

## INTERPOPULATION GENETIC VARIANCES AND HYBRID BREEDING PROGRAMS

Cláudio Lopes de Souza Jr.

### ABSTRACT

This paper reports the implications of interpopulation genetic variances ( $\sigma_{A12}^2$ ,  $\sigma_{A21}^2$ , and  $\sigma_{D(12)}^2$ ) for the breeding programs of hybrids from inbred lines. The genetic variances of normal hybrids, hybrids from partly inbred lines, and of modified hybrids, were derived in the assumption of linkage equilibrium of the parental populations. Comparisons among several types of hybrids were made by comparing their genetic variances. The results showed that for the same inbreeding coefficient, the interpopulation genetic variances of single-crosses (SC), three-way crosses (TWC), and double crosses (DC) of normal hybrids follow the order  $\sigma_{SC}^2 > \sigma_{TWC}^2 > \sigma_{DC}^2$ , with the response to selection following the same pattern. There were differences between the two possible types of three-way crosses, and the appropriate crosses should be made by taking into account the magnitudes of the additive variances that are related to the populations that gave rise to the inbred lines and to the single-crosses. The implications of the use of lines with lower inbreeding levels ( $F < 1.0$ ) and of hybrids from full- and half-sib progenies were also included. The three types of modified single-crosses and two types of modified three-way crosses were compared with the normal hybrids, and with the hybrids produced from partly inbred lines. The results showed modified hybrids have some advantages over normal hybrids and over hybrids from partly inbred lines.

### INTRODUCTION

The production of hybrids by inbreeding-hybridization as outlined by Shull (1909) is the main objective of the breeding programs of several crop species. This is because by selecting hybrids from inbred lines the best genotypes of a population or of an interpopulation hybrid can be selected and reproduced annually.

Cockerham (1961) presented the implications of the genetic variances for intrapopulation hybrid breeding programs. He showed that, for the same inbreeding levels of the lines, the genetic variance of single-crosses (SC) is higher than that of three-way crosses (TW), and that the latter is higher than that of double-crosses (DC). Hence, the expected response to hybrid selection follow the same order.

Hybrids generally are produced from crosses of inbred lines from different populations to exploit the heterosis of the population crosses (Comstock, 1964; Hallauer, 1967). The interpopulation genetic variances of single, three-way, and double crosses have been presented by Vencovsky *et al.* (1988) and Melchinger (1988) to extend Cocherham's (1961) paper. The objective of this paper is to extend even further these results of genetic variances of interpopulation hybrids by incorporating other types of hybrids, such as those from partly inbred lines and from modified lines. Comparisons among these types of hybrids were also presented to allow the breeders to choose the suitable type of interpopulation hybrid for their breeding programs.

## METHODS

### *Genetic model*

The model used to describe the genotypic value of an interpopulation individual produced by crossing individuals taking at random from two outbred diploid populations (1 and 2) in hardy-Weinberg and in linkage equilibrium (Griffing, 1962; Stuber and Cockerham, 1966) is:

$$G_{ij(12)}^k = \mu^k + \alpha_{i12}^k + \alpha_{j21}^k + \delta_{ij(12)}^k ,$$

where  $G_{ij(12)}^k$  refers to the genotypic value of an individual with the  $i^{\text{th}}$  and  $j^{\text{th}}$  alleles at the  $k^{\text{th}}$  locus from populations 1 and 2, respectively;  $\alpha_{i12}^k$  and  $\alpha_{j21}^k$  are the additive effects of the  $i^{\text{th}}$  and  $j^{\text{th}}$  alleles at the  $k^{\text{th}}$  locus of the populations 1 and 2 respectively;  $\delta_{ij(12)}^k$  is the dominance effect of the  $i^{\text{th}}$  and  $j^{\text{th}}$  alleles; and  $\mu^k$  is the mean for the  $k^{\text{th}}$  locus.

If we let  $p_i^k$  and  $p_j^k$  refer to the frequencies of the  $i^{\text{th}}$  and  $j^{\text{th}}$  alleles at the  $k^{\text{th}}$  locus from populations 1 and 2, respectively, then:

$$\sigma_{A12}^2{}^k = 2 \sum_i p_i^k (\alpha_{i12}^k)^2 \text{ is the additive variance 12,}$$

$$\sigma_{A21}^2{}^k = 2 \sum_j p_j^k (\alpha_{j21}^k)^2 \text{ is the additive variance 21, and}$$

$$\sigma_{D(12)}^2{}^k = \sum_{ij} p_i^k p_j^k (\delta_{ij(12)}^k)^2 \text{ is the dominance variance (12),}$$

and for several loci:  $\sigma_{A_{12}}^2 = \sum_k \sigma_{A_{12}}^2$ ,  $\sigma_{A_{21}}^2 = \sum_k \sigma_{A_{21}}^2$ , and  $\sigma_{D(12)}^2 = \sum_k \sigma_{D(12)}^2$ .

Then, the interpopulation genetic variance is

$$\sigma_{G(12)}^2 = (1/2) (\sigma_{A_{12}}^2 + \sigma_{A_{21}}^2) + \sigma_{D(12)}^2,$$

and the genetic covariance of relatives (X and Y) is (Stuber and Cockerham, 1966):

$$\text{CovG}(X, Y) = a_1 \sigma_{A_{12}}^2 + a_2 \sigma_{A_{21}}^2 + d \sigma_{D(12)}^2, \text{ and}$$

$$a_1 = (1/2) P(X_1 = Y_1),$$

$$a_2 = (1/2) P(X_2 = Y_2), \text{ and}$$

$$d = P(X_1 = Y_1)(X_2 = Y_2),$$

where  $P(X_1 = Y_1)$  and  $P(X_2 = Y_2)$  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. Following Cockerham (1961), the genetic variance among unrelated hybrids was obtained from the genetic covariance of pairs of related individuals of the hybrids. For example, the genetic variance among unrelated single-crosses is the genetic covariance of related individuals within the single-crosses, i.e.  $\sigma_{SC}^2 = \text{Cov}(SC_1, SC_1)$ .

Notice that in this model gene frequencies refer to the parent populations, and the gene effects were defined according to origin and not defined uniquely in a least square sense. The model assumes normal diploid segregation, no epistasis, and the parent populations are in gametic equilibrium.

### *Types of hybrids*

Following Cockerham (1961), the inbred lines were represented by capital letters (A, B, C, and D), and the populations that gave rise to the lines by subscripts 1 and 2. Then,  $A_1B_2$  represents a single-cross from the cross of line A from population 1 with line B from population 2;  $A_1B_1.C_2$  represents a three-way cross from the cross of single-cross A B from population 1 with line C from population 2, and so on.  $A_1A_1^*$  represents a modified line from the cross of sister (related) lines A and  $A^*$  from population 1;  $B_2B_2^*$  represents a modified line from the cross of sister lines B and  $B^*$  from population 2. Then,  $A_1A_1^*. B_2B_2^*$  represents a modified single-cross from the cross of modified line  $A_1A_1^*$  from population 1 with modified line  $B_2B_2^*$  from population 2, and so on.

The types of hybrids were divided in two categories, normal and modified hybrids. The former refers to hybrids produced with unrelated lines, and the latter to hybrids produced with modified lines which are crosses of related lines. The normal hybrids are single-cross (NSC) represented by  $A_1B_2$ ; type I three-way cross (NTWI)- $A_1B_1.C_2$ ; type II three-way cross (NTWII)- $A_2B_2.C_1$ , and double-cross (NDC)- $A_1B_1.C_2D_2$ . The modified hybrids are type I single-cross (MSCI)- $A_1A_1^*.B_2B_2^*$ ; type II single-cross (MSCII)- $A_1A_1^*.B_2$ ; type III single-cross (MSCIII)- $A_1.B_2B_2^*$ ; type I three-way cross (MTWI)- $A_1B_1.C_2C_2^*$ ; and type II three-way cross (MTWII)- $A_1A_1^*.B_2C_2$ .

The lines were considered to be completely inbred ( $F=1.0$ ) for the production of the modified hybrids. The modified lines are also inbred with inbreeding coefficient  $F_{ml}=0.5 (1+F_p)$ , and  $F_p$  is the inbreeding coefficient of the plant that gave rise to the progeny from where the sister lines were isolated. For example, if the sister lines were isolated in an S2 progeny we have  $F_p=0.5$  and  $F_{ml}=3/4$ . Thus,  $F_{ml}$  is the inbreeding coefficient of the plants of the progeny in which they were isolated. For the variance of the normal hybrids, the inbreeding coefficient ( $F$ ) of the lines refer to the plant that gave rise to the line because the gametic array of a plant and of its progeny produced by self-pollination is assumed to be the same. Thus,  $F=0$  for S1 lines because the gametic array of an S1 line represents the gametic array of an S0 plant;  $F=1/2$  for S2 lines, and so on.

## RESULTS AND DISCUSSION

The expected response to hybrid selection is  $G_s = (i \sigma_{H}^2) / \sigma_{Ph}$ , where  $i$  is the standardized selection differential,  $\sigma_{H}^2$  is the genetic variance of the hybrids, and  $\sigma_{Ph}$  is the phenotypic standard deviation of hybrid means. The comparisons of the different types of hybrids were made by taken into account the differences of their genetic variances, instead of comparing them by the ratios of their responses to selection. This procedure was used because as emphasized by Cockerham (1961) the differences of the genetic responses to selection of the hybrids are roughly proportional to the differences of their genetic variances.

The coefficients  $a_1$ ,  $a_2$ , and  $d$  of the interpopulation genetic variances of all types of hybrids considered are in Table I. The genetic variances of normal hybrids are:

$$\sigma_{NSC}^2 = [(1+F)/4] \{ \sigma_{A_{12}}^2 + \sigma_{A_{21}}^2 + (1+F) \sigma_{D(12)}^2 \} \text{ for single-crosses,}$$

$$\sigma_{NDC}^2 = [(1+F)/8] \{ \sigma_{A_{12}}^2 + \sigma_{A_{21}}^2 + [(1+F)/2] \sigma_{D(12)}^2 \} \text{ for double-crosses,}$$

$$\sigma_{NTWI}^2 = [(1+F)/8] [ \sigma_{A_{12}}^2 + 2\sigma_{A_{21}}^2 + (1+F) \sigma_{D(12)}^2 ] \text{ and}$$

$\sigma_{NTWII}^2 = [(1+F)/8] [2\sigma_{A12}^2 + \sigma_{A21}^2 + (1+F) \sigma_{D(12)}^2]$  for three-way crosses type I and II, respectively.

The coefficients of  $\sigma_{A12}^2$  and  $\sigma_{A21}^2$  in the genetic variances of NSC are equal; also, for NDC these coefficients are equal. However, they are different for the two types of normal three-way crosses because the single-crosses used to produce these hybrids may come from population 1 and the inbred lines from population 2, and vice-versa. The magnitudes of the additive genetic variances  $\sigma_{A12}^2$  and  $\sigma_{A21}^2$  tend to be different (Obilana *et al.*, 1979; Vencovsky *et al.*, 1988; Souza Jr. and Miranda Filho, 1989). Thus, the magnitudes of the genetic variances of the two types of three-way crosses are expected to be different; i.e., if  $\sigma_{A12}^2 > \sigma_{A21}^2$  then  $\sigma_{NTWII}^2 > \sigma_{NTWI}^2$ , and if  $\sigma_{A12}^2 < \sigma_{A21}^2$  we have  $\sigma_{NTWI}^2 > \sigma_{NTWII}^2$ .

The expected response from normal single-cross selection is higher than that of normal three-way cross selection, and the latter is higher than that expected from normal double-cross selection, considering the inbreeding coefficient (F) of the inbred lines to be the same. This is due to the amount of genetic variance which each type of cross expresses for the same F value (Tables I and II), with  $\sigma_{NSC}^2 > \sigma_{NTWC}^2 > \sigma_{NDC}^2$ . Consequently, it follows that  $G_{NSC} > G_{NTWC} > G_{NDC}$ . Obviously, greater the inbreeding coefficient greater the genetic variance and the response to selection. These results are identical to those reported by Cockerham (1961) for intrapopulation hybrids, and by Melchinger (1988) for interpopulation hybrids. For the three-way crosses, if  $\sigma_{A12}^2 > \sigma_{A21}^2$  it follows that  $G_{NTWII} > G_{NTWI}$ , and if  $\sigma_{A21}^2 > \sigma_{A12}^2$  it follows that  $G_{NTWI} > G_{NTWII}$ .

Hybrids from partly inbred lines ( $0 < F < 1$ ) should be used when inbreeding depression of a specie or population is so high that precludes the use of highly inbred lines ( $F \approx 1.0$ ). Loeffell (1971), Stangland and Russell (1981), and Carlone and Russell (1988, 1989) reported the use of partly inbred lines for maize hybrids production to overcome inbreeding depression problems. The following relations among the genetic variances of single-, three-way, and double-crosses from S1, S2, S3, and S $\infty$  inbred lines (Table II) hold:

$$\sigma_{NSCS1}^2 = \sigma_{NDCS\infty}^2; \sigma_{NSCS2}^2 \text{ and } \sigma_{NSCS3}^2 > \sigma_{NDCS\infty}^2,$$

$$\sigma_{NTWS3}^2 > \sigma_{NTWS\infty}^2; \sigma_{NTWS2}^2 \text{ and } \sigma_{NTWS3}^2 > \sigma_{NDCS\infty}^2,$$

where  $\sigma_{NSCSn}^2$  and  $\sigma_{NTWSn}^2$  refer to genetic variances of normal single- and three-way crosses from S1, S2, or S3 lines, and  $\sigma_{NTWS\infty}^2$  and  $\sigma_{NDCS\infty}^2$  refer to genetic variances of normal three-way and double-crosses from highly inbred lines ( $F \approx 1.0$ ), respectively.

Table I - Coefficients of the interpopulation genetic variances of the normal single-crosses ( $\sigma_{NSC}^2$ ), normal three-way crosses ( $\sigma_{NTW}^2$ ), normal double-crosses ( $\sigma_{NDC}^2$ ), and of the modified single-crosses ( $\sigma_{MSC}^2$ ), and modified three-way crosses ( $\sigma_{MTW}^2$ ).

Variances	Genetic variances*		
	$\sigma_{A12}^2$	$\sigma_{A21}^2$	$\sigma_{D(12)}^2$
Normal hybrids			
$\sigma_{NSC}^2$	$(1+F)/4$	$(1+F)/4$	$(1+F)^2/4$
$\sigma_{NTWI}^2$	$(1+F)/8$	$(1+F)/4$	$(1+F)^2/8$
$\sigma_{NTWII}^2$	$(1+F)/4$	$(1+F)/8$	$(1+F)^2/8$
$\sigma_{NDC}^2$	$(1+F)/8$	$(1+F)/8$	$(1+F)^2/16$
Modified hybrids			
$\sigma_{MSCI}^2$	$(1+Fml)/4$	$(1+Fml)/4$	$(1+Fml)^2/4$
$\sigma_{MSCII}^2$	$(1+Fml)/4$	$(1/2)$	$(1+Fml)/2$
$\sigma_{MSCIII}^2$	$(1/2)$	$(1+Fml)/4$	$(1+Fml)/2$
$\sigma_{MTWI}^2$	$(1/4)$	$(1+Fml)/4$	$(1+Fml)/4$
$\sigma_{MTWII}^2$	$(1+Fml)/4$	$(1/4)$	$(1+Fml)/4$

\* F and Fml refer to the inbreeding coefficient of the lines and of the modified lines, respectively.

Then, it is possible to select single-crosses from S1 lines that perform as well as double-crosses from highly inbred lines, and single-crosses from S2 or S3 lines superior than double-crosses from  $S^\infty$  lines. Also, it is possible to select single-crosses from S3 lines superior than three-way crosses from  $S^\infty$  lines, and three-way crosses from S2 or S3 lines superior than double-crosses from  $S^\infty$  lines. Furthermore, the differences between the genetic variances of the hybrids from S3 lines and from  $S^\infty$  lines are quite small, especially the additive variances (Table II). Thus, when inbreeding depression precludes the use of single- or three-way crosses even for partly inbred lines the production of double-crosses from S3 lines should not be discarded.

Table II - Coefficients of the interpopulation genetic variances of the single-crosses, three-way crosses, and double-crosses from 4 types of inbred lines.

Types of lines	F <sup>++</sup>	Genetic variances		
		$\frac{2}{\sigma_{A12}^2}$	$\frac{2}{\sigma_{A21}^2}$	$\frac{2}{\sigma_{D(12)}^2}$
Single-crosses				
S1	0.0	0.25000	0.25000	0.25000
S2	1/2	0.37500	0.37500	0.56250
S3	3/4	0.43750	0.43750	0.76563 <sup>+</sup>
S <sup>∞</sup>	1.0	0.50000	0.50000	1.00000
Three-way crosses I <sup>*</sup>				
S1	0.0	0.12500	0.25000	0.12500
S2	1/2	0.18750	0.37500	0.28125
S3	3/4	0.21875	0.43750	0.38281 <sup>+</sup>
S <sup>∞</sup>	1.0	0.25000	0.50000	0.50000
Three-way crosses II <sup>**</sup>				
S1	0.0	0.25000	0.12500	0.12500
S2	1/2	0.37500	0.18750	0.28125
S3	3/4	0.43750	0.21875	0.38281 <sup>+</sup>
S <sup>∞</sup>	1.0	0.50000	0.25000	0.50000
Double-crosses				
S1	0.0	0.12500	0.12500	0.06250
S2	1/2	0.18750	0.18750	0.14063 <sup>+</sup>
S3	3/4	0.21875	0.21875	0.19141 <sup>+</sup>
S <sup>∞</sup>	1.0	0.25000	0.25000	0.25000

<sup>+</sup>0.76563 = 49/64; 0.38281 = 49/128; 0.14063 = 9/64; 0.19141 = 49/256. \*Single-crosses from population 1.

\*\*Single-crosses from population 2. \*\*Refers to the plant that gave rise to the inbred line.

Modified hybrids are produced from crosses involving modified lines, and modified lines are crosses of related lines, namely sister lines (Fehr, 1987). The reasoning for the production of modified hybrids is that selected modified single-crosses (MSC) and modified three-way crosses (MTW) could perform as well as or close to the selected normal single-crosses (NSC) and normal three-way crosses (NTW), respectively, with less inbreeding depression problems in the hybrid seed production.

The genetic variances of the three types of modified single-crosses are (Table I):

$$\sigma_{MSCI}^2 = [(1+Fml)/4] [\sigma_{A12}^2 + \sigma_{A21}^2 + (1+Fml) \sigma_{D(12)}^2],$$

$$\sigma_{MSCII}^2 = [(1+Fml)/4] \sigma_{A12}^2 + (1/2) \sigma_{A21}^2 + [(1+Fml)/2] \sigma_{D(12)}^2, \text{ and}$$

$$\sigma_{MSCIII}^2 = (1/2) \sigma_{A12}^2 + [(1+Fml)/4] \sigma_{A21}^2 + [(1+Fml)/2] \sigma_{D(12)}^2.$$

Then, for the same Fml value we have  $\sigma_{MSCII}^2$  and  $\sigma_{MSCIII}^2 > \sigma_{MSCI}^2$ , and for  $\sigma_{A12}^2 > \sigma_{A21}^2$  we have  $\sigma_{MSCIII}^2 > \sigma_{MSCII}^2$ . The expected responses to selection follow the same order, i.e.,  $G_{MSCII}$  and  $G_{MSCIII} > G_{MSCI}$ ; and if  $\sigma_{A12}^2 > \sigma_{A21}^2$  we have  $G_{MSCIII} > G_{MSCII}$ , and vice-versa.

The coefficients of the genetic variances of modified type I single-crosses (MSCI) are in Table III, and of types II and III are in Table IV, for several Fml values that mean several levels of the relationship of the sister lines. The genetic variances of normal double-crosses (NDC) and of normal single-crosses (NSC) were included in Table III, and the genetic variances of normal three-way (NTW) and of normal single-crosses (NSC) were also included in Table IV for the sake of comparisons.

Tables III and IV showed the genetic variance of MSCI is greater than that of NDC from highly inbred lines, and the genetic variances of MSCII and of MSCIII are greater than that of NTWI and NTWII from highly inbred lines, respectively, for any generation of relationship of the sister lines; i.e.,  $\sigma_{MSCI}^2 > \sigma_{NDCS\infty}^2$ ;  $\sigma_{MSCII}^2 > \sigma_{NTWIS\infty}^2$ ; and  $\sigma_{MSCIII}^2 > \sigma_{NTWIIIS\infty}^2$ . Thus, it is possible to select MSCI superior than NDC from highly inbred lines, and to select MSCII and MSCIII superior than NTWI and NTWII from  $S\infty$  lines, respectively, for any generation of relationship of the sister lines.

The genetic variances of modified three-way crosses type I (MTWI) and type II (MTWII) are (Table I):

$$\sigma_{MTWI}^2 = (1/4) \sigma_{A12}^2 + [(1+Fml)/4] \sigma_{A21}^2 + [(1+Fml)/4] \sigma_{D(12)}^2, \text{ and}$$

$$\sigma_{MTWII}^2 = [(1+Fml)/4] \sigma_{A12}^2 + (1/4) \sigma_{A21}^2 + [(1+Fml)/4] \sigma_{D(12)}^2.$$

Table III - Coefficients of the interpopulation genetic variances of modified type I single-crosses ( $A_1A_1^*B_2B_2^*$ ) for several inbreeding values of the modified lines.

Modified lines		Genetic variances		
Relationship generations	Fml <sup>+</sup>	$\sigma_{A12}^2$	$\sigma_{A21}^2$	$\sigma_{D(12)}^2$
S0 <sup>++</sup>	0.0	0.25000	0.25000	0.25000
S1	1/2	0.37500	0.37500	0.56250
S2	3/4	0.43750	0.43750	0.76563
S3	7/8	0.46875	0.46875	0.87891
S4	15/16	0.48438	0.48438	0.93848
S5	31/32	0.49219	0.49219	0.96899
S6	63/64	0.49609	0.49609	0.98444
S $\infty$ <sup>++</sup>	1.0	0.50000	0.50000	1.00000

<sup>+</sup>Fml refers to the modified lines ( $AA^*$  or  $BB^*$ ). <sup>++</sup>The genetic variances of S0 and S $\infty$  correspond to those of normal double-crosses and normal single-crosses, respectively, because the lines are not related in the former and are the same in the latter.

The intrapopulation single-crosses come from population 1 and population 2 for MTWI and MTWII, respectively. The genetic variances of these modified three-way crosses differ in relation to the additive variances. For  $\sigma_{A12}^2 > \sigma_{A21}^2$  it follows that  $\sigma_{MTWII}^2 > \sigma_{MTWI}^2$ , and for  $\sigma_{A21}^2 > \sigma_{A12}^2$  it follows that  $\sigma_{MTWI}^2 > \sigma_{MTWII}^2$  for the same Fml values. Obviously, the expected responses to selection follow the same order.

The genetic variances of modified three-way crosses types I and II are in Table V for several generations of the relationship of the sister lines, i.e., for several Fml values. These genetic variances are greater than that of normal double-crosses from S $\infty$  lines for any generation of relationship of the sister lines, i.e.,  $\sigma_{MTWI}^2$  and  $\sigma_{MTWII}^2 > \sigma_{NDCS\infty}^2$ . Thus, it is possible to select MTW crosses superior to the selected NDC from highly inbred lines.

Notice that the vigor of the modified lines-crosses of the sister lines-corresponds to that of the inbred lines of the selfing generation in which the sister lines were isolated. For example, the vigor of the modified lines isolated in the S1 generation corresponds to that of an S1 inbred line. Hence, it is possible to select MSC superior than NTWC from S $\infty$  lines, and MTWC superior than NDC from S $\infty$  lines, with the vigor of the modified lines being the same of an S1 line.

Table IV - Coefficients of the interpopulation genetic variances of modified type II ( $A_1A_1^*B_2$ ) and type III ( $A_1B_2B_2^*$ ) single-crosses for several inbreeding values of the modified lines.

Modified lines		Genetic variances				
Relationship	Generations	Fml <sup>+</sup>	Type II	$\sigma_{A12}^2$	$\sigma_{A21}^2$	$\sigma_{D(12)}^2$
			Type III	$\sigma_{A21}^2$	$\sigma_{A12}^2$	$\sigma_{D(12)}^2$
S0 <sup>++</sup>		0.0		0.25000	0.50000	0.50000
S1		1/2		0.37500	0.50000	0.75000
S2		3/4		0.43750	0.50000	0.87500
S3		7/8		0.46875	0.50000	0.93750
S4		15/16		0.48438	0.50000	0.96875
S5		31/32		0.49219	0.50000	0.98438
S6		63/64		0.49609	0.50000	0.99219
S <sup>∞</sup>		1.0		0.50000	0.50000	1.00000

<sup>+</sup>Fml refers to the modified lines (AA\* or BB\*). <sup>++</sup>The genetic variances of S0 correspond to those of normal type I and type II three-way crosses, respectively, and of the S<sup>∞</sup> to that of normal single-crosses.

Table V - Coefficients of the interpopulation genetic variances of modified type I ( $A_1B_1.C_2C_2^*$ ) and type II ( $A_1A_1^*.B_2C_2$ ) three-way crosses for several inbreeding values of the modified lines.

Modified lines		Genetic variances				
Relationship	Generations	Fml <sup>+</sup>	Type I	$\sigma_{A12}^2$	$\sigma_{A21}^2$	$\sigma_{D(12)}^2$
			Type II	$\sigma_{A21}^2$	$\sigma_{A12}^2$	$\sigma_{D(12)}^2$
S0 <sup>++</sup>		0.0		0.25000	0.25000	0.25000
S1		1/2		0.25000	0.37500	0.37500
S2		3/4		0.25000	0.43750	0.43750
S3		7/8		0.25000	0.46875	0.46875
S4		15/16		0.25000	0.48438	0.48438
S5		31/32		0.25000	0.49219	0.49219
S6		63/64		0.25000	0.49609	0.49609
S <sup>∞</sup> <sup>++</sup>		1.0		0.25000	0.50000	0.50000

<sup>+</sup>Fml refers to the modified lines (AA\* or CC\*). <sup>++</sup>The genetic variances of S0 correspond to that of normal double-crosses, and of the S<sup>∞</sup> to those of normal type I and type II three-way crosses, respectively.

The increments in the coefficients of the genetic variances of modified hybrids increase sharply from S0 to S2 generation, with increments decreasing thereafter. The differences between the genetic variances of modified hybrids with sister lines isolated in the S2 generation and of their normal counterparts (NSC and NTWC) are quite small. Hence, to combine the vigor of the modified lines with progress from selection, the sister lines isolated in the S2 generation should be the best situation. Then, the performances of the selected modified hybrids and of their selected normal counterparts would show small differences. Obviously, with advantages for the modified hybrids because inbreeding depression problems in the seed production would decrease.

Notice that the modified single-crosses types II and III, and the modified three-way crosses types I and II differ in relation to the coefficients of the additive genetic variances due to the origin of the modified lines. Then, we need to know the magnitudes of these variances to make the suitable choice of the type of MSC and MTWC to increase the improvement of the hybrid breeding programs.

Other comparisons that should be made are those involving modified hybrids and hybrids produced from partly inbred lines ( $0 < F < 1$ ). The inbreeding coefficients ( $F$ ) of the genetic variances of hybrids produced from partly inbred lines correspond to the plants that gave rise to the lines, whereas for the modified hybrids the inbreeding coefficients ( $F_{ml}$ ) of the modified lines correspond to the inbreeding coefficients of the generations in which the sister lines were isolated. Thus, for the same  $F$  value of the partly inbred lines and of the modified lines, which corresponds to the same vigor of the partly inbred lines and modified lines, the genetic variances of modified hybrids will be greater than the genetic variances of the same types of hybrids from partly inbred lines. For example, the genetic variances of normal single-crosses from S2 inbred lines and of type I modified single-crosses from sister lines isolated in the S2 generation are, respectively:

$$\sigma_{NSCS2}^2 = (0.37500) (\sigma_{A12}^2 + \sigma_{A21}^2) + (0.56250) \sigma_{D(12)}^2, \text{ and}$$

$$\sigma_{MSCIS2}^2 = (0.43750) (\sigma_{A12}^2 + \sigma_{A21}^2) + (0.76563) \sigma_{D(12)}^2.$$

For the same vigor of the modified and partly inbred lines we have:  $\sigma_{MSCI}^2$ ,  $\sigma_{MSCII}^2$  and  $\sigma_{MSCIII}^2 > \sigma_{NSC}^2$ , and  $\sigma_{MTWI}^2$  and  $\sigma_{MTWII}^2 > \sigma_{NTW}^2$ . Hence, the modified hybrids have greater advantage over hybrids from partly inbred lines because for the same vigor of the lines it would be possible to select modified hybrids that are superior than their normal counterparts from partly inbred lines.

The production of modified hybrids will be feasible only if the sister lines that gave rise to the modified lines have high combining ability. This aspect is supposed to do not cause any problem because as reported by Jenkins (1935), Sprague (1952), and

Lonquist (1950) the combining abilities of the lines are determined in the first generations and stay relatively stable in the succeeding generations.

Vasal (1986), Cordova (1986), and Magnavaca *et al.* (1989) have suggested the use of hybrids produced from crosses of full-sib progenies, and Mota (1984) from crosses of half-sib progenies to avoid inbreeding depression problems. The genetic variances of these types of hybrids are:

$$\sigma_{FSH}^2 = (1/8) (\sigma_{A12}^2 + \sigma_{A21}^2) + (1/16) \sigma_{D(12)}^2, \text{ and}$$

$$\sigma_{HSH}^2 = (1/16) (\sigma_{A12}^2 + \sigma_{A21}^2) + (1/64) \sigma_{D(12)}^2,$$

for hybrids produced from crosses of full- and half-sib progenies from two populations, respectively. These variances show that little progress is expected from selecting these types of hybrids, mainly for half-sib hybrids. It should be emphasized that full- and half-sib progenies maintained in isolation blocks or in sib-crosses will be inbred with  $F=0.25$  and  $F=0.125$ , respectively. Then, the inbreeding depression problems are not avoided but only reduced. Probably, in this case, due to the time required for extraction and evaluation for general and specific combining ability of the progenies and of the low expected progress from selection, the use of interpopulation hybrids being continually improved by one of the procedures of reciprocal recurrent selection (Hallauer, 1973; Souza Jr., 1987) is expected to be superior to the use of full- or half-sib hybrids.

## ACKNOWLEDGMENTS

Publication supported by FAPESP.

## RESUMO

Este trabalho reporta as implicações das variâncias genéticas interpopulacionais ( $\sigma_{A12}^2$ ,  $\sigma_{A21}^2$ , e  $\sigma_{D(12)}^2$ ) para o melhoramento de híbridos de linhagens endogâmicas. As variâncias genéticas de híbridos normais, híbridos de linhagens parcialmente endogâmicas, e de híbridos modificados, foram derivadas considerando que as populações parentais estão em equilíbrio de ligação. Comparações dos diversos tipos de híbridos foram realizadas através das comparações das suas variâncias genéticas. Os resultados mostraram que, para o mesmo nível de endogamia das linhagens, as variâncias genéticas de híbridos simples (HS), de híbridos triplos (HT), e de híbridos duplos (HD) seguem a ordem  $\sigma_{HS}^2 > \sigma_{HT}^2 > \sigma_{HD}^2$ , e as respostas esperadas com seleção seguem a mesma ordem. Há diferenças entre os dois possíveis tipos de híbridos triplos, e os cruzamentos corretos devem ser feitos considerando as magnitudes das variâncias genéticas interpopulacionais que são relacionadas com as populações que dão origem às linhagens endogâmicas e aos híbridos simples. As implicações do uso de linhagens parcialmente endogâmicas ( $F < 1,0$ ), e de híbridos de progênies de irmãos germanos e de meios

irmãos também foram incluídos. Os três tipos de híbridos simples modificados e os dois tipos de híbridos triplos modificados, foram comparados com os híbridos normais e com os híbridos de linhagens parcialmente endogâmicas. Os resultados mostraram que os híbridos modificados apresentam algumas vantagens sobre os híbridos normais e sobre os híbridos de linhagens parcialmente endogâmicas.

## REFERENCES

- Carlone, M.R. and Russell, W.A. (1988). Evaluation of S2 maize lines reproduced for several generations by random mating within lines. I. Comparisons between the original and maintained S2 lines. *Crop. Sci.* 28: 921-925.
- Carlone, M.R. and Russell, W.A. (1989). Evaluation of S2 maize lines reproduced for several generations by random mating within lines. II. Comparisons for testcross performance of original and advanced S2 and S8 lines. *Crop. Sci.* 29: 899-904.
- Cockerham, C.C. (1961). Implications of genetic variances in a hybrid breeding program. *Crop. Sci.* 1: 47-52.
- Comstock, R.E. (1964). Selection procedures in corn improvement. *Proceedings of the 19th Ann. Hybrid Corn Industry Research Conference 19*: 87-94. Washington, DC, USA.
- Cordova, H.S. (1986). Formacion de híbridos de maiz en base a familias de hermanos completos y sus implicaciones en la produccion de semilla comercial. *Anais do XV Congresso de Milho e Sorgo*, pp. 377-404. Macció, AL, Brazil.
- Fehr, W.R. (1987). *Principles of Cultivar Development*. Vol. I. MacMillan Publishing Company, New York. pp. 536.
- Griffing, B. (1962). Prediction formulae for general combining ability selection methods utilizing one or two random mating populations. *Aust. J. Biol. Sci.* 15: 650-665.
- Hallauer, A.R. (1967). Development of single-cross hybrids from two-eared maize populations. *Crop. Sci.* 7: 192-195.
- Hallauer, A.R. (1973). Hybrid development and population improvement in maize by reciprocal full-sib selection. *Egyptian J. Genet. Cytol.* 2: 84-101.
- Jenkins, M.T. (1935). The effect of inbreeding and of selection within inbred lines of maize upon the hybrids made after successive generations of selfing. *Iowa State J. Sci.* 9: 429-450.
- Loeffel, F.A. (1971). Development and utilization of vigorous parental lines. *Proceedings of the 26th Corn and Sorghum Industry Research Conference*. pp. 209-217. Chicago, IL, USA.
- Lonnquist, J.H. (1950). The effect of selection for combining ability within segregating lines of corn. *Agronomy J.* 42: 503-508.
- Magnavaca, R., Oliveira, A.C., Morais, A.R., Gama, E.E.G. and Santos, M.X. (1989). Family hybrid selection of quality protein maize (*Zea mays* L.). *Maydica* 34: 63-71.
- Melchinger, A.E. (1988). Means, variances, and covariances between relatives in hybrid populations with disequilibrium in the parent populations. *Proceedings of the Second International Conference on Quantitative Genetics*. pp. 400-415. Raleigh, NC, USA.

- Mota, M.G.C. (1984). Potencialidade de um novo sistema de cruzamento a nível interpopulacional com progênies de meios irmãos de milho. Doctoral Thesis, University of São Paulo, Brazil.
- Obilana, A.T., Hallauer, A.R. and Smith, O.S. (1979). Estimated genetic variability in a maize interpopulation. *J. Heredity* 70: 127-132.
- Shull, G.H. (1909). A pure line method of corn breeding. *American Breeders' Assoc. Report*. 5: 51-59.
- Souza Jr., C.L. (1987). Reciprocal recurrent selection with half-sib progenies obtained alternately from non-inbred (S0) and inbred (S1) plants in maize. *Maydica* 32: 19-31.
- Souza Jr., C.L. and Miranda Filho, J.B. (1989). Genetic variability in two maize (*Zea mays* L.) populations and its relationship with intra- and interpopulation recurrent selection. *Rev. Bras. Genet.* 12: 271-285.
- Sprague, G.F. (1952). Early testing and recurrent selection. In: *Heterosis*. (Gowen, J.W., ed.). Iowa State College Press. pp. 400-407.
- Stangland, G.R. and Russell, W.A. (1981). Variability within single crosses of S2 and S8 inbred lines of maize. *Maydica* 26: 227-238.
- Stubber, C.W. and Cockerham, C.C. (1966). Gene effects and variances in hybrid populations. *Genetics* 54: 1279-1286.
- Vasal, S.K. (1986). Approaches and methodology in the development of QPM hybrids. *Anais do XV Congresso de Milho e Sorgo*. pp. 419-430. Macció, AL, Brazil.
- Vencovsky, R., Miranda Filho, J.B. and Souza Jr., C.L. (1988). Quantitative genetics and corn breeding in Brazil. *Proceedings of the Second International Conference on Quantitative Genetics*. pp. 465-477. Raleigh, NC, USA.

(Received July 7, 1989)