in the same manner.

$$c_1 = 1;$$

$$c_2 = \frac{-P_{12}}{P_{22}}; \quad \text{and}$$

$$c_3 = \frac{-P_{13} P_{22} G_4 + (P_{11} P_{22} - P_{12}^2)\, G_5}{P_{22} P_{33} G_4 - P_{13} P_{22} G_5};$$

where

$G_4 = Cov_{(gB,FS)} = \sigma_{gB}^2$ and

$G_5 = Cov_{(gB,SB)} = Cov_{(SB,FS)}$.

All P's can be calculated from the experimental design; G_2 and G_5 are genetic covariances, and they also can be estimated from the experimental design. However, G_1 and G_4 cannot be estimated directly from the experimental design. The genetic variance of the full-sib families (σ_{FS}^2) include G_1, G_4 and one-fourth of the dominance variance (σ_D^2). If σ_D^2 is considered negligible, then by pooling G_1 and G_4, rough estimates of G_1 and G_4 can be obtained as one-half σ_{FS}^2. These estimates will be biased by one-eight σ_D^2. They will not have any effect on estimation of coefficients b_1, b_3, c_1 and c_2, but b_2 and c_3 will be biased downward. Extensive experimental data from maize and other crops have shown that the dominance variance is little important compared to the additive variance.

If the dominance variance is important relative to the additive variance, unbiased estimates of G_1 and G_4 can be obtained by modificating the proposed breeding scheme as follows:

Instead of growing 200 full-sib families (FS), only 150 FS families are grown. In addition, 50 half-sib families (HS) from population A crossed with B and 50 HS families from population B crossed with A are also evaluated. These HS families are obtained in Season 2 by crossing six to eight plants from random S_1 families in one population with bulk pollen from the reciprocal population. At the same time six to eight plants are selfed in each S_1 family to obtain corresponding S_2 families. Thus 650 families instead of 600 will be evaluated in Season 3. The following relations hold:

$$G_1 = \sigma^2_{\mathrm{HSA}} = \mathrm{Cov}\,(\mathrm{gA}, \mathrm{FS})$$

$$G_4 = \sigma^2_{\mathrm{HSB}} = \mathrm{Cov}\,(\mathrm{gB}, \mathrm{FS})$$

$$G_2 = \mathrm{Cov}\,(\mathrm{HSA}, \mathrm{SA}) = \mathrm{Cov}\,(\mathrm{FS}, \mathrm{SA}) = \mathrm{Cov}\,(\mathrm{gA}, \mathrm{SA})$$

$$G_5 = \mathrm{Cov}\,(\mathrm{HSB}, \mathrm{SB}) = \mathrm{Cov}\,(\mathrm{FS}, \mathrm{SB}) = \mathrm{Cov}\,(\mathrm{gB}, \mathrm{SB})$$

Where HSA and HSB refer to half-sib families in populations A and B, respectively.

Individuals producing HS families in A and B are selected at the same time as individuals producing FS families, according to the following selection index:

$$I_{\mathrm{HSA}} = b_1 x_4 + b_2 x_2 + b_3 \bar{x}_3,$$

$$I_{\mathrm{HSB}} = c_1 x_5 + c_2 \bar{x}_2 + c_3 x_3.$$

Where x_4 and x_5 are performances of individual HS families in A and B, respectively. $\bar{x}_2$ and $\bar{x}_3$ are the means of all evaluated S_2 families in A and B, respectively.

More reliable estimates of the genetic parameters can be obtained by pooling data from previous cycles of recurrent selection experiments or from previous research.

Relative Efficiency

Comparisons of both methods of selection reduce to comparison of ΔgA (FS) with ΔgA (C) and ΔgB (FS) with ΔgB (C). Examination of the first of these comparisons shows:

$$\Delta \mathrm{gA}\,(\mathrm{FS}) = \frac{\mathrm{Cov}_{(\mathrm{gA},\mathrm{FS})} \sqrt{P_{11}}\, i}{P_{11}} = \frac{G_1\, i}{\sqrt{P_{11}}} = h_A \sqrt{G_1}\, i, \tag{11}$$

where $h^2_A = \frac{G_1}{P_{11}}$ (12) is the heritability of population A for the population cross; and

$$\Delta \mathrm{gA}\,(\mathrm{C}) = \frac{\mathrm{Cov}_{(\mathrm{gA},I_A)}}{\sigma^2_{I_A}}\, \sigma_{I_A} = \frac{\mathrm{Cov}_{(\mathrm{gA},I_A)}}{\sigma_{I_A}\, \sigma\, \mathrm{gA}}\, \sigma\, \mathrm{gA}\, i = R_{(\mathrm{gA},I_A)} \sqrt{G_1}\, i. \tag{13}$$

$R_{(\mathrm{gA},I_A)}$ is the multiple correlation coefficient between gA, and $I_A = b_1 x_1 + b_2 x_2 + b_3 x_3$ because the predictor I_A maximizes the correlation of gA and the set of variables X's. It can be computed in the following manner:

$$R_{(\mathrm{gA},I_A)} = \sqrt{[r_{(\mathrm{gA},X)}]^{1}\ [r_{XX}]^{-1}\ [r_{(\mathrm{gA},X)}]} \tag{14}$$

where $[r_{(\mathrm{gA},X)}]$ is the vector of correlations of gA with the X's and $[r_{XX}]$ is the correlation matrix of the X's.

$$[r_{(\mathrm{gA},X)}] = \begin{bmatrix} r_{(\mathrm{gA},x_1)} \\ r_{(\mathrm{gA},x_2)} \\ r_{(\mathrm{gA},x_3)} \end{bmatrix} \qquad [r_{XX}] = \begin{bmatrix} 1 & r_{12} & r_{13} \\ r_{12} & 1 & r_{23} \\ r_{13} & r_{23} & 1 \end{bmatrix}.$$

The $r_{(\mathrm{gA},x_j)}$ are simple correlation coefficients between gA and x_i, and r_{ij} are phenotypic correlations between x_i and x_j (i and j = 1, 2, 3). The simple correlation coefficients become:

$$r_{(\mathrm{gA},x_1)} = \frac{\mathrm{Cov}_{(\mathrm{gA},x_1)}}{\sigma_{\mathrm{gA}}\, \sigma_{x_1}} = \frac{g_1}{\sqrt{P_{11} G_1}} = h_A; \quad \text{and}$$

$$r_{(\mathrm{gA},x_2)} = \frac{\mathrm{Cov}_{(\mathrm{gA},x_2)}}{\sigma_{\mathrm{gA}}\, \sigma_{x_2}} = \frac{G_2}{\sqrt{G_1 P_{22}}} = \frac{G_2}{\sqrt{P_{11} P_{22}}} \sqrt{\frac{P_{11}}{G_1}} = \frac{r_{12}}{h_A}.$$

Assuming that environmental covariances are zero, then $G_2 = P_{12}$;

$$r_{(\mathrm{gA},x_3)} = \frac{\mathrm{Cov}_{(\mathrm{gA},x_3)}}{\sigma_{\mathrm{gA}}\, \sigma_{x_3}} = 0; \quad \text{and} \quad r_{23} = 0.$$

Substituting in Eq. (14) with the appropriate terms, the following expression is obtained:

$$R_{(\mathrm{gA},\mathrm{IA})} = h_A \sqrt{\frac{1 - \frac{2 r^2_{12}}{h^2_A} + \frac{r^2_{12}(1 - r^2_{13})}{h^4_A}}{1 - r^2_{12} - r^2_{13}}}.$$

The efficiency (E_A) of the CRRS method relative to the FSRRS method for response in population A with respect to the cross is obtained by comparing Eq. (13) and (11):

$$E_A = \frac{\Delta \mathrm{gA}\,(\mathrm{C})}{\Delta \mathrm{gA}\,(\mathrm{FS})} = \sqrt{\frac{1 - \frac{2 r^2_{12}}{h^2_A} + \frac{r^2_{12}(1 - r^2_{13})}{h^4_A}}{1 - r^2_{12} - r^2_{13}}}. \tag{15}$$

Similarly, efficiency (E_B) for population B would be:

$$E_B = \sqrt{\frac{1 - \frac{2 r^2_{13}}{h^2_B} + \frac{r^2_{13}(1 - r^2_{12})}{h^4_B}}{1 - r^2_{12} - r^2_{13}}}, \tag{16}$$

where $h^2_B = \frac{G_4}{P_{11}}$ (17) is the heritability of population B for the population cross. E_A has a minimum for $h^2_A = 1 - r^2_{13}$ and E_B for $h^2_B = 1 - r^2_{12}$. It can be shown that E_A and E_B are greater than one for any value of h^2_A and h^2_B, provided that $r^2_{12} + r^2_{13} < 1$.

The multiple coefficient of determination, R^2, obtained from regressing x_1 on x_2 and x_3 is:

$$R^2 = [r_{12} \quad r_{13}] \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix}^{-1} \begin{bmatrix} r_{12} \\ r_{13} \end{bmatrix} = r^2_{12} + r^2_{13}.$$

Therefore, $r^2_{12} + r^2_{13}$ cannot exceed the unity.

Because P_{11} includes G_1, G_4, and the dominance and the environmental components, the following relation is obtained:

$$h^2_A + h^2_B = \frac{G_1 + G_4}{P_{11}} < 1. \tag{18}$$

Results and Discussion

Figure 1 is a graphical representation of Eqs. (15) and (16) for the simple case $r_{12} = r_{13}$ and $h^2_A = h^2_B = h^2$. It shows that the CRRS method is more efficient than the FSRRS method for any value of h^2. The relative efficiency (E) increases as the phenotypic correlations r_{12} and r_{13} increase. E increases rapidly as h^2 decreases below $1 - r^2_{13}$ and $1 - r^2_{12}$. The CRRS method is especially efficient for values of r_{12} and r_{13} close to, but below, 0.7 and for low values of h^2.

Heritability estimates in maize testcrosses for grain yield have been obtained by several authors (Table 2). The magnitude of these estimates was about 0.45 in experiments including three or four locations and two replications per location. Heritabilities (h^2) of breeding values in populations A and B (Eqs. 12, 17) are expected to be lower that those of testcrosses because of a larger

Table 2. Estimates of heritability (h^2) in maize testcrosses for yield

Author	Number of estimates	Range of h^2 estimates
Goulas and Lonnquist (1976)	2	0.48 – 0.56
Horner et al. (1973)	5	0.39 – 0.62
Darrah et al. (1972)	3	0.42 – 0.55
Carangal et al. (1971)	3	0.27 – 0.54

genetic component in the phenotypic variance of the full-sib families, as illustrated in the following formula:

$$h_A^2 = \frac{G_1}{P_{11}} = \frac{G_1}{\sigma_{FS}^2 + \frac{\sigma_{ge}^2}{l} + \frac{\sigma_e^2}{r}}$$

where σ_{ge}^2, σ_e^2, l, and r are the variance of genotype-environment interaction, error variance, number of locations, and number of replications, respectively. From Eq. (18), values of heritabilities (h_A^2 and h_B^2) are expected to be lower than 0.5 in most practical situations. Estimates of h_A^2 and h_B^2 depend on how large the environmental and genetic-environmental components are relative to the genetic variances.

Phenotypic correlations (r_p) between S_1 families and testcrosses have been estimated by several authors in different studies for maize grain yield (Table 3). In these studies most of the r_p estimates ranged between 0.3 and 0.6.

r_{12} can be expressed as:

$$r_{12} = h_A^2 \frac{G_2}{G_1} \sqrt{\frac{P_{11}}{P_{22}}} \, . \tag{19}$$

From this formula, r_{12} is expected to be higher tan h_A^2, because P_{22} is expected not to exceed twice P_{11} and G_2 is expected to be about twice G_1. Similarly, r_{13} is expected to be higher than h_B^2. Therefore, the favorable

Table 3. Estimates of phenotypic correlations (r_p) between S_1 families and testcrosses for maize yield

Author	Number of estimates	Range r_p estimates	Number of estimates >0.7
Goulas and Lonnquist (1977)	2	0.36 – 0.48	0
Harris et al. (1972)	12	0.08 – 0.45	0
Carangal et al. (1971)	4	0.24 – 0.68	0
Genter and Alexander (1962)	2	0.47 – 0.61	0
Genter and Alexander (1966)	12	0.30 – 0.74	1
Lonnquist and Lindsey (1964)	2	0.28 – 0.30	0

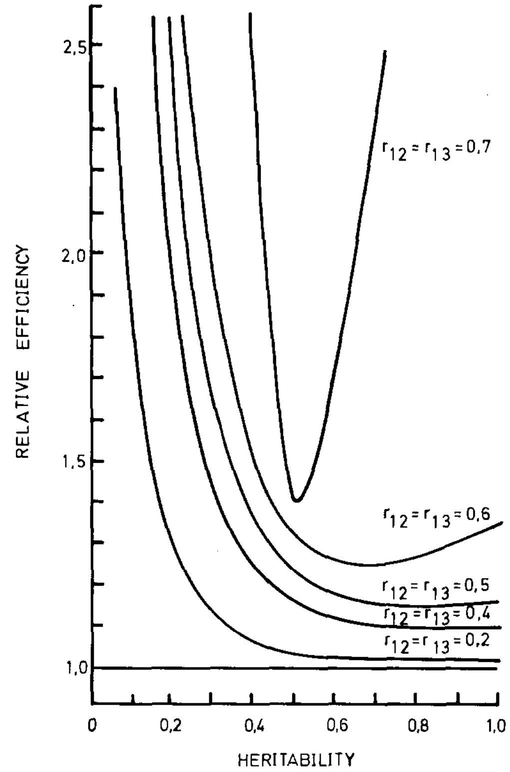

Fig. 1. Relative efficiency of CRRS compared with FSRRS for different values of phenotypic correlated coefficients (r_{12}, r_{13}) when same selection intensity is applied to both methods

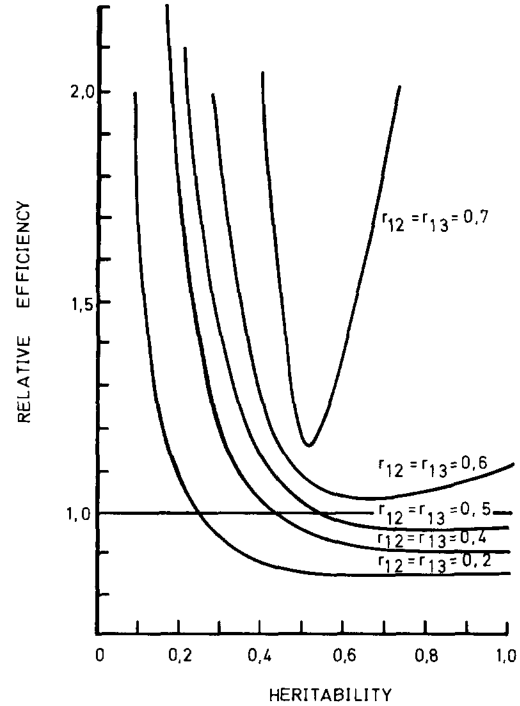

Fig. 2. Relative efficiency of CRRS compared with FSRRS for different values of phenotypic correlation coefficients (r_{12}, r_{13}) considering equivalent amount of effort in both methods, and selection intensities $i_c = 1.5544$ and $i_{FS} = 1.8874$ are applied to CRRS and FSRRS, respectively

situations with low h_A^2 and h_B^2 values and higher r_{12} and r_{13} values are the most likely to occur. These situations result in a better efficiency of the CRRS compared with the FSRRS method as can be seen by Figs. 1 and 2.

Both methods, CRRS and FSRRS, however, should be compared on the basis of the same number of progenies. The FSRRS method would be able to evaluate three times the number of full-sib families as the CRRS method during Season 3. To create such a number of families, however, it would be necessary to obtain three times the number of selfed ears in the Season 1 generation, to grow three times the number of paired rows, and to make the crosses during Season 2. Therefore, if comparisons of both methods are made on the basis of equivalent amount of effort through the four generations of a cycle, the FSRRS method would not permit the evaluation of three times, but about twice the number of full-sib families as the CRRS method. It is especially true, when only one or two locations and two or three replications are used for evaluating the families. For selecting the same number of families in both methods, let the portion selected for CRRS be the top 15% ($i_C = 1.5544$); the portion selected for FSRRS, therefore, would be the top 7.5% ($i_{FS} = 1.8874$). Figure 2 shows the relative efficiency of CRRS compared to with FSRRS when selection intensities i_C and i_{FS} are applied to CRRS and FSRRS, respectively. From equation (19), r_{12} will be about $\sqrt{2}\, h_A^2$. For the simple case, $r_{12} = r_{13} = \sqrt{2}\, h_A^2$. The relative efficiency (E_1) of the CRRS method compared with the FSRRS method, under selection intensities i_C and i_{FS}, respectively, becomes:

$$E_1 = 0.8235 \sqrt{1 + \frac{2}{1 + 2\, h_A^2}}\,.$$

E_1 is always greater than 1.16 for the situation $h_A^2 < 0.5$.

We can conclude that, for low heritability of the trait under selection (i.e., maize grain yield) and when only one or two locations with two replications are involved in the selection experiment, CRRS has an advantage over FSRRS. Under equivalent amount of effort, this advantage is larger as the heritabilities, h_A^2 and h_B^2, are smaller and as r_{12} and r_{13} are larger relative to h_A^2 and h_B^2. Also, in applied breeding programs, CRRS would have advantage because additional pressure can be applied to the S_2 progenies.

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