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Genetic evaluation of tropical popcorn inbred lines using BLUP

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Abstract

The objectives were to identify superior inbred lines and single-crosses, predict untested hybrids and analyze the importance of pedigree information and the prediction efficiency. We analyzed 24 experiments in the incomplete block design, including 20 tests of hybrids and 4 tests of inbred lines. The expansion volume (EV) and grain yield were measured in each plot. The analyses were made using ASReml software. Analyses of the general combining ability (GCA) effects and the additive genetic values of the inbred lines, and the genotypic values of the hybrids in relation to EV showed that no inbred line selection strategy resulted in a set of clearly superior or inferior inbred lines and hybrids. Including pedigree information resulted in an increase in the variance of the GCA effects in relation to EV and a reduction in relation to yield. For both traits, there was an increase in the variance of the specific combining ability effects. The cross-validation study showed that the prediction of the genotypic value of a hybrid based only on the GCA effects is not efficient in the presence of dominance. With dominance, the efficiency of the hybrid prediction depends on the degree of relationship among the inbred lines.

Keywords: combining ability analysis, prediction of single-cross hybrids, cross-validation

Introduction

Diallel analysis is the quantitative genetics methodology most commonly used by plant breeders. This is due to the multiple uses and the diversity of inferences that it provides, relative to the genetic control of quantitative traits and the identification of pure/inbred lines, clones and superior open pollination populations, for the development of new pure lines and clones, hybrids and populations for intra- and interpopulational breeding. The theoretical aspects and methodologies of diallel analysis have been presented by Hayman (1954), Griffing (1956), Kempthorne and Curnow (1961) and Gardner and Eberhart (1966). Griffing's combining ability analysis stands out as the most commonly used because the genetic model is simple, the interpretation is easy, it is applicable to all animal and plant species, and it theoretically results in the same inferences as the heterosis analysis proposed by Gardner and Eberhart (Viana, 2000). Although Hayman's methodology is certainly the most informative for the study of genetic control of quantitative traits, it is less frequently used due to its restricted application to pure/inbred lines. The method of Kempthorne and Curnow aimed to reduce the number of hybrids to be assessed, and it is also a widely applicable method of combining ability analysis.

The merit of diallel analysis became even greater with the use of the Best Linear Unbiased Prediction (BLUP), proposed by Henderson (1974), because pedigree information can be included and untested single-cross hybrids can be predicted in the presence of dominant gene action. Moreover, variance component estimation in unbalanced experiments using restricted/residual maximum likelihood estimation, proposed by Patterson and Thompson (1971), offers greater efficiency than the least squares process (Piepho and Möhring, 2006).

The BLUP methodology is considered the best technique for animal and forestry genetic evaluation, and it is regularly used in annual crop breeding, as demonstrated in the revision by Piepho et al (2008). Its initial application to annual crops followed the prediction of the performance of untested maize single-crosses from diallel analysis. In a series of papers Bernardo (1994, 1995, 1996a, b, c) demonstrated that BLUP is an efficient prediction methodology, whether or not the pedigree information is obtained from molecular markers. Its results, however, were not corroborated by Reis et al (2005), who used BLUP/EM (Expectation Maximization) in partial circulant diallel analysis with maize S1 families. These authors reported lower efficiency in prediction based only on general combining ability effects. It is worth pointing out, however, that BLUP was superior to least squares analysis. In a study on the efficiency of six methods of predicting single-cross maize hybrids, Schrag et al (2009) used phenotypic and pedigree information as well as molecular marker data from a factorial cross (partial diallel) involving dent and flint lines. Based on a cross-validation analysis, they dem-

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onstrated that on the basis of marker assayed inbred lines, the performance of maize hybrids can be predicted efficiently for heterotic and non-heterotic traits for crosses in which one or even both inbred parents have not been evaluated.

Diallel analysis provided additional information for the improvement of maize regardless of whether it incorporated BLUP methodology. For the study of inheritance of maize seedling resistance to pathogens causing lodging, Moreno-González et al (2004) considered the Analysis III of Gardner and Eberhart, Griffing's Models 2 and 4 and an additive model for inbred lines alone, and two statistical approaches: BLUP and ANOVA. They concluded that the methods produced equivalent GCA effects and that the specific combining ability (SCA) effects were important in determining the resistance of the hybrids. From two diallel analyses with popcorn (one with populations and the other with inbred lines), Larish And Brewbaker (1999) found negative heterosis in relation to expansion volume (EV) and positive heterosis for grain yield. The average heterosis in relation to the EV was equivalent in both diallel analyses, but the heterosis for yield in the hybrids of inbred lines was almost twice that in the interpopulation hybrids.

The objectives of the present study were to identify superior inbred lines and single-crosses, predict untested hybrids and analyze the importance of pedigree information and the prediction efficiency.

Materials and Methods

Materials

Eighteen inbred lines from the Beija-Flor population and 29 from the Viçosa population were assessed. As in Brazil there is not a definition of heterotic groups of popcorn, we cannot state that the populations represent different heterotic pools. Both are similar in cycle, vegetative development, shape of grain (pearl), quality (expansion volume around 25 ml/g) and grain yield, although Beija-Flor shows grain color variation (white to purple). Viçosa has yellow grains. In this first stage of evaluation of specific combining ability, only intrapopulation crosses were performed. To minimize the number of hybrids to be assessed, two diallels were carried out with the Beija-Flor inbred lines: one with seven and the other with eleven parents in the 2003/2004 and 2004/2005 growing seasons. Five diallels were conducted with the Viçosa inbred lines: one with eight parents and four with five parents, repeated in the 2006/2007 and 2007/2008 growing seasons, respectively.

The Beija-Flor inbred lines were developed by among and within selection (Viana, 2009). Three lines from the first group of inbred lines were sampled randomly among the 17 selected in two of the eight strategies assessed by Viana (2009) (03-583, 03-548 and 03-566), two were sampled randomly among the 13 selected in one of the strategies (03-597 and 03-701) and two were sampled randomly among those not selected in any of the strategies (03-693 and 03-594), but obtained from families and plants with high expansion volume (EV) and good genealogy. The inbred lines in the second group of the Beija-Flor population were also sampled randomly among the other 14 selected in at least two strategies (03-546, 03-604, 03-579, 03-628, 03-589, 03-637, 03-690, 03-602, 03-608, 03-580 and 03-630). The pedigree showed that there was a relationship between only two lines of the second group and among four lines of the second group and three lines of the first group. Of the possible 153 hybrids, only five would be from related inbred lines. Thus, in the case of dominance, only a small part of the 77 untested hybrids could be predicted.

Regarding the Viçosa inbred lines, in one of the groups of five parents the inbreds (05-284, 05-301, 05-351, 05-406 and 05-447) were chosen among the 20 identified as superior by the systematic use of mass selection based on EV. In another group of parents, the five inbreds (05-382, 05-383, 05-388, 05-423 and 05-456) were chosen among the 20 obtained by among and within selection based on EV. In a third group, the 5 inbreds (05-299, 05-328, 05-393, 05-402 and 05-462) were chosen among the 20 developed by combined selection of families followed by within family selection, both based on EV. In the fourth group of five parents, the inbreds (05-374, 05-379, 05-380, 05-466 and 05-477) were chosen among the 20 superior inbred lines derived from one hundred S3 families with best performance for EV in crossing with the Beija-Flor tester. The eight inbred lines of the fifth group (05-274, 05-345, 05-356, 05-381, 05-391, 05-408, 05-425 and 05-426) were chosen because they were identified as superior in at least three of the four selective processes systematically employed by Arnhold et al (2009), described previously. The pedigree analysis revealed two groups of five unrelated parents, two groups of five parents with only two related inbred lines, a relationship among three pairs of inbred lines of the largest group and parentage among inbred lines of the different groups. Of the 378 possible hybrids, only 39 would be from related inbred lines. Thus, in the case of dominance, only part of the 310 untested hybrids could be predicted.

Ten experiments were carried out in the 2004/2005 to 2006/2007 growing seasons with hybrids from Beija-Flor inbred lines in an incomplete block design with a plot of three or four rows of 5 m spaced at 0.9 m. The number of replications per environment and per hybrid ranged from one to five. Four experiments included only the 21 hybrids of the seven inbred lines of the first diallel, four included 28 to 53 hybrids of the 11 inbred lines of the second diallel and two included 12 hybrids of the first diallel and 15 of the second diallel. All the experiments had two common checks, the IAC112 single-cross, developed by the Agronomic Institute of Campinas, and the three-way cross Zélia from Pioneer. The experiments were carried out in the Brazilian cities of Capinópolis, Minas Gerais (MG); Governador Valadares, MG; and Maringá, Paraná (PR), in experimental stations belonging to the Federal University of Viçosa (UFV), Vale do Rio Doce University (UNIVALE) and Maringá State University (UEM).

The hybrids from inbred lines of the Viçosa population were assessed in three growing seasons (2007/2008 to 2009/2010) in Capinópolis, MG; Maringá, PR; Ponte Nova, MG; and Coimbra, MG, at experimental stations belonging to UFV and UEM in a total of ten experiments. The design was incomplete block, with a plot of two or three rows of 5 m spaced at 0.9 m. The number of replications per environment and per hybrid ranged from one to four. The checks were IAC112, Zélia and the three-way cross Jade, also from Pioneer, in all the experiments. The number of experimental hybrids in each test ranged from 42 to 64.

The inbred lines of the two populations were also assessed experimentally when the hybrid seeds were obtained. The lines were planted in pairs to facilitate the crosses in two or three periods over two years in 5 m rows (plot) spaced at 0.9 m. In all inbred line and hybrid experiments, final stand (covariate), grain yield, grain moisture (covariate) and EV were measured in each plot. In the inbred line quality assessment, a hot air popcorn machine (1,200 W) was used with 30 g samples. In the experiments with the hybrids, the EV was assessed in a 27l microwave oven (900 W) using 30 g samples and in the Metric Weight Volume Tester (MWVT) using 250 g samples. The yield was corrected in all analyses for the ideal stand per row (25 plants in the inbred line tests and 30 plants in the hybrid tests) and for 14.5% moisture.

Methods

The genotypic value of a single-cross hybrid is (Griffing, 1956)

$$G_{ij} = M_H + g_i + g_j + s_{ij}$$

where M_H is the mean of the hybrids, g_i and g_j are the general combining ability effects (GCA) of the inbred lines and s_{ij} is the specific combining ability effect (SCA).

In matrix notation, assuming the effects of environment and block within environment as fixed and the genetic effects and the effects of GCA x environment and SCA x environment interaction as random we have

$$y = X\beta + Z_1 g + Z_2 s + Z_3 u_1 + Z_4 u_2 + \varepsilon$$

where y is the observation vector, X, Z_1, Z_2, Z_3 and Z_4 are the incidence matrices, ß is the fixed effects vector, g and s are the vectors of the general and specific combining ability effects, respectively, u_1 and u_2 are the vectors of the effects of GCA x environment and SCA x environment interaction, respectively, and ε is the residuals vector. The checks were inserted in the pedigree as unrelated individuals. Because they stemmed from populations different from the inbred lines, the model also included fixed effects of population and population x environment.

Assuming $Var(g_i) = \sigma_g^2$ and $Var(s_{ij}) = \sigma_s^2$ then

$$Cov(g_i, g_j) = \mathrm{P}\begin{pmatrix}\text{inbred lines i and j have geno-} \\ \text{types identical by descent}\end{pmatrix} .\sigma_g^2$$

$$= \mathrm{P}(\text{gene of inbred line i} \equiv \text{gene of inbred line j}).\sigma_g^2 = r_{ij}\sigma_g^2$$

$$Cov(s_{ij}, s_{kl}) = \mathrm{P}\begin{pmatrix}\text{hybrids have genotypes} \\ \text{identical by descent}\end{pmatrix} .\sigma_s^2$$

$$= u_{(ij)(kl)}\sigma_s^2$$

$$= [r_{ik}r_{jl} + r_{il}r_{jk} - r_{ij}r_{kl}.(1/4)(r_{ik} + r_{jl} + r_{il} + r_{jk})]\sigma_s^2$$

where r_{ij} is the coefficient of relationship among the lines i and j, and $u_{(ij)(kl)}$ is the probability of the hybrids of lines i and j, and k and l have genotypes identical by descent (Mrode, 2005). Then

$$Var(g) = \frac{1}{2}\sigma_g^2 \begin{bmatrix} 2r_{11} & \cdots & 2r_{1n} \\ \cdots & \cdots & \cdots \\ 2r_{1n} & \cdots & 2r_{nn} \end{bmatrix} = \frac{1}{2}\sigma_g^2 A$$

$$Var(s) = \sigma_s^2 \begin{bmatrix} 1 & \cdots & u_{1t} \\ \cdots & \cdots & \cdots \\ u_{1t} & \cdots & 1 \end{bmatrix} = \sigma_s^2 D$$

where A and D are the additive and dominance relationship matrices (Mrode, 2005), n is the number of parents and t = n(n – 1)/2 is the number of hybrids. For the interactions GCA x environment and SCA x environment we assumed

$$\mathrm{Var}(\mathrm{u}_1) = \sigma_{gxe}^2 I \text{ and } \mathrm{Var}(\mathrm{u}_2) = \sigma_{sxe}^2 \mathrm{I}.$$

The accuracies of the predictions of the general and specific combining ability effects are

$$r_{g_i\tilde{g}_i} = \sqrt{1-\left(PEV_{\tilde{g}} / \tilde{\sigma}_g^2\right)} \text{ and } r_{s_{ij}\tilde{s}_{ij}} = \sqrt{1-\left(PEV_{\tilde{s}} / \tilde{\sigma}_s^2\right)}$$

where PEV is the prediction error variance (Mrode, 2005).

The inbred line tests were analyzed following Viana et al (2011). The study of prediction efficiency considered the diallel of seven non-related Beija-Flor inbreds, a diallel of five non-related Viçosa inbreds and the diallel of eight Viçosa inbreds, among which there were three pairs of related lines, using the delete-one cross-validation procedure of Bernardo (1996a). For a diallel with N hybrids, N analyses are made by removing one hybrid at a time. With dominance, the prediction of the SCA effect of the hybrid removed depends on the pedigree information. All the analyses were performed by ASReml v3.00 software (Gilmour et al, 2009) (see code in Appendix). It is important to point out that when associating the general combining ability to the pedigree (by the !p qualifier) ASReml calculate a dominance relationship matrix for the specific combining ability (gm.gf interaction).

Results

Beija-Flor inbred lines and single-crosses

The likelihood ratio tests show variability for EV and grain yield (Table 1). The variance of general combining ability was systematically lower than the variance of the specific combining ability. Dominance was observed in relation to EV evaluated in microwave and MWVT and grain yield. A GCA x environment interaction was also observed in relation to the two measures of quality and grain yield, but SCA x environment interaction was only observed in relation to the two quality measures.

The variability of quality was certainly less in the group of seven inbred lines because the likelihood ratio tests in the individual analyses were generally not significant. No test was significant regarding the EV assessed in a microwave. Regarding EV measured in the MWVT, only one likelihood ratio test was significant. For EV assessed in a microwave, trials involving only hybrids of inbred lines from the other group systematically showed a significant LRT, with one exception. For the EV measured in the MWVT, the likelihood ratio test was significant in only three of the environments. The variability for grain yield should be greater in the group of seven inbred lines because the likelihood ratio test was significant in all individual analyses. In the experiments with hybrids from inbred lines of the second group, two-thirds of the likelihood ratio tests were significant.

Analysis of the GCA effects showed a correlation of 0.73 among the predictions for the two quality measurements and correlations of -0.12 and -0.19 among the predictions for the quality measurements and grain yield, respectively. The inbred lines with the highest number of favorable genes for quality were 03-637, 03-604 and 03-594. Because only a single-specific combining ability effect of an inbred line (03-546) with itself was obtained (0.5575 for EV assessed in a microwave, -0.0993 for EV measured in the MWVT and -45.5 for yield), no inference can be made regarding gene differences among the inbreds because the dominance direction is not known (Viana 2000). Presuming negative unidirectional dominance for EV (Larish and Brewbaker, 1999), the most divergent inbred lines were 03-628 and 03-589, 03-602 and 03-608, and 03-690 and 03-630 for EV assessed in a microwave, and 03-628 and 03-589, 03-701 and 03-628, and 03-628 and 03-546 for EV accessed in the MWVT. For yield, the superior inbred lines were 03-602, 03-589 and 03-701. Presuming positive unidirectional dominance for yield (Larish and Brewbaker, 1999), the most divergent inbred lines were 03-566 and 03-594, 03-693 and 03-594, and 03-693 and 03-583.

In relation to non-assessed hybrid prediction, 31 of the 79 (39.2%) untested hybrids could be predicted in the presence of dominance. The microwave EV mean of the 10 top quality hybrids was 31.6 ml/g, and the maximum EV was 32.0 ml/g. Only one of these was not assessed, and seven were obtained from at least one of the three inbred lines identified as superior relative to quality. Regarding the EV accessed in the MWVT, the mean of the 10 best hybrids was 29.4 ml/g, and the maximum was 29.7 ml/g. Three hybrids were not assessed and six were obtained from at least one of the inbred lines identified as superior in quality. The average grain yield of the 10 top hybrids was 2,363.5 kg/ha. The best hybrid produced 2,384.7 kg/ha. Out of these 10 hybrids, only one was not assessed and five others were obtained from inbred lines identified as superior. Among the 10 top yielding hybrids were the three derived from the most divergent inbreds. It should be emphasized that of the 20 top EV and/or grain yield hybrids, 17 were obtained from at least one line identified as superior. The EV and grain yield means of the commercial checks ranged from 32.5 to 34.5 ml/g for EV assessed in a microwave, between 30.2 and 31.1 for EV assessed in the MWVT and between 2,432.6 and 2,659.2 kg/ha.

The analysis of the inbred lines showed genetic variability for quality and grain yield (Table 1), but the correlation between performance per se and in cross (between additive genetic value and general combining ability effect) was negative for the quality measurements (-0.18 and -0.22) and positive for yield (0.20), with reduced magnitude. For quality, this result may have been due in part to differences in the assessment equipment. The outstanding inbred lines for quality in the individual assessment were 03-583, 03-630 and 03-579. The inbreds with highest number of favorable genes for grain yield were 03-566, 03-579 and 03-701. Regarding quality, three lines (03-583, 03-693 and 03-604) presented positive additive genetic value and GCA effect, systematically showing a greater number of favorable genes than the mean number of the parents of the diallel (Viana, 2000). Five lines presented positive additive value and GCA effect for grain yield. The predicted EV and grain yield means of the inbred lines ranged from 31.4 to 36.7 ml/g and from 311.0 to 468.9 kg/ha, respectively.

Viçosa inbred lines and single-crosses

The inbreds of this population also presented reduced variability, mainly for yield (Table 1). In the joint analysis and in all environments where variability was verified for quality and yield, dominance was shown only for yield. Interaction between genetic and environmental effects was observed only for yield.

Because the correlation among the GCA effects for the quality means was positive (0.60), the lines 05-345, 05-402, 05-383, 05-456, 05-380 and 05-284 could be established as superior for quality. The correlations between the GCA effects for the quality measurements and grain yield were practically nil (-0.10 and 0.10). The inbred lines with the highest number of favorable genes for grain yield were 05-402, 05-345, 05-408, 05-379 and 05-406. Consequently, at least one top quality line and one top yielding line were obtained from each group, with one exception.

Table 1 - Parameters estimated by BLUP/REML, relative to EV (ml/g) measured in microwave or hot air popcorn machine (EV) and the MWVT (EV_{MWVT}), and yield (kg/ha).

Pop.	Source	EV		EV_{MWVT}		Yield	
		Var comp (95% conf int)	P value LRT	Var comp (95% conf int)	P value LRT	Var comp (95% conf int)	P value LRT
B.-Flor	GCA	0.2620 (0 – 0.9867)	$2.8E^{-21}$	0.0445 (0 – 0.3109)	$1.2E^{-10}$	4601.72 (0 - 16721.38)	$3.8E^{-17}$
	SCA	0.8965 (0.1654 – 1.6276)	$5.1E^{-11}$	0.1996 (0 – 0.4688)	$2.5E^{-05}$	6498.44 (0 – 12996.99)	0.0006
	GCAxEnv	0.4383 (0.0534 – 0.8232)	0.0040	0.2062 (0.0084 – 0.4040)	0.0113	9301.22 (2739.02 - 15863.42)	$3.2E^{-05}$
	SCAxEnv	2.1359 (0.6918 – 3.5800)	0.0010	1.0797 (0.2734 – 1.8860)	0.0034	4895.78 (0 - 18869.22)	0.4708
	Error	11.0804		7.4383		111076.00	
	Accuracy(g)	0.5425		0.3904		0.5474	
	Accuracy(s)	0.2828		-		0.1022	
	Additive	2.1312 (0 – 4.8000)	0.0064			1773.35 (0.06 - 3979.04)	0.0073
	Error	41.3949				37417.90	
	Accuracy(A)	0.3976				0.3967	
Viçosa	GCA	0.3712 (0.0577 – 0.6846)	$1.3E^{-07}$	0.2717 (0.0507 – 0.4928)	$2.6E^{-07}$	1060.29 (0 – 6801.29)	$1.5E^{-30}$
	SCA	0.0000		0.0000		10485.70 (4072.63 – 16898.76)	$3.5E^{-18}$
	GCAxEnv	0.0790 (0 – 0.1622)	0.0223	0.0581 (0.0022 – 0.1139)	0.0200	4726.41 (1780.95 – 7671.87)	$2.6E^{-05}$
	SCAxEnv	0.0000		0.0000		9823.75 (0 – 20503.21)	0.0544
	Error	8.9029		6.5242		194304.00	
	Accuracy(g)	0.8603		0.8642		0.3803	
	Accuracy(s)	-		-		0.5109	
	Additive	1.5338 (0 – 3.5100)	0.0420			12466.40 (2240.00 – 22700.00)	$1.3E^{-05}$
	Error	21.6066				288067.00	
	Accuracy(A)	0.3292				0.6850	

Moreover, the reduced prediction of SCA effects of a inbred line with itself (4/28) did not permit inferences to be established on the genotype differences among the inbreds. Assuming positive dominance for yield (Larish and Brewbaker, 1999), the most divergent lines were 05-393 and 05-402, 05-393 and 05-345, 05-388 and 05-423, 05-388 and 05-391, and 05-284 and 05-406. Three of these pairs were inbred lines from the same group. Because dominance was not shown for the quality measurements, all the untested hybrids could be predicted. Regarding yield, 43.6% of the untested hybrids were predicted (137/314). The EV mean of the 10 top quality hybrids was 35.0 and 32.7 ml/g, when the quality was assessed in a microwave and the MWVT, respectively. The maximum values were 35.1 and 32.8 ml/g. Only three of the 19 superior quality hybrids assessed in a microwave and the MWVT were not assessed. Of these 19, 14 derived from two of the superior quality inbreds, and the rest derived from a line identified as superior. The mean of the 10 top yielding hybrids was 3,063.3 kg/ha, and the maximum value was 3,171.4 kg/ha. Seven were obtained from one of the inbred lines identified as superior in yield, and three were not assessed. Four of these superior hybrids derived from the most divergent lines. The means of the commercial checks ranged from 34.9 to 37.4 ml/g for EV assessed in a microwave, between 32.4 and 34.3 ml/g for EV measured in the MWVT and from 2,630.8 to 2,739.8 kg/ha.

The inbred line analysis showed variability for quality and yield (Table 1). For quality, the correlations between the additive genetic values and the general combining ability for EV assessed in a microwave and the MWVT were 0.33 and 0.23, respectively, whereas 0.05 was obtained for grain yield. For quality, the increase in the correlations compared to that obtained with inbred lines of the Beija-Flor population may be attributed in part to the statistical evidence for absence of dominance. Because of the reduced correlations between the additive genetic value and the GCA effect, only two of the six lines with greater genetic additive value were among those superior in GCA (05-383 and 05-284). The other superior lines were 05-351, 05-356, 05-447 and 05-382, of which three were obtained by the systematic use of mass

Table 2 - Parameters estimated by BLUP/REML without pedigree information, relative to EV (ml/g) measured in microwave or hot air popcorn machine (EV) and the MWVT (EV_{MWVT}), and yield (kg/ha).

Pop.	Source	EV Var comp (95% conf int)	P value LRT	EV_{MWVT} Var comp (95% conf int)	P value LRT	Yield Var comp (95% conf int)	P value LRT
B.-Flor	GCA	0.2609 (0 – 0.9646)	2.7E^{-21}	0.1083 (0 – 0.3902)	1.2E^{-10}	6202.60 (0 – 18950.38)	8.1E^{-17}
	SCA	0.8595 (0.1338 – 1.5852)	7.4E^{-11}	0.1698 (0 – 0.4336)	2.4E^{-05}	5675.15 (0 – 11889.28)	0.0024
	GCAxEnv	0.4182 (0.0404 – 0.7960)	0.0058	0.1718 (0 – 0.3598)	0.0285	9373.07 (2781.46 – 15964.68)	0.0002
	SCAxEnv	2.1739 (0.7107 – 3.6370)	0.0008	1.1379 (0.3121 – 1.9638)	0.0024	4465.45 (0 – 18657.46)	0.5271
	Error	11.0682		7.4359		111222.00	
	Accuracy(g)	0.5102		0.5289		0.5770	
	Accuracy(s)	0.2307		-		-	
Viçosa	GCA	0.2312 (0.0326 – 0.4298)	1.3E^{-07}	0.1741 (0.0286 – 0.3196)	3.2E^{-08}	6456.78 (0 – 14142.57)	6.0E^{-30}
	SCA	0.0000		0.0000		6001.60 (1144.92 – 10858.28)	1.4E^{-06}
	GCAxEnv	0.0780 (0 – 0.1641)	0.0489	0.0800 (0.0206 – 0.1394)	0.0010	4135.91 (1431.01 – 6480.81)	0.0005
	SCAxEnv	0.0000		0.0000		9808.88 (0 – 21160.07)	0.0701
	Error	8.8930		6.4405		194519.00	
	Accuracy(g)	0.8051		0.8068		0.6939	
	Accuracy(s)	-		-		0.1330	

selection based on EV. Regarding yield, there was no coincidence among the five inbred lines superior in additive genetic value and GCA. The lines identified as superior were 05-423, 05-425, 05-391, 05-356 and 05-274. Furthermore, eight inbred lines systematically presented a positive GCA effect and additive genetic value, among which were the six lines identified as superior based on the GCA effects. The analysis of the GCA effects and the additive genetic values for yield showed that five inbreds systematically presented positive values, including three of the five identified as superior based on GCA. The predicted EV and yield means of the inbred lines ranged from 30.5 to 35.5 ml/g and from 1,206.6 to 1,642.7 kg/ha.

Discussion

Regarding the different processes of obtaining the inbred lines from the Viçosa population, the analysis of the GCA effects and the additive genetic values of the lines as well as the mean genotypic values of the hybrids in each group for EV showed that no selection strategy resulted in a set of clearly superior or inferior inbreds and single-crosses. Each process generally resulted in at least one top quality inbred line and hybrid groups with comparable EV means (approximately 34 and 32 ml/g for EV assessed in a microwave and the MWVT, with a maximum difference of 0.6 mL/g in favor of the hybrids from the lines obtained using among and within selection). When the means of the GCA effects and the additive genetic values were analyzed for each group of inbred lines and for the quality measurements, greater mean GCA was observed in the group of lines obtained by among and within selection, and greater mean additive genetic value was observed for the group of lines obtained by mass selection. Arnhold et al (2009), based on least-squares estimation, assessed inbred families from the Viçosa population and concluded that the best strategy to obtain inbred lines superior for EV was combined selection, followed by among and within selection and, finally, mass selection. The maximum differences among the means for the families selected by the different strategies from S1 to S4 ranged from 0.7 to 2.7 ml/g.

For yield, a secondary trait in the inbred line selection process, most of the lines identified as superior based on additive genetic values belonged to the group consisting of lines superior in at least two strategies. Considering the GCA effects, at least one superior line was also obtained in each group, except for the group obtained using among and within selection. Regarding the genotypic means of the hybrid groups, a difference was observed among the hybrids from inbreds obtained using among and within selection (2,579 kg/ha) and the hybrids of the other groups (2,831 to 2,898 kg/ha). The group of inbred lines with the highest mean of the GCA effects was obtained by combined selection.

Including pedigree information resulted in an increase in the magnitude of the variance of the GCA effects relative to EV, with one exception, and a reduction in relation to grain yield (Tables 1 and 2). The changes were 60.5% and 56.1% for EV in the Viçosa population and -25.8% and -83.6% for the yield in the two populations. The variance of the SCA effects also increased from 4.3% and 17.5% for EV and from 14.5% to 74.7% for yield. In general, the variance of the SCA effects was greater than the variance of the GCA effects regardless of the pedigree information. Including pedigree information increased the ratio of these variances. With one exception, an increase was observed in the accuracy of the GCA effects for EV, but a decrease was noted in relation to yield. The changes were generally of small magnitude (less than 10% in absolute value). For EV and yield, the inclusion of the pedigree information increased the accuracy of the SCA effects. However, the predictions of the GCA and SCA effects and the genotypic means of the hybrids, were positively correlated for the analyses with and without pedigree information, with magnitudes in the range of 0.82 to practically 1 (Table 3). This should not be understood as equivalence of the two analyses because, without pedigree information, untested hybrids cannot be predicted when taking into account the effects of SCA in the case of dominance.

In the work of Schrag et al (2009), the ratio of SCA variance to GCA variance (average of dent and flint GCA variance components) was 0.07 for yield and 0.04 for dry matter. Investigating how different depths of pedigree and amounts of data affect the reliability of estimating breeding values of sugarcane parents, Atkin et al (2009) verified an increment in the accuracy of estimating additive variance components and breeding values as more pedigree information and historical data were included in analyses. Bernardo (1996b) concluded that BLUP is robust when estimates of genetic relationship among inbreds are erroneous. The deviations between erroneous and calculated Malecot's coefficients of coancestry ranged from near zero to approximately 0.30, but the correlations between predicted and observed single-cross performance were not affected by the relatively large errors.

The study of cross-validation showed that prediction of the genotypic value of a hybrid based only on the GCA effects was not efficient in the presence of dominance. Regarding the diallels of seven Beija-Flor and five Viçosa unrelated inbred lines, no SCA effect was predicted. Because the EV and grain yield analyses for the Beija-Flor inbred lines and the yield analysis for the Viçosa inbreds showed dominance, the correlation among the genotypic values predicted based only on the GCA effects and those based on the GCA and the SCA effects were negative or positive and of low magnitude, ranging from -0.22 to 0.24 (Table 3). There was greater efficiency in the absence of dominance. The values of the correlations for the quality measurements in the diallel analyses of the Viçosa inbred lines in which dominance was not shown were generally above 0.88. In the cross-validation study with the diallel of related Viçosa inbred lines, the analysis for yield of the 14 predicted SCA effects (50%) showed that nine were correctly predicted in terms of magnitude and sign. Consequently, the correlation among the genotypic means of the nine hybrids predicted in the cross-validation study and in the analysis with pedigree information

Table 3 – Correlations among predictions of GCA, SCA and hybrid genotypic means, from BLUP analyses with and without pedigree information, and among hybrid genotypic means from the cross-validation analyses, relative to EV (ml/g) measured in microwave (EV) and the MWVT (EV_{MWVT}), and yield (kg/ha)

Population	Prediction	EV	EV_{MWVT}	Yield
Beija-Flor	GCA	0.9340	0.8940	0.8318
	SCA	0.9951	0.9940	0.9843
	Gen mean	0.9683	0.9404	0.9538
	Gen mean[1]	0.1028	-0.1983	0.2444
Viçosa	GCA	0.9547	0.9765	0.8167
	SCA	-	-	0.9291
	Gen mean	0.9567	0.9767	0.9852
	Gen mean[2]	0.6200	0.9600	-0.2200
	Gen mean[3]	0.9247	0.8885	0.8270

[1]diallel with 7 non related inbred lines; [2]diallel with 5 non related inbred lines; [3]diallel with 8 inbred lines, with three pairs of related inbred lines

was approximately 0.83. Therefore, because the correlation was dependent on the degree of relationship among the inbreds, the hybrid prediction was not equally efficient in the presence of dominance. In this study, the prediction was effective for about 60% of the hybrids predicted.

Predicting maize single-crosses from groups of predictor hybrids, Bernardo (1994) estimated pooled correlations between predicted and observed grain yield ranging from 0.65 to 0.80. Values slightly higher were produced when dominance variance was included in the model or when the additive relationship matrix was determined from molecular data rather than pedigree data. Also using predictor hybrids, Bernardo (1995) obtained, for unbalanced yield data, correlations ranging from 0.58 to 0.75. The correlations relative to missing and predictor hybrids with no inbred lines in common ranged from 0.39 to 0.49. He also noted ineffective prediction of specific combining ability, which he attributed to the reduced magnitude of the SCA variance, and equivalence between the additive-dominant model and the models with epistasis. Based on a delete-one cross-validation procedure, Bernardo (1996a) verified correlations between predicted and observed yield performances ranging from 0.43 to 0.76. In another cross-validation study with maize, Bernardo (1996c) verified that the correlations between predicted and observed performances were highest when testcross data for both parents of a single-cross were utilized. Except for moisture, these correlations were severely reduced to less than 0.50 when both inbreds were assumed untested. Predicting yields of maize hybrids from S1 families, Reis et al (2005) obtained average correlations between predicted and observed performances in the range of 0.10 to 0.41 based on GCA effects from ordinary least square and BLUP approaches. The values were systematically lower in the least square analysis. The efficiency of the predictions was even lower when the number of crosses of each parent decreased from five to two.

The lower prediction efficiency in our work, compared to the results obtained by Bernardo (1994, 1995, 1996a, b, c) and Schrag et al (2009), is due to the reduced number of related inbred lines. The average coefficients of coancestry for the inbred lines of Beija-Flor and Viçosa are 0.0266 and 0.0592. In the study of Bernardo (1996a), the values for each heterotic group ranged from 0.108 to 0.442.

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Appendix

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BLUP analysis, diallel with 18 inbred lines of Beija-Flor (title line)
 gm 123 !p # gca effects
 gf 123 !p # gca effects
 env 10 # environment
 blo 5 # block
 pop 2 # population
 s # average stand/row - 30
 m # moisture - 14.5
 y # yield
 evm # expansion volume assessed in microwave
 evmwvt # expansion volume assessed in the MWVT
ped.txt # pedigree file
data.asd # data file
#!filter env !select 1 # for individual analysis
!ddf # correction of df by the Kenward-Roger method
!continue # more than 10 iterations (default), if necessary
!maxit 30 # maximum number of iterations

#individual analyses
#evm ~ mu blo pop !r gm and(gf) gm.gf !f mv # mv estimate missing values
#evmwvt ~ mu blo pop !r gm and(gf) gm.gf !f mv
#y ~ mu blo pop s m !r gm and(gf) gm.gf !f mv

#joint analyses
#evm ~ mu env env.blo pop env.pop !r gm and(gf) gm.gf -env.gf env.gm
and(env.gf) env.gm.gf !f mv
#evmwvt ~ mu env env.blo pop env.pop !r gm and(gf) gm.gf -env.gf env.gm
and(env.gf) env.gm.gf !f mv
y ~ mu env env.blo pop env.pop s m !r gm and(gf) gm.gf -env.gf env.gm
and(env.gf) env.gm.gf !f mv

#fitting the first order autoregressive correlation model
1 1 0 # one R structure and no definition for the G structures
0 0 ar1 0.3 # initial value of the correlation
```

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