

Variability and inbreeding in semiexotic maize populations

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ABSTRACT. Three semiexotic populations (CRE-01, CRE-02, CRE-03) obtained by incorporation of exotic germplasm (lines from CIMMYT, Colombia; selected for resistance to corn stunt complex) were evaluated in two cycles of recurrent selection with half-sib families. In cycle-I, samples comprising 50, 70, and 50 half-sib families were evaluated at Jataí (GO) and traits analyzed were ear yield, plant height, and ear height. For yield (t/ha), populations means were 5.86, 6.19, and 5.31, representing approximately 73% of hybrid check. Sets of parameters estimates representing the three populations were: [237, 485, and 608] for the additive genetic variance $(\sigma_A^2: g/plant); [0.393, 0.584, 0.658]$ for the coefficient of heritability (h_m^2) progeny mean basis), and [0.464, 0.684, and 0.801] for the index of variation (θ). In cycle-II, materials analyzed included 60 non-inbred (half-sib) and 60 inbred (S₁) families from each population, evaluated at Anhembi (SP) with two replications; traits analyzed included ear yield plus ear weight and grains weight of four ears, two plant traits (plant height and ear height), two ear traits (length and diameter), two tassel traits (branch number and length), and resistance to corn stunt complex. Means of half-sib families for ear yield (t/ha) were [10.614, 10.419, 10.842], representing 83 to 86% of the hybrid check. The same pattern of variation was observed for ear

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weight and grain weight of four ears. Means of S_1 families were [6.465, 5.527, 5.925] and the inbreeding depression in percent of the non-inbred families were [39.1, 46.9, 45.3]. Estimates for other traits are also shown.

Key words: Genetic variability; Inbreeding depression; Exotic germplasm

INTRODUCTION

The germplasm of maize (*Zea mays* L.) in Brazil is characterized by a wide variability, including local or indigenous races, adapted populations and exotic or semiexotic germplasm. Collections of inbred lines and other sources used in active breeding programs also express potentially useful germplasm (Nass et al., 2001). However, only a small portion of the variability has been effectively utilized, which is representative of the worldwide situation. Goodman (1985) emphasized that less than 5% of the available germplasm has been effectively used in breeding programs. Additionally, the use of exotic germplasm in breeding programs still remains at a very inexpressive level. Goodman (2005) stressed that the use of exotic germplasm in USA changed from 1% in 1984 to 2.9% in 1996 and it was represented mainly by germplasm of temperate origin, which changed from 0.8 to 2.6%; tropical exotics comprised 0.1 and 0.3%, respectively. Recently, the global strategy of seed companies for maize breeding programs over the world may increase the interchange of exotic germplasm (Goodman, 2005).

Historically, the maize breeding in Brazil under scientific basis initiated in the 1930s when seeds of the first commercial hybrid were produced (Krug et al., 1943). Subsequently, the introduction of exotic germplasm, particularly Tuxpeño and related races of Mexico and Central America, as well as other important germplasm sources from Colombia, Cuba, and Caribbean region greatly contributed for the development of outstanding semi-dent hybrids (Miranda Filho and Viégas, 1987). Brieger et al. (1958) described 52 races from Brazil and adjacent countries and about 3,000 collected samples originated the Brazilian germplasm bank. Other introductions of exotic germplasm were further reported (Môro et al., 1981; Lima et al., 1982; Miranda Filho, 1985, 1992; Miranda Filho and Viégas, 1987).

The primary objective of the present study was to introduce exotic germplasm of tropical origin with potential resistance to corn stunt complex, an important leaf disease of the corn crop in Brazil (Pereira, 1995; Basso and Miranda Filho, 2001). Subsequently, following the introgression of the exotic germplasm into three local adapted populations, the final objective was the evaluation of the yield potential and variability of the three semiexotic populations.

MATERIAL AND METHODS

The present project initiated with the introduction of 682 inbred (S_4) lines from CIMMYT (Centro Internacional de Mejoramiento de Maíz y Trigo, Colombia), which were previously selected for resistance to corn stunt complex (*achaparramiento*). The entire set of lines were planted in the year 2000 for visual evaluation in lines 3 m long with 15 plants per plot. The main focus of the evaluation was for resistance to the corn stunt disease, but other important traits including disease symptoms were also observed; to evaluate corn stunt, a 5-point scale was used, with 1 indicating resistance and 5 indicating susceptibility. In the next stage, 51 outstanding lines were incorporated into three local and adapted base populations,

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which were referred to as testers: P-3041, represented by the F_2 generation of the commercial hybrid (Pioneer Hy-Bred Seeds); CMS-14C, an open pollinated population derived from *Pool-25* (CIMMYT, Mexico) and released by Centro Nacional de Pesquisa de Milho e Sorgo/EMBRAPA; and ESALQ-PB23, a broad base population obtained from the cross ESALQ-PB2 (dent type) and ESALQ-PB3 (flint type), as described by Miranda Filho and Vencovsky (1974).

The 51 lines were planted and crossed with the three testers. Poor plant development and low quality or quantity of available seeds resulted in the following numbers of testcrosses: 27, 29, and 19 in crosses with testes P-3041, CMS-14C, and ESALQ-PB23, respectively. The testcrosses of each tester were evaluated individually in two seasons at Piracicaba (SP); the average yield of topcrosses were 7.88, 8.11, and 8.29 t/ha, which are equivalent to 88.6, 91.1, and 93.2%, respectively of the check mean (commercial hybrid Agromen AGN-3050). For plant height and ear height all the topcrosses showed higher means than the hybrid check, averaging 115.2 and 113.1%, respectively. The overall results did not allow the choice of the best tester to be used as base population for the introgression of the inbred lines, suggesting the synthesis of three populations, representing the respective testers. Despite the low quantity of seeds in some crosses (testcrosses), a greater number of lines than mentioned above was used for the introgression into the three testers. Thus, the new semiexotic populations referred to as CRE-01, CRE-02, and CRE-03, were obtained by intercrossing remnant seeds of 30, 39, and 32 testcrosses, respectively.

After the synthesis of the three semiexotic populations, the program was directed to population improvement through recurrent selection with half-sib families. In 2008, a sample of each population was planted in isolated block for seed multiplication to initiate the first cycle of selection. Open-pollinated ears (half-sib families) were then obtained for CRE-01, CRE-02, and CRE-03, with sample sizes of 50, 70, and 50, respectively; families were evaluated in three experiments at Jataí (GO) following the completely randomized block design with three replications. Plots with 4 m spacing by 0.9 m with 20 plants were used. The evaluated traits included ear yield (EY) corrected for stand variation (kg/plot), plant height (PH) in cm, and ear height (EH) in cm. The hybrid AGN-3050 was used as check intercalated after sets of ten plots within replications.

Analyses of variance were performed according to the following model

$$Y_{ii} = m + f_i + b_i + e_{ii}$$
 (Equation 1)

where Y_{ij} is the experimental unit referring to the ith family in the jth block, represented by plot total (EY) or sample means of five plants (PH and EH). In the model, *m* is the general mean, f_i is the random effect of of the ith family, b_j is the random effect of the jth-block, and e_{ij} is the error term (random effect) for plots. For the purposes of this study, the following expectations are of interest:

$$E(f_{i}) = E(e_{i}) = 0, E(f_{i}^{2}) = \sigma_{f}^{2}$$
 (Equation 2)

(genetic variance among half-sib families), and

$$E(e_{i}^{2}) = \sigma^{2}$$
 (Equation 3)

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(plot-to-plot error variance). In the analysis of variance the mean squares for Families and Error have the following expected values:

$$E(M_f) = \sigma^2 + J \sigma_f^2 \qquad (Equation 4)$$

and

$$E(M_{e}) = \sigma^{2}$$
 (Equation 5)

in this analysis, J = 3 (number of replications), so that

$$E(M_{f}) = \sigma^{2} + 3\sigma_{f}^{2}$$
 (Equation 6)

In the first cycle of selection, the main interest was related to the actual potential of the semi-exotic material for population improvement and a preliminary knowledge of parameters related to quantitative variation was emphasized. A mild selection (13/50, 18/70, and 11/50) was used for CRE-01, CRE-02, and CRE-03, respectively.

After recombination of the selected families of each population, seeds were planted in isolated blocks at Jataí (GO) to obtain random samples of 60 half-sib families. Pollination blocks were planted in the same year for selfing, to obtain $60 S_1$ families from each population. The whole set of 360 families, comprising three sets of half-sib families and three sets of S_1 families, were divided in six experiments that were evaluated in randomized block experiments with two replications of plots 3.0 m long with 15 plants, with spaces of 0.90 between rows and 0.20 m between plants. The following traits were analyzed: TB - tassel branch number, TL tassel length (cm), PH - plant height (cm), EH - ear height (cm), EL - ear length (cm), ED - ear diameter (cm), RS - resistance to corn stunt complex (notes: 1 - resistant to 5 - susceptible), EY - total ear weight adjusted for stand variation (g/plot), E4 - ear weight of four normally developed ear in the plot (g), and G4 - grain weight of the four ears sampled for E4. Final stand (ST) was also analyzed to be used as covariate in the correction of for stand variation. The commercial hybrid DOW 2B 587 was used as check and intercalated between sets of ten rows within each replication of the trials with half-sib families. No check plots were included in trials with S₁ families. All the experiments were carried out in the same experimental area.

Analyses of variance with plot totals or plot means from experiments of half-sib families followed the same model as for the Cycle-I; the expectation of effects and mean squares are also similar, except that J (number of replications) = 2, so that

$$E(M_f) = \sigma^2 + 2\sigma_f^2 \qquad (Equation 7)$$

In both cycles, the genetic variance among half-sib families (σ_f^2) expresses ¹/₄ of the additive genetic variance (σ_A^2) in the reference population, i.e.,

$$\sigma_{\rm f}^2 = \frac{1}{4} \sigma_{\rm A}^2 \qquad (\text{Equation 8})$$

then allowing the estimate

$$\hat{\sigma}_{A}^{2} = 4 \hat{\sigma}_{f}^{2}$$
 (Equation 9)

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Formulas for estimating quantitative parameters in both cycles are shown in Table 1.

Table 1. Formulas for the estimation of quantitative parameters in populations represented by random samples of families.

Parameter		Estimators	
	Cycle I*		Cycle II
General mean	$m = \frac{1}{11} \Sigma Y_{ij}$		$m = \frac{1}{120} \Sigma Y_{ij}$
Genetic variance among HS families	$\hat{\sigma}_{f}^{2} = \frac{1}{3} (M_{f} - M_{e})$		$\hat{\sigma}_{\rm f}^2 = \frac{1}{2} \left(M_{\rm f} - M_{\rm e} \right)$
Genetic variance among S ₁ families			$\hat{\sigma}_{f^*}^2 = \frac{1}{2} (M_f - M_e)$
Additive genetic variance (only for HS)		$\hat{\sigma}_{A}^{2} = 4 \hat{\sigma}_{f}^{2}$	-
Error variance		$\hat{\sigma}^2 = M_e$	
Coefficient of heritability (family mean basis)			
Narrow sense for half-sib families		$h_{\rm f}^2 = (M_{\rm f} - M_{\rm e})/M_{\rm f}$	
Broad sense for S ₁ families		$h_{\rm f^*}^2 = ({\rm M_f} - {\rm M_c})/{\rm M_f}$	
Coefficient of variation		CV%=100 $\sqrt{M_{f}}$ /m	
Genetic coefficient of variation		$CVg\% = 100 \ \hat{\sigma}_f/m$	
Index of variation		$\theta = CVg/CV$	

*Values of I: 50, 70, and 50 for CRE-01, CRE-02, and CRE-03, respectively; J = 3.

The analysis of inbred (S₁) families followed the same schedule used for half-sibfamilies, except that the traits TB and TL were not included. Additionally, the genetic variance among inbred families ($\hat{\sigma}_{f^*}^2$) does not allow a direct estimation of the components of the genetic variance, because

$$E(\hat{\sigma}_{f^*}^2) = \sigma_A^2 + \frac{1}{4}\sigma_D^2 + D_1 + \frac{1}{8}D_2$$
 (Equation 10)

In this relationship, σ_A^2 is the additive genetic variance and σ_D^2 the dominance variance in the non-inbred base population; D_1 is the covariance between the additive and dominant effects in the homozygotes and D_2 is the variance of the dominance effects in the homozygotes (Cockerham, 1983; Souza Junior, 1989).

Therefore, because of the complex relationships in the inbred families, estimates were obtained only for the total genetic variance ($\hat{\sigma}_{f^*}^2$) and for the broad sense coefficient of heritability ($h_{f^*}^2$).

The analysis of inbred (S₁) and non-inbred (half-sib) families from the same population allows the estimation of parameters that are functions of the population means. The basic model is given by (Vencovsky and Barriga, 1992). $m_0 = \mu + a^* + d^* = A + d^*$: mean of the non-inbred population and the components are μ : half the difference between the genotypic values of homozygotes over all loci; a^* : overall contribution of homozygotes to the mean; d^* : overall contribution of heterozygotes to the mean.

In a population in Hardy-Weinberg equilibrium, the following definitions hold: $a^* = \sum_i (2p_i - 1)a_i$ and $d^* = \sum_i 2p_i(1-p_i)d_i$, where, at the ith locus, p_i is the frequency of the favorable allele, a_i is the effect of homozygotes, and d_i is the deviation of the heterozygote.

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After generation of selfing, the population mean for 50% expected homozygosity is $m_1 = \mu + a^* + \frac{1}{2} d^*$, and the following effects can be estimated: $\hat{A} = 2m_1 - m_0$: expected mean of a random sample of completely homozygous lines extracted from the base population; $E(\hat{A}) = \mu + a^*$. $d^* = 2(m_0 - m_1)$: overall contribution of heterozygotes to the mean Id = $m_1 - m_0$: inbreeding depression for 50% expected homozygosity.

RESULTS AND DISCUSSION

The results of the present study are shown independently for Cycle I and Cycle II.

Cycle I: Evaluation of half-sib families in three semi-exotic populations

The observed means and the coefficients of variation are shown in Table 2 for three traits. For yield (t/ha), the population means (5.86, 6.19, and 5.31 for CRE-01, CRE-02, CRE-03, respectively) did not differ (non significance of the three contrasts between the population means) with estimates around 73% of the check mean. Means for PH and EH were close to 230 and 120 cm, respectively; and were higher than the check mean for all populations, with differences of 1.6, 4.9, and 7.9% in PH and 5.9, 12.7, and 15.8% in EH. For yield, the small difference of CRE-03 may be attributable to the base population (ESALQ-PB23) used for introgression, representing a wide base and low improved germplasm, as compared with the genetic base of the other two populations that were the hybrid P3041 (Pioneer) in CRE-01 and CMS-14 (EMBRAPA) in CRE-02. The higher means for PH and EH in CRE-03 have the same explanation. The coefficients of variation ($\leq 16.1\%$ for EY, $\leq 5.5\%$ for PH and $\leq 9.61\%$ for EH) were within the acceptable pattern for field experiments.

Table 2. Observed means⁶ and coefficient of variation for three traits in half-sib families of three semiexotic populations (CRE-01, CRE-02, CRE-03). Jataí (GO).

Parameters	Ear yield (t/ha)			Р	Plant height (cm)			Ear height (cm)		
	CRE-01	CRE-02	CRE-03	CRE-01	CRE-02	CRE-03	CRE-01	CRE-02	CRE-03	
m	5.86	6.19	5.31	233	234	238	119	123	126	
m	7.26	7.50	7.31	252	269	275	141	155	152	
m,	4.27	4.12	3.68	215	205	199	99	96	89	
m_%	73.4	73.4	72.02	101.6	104.9	107.9	105.9	112.7	115.8	
m	7.99	8.43	7.37	229	223	220	112	109	109	
CV%	15.71	14.46	16.09	4.26	5.12	5.50	7.30	9.62	9.56	

 ${}^{\Phi}m_0$ = mean of half-sib families; m_{μ} and m_{μ} = higher and lower means; $m_0\%$ = in percent of the check mean (m_c).

The analysis of variance is summarized in Table 3, that showed significance (*F* test; P < 0.01) for the variation among families for the three traits in all populations. The relative values of mean squares for families were in the order CRE-01 < CRE-02 < CRE-03 for the three traits, with higher expression of variability in CRE-03. Other parameters shown in Table 4 had the same tendency. In fact, the additive genetic variance (σ_A^2), the most important parameter for breeding purposes, showed estimates of 237, 485, and 608 (g/pl)² for EY, 189, 410, and 708 cm² for PH, and 253, 406, and 560 cm² for EH in the sequence of populations. Miranda Filho and Nass (2001) reported estimates in the ranges $200 < \hat{\sigma}_A^2 < 750$ (g/pl)² for EY, 250 $< \hat{\sigma}_A^2 < 600$ cm² for PH and $220 < \hat{\sigma}_A^2 < 590$ cm² for EH in five semi-exotic populations, from which three involved crosses with the race cravo and two with the race entrelaçado. Kist et al. (2010)

reported estimates of 276.8 for EY and 579.3 for PH using the same unities. The estimates given by Andrade and Miranda Filho (2008) in the population ESALQ-PB1 were equally expressive: 582, 324, and 170 for EY, PH, and EH, respectively. The described populations, used as references, are characterized by a wide genetic base, so that the results presented in this study express a very favorable condition for all traits.

Table 3. Mean squares in the analysis of variance for three traits in half-sib families of three semiexotic populations (CRE-01, CRE-02, CRE-03).

Source of variation ^f	Ear yield (t/ha)			Plant height (cm)			Ear height (cm)		
	CRE-01	CRE-02	CRE-03	CRE-01	CRE-02	CRE-03	CRE-01	CRE-02	CRE-03
Replications	5.2235	40.190	6.6910	1431.5	574.66	2735.7	658.14	509.66	1496.6
Families	1.3956	1.9206	2.1342	239.76	451.66	701.72	265.12	444.30	564.53
Error	0.8472	0.7995	0.7302	98.233	143.89	170.87	74.871	139.79	144.37

⁷Degrees of freedom for Families and Error: 49 and 98 for CRE-01 and CRE-03; 69 and 138 for CRE-02.

Table 4. Parameters estimates for three quantitative traits in half-sib families of three semiexotic populations (CRE-01, CRE-02, CRE-03).

Parameters ⁿ	I	Ear yield (t/ha))	Pl	ant height (cn	n)	E	ar height (cm)
	CRE-01	CRE-02	CRE-03	CRE-01	CRE-02	CRE-03	CRE-01	CRE-02	CRE-03
$\sigma_{\rm f}^2$	59.35	121.33	151.94	47.17	102.59	176.95	63.42	101.50	140.05
σ_A^2	237.39	485.31	607.75	188.70	410.36	707.80	253.67	406.01	560.21
σ_m^2	0.465	0.640	0.711	79.92	150.55	233.91	88.37	148.10	188.18
h ² _m	0.393	0.584	0.658	0.590	0.681	0.756	0.718	0.685	0.744
CVg	7.30	9.88	12.88	2.95	4.33	5.59	6.71	8.20	9.42
θ	0.464	0.684	0.801	0.693	0.844	1.018	0.920	0.852	0.985
ds	0.795	0.984	1.240	18.2	15.1	39.1	19.9	14.3	36.4
Gs	0.312	0.575	0.816	10.7	10.3	29.6	14.3	9.8	27.1
Gs%	5.3	9.3	15.4	4.6	4.4	12.4	12.1	8.0	21.5
$E(m_1)$	6.172	6.760	6.125	222.1	223.9	208.2	104.3	113.1	98.6
i	1.248	1.248	1.346	1.248	1.248	1.346	1.248	1.248	1.346
<u>G</u> s	0.334	0.583	0.747	6.58	10.43	15.57	8.42	10.41	13.74
<u>G</u> s%	5.7	9.4	14.1	2.8	5.1	6.5	7.1	10.9	10.9
$\underline{E}(m_{1})$	6.194	6.768	6.056	226.3	223.7	222.2	110.2	112.5	112.0

ⁿds, *i* - differential of selection: observed and standardized, respectively; $Gs = ds.h_m^2$ and $\underline{Gs} = i.h_m^2.\sigma_m$: expected gain from selection using ds and *i*, respectively; σ_m^2 is the phenotypic variance among family means; $E(m_1)$ and $\underline{E}(m_1)$ are the expected means $m_0 + Gs$ and $m_0 + \underline{Gs}$.

Other parameters related to the genetic variability showed a similar trend. The coefficient of heritability for family means in the set of populations was [0.393; 0.584; 0.658] for EY, [0.590; 0.681; 0.756] for PH, and [0.718; 0.685; 0.744] for EH; for EY and PH the estimates followed the same trend as for $\hat{\sigma}_A^2$. Estimates reported by Miranda Filho and Nass (2001) varied from 0.282 to 0.537, from 0.597 to 0.723, and from 0.618 to 0.745 for EY, PH, and EH, respectively, in five semiexotic populations. The results of Andrade and Miranda Filho (2008) were 0.398, 0.751, and 0.686 respectively. Kist et al. (2010) reported estimates of 0.344 and 0.771 for EY and PH, respectively. The index of variation (θ) was very promising in all instances and for EY followed the same pattern as other parameters, with estimates [0.464; 0.684; 0.801] in the sequence of populations. Vencovsky and Barriga (1992) hypothesized that values of θ near or greater than 1 indicate a favorable condition for selection. In this sense, the population CRE-03 appeared to be the most promising for selection; in fact the expected gains from truncate selection (13/50, 18/70, and 11/50) were 5.7, 9.4, and 14.1% in the sequence of populations. For PH and EH, the results were slightly more favorable for selection with estimated θ sets of [0.693, 0.844, 1.018] and [0.920, 0.852, 0.985].

Cycle II: Evaluation of half-sib and S₁ families in three semiexotic populations

The observed means for ten traits evaluated in half-sib families and eight traits in S_1 families are shown in Table 5. In the set of three semiexotic populations [CRE-01, CRE-02, CRE-03], the observed means were [16.8, 18.9, 19.9] for tassel branch number (TB), [39.8, 42.7, 41.0] for tassel length (TL), [212.5, 237.9, 241.4] for plant height and [120.1, 136.9, 139.9] for ear height; the sets of means followed approximately the same pattern, i.e., CRE-01 < CRE-02 < CRE-03. For these plant traits, most of the population means were slightly higher than the check means, which were 16.6 branches, 39.4, 185.2, and 98.8 cm. Farias Neto and Miranda Filho (2001) reported values between 6.3 to 43.0 for TB and from 38.2 to 43.6cm for TL in the population ESALQ-PB1. The higher means of CRE-3 for the plant traits is associated to the origin of the base population (ESALQ-PB23) used for introgression of the exotic germplasm. Means for ear length (EL) and ear diameter (ED) were around 17 and 5 cm, respectively. Compared with the hybrid check means (16.7 cm for EL and 5.4 cm for ED), the semiexotic populations showed means slightly higher for EL and slightly lower for ED. Andrade and Miranda Filho (2008) reported means of 17.5 cm for EL and 4.8 cm for ED in the population ESALQ-PB1.

	F	Population CRE-0	1	P	Population CRE-0	12	Р	opulation CRE-0	3
Traits ^ψ	m ₀	m _H	m _L	m ₀	m _H	m _L	m ₀	m _H	m _L
				Half-si	b (HS) progenies	(F=0)			
TB	16.8	20.9	11.6	18.9	24.0	13.5	19.9	26.1	14.1
TL	39.8	46.0	34.4	42.7	48.4	37.9	41.0	44.9	36.1
PH	212.5	241.9	170.6	237.9	273.1	205.6	241.4	280.6	191.9
EH	120.1	150.0	90.6	136.9	165.0	110.0	139.9	170.6	106.3
EL	17.9	20.0	16.0	18.1	20.0	16.1	17.9	19.9	16.3
ED	5.01	5.38	4.31	4.99	5.44	4.50	5.07	5.56	4.63
CS	1.93	3.50	1.00	1.89	3.00	1.00	1.69	2.75	1.00
EWª	10.614 (83.9)	12.963 (102.4)	6.880 (54.4)	10.419 (82.3)	13.019 (102.9)	7.933 (62.7)	10.842 (85.7)	12.777 (101.0)	8.586 (67.8)
E4ª	10.160 (91.3)	12.656 (113.8)	7.156 (64.3)	10.618 (95.4)	13.313 (119.7)	8.094 (72.8)	11.382 (102.3)	13.531 (121.6)	9.375 (84.3)
G4ª	8.540 (87.2)	10.844 (110.7)	6.438 (65.7)	8.680 (89.3)	10.156 (114.8)	6.594 (67.3)	9.440 (96.3)	11.156 (113.9)	7.781 (79.4)
				Inbred ((S_1) progenies (F	$= \frac{1}{2}$			
PH	200.5	238.1	166.9	199.9	258.8	140.6	214.6	268.1	167.5
EH	110.2	129.4	82.5	119.2	178.1	78.1	120.7	154.4	87.5
EL	16.5	18.7	13.6	15.7	18.0	13.2	15.8	18.7	12.3
ED	4.52	5.13	3.56	4.29	4.75	3.19	4.46	5.06	3.63
CS	2.45	4.00	1.00	2.25	3.25	1.25	1.93	3.25	1.00
EW	6.465	9.372	3.396	5.527	10.948	2.276	5.925	10.880	2.407
E4	6.910	9.375	4.031	6.582	8.750	2.781	7.157	11.781	5.188
G4	5.719	7.844	3.625	5.117	7.375	1.844	5.677	9.188	3.625

Table 5. Observed means of ten traits in three semiexotic populations under two levels of inbreeding (F = 0 and $F = \frac{1}{2}$)^b.

^b*F* is Wright's coefficient of inbreeding. $^{\mathbb{V}}TB$ = tassel branch number; TL = tassel length (cm); PH = plant height (cm); EH = ear height (cm); ED = ear diameter (cm); CS = resistance to "corn stunt" disease (notes from 1; resistant to 5: susceptible); EW = total ear weight; E4 = yield of four regular ears in the plot; G4 - grain yield of the same four ears of E4 (yield traits are expressed in t/ha and in percent of check means, in parenthesis).

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The trait CS (resistance to corn stunt complex; scale from 1-resistant to 5-susceptible) revealed a good pattern of resistance in the three populations, particularly in CRE-3 because of its essentially tropical origin. The pattern of resistance was CRE-1 \approx CRE-2 < CRE-3, with set means [1.93; 1.89; 1.69] and ranges 1.00-3.50, 1.00-3.0, and 1.00-2.75, respectively. Thus, the three semiexotic populations showed excellent pattern for resistance to the corn stunt complex, thus corroborating the efficiency of the introgression of exotic germplasm into local and adapted populations.

The trait EY (ear yield, t/ha) showed means [10.614, 10.419, 10.842] very similar among the three populations, corresponding to 83.9, 82.3, and 85.7% of the hybrid check. Probably the small differences among populations are not significant, but maintained the order CRE-1 < CRE-2 < CRE-3 observed for the plant traits. The same yield pattern was observed for E4 (weight of four ears) and G4 (grain weight of the same four ears), whose means (t/ha) are in the sets [10.160, 10.618, 11.382] and [8.540, 8.680, 9.440], respectively. The trait E4, expressed in t/ha, showed no great differences with EY representing 95.8, 101.9, and 105.0% of EY, respectively. Although both EY and E4 refer to ear yield, they are not the same trait because the difference in the criterion for sampling. Overall, the three semi-exotic populations showed relatively high levels of productivity for the tropical environment represented by the conditions in the experiments.

The analysis of variance of ten traits evaluated in half-sib families is shown in Table 6, where the mean squares for families were not significant in several instances. The estimates of quantitative parameters are shown in Table 7. The additive genetic variance (σ_A^2) is particularly important for breeding purposes. For the plant traits (TB, TL, PH, and EH), the sets representing the respective populations are [11.69, 5.905, 21.03], [9.216, 2.508, 3.907], [484.2, 349.8, 529.8] and [310.1, 216.2, 399.1], respectively. For comparison, the estimates reported by Andrade and Miranda Filho (2008) are shown: 15.89, 11.15, 323.8, and 170.3 for the same sequence of traits. The coefficients of heritability (h_f^2) for the plant traits were [0.511, 0.240, 0.640], [0.449, 0.154, 0.286], [0.607, 0.578, 0.547] and [0.667, 0.488, 0.623]. The estimates of h_f^2 reported by Andrade and Miranda Filho (2008) were 0.753, 0.727, 0.751, and 0.686, respectively. The higher estimates reported by Andrade and Miranda Filho (2008) resulted from the wide genetic base of the population ESALQ-PB1. For plant height, Kist et al. (2010) found estimates of 0.74-0.82 for the population MPA1 evaluated in four locations.

For the ear traits (EL and ED) the sets of σ_A^2 estimates were [158.4, 52.46, 68.66] x 10⁻², [29.98, 59.32, 73.18] x 10⁻³, which are below the estimates of 264 x 10⁻² and 44 x 10⁻³ reported by Andrade and Miranda Filho (2008). The corresponding sets for h_f^2 were [0.471, 0.168, 0.292] and [0.232, 0.390, 0.423], respectively. The sets of σ_A^2 estimates for EY were [962.50, 159.67, 231.43] (g/plant), which were beyond the range of 200 < $\hat{\sigma}_A^2$ < 750 reported by Miranda Filho and Nass (2001); the average (451.2) of the three populations was slightly lower than the estimate of 581.7 reported by Andrade and de Miranda Filho (2008). The order of magnitude of the σ_A^2 estimates was CRE-01 < CRE-02 < CRE-03 in Cycle-I and CRE-01 > CRE-02 < CRE-03 in Cycle-II and the discrepancies were attributed to differences in planting dates and locations, that was off-season ("safrinha") in Jataí (GO) and normal season (summer) in Anhembi (SP), respectively. For the other traits related to yield (E4 and G4) the sets of σ_A^2 estimates (g/pl) were [763.1, 723.4, 595.4] and [155.8, 399.5, 215.1], respectively. For these traits, no large differences were observed among populations. For all traits reflecting yield potential (EY, E4, and G4) identifying the population with the higher variability, mainly

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when considering the different environments of the two cycles, was difficult mainly when considering the different environments of the two cycles. Nevertheless, the higher expression of the additive variation for EY was for CRE-03 in Cycle-I and for CRE-01 in cycle-II. Generally, all the populations expressed genetic variability in an appropriate level for selection toward intrapopulation improvement.

Table 6. Mean squares in the analysis of variance of ten quantitative traits in half-sib families of three semiexotic populations under the model of completely randomized blocks.

Plant traits [◊]	TB	TL	РН	EH	CS ^[2]				
Sources			Population CRE-01						
Blocks	19.805	31.136	8526.1	2031.5	0.4492				
Families	11.430	10.268	398.89	232.32	6.6799				
Error	5.5865	5.6602	156.82	77.259	5.9779				
			Population CRE-02						
Blocks	28.6001	140.67	833.45	455.33	18.567				
Families	12.2856	8.1540	302.84	221.76	5.8258				
Error	9.3331	6.8998	127.94	113.64	5.6731				
			Population CRE-03						
Blocks	37.4083	0.0105	787.97	166.26	10.536				
Families	16.4422	6.8284	484.57	320.03	5.7147				
Error	5.9253	4.8750	219.67	120.50	4.5847				
Ear traits	$EL^{[1]}$	ED ^[2]	EW ^[3]	E4 ^[3]	G4 ^[3]				
		Population CRE-01							
Blocks	3.9388	1.5755	267.81	119.00	7.0083				
Families	16.810	6.4643	2069.8	128.39	79.427				
Error	8.8911	4.9654	986.96	67.345	66.962				
			Population CRE-02						
Blocks	11.021	0.6380	865.69	0.3000	0.0333				
Families	15.604	7.6031	1611.6	137.70	97.996				
Error	12.981	4.6370	1432.0	79.834	66.038				
			Population CRE-03						
Blocks	15.470	4.2188	14.753	151.88	282.13				
Families	11.758	8.6458	1506.8	105.61	66.249				
Error	8.3249	4.9868	1246.4	57.972	49.044				

^oDegrees of freedom: 1, 59, 59 for Blocks and Progenies, respectively. ^oAnalysis of variance with plot means for EL, ED, TB, TL, PH, and EH; plot totals for EW; and sample means for E4 and G4. ^[1], ^[2], ^[3]: mean squares multiplied by 10, 10², and 10⁻², respectively.

The sets of h_f^2 (coefficient of heritability) for the yield traits were [0.523, 0.111, 0.173], [0.475, 0.420, 0.451] and [0.157, 0.326, 0.260], respectively; the estimates for all these traits were generally at a lower level compared to values reported by previous studies. Additionally, the index of variation (θ) was relatively low, in the range of 0.25 to 0.75 for the yield traits in the three populations, thus indicating some limitation for the use of recurrent selection for population improvement. The environmental control and use of larger plots with more than two replications should increase substantially the efficiency of selection (Hallauer and Miranda Filho, 1988).

The observed means of selfed (S_1) families for eight traits are also shown in Table 5. The means of inbred families were smaller than the non-inbred families (HS) for all traits, except for resistance to corn stunt because an inverse scale was used, i.e., larger values for susceptibility and lower values for resistance; thus, inbreeding led to an increase in the observed values on the scale by decreasing the resistance to that disease. The larger differences between S_1 and non-inbred families (HS) were for the ear traits, in the range of 30 to 45% when considering the three populations.

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	$\hat{\sigma}^2$	$\hat{\sigma}^2$	$\hat{\sigma}^2$	h ²	CV0/	CV/c9/	0
	0 _f	0 _A	0	п _f	C V %	CVg‰	θ
Traits				Population CRE-0	1		
TB	2.9219	11.687	1.5030	0.511	14.07	10.18	0.723
TL	2.3040	9.2159	2.3078	0.449	5.97	3.81	0.638
PH	121.04	484.15	93.002	0.607	5.89	5.18	0.879
EH	77.532	310.13	57.944	0.667	7.32	7.33	1.002
CS	3.5107	14.043	33.400	0.105	17.89	4.34	0.242
EL	39.595	158.38	84.050	0.471	5.27	3.51	0.667
ED	7.4947	29.979	32.321	0.232	4.45	1.73	0.389
EY	240.63	962.50	438.65	0.523	11.0	8.12	0.741
E4	190.77	763.06	420.91	0.475	10.1	6.80	0.673
G4	38.955	155.82	418.51	0.157	12.0	3.65	0.305
			1	Population CRE-02	2		
TB	1.4762	5.9049	3.5093	0.240	16.2	6.42	0.398
TL	0.6271	2.5084	3.7740	0.154	6.15	1.85	0.301
PH	87.447	349.79	43.771	0.578	4.75	3.93	0.827
EH	54.057	216.23	90.668	0.488	7.79	5.37	0.690
CS	0.7636	3.0544	29.129	0.026	17.59	2.04	0.116
EL	13.116	52.463	78.019	0.168	6.30	2.00	0.318
ED	14.831	59.322	38.015	0.390	4.31	2.44	0.566
EY	39.917	159.67	636.45	0.111	11.0	8.12	0.250
E4	180.85	723.39	498.96	0.420	10.1	6.80	0.602
G4	99.869	399.48	412.73	0.326	12.0	3.65	0.492
				Population CRE-03	3		
TB	5.2585	21.034	1.0586	0.640	12.21	11.50	0.942
TL	0.9767	3.9069	1.7208	0.286	5.38	2.41	0.448
PH	132.45	529.80	135.01	0.547	6.14	4.77	0.777
EH	99.764	399.06	90.375	0.623	7.84	7.14	0.910
CS	5.6503	22.601	28.574	0.198	16.74	5.88	0.351
EL	17.165	68.662	58.790	0.292	5.09	2.31	0.454
ED	18.295	73.181	43.229	0.423	4.40	2.67	0.606
EY	57.859	231.43	553.95	0.173	12.1	3.90	0.323
E4	148.86	595.44	362.33	0.451	8.36	5.36	0.641
G4	53 766	215.06	306.53	0.260	9.27	3.88	0.419

Some parameters of breeding interest were estimated by using the non-inbred and inbred population means: 1) Id is the inbreeding depression, calculated by the difference between the inbred and non-inbred population means. 2) $A = u^* + a^*$ represents the expected mean of a random sample of completely homozygous lines developed from the respective base population; for populations with heavy genetic load (presence of recessive alleles with strong negative effects on morphological or physiological traits) the A estimates are biased downward and making interpretation of the results difficult. 3) d* is the overall contribution of the heterozygotes to the population mean and is expected to be low for traits with low levels of dominance; heavy genetic load due to deleterious alleles that cause strong depressive effects also cause an upward bias in the estimates. For the trait CS (resistance to corn stunt) A and d* were not calculated because the model is not fully appropriate for the analysis based on scale of notes.

The quantity A (Table 8) was fairly consistent among populations with sets [188, 162, 187], [100, 102, 101], [15.2, 13.4, 13.7] and [4.03, 3.59, 3.85] for PH, EH, EL, and ED, respectively, in the sequence of populations; the most prominent populations were CRE-03 for PH and EH and CRE-01 for EL and ED. The quantity d* was smaller than A for all plant and ear traits in the three populations and varied from 12.8 to 46.9%, when expressed in percent of

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A. For yield traits, estimates of d* were biased upward as explained above. However, the estimates of A, although presumably biased downward, seems to be more close to the expected real effect. In percent of the original (non-inbred) population means, the effects A were observed in the sets: [21.9, 6.1, 9.3], [36.0, 24.0, 25.7] and [34.0, 17.9, 20.2] for EY, E4, and G4, respectively, in the sequence of populations. Hallauer and Miranda Filho (1988) showed the change in the population mean for 12 traits over generations of inbreeding representing 0 to near 100% homozygosity; the extreme 100% represents theoretically the component A, as explained. The example shown by Hallauer and Miranda Filho (1988) was for the population Iowa Stiff Stalk Synthetic, and the population means were 7.0 t/ha and 2.4 t/ha, so that the component A should be around 35% of the original population mean. These comparisons indicate that a downward bias in A should be observed for the trait EY in all populations, but less expressive in CRE-01, likely because its lower genetic load. For the other yield traits, evidence for downward bias in A is not clear but; however, CRE-01 showed A% of the same order of that reported by Hallauer and Miranda Filho (1988); it must be emphasized that Iowa Stiff Stalk Synthetic is a synthetic population formed by intercrossing outstanding inbred lines, possibly with a low genetic load represented by deleterious recessive alleles (Silva and Hallauer, 1975).

Table 8. Estimates of the inbreeding depression (Id), and the contribution of homozygotes ($A = u^* + a^*$) and	ıd
heterozygotes (d*) to the population mean of eight traits.	

Traits	Ро	Population CRE-01			Population CRE-02			Population CRE-02		
	Id%	А	d*	Id%	А	d*	Id%	А	d*	
PH	5.64	188	24.0	16.0	162	76.0	11.1	187	53.5	
EH	8.24	100	19.8	13.0	101	35.5	13.8	101	38.6	
CS	+26.8	-	-	+19.2	-	-	+14.6	-	-	
EL	7.63	15.2	2.73	13.1	13.4	4.72	11.8	13.7	4.24	
ED	9.74	4.03	0.98	14.1	3.59	1.40	12.0	3.85	1.22	
EY	39.1	2.32	8.30	46.9	0.64	9.78	45.3	1.01	9.83	
E4	32.0	3.66	6.50	38.0	2.55	8.07	37.1	2.93	8.45	
G4	33.0	2.90	5.64	41.0	1.55	7.13	39.9	1.91	7.53	

Id% - Expressed in percent of the non-inbred population mean; all values of Id are negative, except for CS because the use of an inverse scale.

Estimates of the inbreeding depression (Id) in Table 7 showed that the population CRE-01 was the less depressive among the three semi-exotic populations for all traits. In fact, from the three base populations used for the incorporation of exotic germplasm, CRE-01 was the only one that originated from commercial hybrid. Lima et al. (1984) also reported that the less depressive material among 32 populations were those that had already submitted to some degree of inbreeding, as was the case of hybrids derived from from inbred lines. The same point had been already reinforced by Miranda Filho and Viégas (1987). Farias Neto and Miranda Filho (2000) reported on inbreeding depression for plant and ear height and for tassel traits (weight, length, and branch number) in two subpopulations divergently selected for tassel size; except for plant height, depression rates were higher for the subpopulation selected for smaller tassel size. For yield traits (ear weight or grain weight), several reports observed inbreeding depression in the range of 37.5 to 68.0% (Mota, 1974; Vianna et al., 1982; Gama et al., 1985; Miranda Filho and Meirelles, 1988; Nass and Miranda Filho, 1995; Packer, 1998; Simon et al., 2004). Lima et al. (1982) introduced two sources of maize germplasm for downy mildew resistance and found inbreeding depression of 43.0% in both populations, Suwan-DMR and

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Thai Composite-DMR. Lima et al. (1984) studied 32 Brazilian populations with 50% expected homozygosity and found inbreeding depression varying from 27.0 to 57.9% for grain yield, 7.5 to 20.3% for plant height and 6.9 to 27.7% for ear height. Maldonado and Miranda Filho (2002) studied the effect of inbreeding in subpopulations of small effective size in four generations (F = 0.125, 0.234, 0.291, and 0.379; F is the Wright's coefficient of inbreeding in the sequence of generations) of three populations; for grain yield, the inbreeding depression adjusted to 50% homozygosity (expected level for S₁ progenies) varied from 18.1 to 24.8% when considering all populations and generations, which were below the results reported by Lima et al. (1984), probably because the lower exposure of deleterious recessive genes of large effects, under a less severe inbreeding system.

Results of the present study (Table 7) showed a consistent pattern of inbreeding depression for yield traits among the three populations; in fact, the higher estimates of Id were for EY in the sequence CRE-01 < CRE-03 \simeq CRE-02 with estimates of [39.1, 46.9, 45.3%], respectively. The traits E4 and G4 followed the same relative pattern for Id estimates, which were [32.0, 38.0, 37.1%] for E4 and [33.0, 41.0, 39.9%] for G4. Inbreeding depression for vield was considered to be high as compared to results from other studies, thus limiting the use of the semiexotic populations for the development of highly inbred lines for use in hybrid crosses; in such cases, the use of recurrent selection under inbreeding may improve the potencial of the base population as source of inbred lines (Hallauer, 1980; Miranda Filho, 1981). For plant and ear traits (PH, EH, EL, and ED) the pattern for Id variation was very similar, in the sequence CRE-01 < CRE-03 < CRE-02 (except for EH, which had very close values for CRE-03 and CRE-02). For these traits, estimates of Id varied from 5.6 to 16.0%, which agree with the ranges in other reports. Id estimates for corn stunt resistance were positive, because the scale used was inverse for the expression of the trait that is inverse for the expression of the trait; i.e., larger notes in the scale (1-resistant to 5 susceptible) indicated higher susceptibility. In this sense, the expression of Id [+26.8, +19.2, +14.6] or [CRE-01> CRE-02> CRE-03] indicated a higher increase in susceptibility (or higher decrease in resistance) in the population CRE-01. Then, considering the resistance level the appropriate sequence should be CRE-03 > CRE-02 > CRE-01. Despite the difference for the expression of corn stunt complex, all the three populations showed favorable levels for this trait, indicating that the original introduction of exotic germplasm into local populations was effective towards the development of populations with acceptable pattern of resistance.

Analyses of variance of inbred families for eight traits are shown (Table 9). The mean squares for the variation among families showed the same pattern of variation (CRE-01 < CRE-02 < CRE-03) for the three yield traits, and showed lower variability for the less depressive population (CRE-01). The same trend was observed for the estimates of the variance among S_1 families and for the broad sense coefficient of heritability (h_f^2) for EY (Table 10). The estimates of h_f^2 for E4 and G4 changed the order slightly, but the nine estimates were in the interval 0.54 < h_f^2 < 0.83.

Based on our results, the semiexotic condition of the studied populations all showed acceptable levels of productivity and excellent levels of variability for yield and other important traits, enabling their use in recurrent selection programs. The level of resistance to corn stunt complex which motivated the introduction of exotic germplasm revealed the effectiveness of this strategy and indicated that these traits will be maintained or even enhanced in the new populations. The negative effects of inbreeding (inbreeding depression) were considered higher than acceptable, particularly in populations with a broader genetic base (CRE-02 and CRE-03), suggesting that at least one cycle of recurrent selection under inbreeding (e.g., se-

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lection of S_1 families) should be conducted before developing inbred lines for use in hybrid combinations.

Table 9. Mean squares in the analysis of variance of eight quantitative traits in selfed (S_1) families of three semiexotic populations under the model of completely randomized blocks.

Source	PH	EH	EL	ED ^[1]	RS ^[4]	EY ^[5]	E4 ^[5]	G4 ^[5]
			Р	opulation CRE-0	1			
Blocks	200.85	17.83	1.3283	0.3255	6.2000	1.9	2.70	18.80
Families	573.44	285.14	2.9992	21.782	9.8677	2609.2	123.01	95.69
Error	179.49	150.72	0.9517	3.3711	6.0085	840.3	47.05	34.71
			Р	opulation CRE-0	2			
Blocks	846.68	337.51	0.9408	1.0547	0.2733	14.8	12.14	94.52
Families	787.30	536.12	2.9031	16.521	5.5525	3025.4	152.92	114.95
Error	138.05	131.42	1.6391	5.5568	4.7833	656.2	66.96	52.13
			Р	opulation CRE-0	3			
Blocks	1267.5	515.64	3.3963	5.2083	9.1199	8492.4	57.41	62.11
Families	796.30	446.54	3.3963	18.517	8.9440	3977.7	192.63	128.17
Error	127.59	120.25	0.9759	4.6787	3.5402	686.7	61.03	54.78

^[1], ^[4], ^[5]: Mean squares multiplied by 10^2 , 10^{-2} , 10^{-4} , respectively.

Traits			Parameters estimates	5		
	$\hat{\sigma}_{ m f}^2$	$\hat{\sigma}^2$	h_{f}^{2}	CV%	CVg%	θ
			Population CRE-01			
PH	196.97	179.49	0.687	6.681	6.999	1.048
EH	67.210	150.72	0.471	11.14	7.438	0.668
CS	1.9296	6.0085	0.391	31.90	21.49	0.674
EL	1.0238	0.9517	0.683	5.899	6.118	1.037
ED	9.2055	3.3711	0.845	4.062	6.713	1.652
EY	8.8444	8.4033	0.678	16.61	17.04	1.026
E4	3.7979	4.7047	0.618	12.41	11.15	0.898
G4	3.0492	3.4709	0.637	12.88	12.07	0.937
			Population CRE-02			
PH	324.62	138.05	0.825	5.876	9.011	1.533
EH	202.35	131.42	0.755	9.621	11.94	1.241
CS	0.3846	4.7833	0.139	28.37	11.22	0.396
EL	0.6320	1.6391	0.435	8.142	5.056	0.621
ED	5.4820	5.5568	0.664	5.494	5.457	0.993
EY	11.846	6.5615	0.783	17.16	23.06	1.344
E4	4.2979	6.6964	0.562	15.54	12.45	0.801
G4	3.1411	5.2129	0.547	17.64	13.69	0.776
			Population CRE-03			
PH	334.35	127.59	0.840	5.263	8.520	1.619
EH	163.15	120.25	0.731	9.088	10.59	1.165
CS	2.7019	3.5402	0.604	26.22	27.74	1.058
EL	1.2102	0.9759	0.713	6.255	6.965	1.114
ED	6.9191	4.6787	0.747	4.847	5.895	1.216
EY	16.455	6.8673	0.827	16.38	25.36	1.548
E4	6.5800	6.1031	0.683	13.64	14.17	1.038
G4	3.6697	5.4777	0.573	16.30	13.34	0.818

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