

COMPARISONS OF INTRA-, INTERPOPULATION, AND MODIFIED RECURRENT SELECTION METHODS

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ABSTRACT

Interpopulation and intrapopulation recurrent selection are the selection methods that have been used for germplasm improvement. However, neither intra- nor interpopulation (reciprocal) selection can improve at reasonable rates the population crosses and the populations *per se* simultaneously. Thus, this work was carried out to investigate the drawbacks of these selection schemes, to introduce a modified selection method, and to compare this modified selection method with reciprocal (interpopulation) and with intrapopulation half-sib selection. The effectiveness of these selection methods on populations *per se*, population crosses, and heterosis improvement were compared from a theoretical approach. The results showed that reciprocal selection is more efficient than intrapopulation half-sib selection in a general way. A further analysis of the contribution of each population for the breeding showed neither reciprocal nor intrapopulation half-sib selection is the suitable choice. The use of testcross (interpopulation) selection for population 1 and intrapopulation half-sib selection for population 2, with population 2 (lower yielding than population 1) as the tester for both populations, is the suitable choice. Testcross half-sib selection is more efficient than intrapopulation half-sib selection and as efficient as reciprocal selection for population 1; more efficient than reciprocal and as efficient as intrapopulation half-sib selection for population 2; less than reciprocal and more efficient than half-sib selection for heterosis; and more efficient than both intrapopulation half-sib and reciprocal selection for population cross improvement.

INTRODUCTION

Recurrent selection methods have two main categories: intrapopulation and interpopulation selection. The former was devised to improve the populations *per se*, and the latter to improve the population crosses (Moll and Stuber, 1971).

Responses to intra- and interpopulation selection in maize (*Zea mays* L.) have been reported (Moll and Robinson, 1966; Moll and Stuber, 1971; Darrah *et al.*, 1972; Russell *et al.*, 1973; Moll *et al.*, 1978; Smith, 1983, 1984). Also, theoretical comparisons between these selection procedures have been reported (Griffing, 1962, 1963; Cress, 1966, 1967). In general, these results showed that interpopulation selection improves the population crosses but is not suitable for the improvement of the populations *per se*, whereas intrapopulation selection improves the populations *per se* but is not suitable for the improvement of the population crosses. There is also some evidence that heterosis increases with inter- and decreases with intrapopulation selection methods (Moll *et al.*, 1978; Jiang *et al.*, 1990).

Improvement of crop species that is based on the selection of hybrids produced from inbred lines requires that the populations *per se* and the population crosses be improved as efficiently as possible, because the rates of improvement of inbred lines *per se* and of hybrids produced from inbred lines are expected to be similar to the rates of improvement of the populations *per se* and of the population crosses, respectively. Hence, neither intra- nor interpopulation selection can fulfill these requirements simultaneously.

This paper reports theoretical comparisons of intra- and interpopulation selection by using expected responses to selection in the base populations, in the interpopulation hybrid, and in the heterosis, to investigate the drawbacks of these selection procedures. Then, a modified recurrent selection procedure is introduced to try to fulfill the requirements of the breeding programs for hybrids development, and this procedure is compared with intra- and interpopulation selection.

METHODS

The breeding populations

The two populations (1 and 2) are assumed to be in both Hardy-Weinberg and linkage equilibrium. For comparison, the two populations are under reciprocal recurrent selection (RRS) (Comstock *et al.*, 1949), and simultaneous half-sib intrapopulation recurrent selection (HSS) (Empig *et al.*, 1972). These methods were considered because they both require half-sib progenies (inter- and intra-) for evaluation, and S₁ progenies for recombination. It was also assumed that the phenotypic variances of these methods were equal because they are all from half-sib progenies, and for quantitative traits such as grain yield most of the phenotypic variance is due to environmental variance. These populations were presumed genetically divergent with average frequencies of favorable alleles in population 1 greater than that in population 2.

The genetic model

The models used to describe the genotypic values of the intra- and interpopulation random individuals from two random mating diploid populations (Griffing, 1962; Stuber and Cockerham, 1966) are:

$$G_{ii' (11)} = \mu_{11} + \alpha_{i11} + \alpha_{i'11} + \delta_{ii' (11)} \quad (1)$$

$$G_{jj' (22)} = \mu_{22} + \alpha_{j22} + \alpha_{j'22} + \delta_{jj' (22)} \quad (2)$$

$$G_{ij(12)} = \mu_{12} + \alpha_{i12} + \alpha_{j21} + \delta_{ij(12)} \quad (3),$$

where μ is the intra- or interpopulation mean, α_i and α_j are the additive effects, and $\delta_{ii'}$, $\delta_{jj'}$, and δ_{ij} are the dominance effects. These models are defined for the populations (models 1 and 2) and for the population cross (model 3). The models assume no epistasis, and in model 3, gene frequencies refer to the parent populations and the genetic effects are defined according to origin.

If we let p_i and p_j refer to the frequencies of the i^{th} and j^{th} alleles of the populations 1 and 2, we have:

$$\sigma_{A11}^2 = 2 \sum_i p_i (\alpha_{i11})^2 \quad \text{and} \quad \sigma_{D11}^2 = \sum_{i,i'} p_i p_{i'} (\delta_{ii' (11)})^2,$$

$$\sigma_{A22}^2 = 2 \sum_j p_j (\alpha_{j22})^2 \quad \text{and} \quad \sigma_{D22}^2 = \sum_{j,j'} p_j p_{j'} (\delta_{jj' (22)})^2,$$

$$\sigma_{A12}^2 = 2 \sum_i p_i (\alpha_{i12})^2,$$

$$\sigma_{A21}^2 = 2 \sum_j p_j (\alpha_{j21})^2, \quad \text{and} \quad \sigma_{D(12)}^2 = \sum_{i,j} p_i p_j (\delta_{ij(12)})^2.$$

Where σ_A^2 and σ_D^2 are the additive and dominance variances of the populations 1 and 2, and of the interpopulation hybrid (1x2).

Now, let: $\alpha_{i12} = \alpha_{i11} + \tau_{i12}$ and

$$\alpha_{j21} = \alpha_{j22} + \tau_{j21},$$

and the interpopulation additive effects are expressed as intrapopulation additive effects (α_{i11} and α_{j22}) plus the deviations from them (τ_{i12} and τ_{j21}). Note that, $\tau_{i12} = \alpha_{i12} - \alpha_{i11}$, and $\tau_{j21} = \alpha_{j21} - \alpha_{j22}$.

Then, the interpopulation additive genetic variances can be defined as:

$$\sigma_{A12}^2 = 2\sum_i p_i(\alpha_{i11} + \tau_{i12})^2 = 2\sum_i p_i(\alpha_{i11})^2 + 2\sum_i p_i(\tau_{i12})^2 + 4\sum_i p_i\alpha_{i11}\tau_{i12}$$

and

$$\sigma_{A21}^2 = 2\sum_j p_j(\alpha_{j22} + \tau_{j21})^2 = 2\sum_j p_j(\alpha_{j22})^2 + 2\sum_j p_j(\tau_{j21})^2 + 4\sum_j p_j\alpha_{j22}\tau_{j21}.$$

Thus, one can define:

$$\sigma_{\tau12}^2 = 2\sum_i p_i(\tau_{i12})^2, \text{ and}$$

$$\sigma_{\tau21}^2 = 2\sum_j p_j(\tau_{j21})^2$$

as the genetic variances of the deviations from inter- and intrapopulation additive effects.

Also,

$$\text{Cov}(A_1\tau_{12}) = \sum_i p_i\alpha_{i11}\tau_{i12}, \quad \text{and}$$

$$\text{Cov}(A_2\tau_{21}) = \sum_j p_j\alpha_{j22}\tau_{j21}$$

can be defined as the genetic covariances of the intrapopulation additive effects with the deviations from inter- and intrapopulation additive effects.

The interpopulation additive genetic variances become:

$$\sigma_{A12}^2 = \sigma_{A11}^2 + \sigma_{\tau12}^2 + 4\text{Cov}(A_1\tau_{12}) \quad ,$$

and

$$\sigma_{A21}^2 = \sigma_{A22}^2 + \sigma_{\tau21}^2 + 4\text{Cov}(A_2\tau_{21}) \quad .$$

Thus, the genetic variances of the populations (1 and 2) and of the populations cross are:

$$\sigma_{G11}^2 = \sigma_{A11}^2 + \sigma_{D11}^2 \quad , \quad \sigma_{G22}^2 = \sigma_{A22}^2 + \sigma_{D22}^2 \quad ,$$

and

$$\sigma_{G12}^2 = \frac{1}{2} [\sigma_{A11}^2 + \sigma_{A22}^2 + \sigma_{\tau12}^2 + \sigma_{\tau21}^2 + 4\text{Cov}(A_1\tau_{12}) + 4\text{Cov}(A_2\tau_{21}) + \sigma_{D(12)}^2] .$$

The genetic covariance between relatives (x and y) of the population cross is:

$$\text{CovG}(x,y) = g_1[\sigma_{A11}^2 + \sigma_{\tau12}^2 + 4\text{Cov}(A_1\tau_{12})]$$

$$+ g_2[\sigma_{A22}^2 + \sigma_{\tau21}^2 + 4\text{Cov}(A_2\tau_{21})] + t\sigma_{D(12)}^2 ,$$

where $g_1 = \frac{1}{2} P(x_1 \equiv y_1)$, $g_2 = \frac{1}{2} P(x_2 \equiv y_2)$, and $t = P(x_1 \equiv y_1) P(x_2 \equiv y_2)$. These are probabilities that a random allele of one relative (x) is identical by descent to a random allele of the other relative (y) from populations 1 and 2, respectively (Stuber and Cockerham, 1966).

The genetic covariances between inter- (x_{12}) and intrapopulation (y_1 or y_2) relatives are:

$$\text{CovG}(x_{12}, y_1) = g_1[\sigma_{A11}^2 + 2\text{Cov}(A_1\tau_{12})], \text{ and}$$

$$\text{CovG}(x_{12}, y_2) = g_2[\sigma_{A22}^2 + 2\text{Cov}(A_2\tau_{21})].$$

These covariances are for population cross and populations 1 and 2, respectively.

Notice that the approach used to partition the interpopulation genetic variances was made in a manner similar to that of Cowen (1987).

Following Falconer's (1989) model, for a locus with two alleles, with p and q , r and s as the frequencies of the favorable and unfavorable alleles in populations 1 and 2, respectively; and a as half of the difference of the genotypic values of the homozygotes, and d as the genotypic value of the heterozygote, we have:

$$\sigma_{A11}^2 = 2pq [a + (q-p)d]^2 \quad ; \quad \sigma_{A22}^2 = 2rs [a + (s-r)d]^2 \quad ;$$

$$\sigma_{A12}^2 = 2pq [a + (s-r)d]^2 \quad ; \quad \sigma_{A21}^2 = 2rs [a + (q-p)d]^2 \quad ;$$

$$\sigma_{\tau12}^2 = 8pq (p-r)^2 d^2 \quad ; \quad \sigma_{\tau21}^2 = 8rs (p-r)^2 d^2 \quad ;$$

$$\text{Cov}(A_1\tau_{12}) = 2pq (p-r) [a + (q-p)d]d \quad \text{and}$$

$$\text{Cov}(A_2\tau_{21}) = 2rs (r-p) [a + (s-r)d]d .$$

The relative magnitudes of the parameters that constitute σ_{A12}^2 and σ_{A21}^2 were obtained by assuming that the population gene frequencies fit a Beta distribution. Then, the genetic variances and covariances represent the mean expected value of a population or of a population cross, and are expressed as a function of a and d genotypic values (Souza Jr., 1985, 1987). Three types of base populations (A, B, and C) that represent three levels of favorable allele frequencies (A with $\bar{p} = 0.4$, B with $\bar{p} = 0.5$, and C with $\bar{p} = 0.6$), and the population crosses $A \times C$ and $B \times C$ were used (Table I). Thus, two population crosses that represent two different levels of genetic divergence of the base populations were used, with the population cross $A \times C$ produced from more divergent base populations than the cross $B \times C$. The expected values of the variances were obtained as:

$\epsilon(\sigma_x^2) = \int_0^1 \sigma_x^2 \phi p dp$ or $\epsilon(\sigma_x^2) = \int_0^1 \sigma_x^2 \phi r dr$ for the population parameters, and $\epsilon(\sigma_x^2) = \int_0^1 \int_0^1 \sigma_x^2 \phi p dp \phi r dr$ for the interpopulation parameters. The expected values of the covariances were obtained in the same way, only substituting the variances by the covariances in the integral expressions.

Notice that the genetic model assumes two alleles per locus, no epistasis, linkage and Hardy-Weinberg equilibrium, and that the base populations were characterized by a definite Beta distribution of allele frequencies controlling a quantitative trait.

Table I - Three types of populations and their crosses in terms of gene frequencies distributions as defined by Beta distributions.

Population	Beta distribution	Density function ($\phi(p$ or $\phi(r)$) ^a	Mean gene frequency
A	Beta (2,1)	$12p(1-p)^2$	0.4
B	Beta (2,2)	$6p(1-p)$	0.5
C	Beta (3,2)	$12p^2(1-p)$	0.6
AxC	$\phi(p,r)^*$	$144p^2r(1-p)(1-r)^2$	
BxC	$\phi(p,r)^*$	$72p^2r(1-p)(1-r)$	

^aConsidering the independent distributions: $\phi(p,r) = \phi_p\phi_r$; and p or r for the populations A, B, or C.

The expressions of the expected responses from selection (G_s) were obtained in the usual manner:

$$G_s = i \text{Cov}G(x,y)/\sigma_{Ph},$$

where i and σ_{Ph} are the standardized selection differential and the phenotypic standard deviation of the selection units (half-sib progenies), respectively. The $\text{Cov}G(x,y)$ is the genetic covariance among the selection units (x) and the members of the improved population after one cycle of selection and recombination (y).

DISCUSSION

The derived parameters $\sigma_{\tau_{12}}^2$, $\sigma_{\tau_{21}}^2$, $\text{Cov}(A_1\tau_{12})$, and $\text{Cov}(A_2\tau_{21})$ are related to the genetic divergence ($p-r$) of the base populations and to the level of dominance (d) of the traits. Hence, these parameters are related to heterosis because heterosis depends on these two factors, e.g., $h=(p-r)^2d$ for a locus with two alleles as defined by Falconer (1989). The genetic variances ($\sigma_{\tau_{12}}^2$ and $\sigma_{\tau_{21}}^2$) will be always positive, but for $p>r$ we have $\text{Cov}(A_1\tau_{12})>0$ and $\text{Cov}(A_2\tau_{21})<0$, and vice-versa for $p<r$. Thus, these covariances will be positive for the population with higher average frequencies of favorable alleles, and negative for the one with lower average frequencies of those alleles. If the two populations are not divergent we have: $\sigma_{\tau_{12}}^2 = \sigma_{\tau_{21}}^2 = \text{Cov}(A_1\tau_{12}) = \text{Cov}(A_2\tau_{21}) = 0$.

Ratios of these genetic variances and covariances that form the interpopulation additive variances σ_{A12}^2 and σ_{A21}^2 for the two types of population crosses considered, showed that the intrapopulation additive variances σ_{A11}^2 and σ_{A22}^2 are larger than the σ_{τ}^2 's and $\text{Cov}(A\tau)$'s parameters, but the differences decrease as the level of dominance increases. For example, for partial dominance [(d/a)=0.5] the σ_A^2 's are 8.9 to 16.5 times larger than σ_{τ}^2 's, and 11.8 to 50.0 times larger than $\text{Cov}(A\tau)$'s. However, for complete dominance [(d/a)=1] the σ_A^2 's are 2.14 to 5.0 times larger than σ_{τ}^2 's, and 6.3 to 10 times larger than $\text{Cov}(A\tau)$'s; but $\sigma_{A11}^2/\text{Cov}(A_1\tau_{12}) = 160/0 = \infty$ (Table II).

Table II - Ratios of the expected genetic variances and covariances for several levels of dominance (d/a), and two types of population.^a

Ratios	Level of dominance (d/a)					
	0.25	0.50	0.75	1.00	1.25	1.50
	Population AxC					
$\sigma_{A11}^2 / \sigma_{\tau_{12}}^2$	37.50	8.93	3.85	2.14	1.39	0.99
$\sigma_{A11}^2 / \text{Cov}(A_1\tau_{12})$	25.00	13.89	10.78	10.00	10.78	13.89
$\sigma_{\tau_{12}}^2 / \text{Cov}(A_1\tau_{12})$	0.67	1.56	2.80	4.67	7.78	14.00
$\sigma_{A22}^2 / \sigma_{\tau_{21}}^2$	60.50	16.50	8.06	5.00	3.54	2.72
$\sigma_{A22}^2 / \text{Cov}(A_2\tau_{21})$	-23.27	-11.79	-8.06	-6.25	-5.28	-4.54
$\sigma_{\tau_{21}}^2 / \text{Cov}(A_2\tau_{21})$	-0.39	-0.71	-1.00	-1.25	-1.47	-1.67
$\text{Cov}(A_2\tau_{21})/\text{Cov}(A_1\tau_{12})$	-1.24	-1.56	-2.00	-2.67	-3.78	-6.00
	Population BxC					
$\sigma_{A11}^2 / \sigma_{\tau_{12}}^2$	43.75	10.42	4.49	2.50	1.62	1.16
$\sigma_{A11}^2 / \text{Cov}(A_1\tau_{12})$	70.00	50.00	64.67	∞^b	-38.80	-16.67
$\sigma_{\tau_{12}}^2 / \text{Cov}(A_1\tau_{12})$	1.60	4.80	14.40	∞^b	-24.00	-14.40
$\sigma_{A22}^2 / \sigma_{\tau_{21}}^2$	47.08	12.08	5.60	3.33	2.28	1.71
$\sigma_{A22}^2 / \text{Cov}(A_2\tau_{21})$	-34.24	-15.26	-9.38	-6.67	-5.17	-4.25
$\sigma_{\tau_{21}}^2 / \text{Cov}(A_2\tau_{21})$	-0.73	-1.26	-1.67	-2.00	-2.26	-2.48
$\text{Cov}(A_2\tau_{21})/\text{Cov}(A_1\tau_{12})$	-2.20	-3.80	-8.60	∞^b	10.60	5.80

^a Populations A, B, and C are characterized in Table I, and the average frequencies of favorable alleles of these populations are 0.4, 0.5, and 0.6, respectively.

^b ∞_1 , ∞_2 , and ∞_3 come from divisions by zero, because for BxC population cross the expectation of the parameter $\text{Cov}(A_1\tau_{12})$ is zero.

Increase of the level of dominance, increases the magnitude of the σ_{τ}^2 and $\text{Cov}(A\tau)$ parameters as expected, because both depend on the d genotypic value. The parameters $\sigma_{\tau_{12}}^2$ and $\sigma_{\tau_{21}}^2$ are larger than $\text{Cov}(A_1\tau_{12})$ and $\text{Cov}(A_2\tau_{21})$ for $(d/a) > 0.5$, respectively, and the differences between them increase with the increase of the level of dominance. Hence, for traits whose levels of dominance (d/a) are close to or below 0.5 these new parameters will be negligible; however, for traits with d/a between 0.75 and 1.25 they could be important. Examples of these traits in maize are plant height and ear height with $(d/a) \approx 0.5$, and grain yield with $(d/a) \approx 1.0$ (Gardner and Lonquist, 1959).

Table III - Expected genetic responses (Gs) of interpopulation selection (RRS) with half-sib and S_1 progenies for evaluation and recombination, respectively.^a

Response on	Gs
Population cross (PC)	$\frac{i_1}{4\sigma_{Ph12}} [\sigma_{A_{11}}^2 + \sigma_{\tau_{12}}^2 + 4\text{Cov}(A_1\tau_{12})] + \frac{i_2}{4\sigma_{Ph21}} [\sigma_{A_{22}}^2 + \sigma_{\tau_{21}}^2 + 4\text{Cov}(A_2\tau_{21})]$
Population 1 (P_1)	$\frac{i_1}{2\sigma_{Ph12}} [\sigma_{A_{11}}^2 + 2\text{Cov}(A_1\tau_{12})]$
Population 2 (P_2)	$\frac{i_2}{2\sigma_{Ph21}} [\sigma_{A_{22}}^2 + 2\text{Cov}(A_2\tau_{21})]$
Heterosis (h)	
$h - \text{GsPc} - (\text{GsP}_1 + \text{GsP}_2)/2$	$\frac{i_1}{4\sigma_{Ph12}} [\sigma_{\tau_{12}}^2 + 2\text{Cov}(A_1\tau_{12})] + \frac{i_2}{4\sigma_{Ph21}} [\sigma_{\tau_{21}}^2 + 2\text{Cov}(A_2\tau_{21})]$

^a i and σ_{Ph} are selection differential in standard units, and phenotypic standard deviations of interpopulation half-sib progenies. The subscripts 11, 22, 12 or 21 refer to population 1, 2, and population cross, respectively.

Expected genetic responses for inter- and intrapopulation half-sib selection are shown in Tables III and IV. Comparisons or contrasts between expected responses of inter- and intrapopulation selection for the population cross, for the populations *per se*, and for heterosis follow.

For the population cross:

$$\text{Gs}_{(\text{RRS})} - \text{Gs}_{(\text{HSS})} = \frac{i_1}{4\sigma_{Ph}} [\sigma_{\tau_{12}}^2 + 2\text{Cov}(A_1\tau_{12})] + \frac{i_2}{4\sigma_{Ph}} [\sigma_{\tau_{21}}^2 + 2\text{Cov}(A_2\tau_{21})],$$

For the populations *per se*:

$$\text{Gs}_{(\text{RRS})} - \text{Gs}_{(\text{HSS})} = \frac{i_1}{\sigma_{Ph}} [\text{Cov}(A_1\tau_{12})] \text{ for population 1, and}$$

$$G_{s(RRS)} - G_{s(HSS)} = \frac{i_2}{\sigma_{Ph}} [\text{Cov}(A_2\tau_{21})] \text{ for population 2.}$$

For heterosis:

$$G_{s(RRS)} - G_{s(HSS)} = \frac{i_1}{4\sigma_{Ph}} (\sigma_{\tau_{12}}^2) + \frac{i_2}{4\sigma_{Ph}} (\sigma_{\tau_{21}}^2).$$

The expected responses from selection, the contrasts between inter- and intrapopulation selection, and the ratios of the genetic variances and covariances (Tables II, III and IV), show that the RRS is more efficient than HSS to improve population crosses for traits whose gene effects are close to complete dominance [(d/a) = 0.75 to 1.25], such as grain yield of maize (Gardner and Lonngquist, 1959), because the σ_{τ}^2 's parameters are positive and larger than $\text{Cov}(A\tau)$'s parameters. The population with the highest frequencies of favorable alleles (the best population) will have $\text{Cov}(A\tau) > 0$ and will be more efficiently improved with RRS. Conversely, the other population will be more efficiently improved with HSS [$\text{Cov}(A\tau) < 0$]. The changes in heterosis with RRS will be positive. However, with HSS the changes in heterosis will be negative or less likely zero, because $\text{Cov}(A_2\tau_{21})$ is negative and greater than $\text{Cov}(A_1\tau_{12})$ (Table II), except for (d/a) ≥ 1.25 for the less divergent population. The changes in heterosis with HSS will be zero for $\text{Cov}(A_1\tau_{12}) = -\text{Cov}(A_2\tau_{21})$, but the ratios from Table II show that this result is unlikely.

Table IV - Expected genetic responses (Gs) of intrapopulation selection (HSS) with half-sib and S_1 progenies for evaluation and recombination, respectively.^a

Response on	Gs
Population cross (PC)	$\frac{i_1}{4\sigma_{Ph1}} [\sigma_{A_{11}}^2 + 2\text{Cov}(A_1\tau_{12})] + \frac{i_2}{4\sigma_{Ph2}} [\sigma_{A_{22}}^2 + 2\text{Cov}(A_2\tau_{21})]$
Population 1 (P ₁)	$\frac{i_1}{2\sigma_{Ph1}} (\sigma_{A_{11}}^2)$
Population 2 (P ₂)	$\frac{i_2}{2\sigma_{Ph2}} (\sigma_{A_{22}}^2)$
Heterosis (h)	$\frac{i_1}{2\sigma_{Ph1}} [\text{Cov}(A_1\tau_{12})] + \frac{i_2}{2\sigma_{Ph2}} [\text{Cov}(A_2\tau_{21})]$
$h - G_{sPC} - (G_{sP_1} + G_{sP_2})/2$	

^a i and σ_{Ph} are selection differential in standard units, and phenotypic standard deviations of intrapopulation half-sib progenies. The subscripts 11, 22, 12 or 21 refer to populations 1, 2, and population cross, respectively.

Interpopulation selection makes use of intrapopulation additive effects (σ_{A11}^2 and σ_{A22}^2), and of the dominance effects ($\sigma_{\tau12}^2$ and $\sigma_{\tau21}^2$) in the loci where the populations are divergent and there is some level of dominance [(p-r)d]. Hence, RRS is able to exploit and enhance the heterosis of the crosses.

For the one locus-two allele model and complete dominance of favorable alleles, Moll *et al.* (1978) concluded that interpopulation selection will increase the heterosis and intrapopulation selection will decrease it for most of the situations considered. Jiang *et al.* (1990), using a different and complex approach, stated that RRS will increase the heterosis, and intrapopulation full-sib selection could either increase or decrease heterosis, but heterosis decreased for most of situations considered. Cress (1966) stated that the superiority of interpopulation selection over intrapopulation selection is related to the level of dominance and the sum of the frequencies of the favorable alleles in the two source populations. Cress (1967) also showed that the changes in the source populations with reciprocal recurrent selection (interpopulation selection) depend on the covariances of the source populations with the population cross, and that covariances are non-negative for partial and complete dominance. Therefore, the means of the source populations will not decrease except by chance. Moll *et al.* (1978) and Smith (1983) reported results of several cycles of interpopulation selection in maize. The outcomes showed the population crosses and one of the source populations were improved at reasonable rates (3.22% and 4.23% for the hybrid, and 2.49% and 2.39% for one of the base populations, per cycle, respectively), but the other population was not improved at acceptable rates (1.42% and 0.75% per cycle, respectively). The results reported by these authors are in agreement with the results of this paper.

Hence, interpopulation selection seems to be more efficient than intrapopulation selection in a general way, but breeders should be aware that with the use of RRS one of the populations will be improved at a slower rate than it would be with intrapopulation selection. Once it is identified which population will be improved at a slower rate, the breeder could use intense mass selection for traits correlated with the primary trait during the progenies production, to assure further improvements for the primary trait in this population.

A further analysis of the contribution of each population to the expected response to selection shows that the contribution of population 1 to population cross, heterosis, and population 1 *per se* improvement will be greater with RRS than with HSS. Conversely, population 2 *per se* will be improved faster with HSS than with RRS, and if $|2\text{Cov}(A_2T_{21})| > \sigma_{\tau21}^2$ the contribution of population 2 to population cross improvement will be superior with HSS than with RRS. One can estimate from Table II that $|2\text{Cov}(A_2T_{21})| > \sigma_{\tau21}^2$ for the levels of dominance above 0.75 for the more divergent populations (AxC). For the less divergent populations (BxC) we have $|2\text{Cov}(A_2T_{21})/\sigma_{\tau21}^2| = 1.2, 1.0, \text{ and } 0.9$, for $(d/a) = 0.75, 1.0, \text{ and } 1.25$, respectively. Thus,

there is a trend for $|2\text{Cov}(A_2\tau_{21})| > \sigma_{\tau_{21}}^2$. Even with the ratio values of 1.0 or 0.9 the difference between RRS and HSS for population 2 contribution to population cross improvement will be negligible. Obviously, if $|2\text{Cov}(A_2\tau_{21})| = \sigma_{\tau_{21}}^2$ we have RRS = HSS for population 2.

The foregoing results and discussion showed that neither intrapopulation selection, applied simultaneously in two divergent populations, nor interpopulation selection are able to improve efficiently the base populations and the population crosses. Therefore, a modification of these selection procedures might be introduced to overcome these drawbacks as follows: the population 2 (the lower yielding population) should be used as a tester for the two populations. Then, we will have testcross selection for population 1 and intrapopulation half-sib selection for population 2. This selection procedure will be named testcross half-sib selection (THS) thereafter.

Expected relative effectiveness (RE%) of RRS (inter-), HSS (intra-), and THS (testcross selection for population 1, and half-sib selection for population 2), were estimated for three types of populations (A, B, and C) and three levels of dominance (Table V). The RE outcomes showed that for the more divergent populations (A and C) RRS was more efficient than HSS for P_1 , population cross (PC), and heterosis (h) improvement; nearly 30% less efficient than HSS for P_2 improvement. THS was more efficient than HSS and as efficient as RRS for P_1 ; more efficient than RRS and as efficient as HSS for P_2 ; less than RRS and more efficient than HSS for heterosis, and more efficient than both methods for population cross improvement. For the less divergent populations the results are nearly the same even though they are not so evident. The more divergent the populations, the greater will be the superiority of the THS method over the other procedures. If the source populations are not divergent, RRS=HSS=THS.

Hence, it seems that the more suitable choice is the use of THS instead of using either RRS or HSS for both populations. With this choice, heterosis will be improved at a slower rate than it would be with RRS, but the improvement of the population cross and of the populations *per se* will be greater than would be with RRS or HSS. The improvement of heterosis depends on the difference between the rates of improvement of populations *per se* and of the population crosses. With RRS, population cross improvement is greater than populations *per se* and heterosis increases. Conversely, with HSS the populations *per se* improvement is greater than population cross improvement and heterosis decreases. For breeders, improvement of the population crosses as well as the populations *per se* should be made as efficient as possible, because their rates of improvement are approximately the same as for hybrids produced from inbred lines, and as for inbred lines *per se*, respectively.

Estimates of those genetic variances and covariances can be obtained with the use of intra- and interpopulation half-sib progenies from the same genotype (plant or inbred line) taken at random from two populations. For example, in maize one can

Table V - Expected relative effectiveness (RE%) of three selection procedures on the population cross (PC), on population 1 (P₁), on population 2 (P₂), and on heterosis (h), for three levels of dominance (d/a) and three types of populations.^a

Comparisons ^b		RE% - $[(Gs1-Gs2)/Gs2] \times 100$			
		d/a	0.75	1.0	1.25
Populations A and C					
GsRRS vs. GsHSS	PC		11.25	20.00	31.25
	P ₁		18.56	20.00	18.56
	P ₂		-24.83	-32.00	-38.42
	h		240.00	240.00	240.00
GsTHS vs. GsRRS	PC		7.22	7.14	6.12
	P ₁		0.00	0.00	0.00
	P ₂		33.03	47.06	62.39
	h		-71.43	-71.43	-71.43
GsTHS vs. GsHSS	PC		19.29	28.57	39.29
	P ₁		18.56	20.00	18.56
	P ₂		0.00	0.00	0.00
	h		140.00	140.00	140.00
Populations B and C					
GsRRS vs. GsHSS	PC		10.45	20.70	35.23
	P ₁		3.10	0.00	-5.16
	P ₂		-21.32	-30.00	-38.69
	h		189.47	200.00	206.90
GsTHS vs. GsRRS	PC		1.95	0.00	-2.94
	P ₁		0.00	0.00	0.00
	P ₂		27.10	42.86	63.10
	h		-105.88	0.00 ^c	-96.77
GsTHS vs. GsHSS	PC		12.60	29.69	31.25
	P ₁		3.10	0.00	-5.16
	P ₂		0.00	0.00	0.00
	h		5.26	0.00 ^c	103.45

^a Populations A, B, and C are characterized in Table I. Phenotypic variances and selection differentials were assumed to be the same for all comparisons.

^b RRS, HSS, and THS are reciprocal recurrent selection, intrapopulation half-sib selection, and testcross selection for P₁ and half-sib selection for P₂, respectively.

^c GshTHS = 0.0.

produce these two types of progenies by using prolific plants or highly inbred lines. Analyses of variance of each population and population crosses, and covariance analyses of the intra- and interpopulation progenies are required to provide the estimates of genetic variances of intrapopulation (σ_{p11}^2 and σ_{p22}^2) and interpopulation (σ_{p12}^2 and σ_{p21}^2) progenies, and for the genetic covariance of intra- and interpopulation progenies ($\text{Cov}(p_1p_{12})$ and $\text{Cov}(p_2p_{21})$). Thus, with these estimates it is possible to estimate all the variances and covariances considered in this paper, i.e.:

$$\sigma_{A11}^2 = [4/(1+F)]\sigma_{p11}^2 \quad , \quad \sigma_{A22}^2 = [4/(1+F)]\sigma_{p22}^2 \quad ,$$

$$\sigma_{A12}^2 = [4/(1+F)]\sigma_{p12}^2 \quad , \quad \sigma_{A21}^2 = [4/(1+F)]\sigma_{p21}^2 \quad ,$$

$$\sigma_{\tau12}^2 = [4/(1+F)] [\sigma_{p12}^2 - 2\text{Cov}(p_1p_{12}) + \sigma_{p11}^2] \quad ,$$

$$\sigma_{\tau21}^2 = [4/(1+F)] [\sigma_{p21}^2 - 2\text{Cov}(p_2p_{21}) + \sigma_{p22}^2] \quad ,$$

$$\text{Cov}(A_1\tau_{12}) = [2/(1+F)] [\text{Cov}(p_1p_{12}) - \sigma_{p11}^2] \quad ,$$

$$\text{Cov}(A_2\tau_{21}) = [2/(1+F)] [\text{Cov}(p_2p_{21}) - \sigma_{p22}^2] \quad .$$

In these expressions F is the inbreeding coefficient of the genotypes that give rise to the progenies (Falconer, 1989).

The discussion of the effectiveness of the selection procedures was restricted to levels of dominance close to the complete dominance [$(d/a) \approx 1.0$], because they are nearest to values usual for complex traits such as grain yield of maize. For traits with $(d/a) \leq 0.5$, the σ_{τ}^2 's and $\text{Cov}(A\tau)$'s terms are likely to be negligible, and, therefore, the intrapopulation selection is the appropriate choice.

The genetic model used did not consider linkage and/or Hardy-Weinberg disequilibrium and epistasis. Hence, it would be interesting to estimate these variances and covariances for original populations (cycle 0) and improved populations (cycle n) from intra- and interpopulation selection programs to study their magnitude and changes with selection. One can expect that σ_{τ}^2 's and $|\text{Cov}(a\tau)|$'s magnitude will decrease and increase with intra- and interpopulation selection, respectively.

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RESUMO

Os métodos de seleção recorrente intra e interpopulacionais são os esquemas seletivos que têm sido utilizados para o melhoramento de germoplasmas. Entretanto, nenhum destes métodos pode melhorar a taxas razoáveis os híbridos interpopulacionais e as populações *per se* simultaneamente. Assim, este trabalho foi conduzido para investigar as limitações destes esquemas seletivos, para introduzir um esquema modificado de seleção, e para comparar este esquema modificado com a seleção recíproca (interpopulacional) e com a seleção intrapopulacional com meios irmãos. As eficiências destes métodos seletivos no melhoramento das populações *per se*, do híbrido interpopulacional, e da heterose foram investigados teoricamente. Os resultados mostraram que a seleção recíproca é mais eficiente que a seleção intrapopulacional com meios irmãos de uma maneira geral. A análise da contribuição de cada população para o melhoramento mostrou que a seleção recíproca e a seleção intrapopulacional com meios irmãos não são as mais apropriadas. A utilização de seleção com testcross (interpopulacional) para a população 1 e seleção intrapopulacional com meios irmãos para a população 2, com a população 2 (menos produtiva que a população 1) como testadora para as duas populações é mais apropriado. A seleção com testcross e meios irmãos é mais eficiente que a seleção intrapopulacional com meios irmãos e tão eficiente quanto a seleção recíproca para a população 1; mais eficiente que a seleção recíproca e tão eficiente quanto a seleção intrapopulacional para a população 2; menos eficiente que a seleção recíproca e mais eficiente que a seleção intrapopulacional para a heterose; e mais eficiente que a seleção recíproca e a seleção intrapopulacional para o melhoramento de híbridos interpopulacionais.

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