

INBREEDING DEPRESSION IN MAIZE POPULATIONS OF REDUCED SIZE¹

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ABSTRACT: Inbreeding is a well known phenomenon in living beings and its immediate consequence is the decrease in the expression of quantitative traits, known as *inbreeding depression*. Selfing is the most common system of inbreeding in plant species; however, little has been studied with other less severe inbreeding systems, such that resulting from small population sizes. The present work consisted of the study of the inbreeding effect on quantitative traits as a consequence of reduced population size under panmixy. Three maize (*Zea mays* L.) populations were used in this study: P₁ – ITA, population derived from the variety IAC-Taiúba; P₂ – represented by 30 subpopulations already submitted to reduced size (N = 5); and P₃ – population derived from the interpopulation cross ESALQ-PB2 x ESALQ-PB3. The subpopulations and the respective parental populations were evaluated in six experiments using completely randomized blocks with four replications in Piracicaba (SP) and Anhembi (SP), Brazil, from 1997 to 1999. Estimates of inbreeding depression and components of means were obtained for the two generations in the three populations for the following traits: plant height, ear height, ear length, ear diameter, and yield traits (total ear weight and total grain weight). In all populations and for all traits and sampling generations, means of subpopulations were always smaller than mean of the base populations, however the inbreeding depression levels were smaller than expected. The highest inbreeding depression was exhibited by the yield traits, while a very small depressive effect was observed for plant height and ear height in the first generation of reduced size in populations P₁ and P₃. The component A (expected mean of a random sample of completely homozygous lines) was always higher than d (contribution of the heterozygotes to the mean) for all traits and populations.

Key words: *Zea mays*, genetic drift, effective size

DEPRESSÃO POR ENDOGAMIA EM POPULAÇÕES DE MILHO DE TAMANHO REDUZIDO

RESUMO: A endogamia é um fenômeno bastante conhecido nos seres vivos e sua consequência imediata é o decréscimo na expressão de caracteres quantitativos, conhecido por *depressão por endogamia*. A autofecundação é o sistema mais comum de endogamia nas espécies vegetais; entretanto, pouco tem sido estudado com outros sistemas menos severos de endogamia, como o que resulta de pequeno tamanho populacional. O presente trabalho teve por objetivo o estudo do efeito da endogamia em caracteres quantitativos, como consequência da redução do tamanho de população sob panmixia. Três populações de milho (*Zea mays* L.) foram utilizadas neste estudo: P₁ – ITA, população derivada da variedade IAC-Taiúba; P₂ – representada por 30 subpopulações previamente submetidas a tamanho reduzido (N = 5); P₃ – população derivada do híbrido interpopulacional ESALQ-PB2 x ESALQ-PB3. As subpopulações e as respectivas populações parentais foram avaliadas em seis experimentos em blocos casualizados com quatro repetições em Piracicaba (SP) e Anhembi (SP) entre os anos de 1997 e 1999. Foram obtidas estimativas de depressão por endogamia e dos componentes de médias para as duas gerações nas três populações para os caracteres: altura da planta, altura da espiga, comprimento da espiga, diâmetro da espiga, peso de espigas e peso de grãos. Em todas as populações, para todos os caracteres e gerações de amostragem, as médias das subpopulações foram menores do que as médias das populações base, porém os níveis de depressão por endogamia foram menores do que o esperado. A partir das estimativas dos componentes A (média esperada de linhagens totalmente homozigóticas) e d (contribuição dos heterozigotos para a média), foi estimada a relação A/d, com valores maiores que 1,0 para todos os caracteres e populações.

Palavras-chave: *Zea mays*, deriva genética, tamanho efetivo

INTRODUCTION

One of the main objectives in maize breeding is to develop outstanding hybrids from inbred lines and selfing has been recognized as the most used method for the development of inbred lines (Hallauer, 1990).

Selfing has some advantages over other methods of inbred line development that are less severe in relation to the rate of inbreeding in each generation. One advantage is the time necessary to reach the desired level of homozygosity; however, reaching a high level of homozygosity in few generations of inbreeding may turn

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to be a disadvantage in highly depressive populations, because many potentially useful lines are eliminated in the first generations as a consequence of the high homozygosity for lethal, semi-lethal and deleterious genes of large effects (Hallauer & Miranda Filho, 1995).

Methods for inbred line development under less severe inbreeding than selfing are based on crosses between half-sibs, crosses between full-sibs, backcrossing and random mating within small size subpopulations. Crossing a small number of plants to generate subpopulations will lead to a dispersive process that causes variation of allele frequencies among subpopulations. Such a dispersive process also leads to an increase in the level of homozygosity and consequently to a decrease in the expression of quantitative traits under the control of dominant gene action (Miranda Filho, 1999). Paterniani (1995) reported on inbreeding depression in subpopulations of size $N = 5$, obtained from two populations represented by the F_2 generations of crosses between inbred lines from the base populations ESALQ-PB2 and ESALQ-PB3. In this study, inbreeding depression varied with the base population, the studied trait and the local of evaluation; in general, inbreeding depression was higher for tassel branch number, 300 kernel weight and yield (total plot grain weight). Corrales Blandon (1996) also studied the possibility of using the random dispersive process, caused by reduced population size, as a means for the development of superior inbred lines with the accumulation of favorable factors. It was found that the increase in the proportion of homozygotes within subpopulations resulted in inbreeding depression in several traits, mainly plant height, ear height, tassel branch number and grain yield. Also, some estimates of subpopulation means and general combining ability in partial diallel cross were higher than the parental population for all the studied traits.

To study the inbreeding effect on quantitative traits, as a consequence of reduced population size under panmixy, this work was carried out using maize subpopulations of size $N = 4$ in two non-inbred populations and one set of inbred subpopulations already submitted to reduced size in two generations with $N = 5$

MATERIAL AND METHODS

Three maize (*Zea mays* L.) populations were submitted to sampling of reduced effective size: P_1 – ITA, population derived from the variety IAC-Taiúba; P_2 – represented by 30 subpopulations obtained by sampling in two generations of reduced size ($N = 5$), starting from the F_2 generation of the cross between inbred lines derived from the populations ESALQ-PB2 e ESALQ-PB3; P_3 – population derived from the interpopulation cross ESALQ-PB2 x ESALQ-PB3. In populations P_1 and P_3 , reduced size ($N = 4$) subpopulations were obtained through random pollination within each set of four plants:

51 and 73 in the first generation and 48 and 70 in the second generation, respectively. In P_2 , only 28 subpopulations were advanced for two additional generations of reduced size ($N = 4$).

Subpopulations and respective parental populations were evaluated in six experiments in completely randomized blocks with four replications at Piracicaba (SP) and Anhembi (SP) from 1997 to 1999. Two experiments at Piracicaba (SP), 1997 and 1998, were used to evaluate subpopulations of P_1 and P_3 in the first cycle; two experiments at Anhembi (SP), 1998 and 1999, were used to evaluate subpopulations of P_1 and P_3 in the second cycle; and two experiments in Anhembi (SP), 1999, were used to evaluate subpopulations of P_2 in the third and fourth cycles. The base populations (P_1 , P_2 and P_3) were included as treatments in the respective experiments. The commercial hybrid (three-way cross) MASTER (Novartis Seeds) was used as check and was intercalated systematically after ten plots within replications.

In all the experiments, the following traits were analyzed: plant height (PH), ear height (EH), ear length (EL), ear diameter (ED), and yield traits (EY- ear yield and GY- grain yield). The inbreeding depression, on the average of subpopulations and expressed in the original unit (I), in per cent of the parental populations (I%), and for 1% expected homozygosity ($I_{1\%}$), were estimated by: $I = m_s - m_0$, $I\% = 100 (m_s - m_0)/m_0$ and $I_{1\%} = (m_s - m_0)/100 F_t$; m_s is the overall mean of sub-populations, m_0 is the parental population mean, and F_t is the inbreeding coefficient in the t^{th} generation ($t = 1$ and 2 for populations P_1 and P_3 and $t = 3$ and 4 for population P_2); F is the general notation for Wright's coefficient of inbreeding. The inbreeding coefficients are: $F_1 = 0.125$ and $F_2 = 0.234$; and $F_3 = 0.291$ and $F_4 = 0.379$. The hybrid check mean (m_c) was included in the results for general comparisons, except for the results referring to inbreeding depression because the check was not submitted to inbreeding.

For comparison with other reports in the literature, which used one generation of selfing (50% expected homozygosity) to study inbreeding depression, our results were adjusted to $F = 0.5$. The expected contribution of the homozygotes ($A = \mu + a$) and heterozygotes (d) to the population mean were estimated by $A = (\frac{1}{F_t}) m_s - (\frac{1-F_t}{F_t}) m_0$ and $d = \frac{1}{F_t} (m_0 - m_s) = -100 I_{1\%}$ (Lima et al., 1984; Paterniani, 1995; Miranda Filho, 1999).

RESULTS AND DISCUSSION

The analysis of variance for the six traits showed significance for the variation among subpopulations in the six experiments at probability $P < 0.01$, except GY in population P_3 at Piracicaba with significance at $P < 0.05$ (Table 1). The expressive difference among subpopulations of reduced size was expected as based on the theory that the subdivision of a population into subpopulations of smaller size leads to a dispersive

Table 1 - Analysis of variance for six traits in six experiments.

Source ¹	d.f.	PH	EH	EL	ED	EY	GY
Population P ¹ : 1 st generation (Piracicaba, SP) ²							
Subpopulation	50	3.598**	2.878**	2.299**	0.175**	1.440**	0.959**
Error	150	0.755	0.562	0.918	0.044	0.224	0.151
Coef. variation %		4.0	6.1	7.4	6.0	15.6	17.7
Population P ¹ : 2 nd generation (Anhembi, SP) ³							
Subpopulation	47	15.100**	12.669**	2.222**	0.176**	1.219**	0.894**
Error	141	2.901	2.044	0.607	0.027	0.163	0.095
Coef. variation %		6.9	11.8	6.1	4.5	13.1	13.8
Population P ² : 3 rd generation (Anhembi, SP) ⁴							
Subpopulation	27	10.491**	6.623**	4.209**	0.165**	1.519**	1.048**
Error	81	5.843	3.051	0.985	0.046	0.316	0.228
Coef. variation %		9.5	13.4	7.9	5.3	14.8	15.7
Population P ² : 4 th generation (Anhembi, SP) ⁴							
Subpopulation	27	10.260**	11.083**	4.509**	0.150**	0.948**	0.635**
Error	81	3.478	2.026	1.045	0.047	0.244	0.152
Coef. variation %		8.9	12.3	8.6	5.6	13.9	14.1
Population P ³ : 1 st generation (Piracicaba, SP) ²							
Subpopulation	72	3.761**	2.978**	3.296**	0.124**	1.061**	0.736*
Error	216	1.745	1.099	1.386	0.058	0.756	0.487
Coef. variation %		6.3	9.0	7.5	6.1	17.7	18.0
Population P ³ : 2 nd generation (Anhembi, SP) ³							
Subpopulation	69	13.372**	10.422**	4.006**	0.153**	2.294**	1.737**
Error	207	6.522	5.075	1.316	0.042	0.410	0.294
Coef. variation %		6.5	9.6	8.0	5.1	13.1	13.7

¹Mean squares for replications (not shown) were significant in most instances.

²1997/98, ³1998/99, ⁴off-season ("safrinha") 1999.

process as a consequence of genetic drift (Crow & Kimura, 1970). The variance ratio (subpopulations : error; values not shown) showed the higher estimates for GY and EY, except for population P₃ at Piracicaba, suggesting a higher dispersion among subpopulations for these traits. It is therefore reasonable to suppose that more complex traits, controlled by a large number of loci, should exhibit a wider dispersion of subpopulation means.

The coefficients of variation (CV) were in general higher than the observed in other reports, particularly for yield traits (GY and EY). However, the results do not indicate necessarily a low precision of the experiments, because CV is influenced by the mean and in all experiments the general mean represents subpopulations with some level of inbreeding, whose means are below the non inbred populations as a consequence of inbreeding depression. In fact CV in the range of 13% to 18% can be considered as acceptable for inbred subpopulations. Bandon (1996) worked with inbred subpopulations and reported CV's of 15.6% and 19.5% for yield in two locations; mean yields were 4.43 and 3.06 t ha⁻¹, respectively.

Observed means in the base populations (P₁, P₂ and P₃) and derived sub-populations are shown for six

traits (Table 2). Some direct comparisons between populations and generations are not possible because differences between locations and planting dates. The performance of populations P₁ and P₃ can be compared in both first and second generations because experiments were conducted in Piracicaba (SP) and Anhembi (SP) in 1997/98 and 1998/99, respectively. Very small differences were observed between populations P₁ and P₃ for PH and EH in both generations; the same conclusion holds for the comparison between populations and hybrid check. For EL and ED, population P₁ showed smaller values than P₃ and check in both generations. Population P₃ showed slightly higher EL and slightly smaller ED than hybrid check in both generations. For yield traits (EY and GY) both populations (P₁ and P₃) showed smaller values than the hybrid check in both generations. However, the lower yielding performance was for P₁ with grain yield representing 43.2% and 44.1% of the check yield in the first and second generations, respectively. On the other hand, grain yield for P₃ represented 77.3% and 79.9% of the check yield, respectively. The superiority of P₃ over P₁ for yield traits is thus evident; grain yield for P₃ represented 178.2% and 178.9% relative to P₁ in the

Table 2 - Observed means for six traits in three base populations (m_0) and respective subpopulations (m_s) derived from reduced effective size and in a hybrid check (m_c).

Traits	Base population P ₁					
	1 st generation (Piracicaba, SP) ¹			2 nd generation (Anhembi, SP) ²		
	m_0	m_s	m_c	m_0	m_s	m_c
Plant height (m)	2.193	2.172	2.116	2.152	2.053	2.118
Ear height (m)	1.237	1.232	1.186	1.238	1.133	1.197
Ear length (cm)	13.17	12.91	14.59	13.24	12.67	14.69
Ear diameter (cm)	3.55	3.52	4.43	3.75	3.66	4.46
Ear yield (t ha ⁻¹)	3.164	3.035	6.181	3.266	3.069	6.543
Grain yield (t ha ⁻¹)	2.293	2.172	5.314	2.516	2.224	5.700
	Base population P ₂					
	3 rd generation (Anhembi, SP) ³			4 th generation (Anhembi, SP) ³		
	m_0	m_s	m_c	m_0	m_s	m_c
Plant height (m)	1.804	1.584	1.953	1.868	1.580	1.943
Ear height (m)	0.953	0.822	1.133	1.010	0.828	1.147
Ear length (cm)	13.67	12.54	14.58	13.43	11.91	14.76
Ear diameter (cm)	4.18	4.07	4.20	4.12	3.91	4.22
Ear yield (t ha ⁻¹)	4.171	3.793	4.62	4.133	3.553	4.312
Grain yield (t ha ⁻¹)	3.401	3.042	3.59	3.201	2.774	3.366
	Base population P ₃					
	1 st generation (Piracicaba, SP) ¹			2 nd generation (Anhembi, SP) ²		
	m_0	m_s	m_c	m_0	m_s	m_c
Plant height (m)	2.105	2.091	2.109	2.180	2.089	2.137
Ear height (m)	1.167	1.160	1.191	1.249	1.176	1.208
Ear length (cm)	15.92	15.59	14.67	14.86	14.35	14.66
Ear diameter (cm)	4.02	3.96	4.48	4.10	3.97	4.46
Ear yield (t ha ⁻¹)	5.143	4.894	5.968	5.391	4.898	6.473
Grain yield (t ha ⁻¹)	4.086	3.880	5.287	4.500	3.971	5.633

¹1997/98, ² 1998/99, ³ off-season ("safrinha") 1999.

first and second generation, respectively. The differences between yields of P₁ and P₃ can be partly attributed to environmental effects by favoring the expression of susceptibility to pests and diseases. However, P₃ has shown good performance in several other experiments (Basso, 1999; Miranda Filho et al., 2001).

The base population P₂ and its sub-populations in the third and fourth generations of reduced size were evaluated only at Anhembi in off-season planting ("safrinha") in 1999. Therefore, the results of these experiments are not directly comparable with those referring to P₁ and P₃, but they are comparable between themselves. For the base population, means of PH and EH were slightly smaller than hybrid check in both generations. EL and ED also showed smaller means than the hybrid check; these two components of grain yield possibly contributed to the lower yield of the base populations in both generations. In fact, grain yield of population P₂ represented 97.2% and 95.1% of the hybrid check in the third and fourth generations, respectively.

Means of sub-populations (m_s) derived from the three populations (P₁, P₂ and P₃) were always smaller than the base populations (m_0) for all the six studied traits in all generations and m_s varied from 82.0% to 99.6% in relation to m_0 . These effects are due to the depression caused by inbreeding as a consequence of the reduced size of the sub-populations. Some parameters related to inbreeding depression and components of means were estimated (Table 3). Inbreeding depression (**I**) was firstly estimated in the original units for all traits. The most negative estimates were for for population P₂, as expected because it was in a higher level of inbreeding; i.e., $F = 0.291$ and $F = 0.379$ in the third and fourth generations, respectively; F being Wright's coefficient of inbreeding. When expressed in percent of the original mean it was seen that the highest **I** was for PH and EH, followed by yield traits. In the populations P₁ and P₃, at a lower level of inbreeding ($F = 0.125$ in the first cycle and $F = 0.234$ in the second cycle), the highest **I** was for grain yield in the first cycle (-5.3% in P₁ and -5.0% in P₃); for PH and EH, **I** was very low (<1%) in the first cycle

Table 3 - Estimates of the inbreeding depression expressed in original units (I), in percent of the base population mean (I%) and for 1% expected homozygosity (I_{1%}) and expected contribution of homozygotes (A) and heterozygotes (d) to the mean for three populations in two different generations of reduced effective size.

	Base population P ₁									
	1 st generation (Piracicaba, SP) ¹					2 nd generation (Anhembi, SP) ²				
	I	I%y	I1%	A	d	I	I%	I1%	A	d
Plant height (m)	0.021	-1.0	-1.7	2.025	0.168	-0.099	-4.6	-4.2	1.730	0.422
Ear height (m)	-0.005	-0.4	-0.4	1.197	0.040	-0.105	-8.5	-4.5	0.790	0.448
Ear length (cm)	-0.26	-2.0	-20.8	11.090	2.080	-0.57	-4.3	-24.3	10.809	2.431
Ear diameter (cm)	-0.03	-0.8	-2.4	3.310	0.240	-0.09	-2.4	-3.8	3.366	0.384
Ear yield (t ha ⁻¹)	-0.129	-4.1	-10.3	2.132	1.032	-0.197	-6.0	-8.4	2.426	0.840
Grain yield (t ha ⁻¹)	-0.121	-5.3	-9.7	1.325	0.968	-0.292	-11.6	-12.5	1.271	1.245
	Base population P ₂									
	3 rd generation (Anhembi, SP) ³					4 th generation (Anhembi, SP) ³				
	I	I%y	I1%	A	d	I	I%	I1%	A	d
Plant height (m)	-0.22	-12.2	-7.6	1.049	0.755	-0.288	-15.4	-7.6	1.110	0.758
Ear height (m)	-0.131	-13.7	-4.5	0.503	0.450	-0.182	-18.0	-4.8	0.531	0.479
Ear length (cm)	-1.13	-8.3	-38.8	9.790	3.880	-1.52	-11.3	-40.0	9.428	4.002
Ear diameter (cm)	-0.11	-2.6	-3.8	3.802	0.378	-0.21	-5.1	-5.5	3.567	0.553
Ear yield (t ha ⁻¹)	-0.378	-9.1	-13.0	2.873	1.298	-0.58	-14.0	-15.3	2.606	1.527
Grain yield (t ha ⁻¹)	-0.359	-10.6	-12.3	2.168	1.233	-0.427	-13.3	-11.2	2.077	1.124
	Base population P ₃									
	1 st generation (Piracicaba, SP) ¹					2 nd generation (Anhembi, SP) ²				
	I	I%y	I1%	A	d	I	I%	I1%	A	d
Plant height (m)	-0.014	-0.7	-1.1	1.993	0.112	-0.091	-4.2	-3.9	1.792	0.388
Ear height (m)	-0.007	-0.6	-0.6	1.111	0.056	-0.073	-5.8	-3.1	0.938	0.311
Ear length (cm)	-0.33	-2.1	-26.4	13.280	2.640	-0.51	-3.4	-21.8	12.685	2.175
Ear diameter (cm)	-0.06	-1.5	-4.8	3.540	0.480	-0.13	-3.2	-5.5	3.546	0.554
Ear yield (t ha ⁻¹)	-0.249	-4.8	-19.9	3.151	1.992	-0.493	-9.1	-21.0	3.288	2.103
Grain yield (t ha ⁻¹)	-0.206	-5.0	-16.5	2.438	1.648	-0.529	-11.8	-22.6	2.244	2.256

¹1997/98, ²1998/99, ³off-season ("safrinha") 1999; I_{1%}: multiplied by 10³ y I% for 50% expected homozygosity is obtained by: 5000 I_{1%}/m₀.

and more expressive (>4%) in the second cycle. Also, in the second cycle, I was around 11% for grain yield in both populations. For all populations, I at the actual inbreeding level was adjusted to 50% expected homozygosity and the results were below the expected. In fact, estimated I for grain yield adjusted to F = 0.5, which is the expected homozygosity for S₁ (selfed) progenies, varied from 18.1% to 24.8% (results not shown), considering all populations and generations. Lima et al. (1984) reported inbreeding depression in S₁ progenies of 32 Brazilian maize populations, varying from 27.0 to 59.9% for grain yield, 6.6 to 20.3% for PH and 6.9 to 27.4% for EH. It was also reported that populations derived from inbred lines exhibited lower inbreeding depression (34% less) than open-pollinated varieties which were never submitted to inbreeding. In conclusion, selection under inbreeding leads to a decrease in the genetic load, mainly that caused by recessive genes of large effects.

Other results of inbreeding depression for yield in S₁ progenies have shown average decreases varying

from 37.5% to 64.0% (Vianna et al., 1982; Gama et al. 1985; Napolini Filho & Vencovsky, 1982; Moro, 1982; Mota, 1984; Miranda Filho & Meirelles, 1986; Marques, 1988; Terasawa Jr., 1983; Nass & Miranda Filho, 1995; Packer, 1998). Farias Neto & Miranda Filho (2000) also reported on inbreeding depression for PH, EH and tassel traits in subpopulations divergently selected for tassel size. The low inbreeding depression expected for 50% homozygosity can be due to the low exposure of the potential genetic load as a consequence of low levels of homozygosity resulting from low inbreeding in populations of reduced size. On the other hand, in S₁ progenies obtained by selfing the exposure of genetic load due to recessive genes of large effects (detrimental and deleterious genes) is much higher than in sub-populations of reduced size.

For EL and ED, small effects of inbreeding depression were observed in general. Population P₂, at a higher level of homozygosity, inbreeding depression was higher for EL (-8.3% and -11.3%) than for ED

(-2.6% and - 5.1%) in the third and fourth generations, respectively. For populations P_1 and P_3 , at lower levels of homozygosity, inbreeding depression was <5% for both traits, considering both populations and generations. Lower inbreeding depression is indicative of lower levels of dominance of genes controlling the trait (Miranda Filho, 1999).

Estimates of the expected mean of completely homozygous lines ($A = m+a$) were always higher than the contribution of heterozygotes (d) to the mean (Table 3). The ratio A/d (not shown) was always smaller for yield traits, indicating higher levels of dominance of genes controlling the trait. Similar results were reported by Nass & Miranda Filho, (1995). Lima et al. (1984) reported on estimates of $A/d < 1$ in some populations, which were indicative of high levels of inbreeding depression.

The low levels of inbreeding depression at moderate levels of homozygosity indicates that more vigorous inbred lines can be developed under a continuous elimination of the potential genetic load, as emphasized by Hallauer (1980) and Hallauer & Miranda Filho (1995).

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