

PROCEDURES FOR ESTIMATING EXPECTED GENETIC PROGRESS IN INBRED LINES VIA RECURRENT INTRAPOPULATIONAL SELECTION

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ABSTRACT

Objective of study was to provide genetical-statistical procedures that permit estimating expected genetic progress for inbred S_1 and S_6 lines through recurrent intrapopulational selection. Two mating schemes involving inbred lines progenies (S_1 and S_6) and half-sib progenies were used. The statistical procedures, genetic interpretations of progeny variance and covariance, and formulae for predicting expected progress in inbred lines (S_1 and S_6) via intrapopulational selection are provided. The formulae of expected gain for the inbred lines are a function of the genetic covariances between half-sib and selfed ($\sigma_{A_1/2A_0}$ and $\sigma_{A_1A_0}$) progenies. The theoretical values for the $\sigma_{A_1/2A_0}/\sigma_A^2$ and $\sigma_{A_1A_0}/\sigma_A^2$ ratios show that they are influenced by the genetic structure of the populations and are higher than 1.0 when the average frequency of favorable alleles is higher than 0.5.

INTRODUCTION

The development of maize (*Zea mays* L.) hybrids by inbreeding and hybridization, as outlined by Shull (1909), is the main objective of applied maize breeding programs. By selecting hybrids from inbred lines it is possible to fix the best genotypes of a population, or of an interpopulational hybrid, and to reproduce them annually. To be commercially useful, an inbred line must have good combining ability and *per se*

performance, with the latter attribute being of greater importance when single rather than three-way or double-cross hybrids are desired.

Although the level of productivity of inbred lines is of fundamental importance in hybrid production programs and empirical information existing on increased inbred line productivity via recurrent selection (Genter, 1971, Burton *et al.*, 1971; Harris *et al.*, 1972) and theoretical assumptions (Comstock, 1964) is available, no procedures are available that permit the quantification of expected gain in inbred lines through recurrent selection. The only procedures available are those for estimating expected genetic gain in populations by different schemes of recurrent selection (Empig *et al.*, 1972; Sprague and Eberhart, 1977; Hallauer and Miranda Filho, 1981) and among hybrids (Cockerham, 1961).

Thus, the objective of the present paper was to present genetical-statistical designs and expressions that permit estimating expected genetic gain for inbred lines (S_1 and S_6) through recurrent intrapopulational selection.

METHODS

Genetic model

A simple genetical model similar to that of Falconer (1960) was used. Genetic variances and covariances are defined in terms of gene frequencies and genotypic effects and based on one locus with two alleles. These quantities are expressed as linear functions of genetic variances and covariances among progenies. Among the genotypic effects, only additive and dominant effects were considered, since epistatic effects have been shown to be negligible in maize (Silva and Hallauer, 1975; Stuber *et al.*, 1966).

Consider a population in Hardy-Weinberg equilibrium and let p and q refer to frequency of favorable and unfavorable alleles, respectively, of any locus and a and d refer to half the difference between homozygotes and dominance effect, respectively. If we let Δp represent the change in p via selection and z_1 and z_2 refer to the selection coefficients associated with the dominant and recessive homozygotes, respectively, the following genetical parameters are obtained (Falconer, 1960):

$\alpha = a + (q-p)d$ is the average effect of a gene substitution;

$\Delta p_1 = z_2 pq^2 / (1 - z_2 q^2)$ and $\Delta p_2 = pq(z_2 q - z_1 p) / (1 - z_1 p^2 - z_2 q^2)$ are the changes in p through intrapopulational selection using models with complete dominance and overdominance, respectively; and

$\sigma_A^2 = 2pq\alpha^2$ is the additive genetic variance.

If $\sigma_{\overline{p}_h}$ and σ_w are the phenotypic standard deviations among progeny means and within progenies, respectively, inherent in each breeding method and K is the standardized selection differential, the following changes in p are obtained through selection (Empig *et al.*, 1972):

$\Delta p = K(1/4)pq\alpha/\sigma_{\overline{p}_h}$ and $\Delta p = K(3/8)pq\alpha/\sigma_w$ are the changes in p through selection among and within half-sib progenies, respectively; and

$\Delta p = K(1/2)pq\alpha/\sigma_{\overline{p}_h}$ and $\Delta p = K(1/4)pq\alpha/\sigma_w$ are the changes in p through selection among and within full-sib progenies, respectively.

Using the same procedures and type of populations employed by Miranda Filho and Hallauer (1978), the $\sigma_{A_F A_0}/\sigma_A^2$ ratio was calculated for inbreeding coefficient $F = 1/2$ and $F = 1.0$ in order to know the relative magnitude of $\sigma_{A_F A_0}$, assuming that the gene frequencies of the populations fit a Beta distribution. Thus, genetic variances and covariances are expressed as functions of a and d and represent the expected mean values of a quantitative trait, assuming that all loci contribute the same genotypic effect (Table I). In Table I, A is representative of composites ($\overline{p} = 0.5$), B is representative of an unimproved population ($\overline{p} = 0.4$), and C is representative of an improved population ($\overline{p} = 0.6$).

Table I - Characterization of three types of populations according to their distribution of gene frequencies defined by Beta distributions.

Population	Beta distribution	Density function (ϕp)	Average gene frequency (\overline{p})
A	Beta (2,2)	$6p(1-p)$	0.5
B	Beta (2,3)	$12p(1-p)^2$	0.4
C	Beta (3,2)	$12p^2(1-p)$	0.6

Mating schemes

Two mating schemes were considered that would permit estimating parameters for one selfing generation ($F = 0.5$) and for six selfing generations ($F \approx 1.0$):

Design (c): Population is planted in an isolation block. At the flowering time, both ears of prolific plants are protected. The lower ear is selfed and after self-

ing, the protection is removed from the upper ear, which is exposed to open pollination. Thus, from each plant (genotype) an S_1 progeny and a half-sib progeny are obtained, which are evaluated in replicated trials.

Design (d): Obtain inbred lines ($F \approx 1.0$) by single-seed descent (without selection) for six generations of selfing. In an isolation block, each inbred line is planted as female, and the males include an equal mixture of all lines. Thus, inbred lines ($F \approx 1.0$) and a half-sib progeny (testcrosses) are obtained from each genotype, which are evaluated in replicated trials.

Experimental design and statistical analysis

Using a randomized complete block design, the two progeny types are evaluated in a split-block arrangement to avoid competition due to inbreeding depression. Analysis of variance is done in the usual manner for the experimental design used for a mixed model: random effects for genotypes and fixed effects for progeny type. The scheme for the analysis of variance is presented in Table II.

Table II - Analysis of variance for a split-block arrangement in a randomized complete block design for the evaluation of two types of progenies.

Sources of variation	D.F.	M.S.	E(M.S.)	F
Blocks	r-1	—	—	—
Genotypes (G)	p-1	M_1	$\sigma_c^2 + 2\sigma_a^2 + 2r\sigma_g^2$	M_1/M_2
Error (a)	(r-1)(p-1)	M_2	$\sigma_c^2 + 2\sigma_a^2$	
Progeny type (T)	1	M_3	$\sigma_c^2 + p\sigma_b^2 + 2r\sigma_{gt}^2 + pr\sum_1 t_1^2$	$M_3/(M_4 + M_5 - M_6)$
Error (b)	(r-1)	M_4	$\sigma_c^2 + p\sigma_b^2$	
G x T	(p-1)	M_5	$\sigma_c^2 + 2r\sigma_{gt}^2$	M_5/M_6
Error (c)	(r-1)(p-1)	M_6	σ_c^2	

For estimating the expected gain in inbred lines, only the phenotypic standard deviations of the half-sib progeny means are used. Thus, separate analyses of variance

were done only for the half-sib progenies for a randomized complete block design (Table III).

Table III - Analysis of variance for half-sib progenies in a randomized complete block design.

Sources of variation	D.F.	M.S.	E(M.S.)
Blocks	r-1	—	—
Progenies	p-1	M ₁	$\sigma_w^2/n + \sigma_e^2 + r\sigma_p^2$
Error	(r-1)(p-1)	M ₂	$\sigma_w^2/n + \sigma_e^2$
Within	pr(n-1)	M ₃	σ_w^2

From Table III we can estimate:

$$\hat{\sigma}_p^2 = (M_1 - M_2)/r: \text{genetic variance among half-sib progenies};$$

$$\hat{\sigma}_e^2 = M_2 - M_3/n: \text{plot-to-plot environmental variance};$$

$$\hat{\sigma}_w^2 = M_3: \text{phenotypic variance within half-sib progenies};$$

For design c, the following estimates of phenotypic variances were obtained from estimates of Table III:

$$\hat{\sigma}_{Ph}^2 = \hat{\sigma}_p^2 + \hat{\sigma}_e^2 + \hat{\sigma}_w^2: \text{phenotypic variance among individual plants};$$

$$\hat{\sigma}_w^2 = M_3: \text{phenotypic variance within half-sib progenies};$$

$$\hat{\sigma}_{Ph}^2 = \hat{\sigma}_p^2 + \hat{\sigma}_e^2/r + \hat{\sigma}_w^2/nr: \text{phenotypic variance among half-sib progeny means.}$$

For design d, the phenotypic variances among half-sib progeny means and within progenies should be obtained considering half-sib progenies obtained from nonselfed plants, because the half-sib and full-sib selection processes presented here are based on progenies obtained from nonselfed plants. Thus, from estimates of Table III we have:

$$\hat{\sigma}_{Ph}^2 = \hat{\sigma}_p^2 + \hat{\sigma}_e^2 + \hat{\sigma}_w^2: \text{phenotypic variance among individual plants};$$

$$\hat{\sigma}_w^2 = M_3 + (1/2)\hat{\sigma}_p^2: \text{phenotypic variance within half-sib progenies};$$

$$\hat{\sigma}_{Ph}^2 = (1/2)\hat{\sigma}_p^2 + \hat{\sigma}_e^2/r + \hat{\sigma}_w^2/nr: \text{phenotypic variance among half-sib progeny means.}$$

Analysis of covariance between the two progeny types is then carried out by the randomized complete block design shown in Table IV.

Table IV - Analysis of covariance between two types of progenies in a split-block arrangement according to a randomized complete block design.

Sources of covariation	D.F.	M.P.	E (M.P.)
Blocks	r-1	-	-
Progenies	p-1	P ₁	COV _e + r COV _p
Error	(r-1)(p-1)	P ₂	COV _e

From Table IV we can estimate:

$\hat{C}ov_p = (P_1 - P_2)/r$: genetic covariance between half-sib progenies and selfed progenies.

RESULTS

a) Genetic interpretation of variances and covariances between progenies

The genetic interpretations of the genetic variance and covariance estimates between progenies according to the model used are as follows:

$$\text{Design (c): } \sigma_p^2 = (1/2)pq\alpha^2 \quad \therefore \hat{\sigma}_A^2 = 4\hat{\sigma}_p^2$$

$$COV_p = pq\alpha[a + (1/2)(q-p)d],$$

$$\text{by defining: } \sigma_{A_{1/2}A_0} = 2pq\alpha[a + (1/2)(q-p)d],$$

$$\text{We have: } \hat{\sigma}_{A_{1/2}A_0} = 2 \hat{C}OV_p$$

$$\text{Design (d): } \sigma_p^2 = pq\alpha^2 \quad \therefore \hat{\sigma}_A^2 = 2\hat{\sigma}_p^2$$

$$COV_p = 2pqa\alpha;$$

$$\text{by defining: } \sigma_{A_1A_0} = 2pqa\alpha,$$

$$\text{We have: } \hat{\sigma}_{A_1A_0} = \hat{C}OV_p$$

b) Expected genetic progress in inbred lines through intrapopulational selection

By using the model described above, we obtain:

$S_{10} = u + (p-q)a + pqd$, S_1 inbred lines mean of the original population;

$S_{11} = S_{10} + 2\Delta p [a + (1/2)(q-p)d]$, S_1 inbred lines mean after one selection cycle;

$S_{60} = u + (p-q)a$, S_6 inbred lines mean of the original population;

$S_{61} = S_{60} + 2\Delta pa$, S_6 inbred lines mean after one selection cycle;

$G_{S_1} = S_{11} - S_{10} = 2\Delta p [a + (1/2)(q-p)d]$, expected genetic gain for S_1 inbred lines through selection;

$G_{S_6} = S_{61} - S_{60} = 2\Delta pa$, expected genetic gain for S_6 inbred lines through selection.

The expressions that permit estimating the expected genetic gain for S_1 and S_6 inbred lines through intrapopulational selection were obtained by substituting the Δp expressions obtained by Empig *et al.* (1972) in $G_{S_1} = 2\Delta p [a + (1/2)(q-p)d]$ and in $G_{S_6} = 2\Delta pa$.

These expressions are presented in Table V.

Table VI shows the theoretical expected values for the ratios $\sigma_{A_1/2A_0}/\sigma_A^2$ and $\sigma_{A_1A_0}/\sigma_A^2$ for three types of populations, i.e. composites (A), unimproved population (B) and improved population (C), for different degrees of dominance. The data for populations A and B show that the two ratios decrease with the increase in degree of dominance, whereas this tendency is not observed for population C (Table VI). The ratios also are influenced by the genetic structure of the populations because they tend to decrease with lower average frequencies of favorable alleles and to increase with higher average frequencies of favorable alleles.

Expected genetic gains for inbred lines and populations from selection among and within half-sib progenies for ear weight were estimated for ESALQ-PB1 and BR-105 maize populations. These were made by using the estimates of genetic and phenotypic parameters for the ESALQ-PB1 and BR-105 maize populations reported by Souza Jr. (1983), using the calculated ratios $\sigma_{A_1/2A_0}/\sigma_A^2 = 0.938$ and $\sigma_{A_1A_0}/\sigma_A^2 = 0.875$ ($d/a = 1.0$, Table VI) and assuming that the average degree of dominance for grain yield was about 1.0 (Comstock and Robinson, 1948; Robinson *et al.*, 1949)

Table V - Expected gains for inbred lines for three different schemes of intrapopulation selection.

Selection process*	Type of inbred line**	Expected genetic gain
I	S ₁	$G_{s_1}^I = K(1/2)\sigma_{A_1/2A_0}/\sigma_{Ph}$
II	S ₁	$G_{s_1}^{II} = K_1(1/4)\sigma_{A_1/2A_0}/\sigma_{Ph} + K_2(3/8)\sigma_{A_1/2A_0}/\sigma_w$
III	S ₁	$G_{s_1}^{III} = K_1(1/2)\sigma_{A_1/2A_0}/(1.18)\sigma_{Ph} + K_2(1/4)\sigma_{A_1/2A_0}/0.98\sigma_w$
I	S ₆	$G_{s_6}^I = K(1/2)\sigma_{A_1A_0}/\sigma_{Ph}$
II	S ₆	$G_{s_6}^{II} = K_1(1/4)\sigma_{A_1A_0}/\sigma_{Ph} + K_2(3/8)\sigma_{A_1A_0}/\sigma_w$
III	S ₆	$G_{s_6}^{III} = K_1(1/2)\sigma_{A_1A_0}/(1.18)\sigma_{Ph} + K_2(1/4)\sigma_{A_1A_0}/0.98\sigma_w$

* I, Mass selection for one sex; II, selection among and within half-sib progenies; III, selection among and within full-sib progenies. II and III, selection for both sexes among progenies, and for one sex for selection within progenies.

** We assumed that $\sigma_{FS} = 1.18 \sigma_{HS}$ and $\sigma_{wFS} = 0.98\sigma_{wHS}$ (Souza Jr., 1983). σ_{FS} and σ_{HS} are the phenotypic standard deviations for full-sib and half-sib progeny means, respectively. σ_{wFS} and σ_{wHS} are the phenotypic standard deviations among plants within full-sib and half-sib plots, respectively.

and a selection intensity of 10%. The results are given in Table VII and show that, in absolute values, most of the population gain was transmitted to the S₁ and S₆ lines.

c) Changes in inbreeding depression (ΔD) through selection

By considering inbreeding depression to be simply the result of a decrease in number of heterozygous loci and by using the adopted model, we have:

$$S_{00} = u + (p-q)a + 2pqd, \text{ original population mean;}$$

$S_{F0} = u + (p-q)a + 2(1-F)pqd$, inbred lines mean at any selfing generation in the original population;

$$S_{01} = S_{00} + 2\Delta p \alpha, \text{ population mean after one selection cycle;}$$

Table VI - Expected values for the $\sigma_{A_1/2A_0}/\sigma_A^2$ and $\sigma_{A_1A_0}/\sigma_A^2$ ratios for three types of populations and different degrees of dominance (d/a).

d/a	$\sigma_{A_1/2A_0}/\sigma_A^2$			$\sigma_{A_1A_0}/\sigma_A^2$		
	A	B	C	A	B	C
0.0	1.000	1.000	1.000	1.000	1.000	1.000
0.1	0.999	0.992	1.007	0.999	0.985	1.013
0.2	0.997	0.984	1.012	0.994	0.968	1.024
0.3	0.994	0.975	1.016	0.987	0.949	1.032
0.4	0.989	0.965	1.018	0.978	0.930	1.038
0.5	0.983	0.955	1.020	0.965	0.909	1.040
0.6	0.975	0.944	1.019	0.951	0.888	1.039
0.7	0.967	0.933	1.017	0.936	0.866	1.034
0.8	0.958	0.922	1.013	0.916	0.844	1.026
0.9	0.948	0.911	1.003	0.896	0.822	1.015
1.0	0.938	0.900	1.000	0.875	0.800	1.000
1.2	0.915	0.881	0.980	0.829	0.759	0.960

Table VII - Expected gain (G_s) for ear weight from selection among and within half-sib progenies of ESALQ-PB₁ and BR-105 for the population (F = 0), S₁ lines (F = 1/2), and S₆ lines (F ≈ 1.0).

Population	F	Mean (g/plant)	G_s /cycle (g/plant)
ESALQ-PB ₁	0	117.99	10.86
ESALQ-PB ₁	1/2	-	10.19
ESALQ-PB ₁	1.0	-	9.51
BR-105	0	112.87	7.68
BR-105	1/2	-	7.57
BR-105	1.0	-	7.06

$S_{F1} = S_{F0} + 2\Delta p [a + (1-F)(q-p)d]$, inbred lines mean at any selfing generation after one selection cycle;

$D_{F0} = S_{F0} - S_{00} = -2Fpqd$, inbreeding depression at any selfing generation in the original population;

$D_{F1} = S_{F1} - S_{01} = D_{F0} - 2F\Delta p(p-q)d$, inbreeding depression at any selfing generation after one selection cycle;

$\Delta D = D_{F1} - D_{F0} = -2F\Delta p(p-q)d$, change in inbreeding depression at any selfing generation through selection.

ΔD values are shown in Table VIII for different gene frequency values. The estimates of ΔD were obtained assuming complete dominance and an overdominance models and unidirectional positive values for d . Selection coefficients equal to 0.20 ($z_1 = z_2 = 0.20$) were used in all instances. When we consider the complete dominance model, the loci in which the frequency of the favorable allele is within the $0 < p < 0.5$ interval will contribute to an increase in inbreeding depression, whereas those loci in which the frequency of the favorable allele is within the $0.5 < p < 1.0$ interval will contribute to a decrease in inbreeding depression (Table VIII). For the overdominance

Table VIII -Changes in inbreeding depression through selection (ΔD) for two degrees of dominance and different gene frequency values (p).

p	ΔD^*	
	Complete dominance	Overdominance
0.0	0.00	0.00
0.1	-309.28	-275.60
0.2	-352.35	-266.67
0.3	-260.72	-152.04
0.4	-124.12	-42.86
0.5	0.00	0.00
0.6	79.32	-42.86
0.7	102.64	-152.04
0.8	77.40	-266.67
0.9	28.80	-275.60
1.0	0.00	0.00

*Multiplied by 10^{-4} dF.

model, loci will contribute to an increase in inbreeding depression in every other situation with the exception of $p = 0.0, 0.5$ and 1.0 .

DISCUSSION

The inbred line *per se* performance is of fundamental importance for its commercial use, especially in the production of single cross hybrids. As demonstrated by Comstock (1964), it is possible to increase hybrid productivity only by population breeding because a hybrid is a genotype that occurs in the population or in the inter-varietal hybrid. Population breeding by recurrent selection also contributes to inbred line improvement. An increase in the frequency of genes that are favorable for increased productivity in the populations will also increase inbred lines productivity.

Expected progress from selection is based on the regression of the selection unit with the improved population (Hallauer and Miranda Filho, 1981) and, therefore, involves genetic covariance among the individuals that are being submitted to selection (selection unit) and their descendants (improved population). Fisher (1918) demonstrated that genetic covariance between parents is a function of genetic variance components at the intrapopulation level. Thus, in intrapopulation recurrent selection methods genetic covariance is a linear function only of intrapopulation additive genetic variance (σ_A^2).

When different inbreeding generations are involved, genetic covariance between parents cannot be expressed by the components defined by Fisher (1918), unless restrictions are made in the genetic models (Cockerham, 1963). Thus, the genetic covariances involved in the expressions of expected gains in the inbred lines by processes of intrapopulation selection are functions of $\sigma_{A_F A_0}$, which is a function of the average effect of a gene substitution in the non-inbred population (α_0) and of this effect on the population within any inbreeding generation (α_F). When they are S_1 and S_6 lines, S_1 ($F = 1/2$): $\alpha_{(1/2)} = a + (q-p)(1/2)d$, and S_6 lines ($F \cong 1.0$): $\alpha_1 = a$.

Estimates of additive genetic variance for several maize traits have been obtained by several investigators after the designs proposed by Comstock and Robinson (1952) and have been summarized by Hallauer and Miranda Filho (1981) for several types of populations. To determine the magnitude of $\sigma_{A_{(1/2)} A_0}$ and $\sigma_{A_1 A_0}$ in relation to σ_A^2 , the theoretical expected ratios $\sigma_{A_{1/2} A_0} / \sigma_A^2$ and $\sigma_{A_1 A_0} / \sigma_A^2$ were estimated considering three types of populations and several degrees of dominance (Table VI). The results suggested that for populations A and B the values of these ratios decreased with increasing levels of dominance. For population C (improved), the values of these relations were above 1.0, except for absence of dominance, complete dominance, and overdominance. These ratios were affected by the differences in population structure

because these relations increased in value with increasing average frequencies of favorable alleles for the same levels of dominance.

Genter (1971), compared the productivity of S_1 lines of populations under selection and reported that the gain obtained for population CBS after 4 cycles with S_1 progenies (1.34 t/ha) was transmitted to the S_1 lines (1.38 t/ha). Burton *et al.* (1971) reported that after 4 cycles of S_1 recurrent selection in population BSK the gain obtained for S_1 lines (1.45 t/ha) was greater than that obtained for the population (0.99 t/ha). After four cycles of half-sib selection, the gain obtained for S_1 lines (0.45 t/ha) was also greater than that obtained for the population (0.38 t/ha). Harris *et al.* (1972), however, reported that the gain obtained for S_1 lines (1.46 t/ha) was a little lower than that obtained for the population (1.80 t/ha) after 9 cycles of mass stratified selection.

The results presented in Table VII for the S_1 lines ($F = 1/2$) agree with those reported in the literature, since the expected gain for the populations ($F = 0$), as an absolute value, was transmitted to the S_1 lines. Since inbreeding depression occurs, the expected gain for the lines as a percentage of the mean was higher than the expected gain for the population. The expected gains for the S_6 lines ($F \cong 1.0$) were also similar to those expected for S_1 lines and for the populations. In all instances, the expected gains were estimated on the basis of some theoretical assumptions, and to estimate the expected gains for the lines by intrapopulation selection it is necessary to use the designs presented here.

The results shown in Table VIII indicate that for loci with complete dominance, inbreeding depression will decrease only when the frequency of the favorable allele (p) is higher than 0.5, whereas when $p < 0.5$ inbreeding depression will tend to become more marked with selection. For overdominant loci, except cases of fixation and intermediate gene frequency ($p = 0.5$), inbreeding depression will be more marked at any gene frequency.

Genter (1971), Burton *et al.* (1971), Harris *et al.* (1972), and Goulas and Lonnquist (1976) reported that population breeding involves a decrease in inbreeding depression. Thus, we may consider that the theoretical model with complete dominance fits the explanation of the results reported in the literature, since it is expected that improved populations and synthetic material would have a greater number of loci with a frequency of the favorable alleles above 0.5.

Inbreeding depression decreases when $p > 0.5$ (complete dominance model) because the number of homozygotes for the favorable allele exceeds the number of homozygotes for the other allele, with inversion occurring for $p < 0.5$. For $p = 0.5$, the two types of homozygotes are present in equal proportions and therefore $\Delta D = 0$. Also, starting from $\bar{p} > 0.5$, the ratios $\sigma_{A_1/2A_0}/\sigma_A^2$ and $\sigma_{A_1A_0}/\sigma_A^2$ become greater than 1.0 (except for absence of dominance, complete dominance, and overdominance). This occurs because the quantity $(q-p)d$ in the average effect of gene substitution

becomes negative for a large number of the loci ($\bar{p} > \bar{q}$), thus contributing to the decrease of $\sigma_{A_F A_0}$ and σ_A^2 . This decrease, however, is more marked in σ_A^2 , since in the $\sigma_{A_1/2 A_0}$ terms this quantity is multiplied by 0.5, and in the $\sigma_{A_1 A_0}$ terms it is null. Thus, when the $\sigma_{A_1/2 A_0} / \sigma_A^2$ ratio in a population under selection is higher than 1.0, this indicates that the average frequency of favorable alleles that control a given trait is above 0.5 and therefore inbreeding depression will tend to decrease and the gain obtained by selection for the inbred lines, as an absolute value, will be higher than that obtained for the population. The $\sigma_{A_1/2 A_0} / \sigma_A^2$ ratio could be considered as an indication of the best time when a population under selection can be utilized as a source of inbred lines.

RESUMO

O objetivo do trabalho é fornecer procedimentos genético-estatísticos que permitam estimar o progresso genético esperado em linhagens endogâmicas S_1 e S_6 via seleção recorrente intrapopulacional. São utilizados dois esquemas de acasalamento envolvendo progênies de linhagens endogâmicas (S_1 e S_6) e progênies de meios irmãos. São fornecidos os procedimentos estatísticos, as interpretações genéticas das variâncias e covariâncias genéticas entre progênies e as fórmulas para a predição dos progressos esperados por seleção intrapopulacional nas linhagens endogâmicas S_1 e S_6 . As fórmulas dos progressos esperados nas linhagens são funções das covariâncias genéticas entre as progênies de meios irmãos e as progênies endogâmicas ($\sigma_{A_1/2 A_0}$ e $\sigma_{A_1 A_0}$). Relações teóricas de $\sigma_{A_1/2 A_0} / \sigma_A^2$ e $\sigma_{A_1 A_0} / \sigma_A^2$ mostram que estas relações são influenciadas pela estrutura genética das populações, sendo superior a 1,0 quando a frequência média dos alelos favoráveis for superior a 0,5.

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