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Inbreeding depression rates of semi-exotic maize (*Zea mays* L.) populations*

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ABSTRACT

Two semi-exotic maize (*Zea mays* L.) populations, ESALQ-PB1 x ENTRELAÇADO 1 (EE1) and ESALQ-PB1 x CRAVO 4 (EC4) were used to evaluate the effects of inbreeding depression of important agronomic traits and the possibilities to use them as sources of inbred lines. Two types of progenies (S_1 and full-sib) were used. The semi-exotic population EC4 had higher means for plant height, ear height, ear diameter, stand, number of ears per plot, ear yield and grain yield for both noninbred and inbred progenies. Population EE1 had greater ear length and tassel branch number. The effects of inbreeding depression were more evident in EE1 for all traits, except ear yield and grain yield. Estimates of inbreeding depression were similar for both populations for ear and grain yield. The estimates per 1% increase in homozygosity were 0.85 for ear yield and 0.71 g/pl for grain yield in EE1, and 1.20 for ear yield and 1.02 g/pl for grain yield in EC4. The expected means of a random sample of homozygous lines ($A = \mu + a$) were smaller than the overall contribution of the heterozygotes to the mean (d) for ear yield and grain yield. Increasing homozygosity through continuous selfing and selection against recessive deleterious genes would contribute to enhance the agronomic pattern of inbred lines in both populations.

INTRODUCTION

Maize (*Zea mays* L.) is a cross-pollinated diploid species and several types of hybrids are possible, although those used for commercial production are usually derived from inbred lines. Different mating systems are available to increase homozygosity, but the most rapid and intense form of inbreeding is self-pollination, which is the standard method used by maize breeders (Hallauer, 1990).

The main consequence of inbreeding is the reduction in the mean phenotypic value of quantitative traits, including those affecting yield components (Falconer, 1989). The effects of inbreeding depression and the estimates reported for maize were presented by Hallauer and Miranda Filho (1988). This survey showed that for grain yield, the inbreeding depression expected for 50% of homozygosity, as a result of one generation of selfing, ranged from 42.2 to 71.9 g/pl; for plant and ear height, the estimates ranged from 7.8 to 33.4 cm and 10.4 to 29.6 cm, respectively.

In Brazil, Vencovsky *et al.* (1988) stated that a great amount of information about inbreeding depression remained unpublished and therefore unknown for a long time. Nevertheless, many studies have been conducted to evaluate inbreeding depression in populations after one generation of selfing. Geraldi and Vencovsky (1980) reported estimates of inbreeding depression varying from 36.7 to 54.8% among nine Brazilian populations of maize. Lima *et al.* (1982) introduced two sources of maize germplasm for downy

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mildew resistance and found an inbreeding depression of 43.0% in both populations, Suwan-DMR and Thai Composite-DMR. Fourteen introduced populations of maize showed inbreeding depression for grain yield in the range from 31 to 65% and 44 to 69% in Sete Lagoas and Piracicaba, respectively (Vianna *et al.*, 1982). In an open-pollinated variety 'Centralmex' the reduction in yield was 39% after one generation of selfing (Valois and Miranda Filho, 1984).

Lima *et al.* (1984) conducted extensive research on the effects of inbreeding in 32 Brazilian populations after one generation of selfing. The ranges for inbreeding depression were 27.0 to 57.9% for grain yield, 7.5 to 20.3% for plant height, and 6.9 to 27.4% for ear height. According to estimates summarized by Vencovsky *et al.* (1988), open-pollinated varieties and populations exhibit almost as much inbreeding depression as do the hybrids; they found slightly lower values for improved varieties.

Despite the importance of information on the inbreeding effects in maize, there are breeding populations where studies would be desirable. Santos and Miranda Filho (1992) evaluated the genetic potential of two Brazilian races of maize, Cravo (large number of kernel rows) and Entrelaçado (long ear), that were crossed to ESALQ-PB1, a local and adapted population. The semi-exotic populations showed encouraging results because a substantial increase in genetic variability was observed, and they were considered promising for use as base populations in recurrent selection programs.

A study similar to that reported by Santos and Miranda Filho (1992) was initiated by using two other samples of the races Cravo and Entrelaçado to obtain two semi-exotic populations after crossing with local variety ESALQ-PB1. Our objective was to evaluate selfed S_1 progenies as a basis to determine the inbreeding effects of several quantitative traits.

MATERIAL AND METHODS

In 1983/84, two Brazilian races (Cravo and Entrelaçado) were introduced into the maize breeding program of the Department of Genetics (ESALQ-USP). These races were described by Paterniani and Goodman (1977). They emphasized the large number of kernel rows expressed in Cravo and the long ear length of Entrelaçado.

Representative samples of each race were crossed with the improved and adapted variety ESALQ-PB1, which was obtained from a composite formed by intercrossing seven short plant varieties (Miranda Filho, 1974). The segregating populations (F_2) that resulted from these crosses were designated by EC1 and EE1. Santos and Miranda Filho (1992) presented a complete description of EC1 and EE1. Concomitantly, other samples of both races were introduced and crossed with ESALQ-PB1, giving rise to F_2 populations designated by EC2, EC3, EC4, EE2, and EE3.

Samples of two semi-exotic populations, ESALQ-PB1 x ENTRELAÇADO 1 (EE1) and ESALQ-PB1 x CRAVO 4 (EC4) after two cycles of selection for yield, were used in this study. The two populations represented introgression of 50% of genes from exotic germplasm, independently, into ESALQ-PB1. The race Cravo has been grown in the Southern Brazil and the race Entrelaçado is an interlocked soft-corn grown by Indians in the North Region of Brazil. Since they are poorly adapted in Piracicaba-SP (24^{o} South latitude), where the experiments were conducted, they were considered as exotic materials.

In 1988/89, a sample of each semi-exotic population was planted in two contiguous blocks. Each block was divided by half to obtain full-sib (FS) and selfed (S_1) progenies. The numbers of progenies were 160 (80 FS and 80 S_1) from EE1 and 240 (120 FS and 120 S_1) from EC4. Two yield trials were conducted in 1989/90 in the experimental area of the Department of Genetics at Piracicaba-SP (Brazil).

Progenies from EE1 were partitioned into four sets of 40 progenies: sets A and B with FS progenies, and sets C and D with S_1 progenies. The randomized complete block design with split plot arrangement with three replications was used; sets (types of progenies) were allocated in the main plots, and progenies (progenies/sets) in the sub-plots. Sub-plots were 3.0 m long, spaced 1.0 m apart and 0.20 m between plants, with 15 plants per plot after thinning.

Progenies from EC4 were partitioned into six sets of 40 progenies: sets E, F and G with FS progenies and sets H, I and J with S_1 progenies. The experimental design and the plots were the same as for EE1. In both experiments, the double-cross Cargill 511 was used as check.

Data were collected for nine traits: plant height, ear height, number of ears per plot, tassel branch number, stand, ear diameter, ear length, ear yield, and grain yield. Plant height, ear height and tassel branch number were analyzed as the mean of five random and competitive plants within each sub-plot. Stand was recorded at physiologic maturity. Data for other traits were taken after harvest; ear diameter and ear length were analyzed as the mean of five ears per sub-plot.

Yield data were adjusted for ideal stand of 15 plants, following the methodology of covariance (Miranda Filho, J.B. - op.cit. Vencovsky and Barriga, 1992). The correction was made for each sub-plot. Thus, Wc = W - b (X - 15), where Wc is the corrected ear yield or grain yield, W is the observed ear yield or grain yield, b is the linear regression coefficient of ear yield or grain yield upon the stand variation, and X is the observed stand.

The analysis of variance was performed as a split-plot randomized complete block design. The error at sub-plot level was partitioned according to the type of progeny analyzed.

The appropriate models for population means are:

$m_0 = \mu + a + d$: for full-sib progenies;
$m_1 = \mu + a + 1/2\ d$: for S_1 progenies,

where μ is half the difference between the genotypic values for the homozygotes, summed over all loci; a is the overall contribution of the homozygotes to the mean, and d is the overall contribution of the heterozygotes to the mean.

The inbreeding depression was estimated by $I = m_1 - m_0$ and $I\% = 100\ (m_1 - m_0)/m_0$, where m_1 and m_0 are the means of S_1 and FS progenies, respectively. The estimates of inbreeding depression per 1% increase of the coefficient of inbreeding were obtained by $I_{1\%} = I/50$. In addition, the quantities $A = \mu + a$, the expected mean of a random sample of completely homozygous lines, and d were estimated by: $\hat{A} = 2\ m_1 - m_0$ and $\hat{d} = -2I$.

RESULTS AND DISCUSSION

The means of the two types of progenies (FS and S_1) obtained from two semi-exotic populations, EE1 and EC4, for nine traits are shown in Table I. The semi-exotic population EC4 had greater means for plant height, ear height, ear diameter, stand, number of ears per plot, ear yield, and grain yield for both noninbred and inbred progenies, while for ear length and tassel branch number EE1 had greater means. The larger means for ear diameter in EC4 and for ear length in EE1 were expected, because of the introgression of genes of the races Cravo (greater number of kernel rows) and Entrelaçado (longer ears). Santos and Miranda Filho (1992) reported that the negative effects of the introgression of these races into the adapted population (ESALQ-PB1) were evident for ear and grain yield, mainly in EE1 for the average of two locations.

For both semi-exotic populations, FS and S_1 progeny means were also expressed in percent of hybrid check (Table I). Full-sib progenies were greater than the check for plant height, ear height and tassel branch number: 9.6, 25.6, and 59.5% in EE1 and 10.4, 26.0, and 17.6% in EC4, respectively. S_1 progeny means were greater only for ear height and tassel branch number: 5.6 and 28.2% in EE1, and 8.1 and 2.9% in EC4, respectively. For ear diameter, ear length, stand, number of ears per plot, ear yield and grain yield, the FS and S_1 progeny means were always less than the check, except for stand in EE1 and ear diameter in EC4, which were similar to the check, when evaluated as FS progenies.

Table I - Means of nine traits in two semi-exotic maize populations (EE1 and EC4) and checks.

Traits	EE1			EC4		
	m_0 %	m_1 %	Check	m_0 %	m_1 %	Check
Plant height, cm	109.6	94.6	245.2	110.4	96.2	247.2
Ear height, cm	125.6	105.6	135.5	126.0	108.1	138.2
Ear diameter, cm	86.7	71.1	4.5	100.0	86.7	4.5
Ear length, cm	93.0	75.9	18.7	87.3	73.5	18.9
Stand, no.	100.0	80.8	14.1	96.0	86.7	15.0
Tassel branch, no.	159.5	128.2	22.7	117.6	102.9	24.4
Ears per plot, no.	78.5	42.4	15.8	84.8	58.2	15.8
Ear yield, g/pl	53.1	29.3	179.3	78.4	43.2	170.5
Grain yield, g/pl	52.3	28.1	146.9	78.5	41.8	139.4

m_0, m_1: means of noninbred and inbred populations, respectively.
%: In percent of check means.

The analysis of variance for all traits (from Nass, 1992; not shown herein) showed highly significant differences ($P < 0.01$) among sets, for the contrast FS vs S_1, and for progenies within sets (progenies/FS and progenies/S_1) for all traits in both semi-exotic populations, except stand (non significant) when evaluated by FS in EE1. Significant ($P < 0.05$ or $P < 0.01$) differences between FS in EE1 were detected for ear diameter, ear length, number of ears per plot, tassel branch number, ear yield and grain yield; in EC4 for stand, number of ears per plot, and grain yield. Ear diameter, stand, ear length, and tassel branch number also showed significant differences between S_1, except tassel branch number in EC4. Frequency distributions of S_1 progeny means in EE1 and EC4 for yield, plant traits, and ear traits are given in Figures 1, 2, and 3, respectively. Significant variability among FS and S_1 progenies was detected within each population for all traits. Thus, for both populations promising results can be attained by intrapopulation improvement as well as through selection of inbred lines for a hybrid program. Inbreeding effects in maize are evident by the reduction in the mean phenotypic value for most of the traits, and it is consequence of the effects of deleterious recessive alleles (Hallauer and Miranda Filho, 1988; Falconer, 1989; Hallauer, 1990).

The semi-exotic population EE1 had higher estimates of inbreeding depression in relation to noninbred progenies for all traits, except ear yield and grain yield (Table II). Although the estimates for ear and grain yield were similar, the means of FS progenies were greater in EC4: 28.7 and 29.8%, respectively (Table I). San Vicente and Hallauer (1993) studied inbreeding depression rates in two groups of maize inbred lines with theoretical levels of homozygosity attained by constant increments (12.5%) in the coefficient of inbreeding. Yield level of the newer group of inbred lines was greater than in the older group of inbred lines, but the rate of inbreeding depression was similar for both groups. For ear and grain yield the results obtained in this study corroborated the preliminary studies conducted by Santos and Miranda Filho (1992), which indicated the better performance of EC1 (introgression of Cravo) on the average of two locations.

The relative change for each trait per 1% increase in homozygosity are included in Table II. We can expect reductions of the same magnitude for plant height, ear height, ear diameter, ear length, stand and number of ears per plot, for both EE1 and EC4. Tassel branch number decreased two times more in EE1 than in EC4, although the values were relatively low in both instances. For ear yield and grain yield the estimates

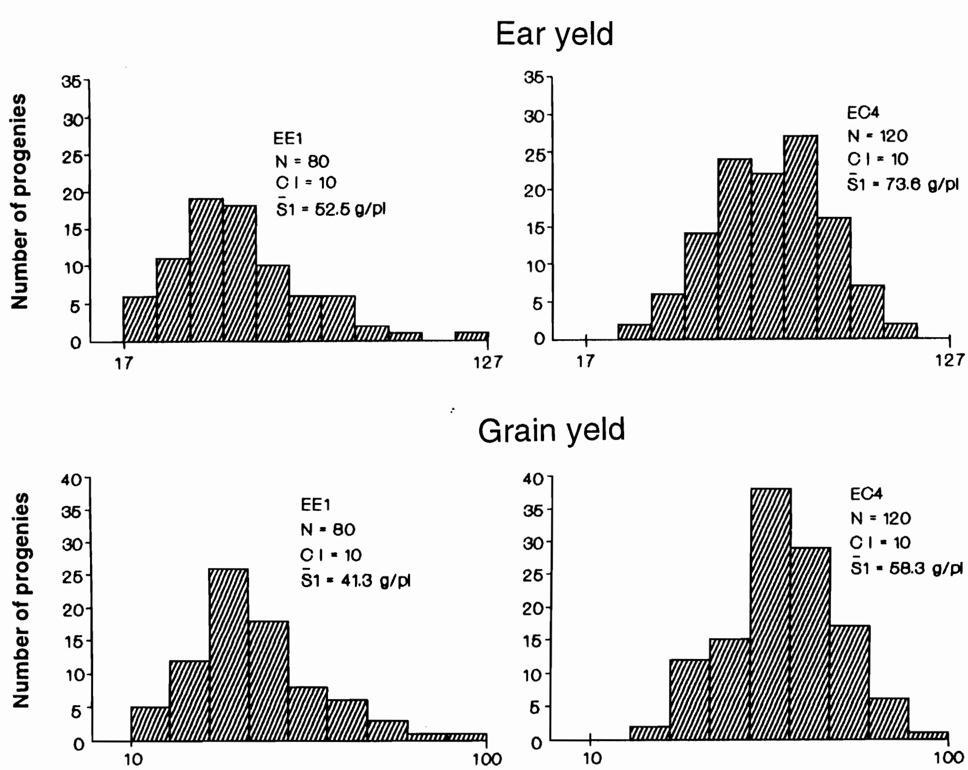

Figure 1 - Frequency distribution of S_1 progeny means in the two semi-exotic maize populations (EE1 and EC4) for ear yield and grain yield. (CI = class interval; N = total number of progenies).

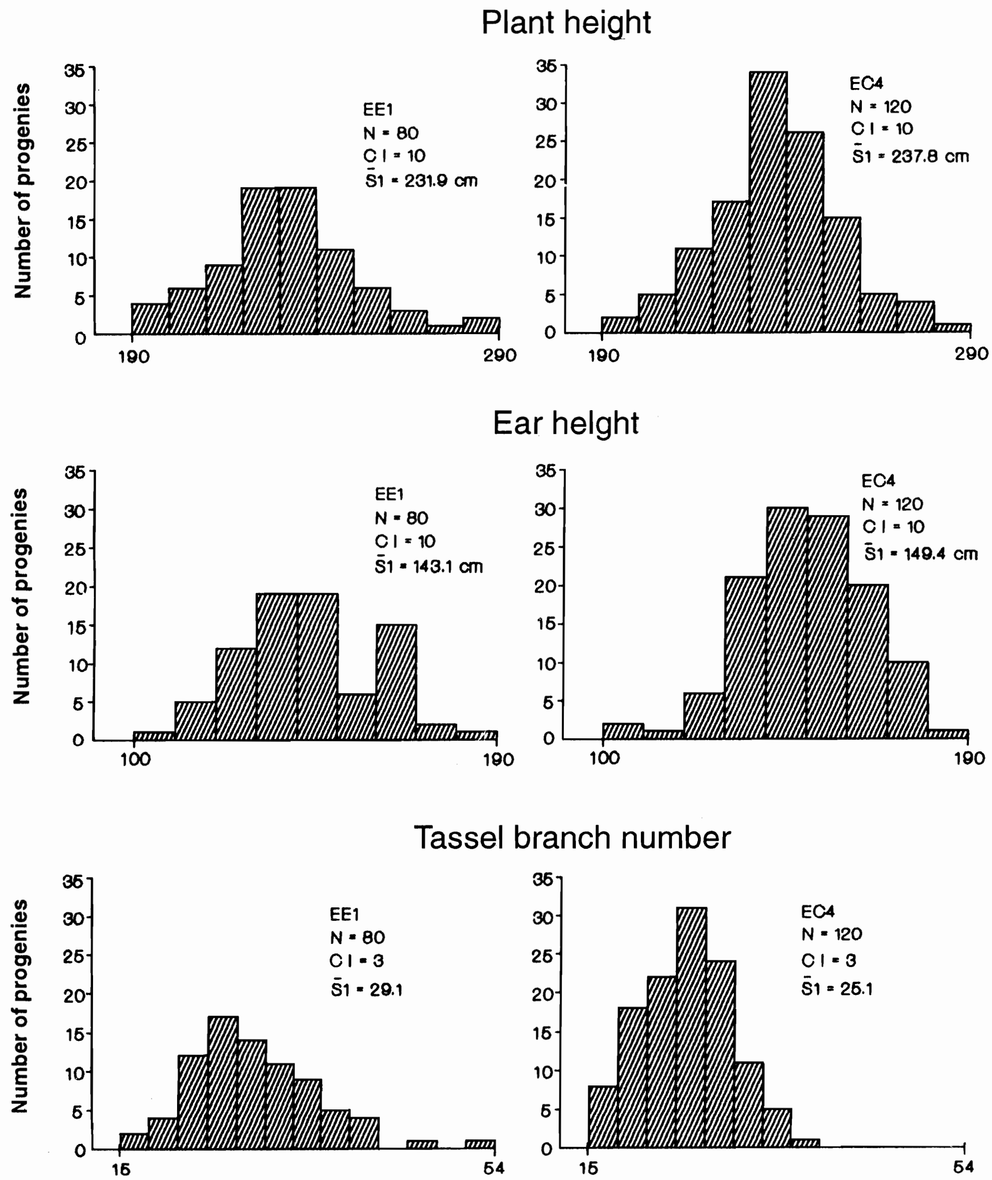

Figure 2 - Frequency distribution of S_1 progeny means in the two semi-exotic maize populations (EE1 and EC4) for plant height, ear height, and tassel branch number. (CI = class interval; N = total number of progenies).

were 0.85 and 0.71 g/pl in EE1 and 1.20 and 1.02 g/pl in EC4, respectively. For each 1% increase in homozygosity, Hallauer and Miranda Filho (1988) reported estimates that ranged from 0.80 to 1.40 g/pl, with a mean of 1.20 g/pl for grain yield. The reduction in grain yield due to increase in the percentage of homozygosity follows a linear regression model (Hallauer and Sears, 1973; Good and Hallauer, 1977; Hallauer and Miranda Filho, 1988).

The expected mean of a random sample of completely homozygous lines was higher than the contribution of the heterozygotes for most traits, except for number of ears per plot, ear yield and grain yield (Table II). According to Lima *et al.* (1984) the A values are expected to be higher than d values for any level of dominance and gene frequency, if a model without epistasis is considered. Thus, higher values of A indicate the potential of populations as a source of high-yielding lines. For both semi-exotic populations the estimates of $\hat{A}$ were lower for ear and grain yield, but negative values of $\hat{A}$ were reported by Lima *et al.* (1984). Lima *et al.* (1984) emphasized the existence of deleterious recessive genes with epistatic effects, which have a negative contribution when in the homozygous state, to explain the relatively lower values of $\hat{A}$ estimates.

Lima *et al.* (1984) evaluated inbreeding depression effects in 32 Brazilian maize populations.

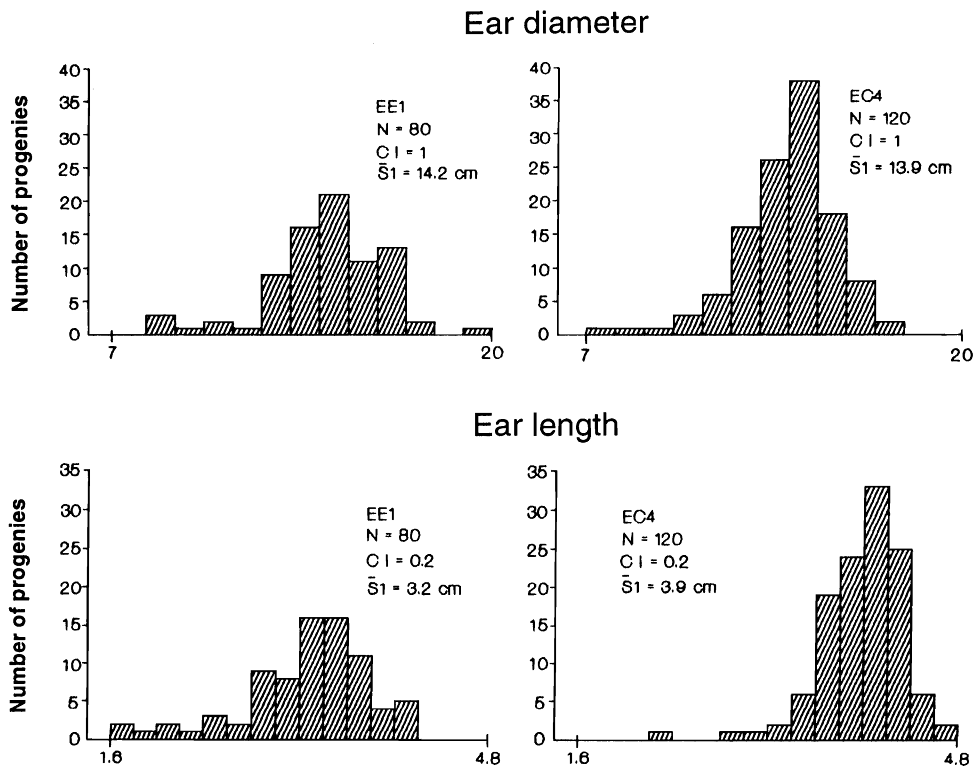

Figure 3 - Frequency distribution of S_1 progeny means in the two semi-exotic maize populations (EE1 and EC4) for ear diameter and ear length. (CI = class interval; N = total number of progenies).

Table II - Estimates of the inbreeding depression (I) and components of the population mean ($\hat{A}$ and $\hat{d}$) for nine traits in two semi-exotic maize populations (EE1 and EC4).

Traits	EE1					EC4				
	I	I%	$I_{1\%}$	$\hat{A}$	$\hat{d}$	I	I%	$I_{1\%}$	$\hat{A}$	$\hat{d}$
Plant height, cm	-36.81	-13.70	0.74	195.09	73.62	-34.95	-12.81	0.70	202.89	69.90
Ear height, cm	-27.12	-15.94	0.54	115.94	54.24	-24.78	-14.23	0.50	124.62	49.56
Ear diameter, cm	-0.67	-17.14	0.01	2.57	1.34	-0.56	-12.39	0.01	3.40	1.12
Ear length, cm	-3.25	-18.66	0.06	10.92	6.50	-2.61	-15.80	0.05	11.30	5.22
Stand, no.	-2.71	-19.17	0.05	8.72	5.42	-1.42	-9.85	0.03	11.57	2.84
Tassel branch, no.	-7.03	-19.44	0.14	22.11	14.06	-3.64	-12.68	0.07	21.43	7.28
Ears per plot, no.	-5.72	-45.98	0.11	1.00	11.44	-4.19	-31.32	0.08	5.00	8.38
Ear yield, g/pl	-42.64	-44.81	0.85	9.87	85.28	-60.10	-44.97	1.20	13.45	120.20
Grain yield, g/pl	-35.52	-46.24	0.71	5.77	71.04	-51.13	-46.74	1.02	7.14	102.26

$\hat{A}$, $\hat{d}$: refer to the expected mean of completely inbred lines and overall contribution of heterozygotes to the mean, respectively.

The mean values observed for the ratio $\hat{A}/\hat{d}$ were 0.28 for yield, 2.69 for plant height and 2.55 for ear height. In this study the estimates were 0.08, 2.65, and 2.13 in EE1 and 0.07, 2.90, and 2.51 in EC4, respectively. Although the $\hat{A}$ estimates were smaller than $\hat{d}$ estimates for EE1 and EC4, for ear and grain yield, the ratio $\hat{A}/\hat{d}$ was positive. According to the model suggested by Lima *et al.* (1984), some deleterious genes may occur where the contribution of the less favorable homozygote is negative, as a consequence of preventing some important pathways and/or some negative epistatic effects. Thus, the quantity A may show relatively small values as a consequence of deleterious recessive genes.

The relatively small values of $\hat{A}$ suggest that the semi-exotic populations have large inbreeding effects and should not be used as sources of outstanding inbred lines. However, small estimates of $\hat{A}$ for yield have also been reported for other populations (Vencovsky *et al.*, 1988) and the hypothesis of epistatic effects of deleterious genes seems to be valid. Continuous selfing to obtain inbred lines would decrease the hidden genetic load and possibly enhance the agronomic value of the inbreds. Continuous inbreeding and selection, therefore, would lead to inbred lines which would perform better than indicated by the relatively small values of $\hat{A}$. In this sense, the $\hat{A}$ estimated to predict the mean of a random sample of completely inbred lines seems to be unrealistic at least for yield.

The effects of inbreeding depression were generally greater in the semi-exotic population EE1 because number of ears per plot, ear diameter, ear length, tassel branch number, stand, plant height, and ear height had greater inbreeding rates than in EC4. For ear and grain yield, the estimates of inbreeding depression were of the same magnitude as for other estimates of Brazilian and introduced populations (Geraldi and Vencovsky, 1980; Vianna *et al.*, 1982; Valois and Miranda Filho, 1984; Lima *et al.*, 1984; Vencovsky *et al.*, 1988).

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RESUMO

Foram estudadas duas populações semi-exóticas de milho, ESALQ-PB1 x ENTRELAÇADO 1 (EE1) e ESALQ-PB1 x CRAVO 4 (EC4), utilizando-se dois tipos de progênies (S_1 e irmãos germanos). Amostras representativas de EE1 e EC4 foram utilizadas para avaliar os efeitos da depressão por endogamia em vários caracteres agronômicos e verificar o potencial de ambas como fonte de linhagens endogâmicas. A população semi-exótica EC4 apresentou as maiores médias para altura de planta, altura de espiga, diâmetro de espiga, estande, número de espigas por parcela, produção de espigas e produção de grãos em ambos os tipos de progênies, enquanto que para comprimento de espiga e número de ramificações do pendão, as maiores médias foram observadas em EE1. Os efeitos da depressão por endogamia foram mais evidentes em EE1 para todos os caracteres, exceto para produção de espigas e produção de grãos, nos quais as estimativas foram de mesma magnitude para ambas as populações semi-exóticas. As estimativas da depressão por endogamia pelo aumento de 1% na homozigose foram de 0,85 e 0,71 g/pl em EE1 e 1,20 e 1,02 g/pl em EC4, para produção de espigas e de grãos, respectivamente. As médias esperadas de uma amostra ao acaso de linhagens completamente homozigotas ($A = \mu + a$) foram inferiores em relação à contribuição total dos efeitos de heterozigotos para a média (d) nos caracteres produção de espigas e produção de grãos; entretanto, tanto em EE1 quanto em EC4, a relação A/d foi positiva. O aumento da homozigose por autofecundações sucessivas e a seleção contra genes recessivos deletérios tende a elevar o potencial genético dessas populações para serem utilizadas como fontes de linhagens endogâmicas.

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