

INBREEDING DEPRESSION RATES OF MATERIALS DERIVED FROM TWO GROUPS OF MAIZE INBRED LINES*

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ABSTRACT

The production of single-cross maize (*Zea mays* L.) hybrids requires the use of inbred lines that have dependable, stable performance. Inbred lines are usually developed by self-pollination, and inbreeding in maize is accompanied by a reduction in the mean phenotypic value for most traits. The objectives of this study were to compare inbreeding depression rates of materials derived from older (pre-1960) and newer (post-1970) maize lines to determine if rate of inbreeding depression and fit of data to a linear model changed between the two groups of lines. Each group included six lines with B14A, B37, L289, L317, M14, and WF9 included in the older group and B73, B75, B76, B77, B79, and B84 included in the newer group. Nineteen generations within each of the two inbred groups representing nine levels of inbreeding (0 to 100% homozygosity at 12.5% intervals) were evaluated in 10 environments to determine rates of inbreeding depression for 15 plant and ear traits. The rates of inbreeding depression were similar for the two groups of lines for nine of the 15 traits. The rate of inbreeding depression was lower for tassel-branch number, ear-leaf width, number of ears per plant, ear length, ear diameter, and cob diameter in the newer lines, suggesting either that the newer lines were segregating at fewer loci than the older lines or that the frequency of favorable alleles was greater than 0.5. The reduction in the phenotypic means was negatively and linearly correlated with the coefficient of inbreeding for all traits except days to anthesis. The linear model explained 89% or more of the variation among the inbreeding level means for nine traits for both groups of lines.

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INTRODUCTION

A major objective of the maize breeder is to develop hybrids that are high yield and are adapted to a wide range of environmental conditions. Inbreeding by selfing was recognized early as a procedure for developing pure lines for use in producing maize hybrids (Shull, 1952). Mean phenotypic values for most plant and ear traits are reduced when inbreeding is initiated in maize populations owing to a genetic phenomenon known as inbreeding depression. Inbreeding depression is the reduction of the mean phenotypic value shown by characters associated with reproductive capacity or physiological efficiency (Falconer, 1989). Genter (1971) and Hallauer and Sears (1973) concluded that inbreeding depression is the result of an increase in the frequency of homozygotes with deleterious recessive alleles.

The rate of inbreeding depression is a function of allele frequency, directional dominance, and the number of segregating loci. If we assume two alleles per locus and directional dominance, the rate of inbreeding depression is maximum at an allele frequency of 0.5 and decreases as the allele frequency approaches 0 to 1 (Lamkey and Smith, 1987). Allele frequencies can be changed by mutation, migration, selection, and random genetic drift (Falconer, 1989).

Previous inbreeding studies in maize (Sentz *et al.*, 1954; Sing *et al.*, 1967; Genter, 1971; Hallauer and Sears, 1973; Cornelius and Dudley, 1974; Good and Hallauer, 1977; Benson, 1991) reported a reduction in the mean and a negative linear relationship to the coefficient of inbreeding for all plant and ear traits except days to silk, plants with second ears, and barren plants. The genetic model based on the cumulative effects of loci with dominance generally explained most of the variation among the generations of inbreeding.

Hallauer and Miranda (1988) summarized the results of seven different inbreeding experiments in maize. On the average, yield was reduced 5.10 mg ha^{-1} from noninbred to 100% inbred generations. Plant height was reduced 44 cm, ear height was reduced 31 cm, and days to silk increased five days upon inbreeding in the maize populations studied. In a more recent study, Benson (1991) reported an average yield decline of 3.21 mg ha^{-1} from noninbred to 100% inbred generations in six synthetic maize populations.

Hallauer *et al.* (1983) reported that newer maize inbred lines obtained from advanced cycles of recurrent selection produced higher-yielding single crosses than did previously released inbred lines. Duvick (1984) found that 1970 inbreds compared with 1930 inbreds had a yield gain of $0.05 \text{ mg ha}^{-1} \text{ yr}^{-1}$, or a total predicted gain of 2.0 Mg ha^{-1} . Meghji *et al.* (1984) obtained no yield increase for 1950-era inbreds compared with 1930-era inbreds, but the 1970-era inbreds had an average yield increase of 14.5% over the 1950-era inbreds. Whereas in earlier years breeders selected lines primarily on the

basis of hybrid performance, more emphasis currently is given to the development of lines that have greater vigor and, thus, greater seed yields. Nevertheless, it is necessary to determine whether newer greater-yielding maize inbred lines are less affected by inbreeding depression than older inbred lines.

The objectives of this experiment were to compare inbreeding depression rates for materials derived from older maize lines and from newer maize lines; to determine if selection of newer lines has affected inbreeding depression; and to determine if there has been a change in fit of data to a linear model with selection of newer lines.

MATERIAL AND METHODS

Genetic materials

The materials used in this study included six relatively old maize inbred lines (B14, B37, L289, L317, M14, and WF9) and six relatively new maize inbred lines (B73, B75, B76, B77, B79, and B84). The older inbred lines were available for commercial use between 1936 and 1958, whereas the newer inbred lines were released between 1972 and 1978.

Two six-parent diallels were produced in 1981. The first diallel included 15 single crosses produced among six older inbred lines. The second diallel included the 15 single crosses produced among the six newer inbred lines. Generations of inbreeding within each of the 15 crosses for the two diallels were produced in the following manner. In 1982, the BC₁, BC₂ (backcrosses to parents 1 and 2, respectively), and the F₂ generation (self of F₁ generation) were produced. In 1983, the BC₁ and BC₂ generations were selfed (BC₁₋₀ and BC₂₋₀), backcrossed to their respective recurrent parents (BC₁₋₁ and BC₂₋₂), and crossed to their nonrecurrent parents (BC₁₋₂ and BC₂₋₁); also F₂ plants were selfed, and F₃ seed was harvested. In 1984, the BC₁₋₂ and BC₂₋₁ generations were selfed (BC₁₋₂₋₀ and BC₂₋₁₋₀) and crossed to their recurrent parents (BC₁₋₂₋₁ and BC₂₋₁₋₂). The BC₁₋₁ and BC₂₋₂ generations were crossed to their nonrecurrent parents (BC₁₋₁₋₂ and BC₂₋₂₋₁), and the F₃ plants were selfed (F₄). In segregating populations (F₂, F₃, F₄, and backcrosses), 125 plants were used to sample a range of genotypes within each population. In each generation, the number of ears was counted and an equal quantity of seed from each ear was counted, and equal quantities of seed from each ear were bulked to form the different generations obtained by backcrossing and self-pollination within the two groups of lines. Seed for the different generations of inbreeding was produced in different years. After the seed was harvested, dried, and shelled for each generation, it was placed in cold storage until evaluated. If there were differences in seed quality because of season and age effects, this could affect the estimates of inbreeding depression.

The entries included in the experiment are listed in Table I. Nineteen generations with different levels of homozygosity within the older and newer groups of lines were used to evaluate nine levels of inbreeding (from 0% to 100% homozygosity at 12.5% intervals). Within the older and newer groups, bulks for each of the 19 generations were formed from the 15 crosses. Two hundred-seventy seeds per cross for each generation were bulked for 18 of the 19 generations. The 100% homozygosity level was represented by bulks of the six older and six newer lines (675 seeds per inbred line). Each entry, therefore, was represented by a bulk of the different generations within each group rather than by evaluation of each generation for each of the 15 crosses within each group.

Table I - Generations of entries for two sets of maize inbred lines and their percentage of expected homozygosity.

Entry number		Generation	Expected homozygosity (%)
Older lines	Newer lines		
1	21	Inbred parents	100.0
2	22	F ₄	87.5
3	23	F ₃	75.0
4	24	BC ₁₋₁	75.0
5	25	BC ₂₋₂	75.0
6	26	BC ₁₋₀	75.0
7	27	BC ₂₋₀	75.0
8	28	BC ₁₋₂₋₀	62.5
9	29	BC ₂₋₁₋₀	62.5
10	30	F ₂	50.0
11	31	BC ₁	50.0
12	32	BC ₂	50.0
13	33	BC ₁₋₂₋₁	37.5
14	34	BC ₂₋₁₋₂	37.5
15	35	BC ₁₋₂	25.0
16	36	BC ₂₋₁	25.0
17	37	BC ₁₋₁₋₂	12.5
18	38	BC ₂₋₂₋₁	12.5
19	39	F ₁	0.0

Experimental procedures and data collection

The 19 entries for each group were evaluated in a randomized complete-block design at five Iowa locations (Ames, Ames Atomic Energy, Ankeny, Crawfordsville, and Martinsburg) in each of 2 years (1988 and 1989). The Crawfordsville location was not harvested in 1989 because of drought stress during pollination. Plots included four-rows, 5.5 m long with 0.76 m between rows. To reduce intergenotypic competition between plots of different generations, all data were collected on the middle two rows of the four-row plots. Plots were machine-planted and thinned to 55,000 plants ha⁻¹ at the five-leaf stage. In 1989, the Martinsburg test site was machine-harvested, and dropped ears were retrieved. All other plots were hand-harvested. Ears were forced-air-dried to a uniform grain moisture content of approximately 6%. Data were obtained for grain yield (Mg ha⁻¹) and stand (plants plot⁻¹) at nine environments. Data for plant height (cm), ear height (cm), ears per plot (no.), ear length (cm), ear diameter (cm), kernel row number (no.), cob diameter (cm), stalk lodging (%), root lodging (%), dropped ears (%), and 300-kernel weight (g) were obtained in eight environments, and data for days to anthesis, tassel-branch number, and ear-leaf width (cm) were obtained in four environments. Plant height was measured from ground level to the node below the flag leaf and, ear height, from ground level to the top ear node. Ear-leaf width was measured at the estimated widest part of the ear leaf. Root and stalk lodging were recorded as the number of plants leaning greater than 30° from vertical and broken below the ear-bearing node, respectively, and expressed as percent of stand. Dropped ears was calculated as the percentage of ears lying on the ground. Days to anthesis were calculated as the number of days from date of planting until 50% of the plants in a plot had shed pollen. Tassel-branch number was counted as the primary branches from the main axis of the tassel. All ear traits were measured to the nearest 0.1 cm from a random sample of 20 ears per plot. Weights of 300-kernel samples were obtained from a random sample of the shelled grain from each plot. Data were analyzed on plot means.

Statistical analysis

Individual environment and combined analysis of variance across environments of a randomized complete-block design with four replications were conducted by considering environments as random effects and entries as fixed effects. The entry and environment-by-entry sums of squares were partitioned for the different comparisons, and the comparisons among entries were tested against the appropriate interaction with environments. Linear and quadratic regression models were fitted to the expected inbreeding levels for 15 plant and ear traits in each group of lines for each location, each year, and combined across locations and years. The estimates of the regression

coefficients are the inbreeding depression rates and measure the change in the mean per 12.5% and 1% increase in homozygosity. Tests of significance were made for the linear and quadratic sums of squares.

RESULTS AND DISCUSSION

Entry differences were highly significant ($P \leq 0.01$) for all 15 traits (analyses of variance not included). Generally, the among-inbred group mean square was highly significant for most traits within both older and newer groups. There were highly significant differences between the older and the newer group of inbred lines for all traits except days to anthesis, cob diameter, root lodging, and dropped ears. In most instances, either significant ($P \leq 0.05$) or highly significant differences were detected among levels of inbreeding within both groups of lines. Exceptions included tassel-branch number, root lodging, dropped ears, and 300-kernel weight within both groups, and stalk lodging in the older group.

The linear model accounted for 89% or more of the variation among levels of inbreeding in each group of lines for yield, plant height, ear height, days to anthesis, ear-leaf width, number of ears plot⁻¹, ear length, ear diameter, and kernel-row number (Table II). Changes in generation means with inbreeding for cob diameter in both groups of lines and for stalk lodging in the newer group were not explained by the additive (linear) model. Only in one instance (cob diameter, in the older group), however, was the quadratic mean square significant. A model that includes the quadratic term indicates epistatic (nonadditive) effects of loci that have segregating alleles (Sentz *et al.*, 1954). There were no significant changes in generation means with inbreeding for tassel-branch number (new lines), root lodging, 300-kernel weight, and dropped ears within both groups of lines and, for stalk lodging (older lines). However, these traits generally had significant linear mean squares, which were dependent on the trait and the group of lines.

The genotype x environment interaction mean squares were highly significant for all plant and ear traits except days to anthesis, ear-leaf width, ear diameter, and kernel row number. The linear component of each group among levels x environment interaction mean square was either significant or highly significant for ear traits, yield, plant height, ear height, root lodging, and for stalk lodging, cob diameter, and dropped ears for the older group of lines. A significant linear component of the among levels x environment interaction mean squares indicates that the magnitude of the linear regression coefficients for a trait varied among environments. The best situation for homogeneity of regression coefficients over environments would be one in which either the residual mean square was the only component that was significant or none of the components was significant.

Table II - Linear regression coefficients (b_i) and their standard errors, rate of inbreeding depression for each 1% increase in homozygosity (IDR), and R^2 values for old and new groups of lines.

	Yield Mg ha ⁻¹	Height cm		Days to anthesis	Tassel branch number
		Plant	Ear		
Old lines					
b_i^+	-0.545 ± 0.01	-4.81 ± 0.21	-2.99 ± 0.21	0.53 ± 0.07	-0.35 ± 0.12
IDR ($\Delta 0.01F$) ⁺⁺	-0.044**	-0.385**	-0.239**	0.042**	-0.028**
R^2	99.3	96.0	95.1	94.0	94.5
New lines					
b_i^+	-0.574 ± 0.03	-5.19 ± 0.23	-3.29 ± 0.14	0.61 ± 0.06	0.0
IDR ($\Delta 0.01F$) ⁺⁺	-0.046**	-0.415**	-0.263**	0.049**	0.0
R^2	98.4	97.9	98.0	97.9	0.0

	Ear leaf width cm	Number of ears per plot no.	Ear		Kernel-row number no.
			Length cm	Diameter (x 10) mm	
Old lines					
b_i^+	-0.14 ± 0.02	-1.67 ± 0.09	-0.50 ± 0.02	-0.67 ± 0.06	-0.21 ± 0.02
IDR ($\Delta 0.01F$) ⁺⁺	-0.011**	-0.13**	-0.040**	-0.054**	-0.017**
R^2	94.6	93.7	98.4	94.0	92.6
New lines					
b_i^+	-0.07 ± 0.01	-1.29 ± 0.09	-0.42 ± 0.02	-0.51 ± 0.04	-0.17 ± 0.01
IDR ($\Delta 0.01F$) ⁺⁺	-0.006**	-0.103**	-0.034**	-0.041**	-0.014**
R^2	89.1	94.5	99.0	93.7	89.5

Continued

Table II - Continued.

	Cob diameter	Lodging		Dropped ears	300-kernel weight
		Stalk	Root		
	(x 10) mm	-----%-----			g
Old lines					
b_l^+	- 0.53 ± 0.05	- 0.61 ± 0.16	- 0.17 ± 0.06	0.0	- 0.95 ± 0.18
IDR ($\Delta 0.01F$) ⁺	- 0.043**	- 0.049**	- 0.014*	0.0	- 0.076**
R ²	76.4	68.1	48.0	0.0	90.4
New lines					
b_l^+	- 0.13 ± 0.02	- 0.49 ± 0.01	- 0.16 ± 0.04	0.0	- 0.54 ± 0.11
IDR ($\Delta 0.01F$) ⁺	- 0.010**	- 0.039**	- 0.013**	0.0	- 0.043**
R ²	69.9	63.1	84.5	0.0	70.4

*, **Significant at the 0.05 and 0.01 probability level, respectively.

⁺Change in the mean per 0.125 increase of the inbreeding coefficient.

⁺⁺Change in the mean per 0.01 increase of the inbreeding coefficient.

The inbreeding depression rates were calculated by the regression of entry means for the nine inbreeding level means for each trait (dependent variable) either on the coefficient of inbreeding (F) or on the percentage of homozygosity (independent variable). The sign (+ or -) of the regression coefficient indicates the direction of the change, and the magnitude indicates the rate of change in the mean as the inbreeding coefficient increases. The rates of inbreeding depression were similar for the older and newer lines for 9 of the 15 traits. Rates of inbreeding depression for the newer lines were less than for the older lines for tassel-branch number, ear-leaf width, number of ears per plot, ear length, ear diameter, and cob diameter (Table II).

Inbreeding depression rates have been estimated in several experiments that included different maize populations evaluated in different environments with theoretical levels of homozygosity attained by different systems of inbreeding. Sing *et al.* (1967) obtained their estimates of inbreeding depression from seven levels of inbreeding within double-double crosses, Genter (1971) and Harris *et al.* (1972) from S₁ lines; and Hallauer and Sears (1973), Cornelius and Dudley (1974), Good and Hallauer (1977), and Benson (1991) from generations of inbreeding by self-fertilization and/or by sibbing. None of these experiments, however, used materials with equal increments in the level of

homozygosity. This study estimated inbreeding depression rates in maize with theoretical levels of homozygosity attained by constant increments (12.5%) in the coefficient of inbreeding. Inbreeding depression rates were estimated by comparing different generations of inbreeding attained by self-fertilization, backcrossing, or a combination of both.

In general, the effects of inbreeding in the two groups of inbred lines studied were similar to data obtained in previous maize inbreeding studies: a reduction in the mean for all traits except an increase for days to anthesis and no change for percentage of dropped ears. The reduction in the mean with inbreeding was greatest for grain yield, intermediate for ears plot⁻¹, plant height, ear height, ear length, and ear diameter, and less for all other traits (Table III). The reduction in the mean with inbreeding was negatively and linearly correlated with the coefficient of inbreeding for all traits except days to anthesis, which was positively associated with the coefficient of inbreeding and dropped ears, which was unchanged with inbreeding (Table II). The linear (additive) model, as estimated by the R² values, explained 89% or more of the variation among the inbreeding level means for yield, plant height, ear height, days to anthesis, ear-leaf width, number of ears per plot, ear length, ear diameter, and kernel-row number for both groups of lines (Table II).

Table III - Combined inbreeding level means of 15 traits for two groups of maize lines measured in nine environments.

Old lines	Yield	Height		Days to anthesis	Tassel branch number	Ear-leaf width	Number of ears per plot
		Plant	Ear				
% Homozygosity	Mg ha ⁻¹	----- cm -----		----- no. -----		cm	no.
0.0	6.11	198.8	112.1	85	12.1	10.7	34
12.5	5.43	193.7	109.7	86	12.2	10.6	33
25.0	4.85	188.8	106.5	87	11.7	10.4	32
37.5	4.47	183.5	101.6	87	11.4	10.4	30
50.0	3.87	174.4	97.1	87	11.1	10.2	29
62.5	3.23	170.5	94.9	87	10.6	10.0	27
75.0	2.88	170.5	95.0	89	10.4	10.0	26
87.5	2.02	165.2	91.5	89	9.3	9.5	22
100.0	1.50	158.8	87.1	89	9.9	9.5	19
Group mean	3.77	177.5	99.1	87.4	10.9	10.2	29

Continued

Table III - Continued.

New lines	Yield	Height		Days to anthesis	Tassel branch number	Ear-leaf width	Number of ears per plot
		Plant	Ear				
% Homozygosity	Mg ha ⁻¹	----- cm -----		----- no. -----		cm	no.
0.0	7.38	197.8	112.5	84	11.4	9.8	42
12.5	6.87	188.4	106.5	85	10.8	9.7	40
25.0	6.19	185.1	104.2	85	10.6	9.6	39
37.5	5.80	180.8	102.1	86	10.7	9.5	39
50.0	5.13	173.3	97.2	87	9.9	9.6	37
62.5	4.21	167.2	93.7	87	9.8	9.4	35
75.0	4.13	166.0	92.4	88	9.5	9.3	35
87.5	3.09	158.9	87.2	89	9.2	9.4	31
100.0	2.82	151.0	82.9	89	9.5	9.2	31
Group mean	5.02	173.7	97.3	86.7	10.1	9.5	37
LSD (0.01)	0.12	1.4	1.0	0.3	0.3	0.1	1

Old lines	Ear		Kernel-row number	Cob diameter	Lodging		Dropped ears	300-kernel-weight
	Length	Diameter			Stalk	Root		
% Homozygosity	----- cm -----		no.	cm	----- % -----			g
0.0	18.3	4.2	15.6	2.7	15	4	1	73.7
12.5	18.0	4.1	15.5	2.7	16	4	1	71.6
25.0	17.6	4.0	15.2	2.7	16	5	1	70.8
37.5	17.2	4.1	15.2	2.7	14	4	1	71.3
50.0	16.7	4.0	14.9	2.6	13	3	1	68.7
62.5	16.0	3.9	14.7	2.6	15	3	0	67.0
75.0	15.7	3.8	14.6	2.5	13	3	1	67.5
87.5	14.8	3.7	14.1	2.3	12	4	1	66.1
100.0	14.3	3.6	13.6	2.2	9	3	0	66.0
Group mean	16.5	3.9	14.8	2.6	14	4	0.7	69.0

Continued

Table III - Continued.

New lines	Ear		Kernl- row number	Cob diameter	Lodging		Dropped ears	300- kernel- weight
	Length	Diameter			Stalk	Root		
% Homozygosity	----- cm -----		no.	cm	----- % -----			g
0.0	16.4	4.3	16.2	2.7	11	3	0	73.8
12.5	16.0	4.2	16.0	2.7	9	2	0	73.3
25.0	15.6	4.2	15.9	2.7	10	3	0	72.5
37.5	15.3	4.2	16.0	2.7	8	2	0	72.5
50.0	14.8	4.1	15.8	2.7	7	2	0	71.8
62.5	14.4	4.1	15.6	2.7	10	2	1	70.1
75.0	14.0	4.0	15.4	2.6	7	2	0	70.0
87.5	13.3	3.9	15.2	2.6	7	2	0	68.9
100.0	13.0	3.9	14.6	2.6	5	2	0	72.0
Group mean	14.7	4.1	15.7	2.7	8	2	0.3	71.4
LSD (0.01)	0.1	0.0	0.1	0.5	1	1	0.2	0.8

The inbreeding depression rate for grain yield had a nonsignificant increase of 0.029 Mg ha^{-1} (- 0.545 vs. 0.574) in the newer lines (Table II), which indicates that inbreeding depression for grain yield was not affected by development of newer lines. In the process of developing newer, more vigorous, greater-yielding maize inbred lines, the rate of inbreeding depression was not changed. Any changes in the inbreeding depression rate resulting either from selection in the number of segregating loci or from allele frequency for a trait are confounded. Knowledge of the allele frequency within the two groups and/or the number of segregating loci would be of great value when comparing inbreeding depression rates between the two groups of lines. Estimates of these parameters were not available for the two groups of inbred lines used in this study.

The most likely explanations for the lower rates of inbreeding depression in the group of newer lines for 9 of 15 traits evaluated are that this group is either segregating at fewer loci than the group of older lines or that the favorable allele frequency has increased beyond 0.5. The number of segregating loci would be expected to be lower in the group of newer lines if selection was effective in substituting favorable alleles for unfavorable alleles and the initial allele frequency was either near or greater than 0.5.

The inbreeding depression rate for grain yield was not significantly different between the two groups of inbred lines. Two possible explanations for the nonsignificant differences in estimates of inbreeding depression rates for yield are 1) that so many loci are involved in the expression of yield that the differences in allele frequencies between the two groups of lines were not large enough to detect changes in the inbreeding depression rates with the genetic models used; or 2) the frequency of favorable alleles increased from either 0.3 to 0.7 or 0.4 to 0.6 with the selection of newer lines. A change in allele frequency of this magnitude would result in an improvement in the mean with no change in the inbreeding depression rate. Yield of the newer group of lines compared with the older group of lines was 20.8% greater at the noninbred level, 32.6% greater at the 50% level, and 88.0% greater at the inbred level (Table III). Although the yield level of the newer group of lines was greater than the older group of lines at all levels of inbreeding, the rate of inbreeding depression was similar for both groups (Table II). Unfortunately, we could not determine allele frequencies, dominance deviations, and number of segregating loci. Although inbreeding depression continued with increased homozygosity and the rate of inbreeding depression remained unchanged, the newer inbred lines, mostly developed from improved source populations, had greater yield and shorter stature than older lines mostly developed from unimproved germplasm sources.

RESUMO

A produção de milho híbrido de um cruzamento (*Zea mays* L.) requer o uso de linhagens consanguíneas que tenham performance estável. Linhagens consanguíneas são usualmente desenvolvidas pela auto-polinização e consanguinidade em milho é acompanhada pela redução no valor médio do fenótipo para a maioria das características. O objetivo deste estudo foi comparar a queda das taxas de consanguinidade dos materiais derivados de linhagens de milho mais velhas (antes de 1960) e mais novas (após 1970) para determinar se a taxa da queda da consanguinidade e a aproximação dos dados para o modelo linear mudou entre os dois grupos de linhagens. Cada grupo incluiu seis linhagens com B14A, B37, L289, L317, M14 e WF9 incluídas no grupo mais velho e B73, B75, B76, B77, B79 e B84 incluídas no grupo mais novo. Dezenove gerações dentro de cada um dos dois grupos cruzados representando nove níveis de consanguinidade (0 a 100% de homozigose com intervalo de 12.5%) foram avaliados em 10 ambientes para determinar a taxa de queda devido a consanguinidade de 15 características de plantas e espigas. As taxas de queda devido a consanguinidade foram similares para os dois grupos de linhagens para 9 das 15 características. Foi menor para o número de ramificações do pendão, largura da folha da espiga, número de espigas por planta, comprimento da espiga, diâmetro da espiga e diâmetro do sabugo da espiga nas linhagens mais novas, sugerindo que qualquer uma das linhagens mais novas foram segregando a loci menores que as linhagens mais velhas ou que a frequência de alelos favoráveis foi maior que 0.5. A redução nas médias fenotípicas foi negativa e linearmente correlacionada com o coeficiente de consanguinidade para todas as características exceto dias até soltar pólen. O modelo linear explicou 89% ou mais da variação entre o nível de consanguinidade para nove características para ambos os grupos de linhagens.

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