

Predicting the range of inbreeding depression of inbred lines in cross-pollinated populations

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ABSTRACT

The objectives of this paper were to derive the genetic variance of inbreeding depression (σ_{GID}^2) and to predict the range of inbreeding depression (RID) in cross-pollinated populations. The variance of inbreeding depression is a function of the genetic variances related to dominance effects (σ_D^2 , D_2 , and \bar{H}), and of the inbreeding coefficients of the two generations in which inbreeding depression is measured (F_t and F_g). The results showed that the higher the level of dominance of a trait, the higher the variance of inbreeding depression. The magnitudes of σ_{GID}^2 were expected to be lower in improved (mean gene frequencies = $\bar{p} > 0.6$) and in unimproved ($\bar{p} < 0.4$) populations, than in composite populations ($\bar{p} = 0.5$). Data from a maize population used to illustrate the study showed that the range of inbreeding depression in the S_{∞} generation of selfing was from 48.7% to 85.3% for grain yield, and from 13.9% to 24.5% for plant height. A mating design outlined to estimate the genetic variance of inbreeding depression, the range of inbreeding depression, and of the range of inbred lines is presented.

INTRODUCTION

Inbreeding depression depends on both the level of dominance of a trait and on the inbreeding coefficient; the higher the level of dominance of a trait the higher the inbreeding depression. The rate of inbreeding depression has a negative linear relationship with the coefficient of inbreeding for most traits (Falconer, 1989; San Vicente and Hallauer, 1993; Benson and Hallauer, 1994).

The major objective in breeding programs of several cross-pollinated species has been to develop hybrids from inbred lines, e.g., maize, sunflower, and sugar beet. Thus, highly inbred lines are obtained, usually by selfing, and subsequently crossed to produce hybrids (Miller, 1987; Smith, 1987; Hallauer, 1990). To be commercially useful, inbred lines must have

outstanding performances themselves and in combining ability. Therefore, selecting lines based on their own performance during the generations of inbreeding is a standard procedure (Hallauer, 1990).

The rates of inbreeding depression vary among populations of the same species, and populations less sensitive to inbreeding depression are selected as a potential source of outstanding inbred lines (Vianna *et al.*, 1982; Lima *et al.*, 1984). Inbreeding depression also is expected to vary within populations, i.e., genotypes of a population have different mean phenotypic values under inbreeding. Thus, inbred lines selected on their own performance are those whose parents were less sensitive to inbreeding depression.

Despite its importance, no information is available on the genetic variability of inbreeding depression within populations. Thus, the purpose of this paper was threefold: 1) to derive the genetic variance of inbreeding depression and present a mating design to estimate it; 2) to present procedures for

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predicting the range of inbreeding depression and of inbred lines in any generation of selfing; 3) to present an example for maize with reported experimental results.

METHODS

Consider a random mating population in both Hardy-Weinberg and linkage equilibrium. Excluding epistasis, the genetic variance of this population in the t th generation of selfing is (Cockerham, 1983): $\sigma_G^2 = (1 + Ft)\sigma_A^2 + (1 - Ft)\sigma_B^2 + 4FtD_1 + FtD_2 + Ft(1 - Ft)\bar{H}$, where σ_A^2 and σ_B^2 are additive and dominance variances, D_1 is the covariance of additive and homozygous dominance effects, D_2 is the variance of homozygous dominance effects, \bar{H} is the sum of squared inbreeding depression effects, and Ft is the inbreeding coefficient in the t th generation of selfing.

Let X_t and X_g be the means of a trait in the t th and g th ($g > t$) generations of inbreeding, with Ft and Fg as their inbreeding coefficients, respectively. The inbreeding depression being measured as $ID = (X_t - X_g)$, its variance is $\sigma_{ID}^2 = \sigma_{X_t}^2 + \sigma_{X_g}^2 - 2Cov_{X_t, X_g}$ where $\sigma_{X_t}^2$ and $\sigma_{X_g}^2$ are the variances in the t th and in the g th generations of inbreeding, respectively, and Cov_{X_t, X_g} is the covariance of individuals in the t th and in the g th generations. Following Cockerham's (1983) notation, the components of the genetic variance of inbreeding depression could be expressed as $\sigma_{X_t}^2 = Ct_{tt}$, $\sigma_{X_g}^2 = Ct_{gg}$, and $Cov_{X_t, X_g} = Ct_{tg}$, where Ct_{tt} is the genetic variance in the t th generation; Ct_{gg} is the genetic covariance among relatives in the g th generation with the last common ancestor in the t th generation, or the genetic variance among progenies in the g th generation stemming from a common ancestor in the t th generation; and Ct_{tg} is the genetic covariance between a relative in the t th generation and the other one in the g th generation.

With $Ct_{tt} = \sigma_G^2$, $Ct_{gg} = (1 + Ft)\sigma_A^2 + [(1 - Fg)^2 / (1 - Ft)]\sigma_B^2 + 2(Ft + Fg)D_1 + [Ft + (Fg - Ft)^2 / 2(1 - Ft)]D_2 + [Ft(1 - Fg)^2 / (1 - Ft)]\bar{H}$, and $Ct_{tg} = (1 + Ft)\sigma_A^2 + (1 - Fg)\sigma_B^2 + (3Ft + Fg)D_1 + FtD_2 + Ft(1 - Fg)\bar{H}$, (Cockerham, 1983), the genetic variance of inbreeding depression in the g th generation was derived as $\sigma_{GID}^2 = Ct_{tt} + Ct_{gg} - 2Ct_{tg}$.

Expected values of the variances of inbreeding depression and of the ratio σ_B^2 / D_2 for several types of populations were obtained by a simulation procedure, assuming the population gene frequencies fit a beta distribution (Souza Jr., 1985, 1987, 1993). Let p and q refer to the frequencies of favorable and unfavorable alleles, and a and d refer to half the difference between homozygotes and the dominance effect, respectively; thus $\sigma_B^2 = (2pqd)^2$ and $D_2 = 4pq(q - p)^2d^2$ (Cockerham

and Matzinger, 1985). The expected values of variances were obtained for populations with favorable gene frequencies ranging from $\bar{p} = 0.1$ to $\bar{p} = 0.9$ as $E(\sigma_x^2) = \int_0^1 \sigma_x^2 \phi p dp$, where σ_x^2 is σ_B^2 or D_2 and ϕp is a Beta density function.

The mean value of a trait in a random mating population is $S_0 = \mu + \alpha + \delta$, where μ is the general mean, $\alpha = \sum (p_i - q_i)a_i$ and $\delta = 2 \sum p_i q_i d_i$ are the contributions of the homozygous and heterozygous loci, respectively, to the mean value (Gardner, 1965). In the g th generation of selfing the mean value can be expressed as $S_g = \mu + \alpha + (1/2)^g \delta$; thus, the mean of all pure lines extracted at random from the population is $S_\infty = \mu + \alpha$, and the mean of random lines from one generation of selfing is $S_1 = \mu + \alpha + (1/2)\delta$. From the means of the S_0 and S_1 generations one can estimate $S_\infty = 2S_1 - S_0$, and $\delta = 2(S_0 - S_1)$, and the mean values of any generation of selfing can be estimated as $S_g = S_\infty + (1/2)^g \delta$. Inbreeding depression in the g th generation of inbreeding was estimated as $ID_g = S_g - S_0$, and in percentage as $ID_g\% = (ID_g / S_0)100$; the range of inbreeding depression in the g th generation was estimated as $RID_g = ID_g \pm 2\sigma_{ID_g}$.

Data from Iowa Stiff Stalk Synthetic (BSSS) maize population reported by Hallauer and Miranda (1988) were used to illustrate this study. The mean grain yield values of non-inbred $S_0 = 168.60$ g/plant, and of the first generation of selfing $S_1 = 112.10$ g/plant, and the average estimate of dominance variance $\sigma_B^2 = 179.0$ were used. For plant height the following values were used: $S_0 = 194.10$ cm/plant, $S_1 = 175.50$ cm/plant, and $\sigma_B^2 = 20.0$. Estimates of D_2 variances were not available, so they were obtained from the ratio $\sigma_B^2 / D_2 = 1.50$ for a population whose average frequencies of favorable alleles is $\bar{p} = 0.6$ from the simulation. Then, it was assumed that the frequencies of favorable alleles in the BSSS population are greater than 0.5, as reported by Hallauer *et al.* (1983). From this ratio, estimates of D_2 used were 119.0 and 13.0 for grain yield and plant height, respectively.

RESULTS AND DISCUSSION

The genetic variance of inbreeding depression is:

$$\sigma_{GID}^2 = [(Fg - Ft)^2 / (1 - Ft)] [\sigma_B^2 + (1/2)D_2 + Ft\bar{H}];$$

therefore σ_{GID}^2 is a function of the genetic variances related to dominance effects (σ_B^2 , D_2 and \bar{H}) and of the inbreeding coefficients in which inbreeding depression is measured (Ft and Fg , $Fg > Ft$). For populations developed from the cross of two highly inbred lines,

e.g., F2 populations, we have $D_2 = 0$ and $\sigma_D^2 = \bar{H}$ (Cockerham, 1983) and $\sigma_{GID}^2 = [(Fg - Ft)^2 (1 + Ft)/(1 - Ft)]\sigma_D^2$.

Usually, inbreeding depression is measured in relation to the non-inbred population ($Ft = 0$), which reduces the variance of inbreeding depression to:

$$\sigma_{GID}^2 = F_g^2 [\sigma_D^2 + (1/2)D_2],$$

and for F2 populations we have:

$$\sigma_{GID}^2 = F_g^2 \sigma_D^2,$$

and σ_{GID}^2 is a function of the square of inbreeding coefficient of the gth generation of inbreeding (Fg) and of the variance of dominance effects (σ_D^2 and D_2). The genetic variance of inbreeding depression of F2 populations does not depend on the variance of homozygous dominance effects. However, this does not mean that σ_{GID}^2 of the F2 is lower than for other types of populations, because the magnitudes of dominance variances arising from F2 populations are expected to be higher than other types of populations, since the frequencies of all segregating alleles in F2 populations are 0.5 (Falconer, 1989).

The ratios of σ_D^2/D_2 for populations defined by average frequencies of favorable alleles ranging from 0.1 to 0.9, depicted in Figure 1, showed that D_2 is greater than σ_D^2 for populations with $\bar{p} < 0.3$ and $\bar{p} > 0.7$, and that $\sigma_D^2 > D_2$ between these values. Then, one could expect that $D_2 > \sigma_D^2$ in unimproved and improved populations, and that the contribution of the D_2 variance to σ_{GID}^2 will be more expressive for these types of populations.

For highly inbred lines ($Fg = 1$), and taking the non-inbred population as a reference ($Ft = 0$), the variance of inbreeding depression reduces to:

$$\sigma_{GID}^2 = \sigma_D^2 + (1/2)D_2,$$

and the expected variances for populations defined by average frequencies of favorable alleles ranging from 0.1 to 0.9 and for two levels of dominance ($d = 2$ and $d = 4$), depicted in Figure 2, showed that the lower the level of dominance of a trait the lower the variance of inbreeding depression, and irrespective of the level of dominance they follow the same pattern of variation. The variance of inbreeding depression increases from $\bar{p} = 0.1$ to $\bar{p} = 0.4$ and decreases from $\bar{p} = 0.6$, reaching a plateau between $\bar{p} = 0.4$ and $\bar{p} = 0.6$, this variation being more expressive for traits with higher levels of dominance. Thus, one would expect that σ_{GID}^2 of improved and unimproved populations will be lower than in populations whose average frequencies of favorable alleles lie between these intervals, which may be representative of composite populations ($\bar{p} \approx 0.5$). These

results indicate that the higher the level of dominance the higher the range of inbreeding depression, and inbred lines extracted from unimproved and improved populations will have similar and lower ranges of inbreeding depression than composite populations.

For the one locus-two alleles model, the expected change in inbreeding depression in populations under selection is $\Delta ID = -2F\sum_i \Delta p_i (q_i - p_i) d_i$, where Δp_i is the change in the allele frequency at the ith locus due to selection, and for complete dominance inbreeding depression will decrease for $\bar{p} > 0.5$ (Souza Jr., 1985). Then, improved ($\bar{p} > 0.5$) populations are expected to be less sensitive to inbreeding depression than unimproved populations ($\bar{p} < 0.5$) and composite populations ($\bar{p} \approx 0.5$). Although the range of inbreeding depression will be lower in improved than in composite populations, the lower inbreeding depression in improved populations assures that the mean values of the lines in the upper limit of the range will be higher than in composite populations. San Vicente and Hallauer (1993) reported that the rates of inbreeding depression of hybrids produced from old and new lines are quite similar, whereas Benson and Hallauer (1994) reported that the rates of inbreeding depression of the BSSS maize population under recurrent selection have

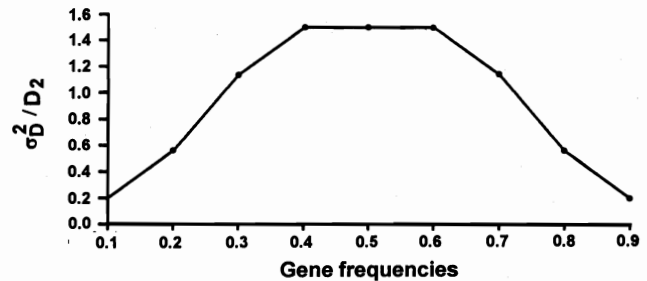


Figure 1 - Ratios of σ_D^2/D_2 for average frequencies of favorable alleles ranging from 0.1 to 0.9.

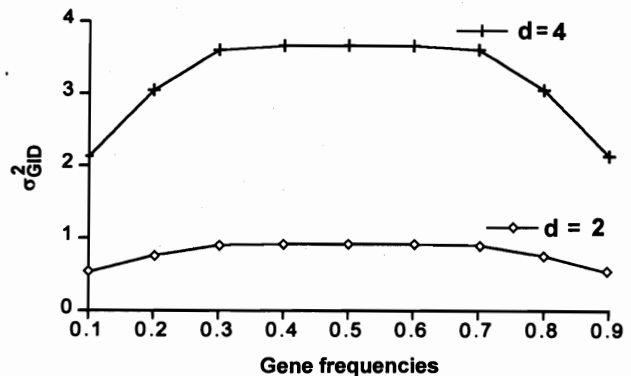


Figure 2 - Genetic variances of inbreeding depression (σ_{GID}^2) of highly inbred lines ($Fg = 1.0$) for average frequencies of favorable alleles ranging from 0.1 to 0.9, and for two levels of dominance ($d = 2$ and $d = 4$).

decreased in the advanced cycles of selection for most of the traits.

The mean values and the genetic variances of inbreeding depression for several generations of selfing for grain yield (GY) and plant height (PH) for the BSSS maize population showed that the expected mean values of random highly inbred lines are 55.60 g/plant and 156.90 cm high; and the genetic variances of inbreeding depression are F_g^2 (238.50) and F_g^2 (26.50) for GY and PH, respectively (Table I). The expected mean inbreeding depression of the highly inbred lines for GY is 113.00 g/plant (67.02%) with the lower limit as 82.12 g/plant (48.71%) and the upper limit as 143.88 g/plant (85.33%) (Table II). For plant height we have 37.20 cm/plant (19.17%) as the mean inbreeding depression, with the lower and upper limit as 26.94 cm/plant (13.88%) and 47.46 cm/plant (24.45%), respectively (Table III). The level of dominance of grain yield ($d/a \approx 1.0$) is higher than that of plant height ($d/a \approx 0.5$) (Gardner and Lonnquist, 1959); thus, as expected, the mean and the range of inbreeding depression of grain yield were greater than those of plant height.

Notice that for $F_t = 0$, the variance of inbreeding depression is directly related to the square of the inbreeding coefficients of the lines (F_g^2). The σ_{GID}^2 increases with F_g , but the increments are not linear, increasing sharply from S1 to S3 generation of selfing and decreasing thereafter. For example, the ratios ($\sigma_{GIDS_g}^2 / \sigma_{GIDS_\infty}^2$)100 are 25%, 56%, and 77% for S1, S2, and S3 generations, respectively, whereas for S4, S5, and S6 generations the ratios are 88%, 94%, and 97%, respectively, for the two traits studied. The ranges of inbreeding depression followed the same pattern, as expected.

Estimates of variance of inbreeding depression can be obtained by producing unrelated single-crosses from highly inbred lines extracted at random from an open-pollinated population, subsequently producing S1 progenies by self-pollinating the single-crosses, then evaluating the single-crosses and their S1 progenies in replicated experiments following a split-block design. Analyses of variance of the single-crosses, of the S1 progenies, and of covariance analyses of single-crosses and S1 progenies are required to provide estimates of genetic variances of SC (σ_{GSC}^2) and S1 progenies (σ_{GS1}^2), and of genetic covariances of SC and S1 (Cov_{SCS1}). Thus we have,

$$\sigma_{GSC}^2 = \sigma_A^2 + \sigma_D^2;$$

$$\sigma_{GS1}^2 = \sigma_A^2 + (1/4)\sigma_D^2 + D_1 + (1/8)D_2, \text{ and}$$

$$Cov_{SCS1} = \sigma_A^2 + (1/2)\sigma_D^2 + (1/2)D_1.$$

Table I - Mean values and genetic variances of inbreeding depression (σ_{GID}^2) for grain yield (GY = g/plant) and plant height (PH = cm/plant) in several generations of selfing (Sg) for the BSSS maize population.

Generations Sg	Inbreeding coefficient Fg+	Mean values		σ_{GID}^2	
		GY	PH	GY	PH
S0	0.00	168.6	194.1	0.0	0.0
S1	0.50	112.1	175.5	59.6	6.6
S2	0.75	83.9	166.2	134.2	14.9
S3	0.88	69.7	161.6	182.6	20.3
S4	0.94	62.7	159.2	209.6	23.3
S5	0.97	59.1	158.1	223.8	24.9
S6	0.98	57.4	157.5	231.1	25.7
S ∞	1.00	55.6	156.9	238.5	26.5

+Rounded values.

Table II - Mean values (ID) and ranges (RID) of inbreeding depression for grain yield (GY) in g/plant and in percentage for several generations of selfing (Sg) for the BSSS maize population.

Generations Sg	ID (g/plant)	RID (g/plant)		RID (%)		
		Lower	Upper	ID%	Lower	Upper
S1	56.5	41.1	71.9	33.5	24.4	42.7
S2	84.8	61.6	107.9	50.3	36.5	64.0
S3	98.9	71.9	125.9	58.6	42.6	74.7
S4	105.9	77.0	134.9	62.8	45.7	80.0
S5	109.5	79.5	139.4	64.9	47.2	82.7
S6	111.2	80.8	141.6	66.0	47.9	84.0
S ∞	113.0	82.1	143.9	67.0	48.7	85.3

ID = S0 - Sg; ID% = (ID/S0)100; RID = ID \pm 2 σ_{GID} ; RID% = (RID/S0)100.

Table III - Mean values (ID) and ranges (RID) of inbreeding depression for plant height (PH) in cm/plant and in percentage for several generations of selfing (Sg) for the BSSS maize population.

Generations Sg	ID (cm/plant)	RID (cm/plant)		RID (%)		
		Lower	Upper	ID%	Lower	Upper
S1	18.6	13.5	23.7	9.6	7.0	12.2
S2	27.9	20.2	35.6	14.4	10.4	18.4
S3	32.6	23.6	41.6	16.8	12.1	21.4
S4	34.9	25.2	44.5	18.0	13.0	23.0
S5	36.0	26.1	46.0	18.6	13.4	23.7
S6	36.6	26.5	46.8	18.9	13.6	24.1
S ∞	37.2	27.0	47.5	19.2	13.9	24.5

ID = S0 - Sg; ID% = (ID/S0)100; RID = ID \pm 2 σ_{GID} ; RID% = (RID/S0)100.

The genetic variance of inbreeding depression of the S1 progenies is: $\sigma_{GIDS1}^2 = \sigma_{GSI}^2 + \sigma_{GSC}^2 - 2Cov_{SCS1}$; therefore, $\sigma_{GIDS1}^2 = (1/4) [\sigma_D^2 + (1/2)D_2]$. As we have shown, for $F_t = 0$ the genetic variance of inbreeding depression in the gth generation of inbreeding is

$\sigma_{GIDg}^2 = F_g^2 [\sigma_D^2 + (1/2)D_2]$; then, the genetic variance of inbreeding depression in the g th generation of inbreeding can be estimated as $\sigma_{GIDg}^2 = 4F_g^2 \sigma_{GIDSI}^2$.

For plant breeders, it would also be important to obtain estimates of the genetic variance and the range of the traits of the highly inbred lines. This could be accomplished by evaluating the highly inbred lines used to develop the single-crosses for the mating design previously described. However, it is difficult to obtain reliable estimates from the evaluation of highly inbred lines because of the genetic load that often is high in cross-pollinated populations. Also, highly inbred lines are more sensitive to environmental variation than partly inbred lines or non-inbred plants, which may interfere in the estimates of genetic variances (Falconer, 1989). The mating design presented also could provide these estimates as follows; the genetic variance of highly inbred lines is (Cockerham, 1983):

$$\sigma_{S_{\infty}}^2 = \sigma_A^2 + 4D_1 + D_2,$$

and can be estimated as:

$$\sigma_{S_{\infty}}^2 = 2(4\sigma_{S1}^2 + \sigma_{SC}^2 - 4Cov_{SC,S1}),$$

and the range of the mean values of the inbred lines can be estimated as $RIL = S_{\infty} \pm 2\sigma_{S_{\infty}}^2$.

The genetic model did not take into account linkage and/or Hardy-Weinberg disequilibrium and epistasis, and it was restricted to a one locus-two alleles model. Furthermore, the study was based on the assumption that the population gene frequencies fit a Beta distribution. Thus, it would be useful to estimate genetic variances of inbreeding depression and of highly inbred lines from experimental studies following the procedures outlined in this paper.

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RESUMO

Os objetivos deste artigo foram derivar a variância genética da depressão por endogamia (σ_{GID}^2) e prever a amplitude da depressão por endogamia (RID) dentro de populações de polinização cruzada. A variância da depressão por endogamia é função das variâncias genéticas relacionadas aos efeitos de dominância (σ_D^2 , D_2 e \bar{H}) e dos coeficientes de endogamia das duas gerações em que é medida a depressão por endogamia (F_t e F_g). Os resultados mostraram que quanto maior o nível de dominância de um caráter maior é a variância da depressão por endogamia, e que as magnitudes de σ_{GID}^2 devem ser menores em populações melhoradas ($\bar{p} > 0,6$) e não melhoradas ($\bar{p} < 0,4$) que em compostos ($\bar{p} \approx 0,5$). Dados de uma população de milho utilizada como exemplo mostraram que a amplitude da depressão por endogamia na geração S_{∞} de autofecundação é de 48,7% a 85,3% para produção de grãos

e de 13,9% a 24,5% para altura da planta. Um delineamento apropriado para estimar a variância da depressão por endogamia, a sua amplitude e a amplitude de linhagens endogâmicas é apresentado.

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