

An accurate prediction of maize crosses using diallel analysis and best linear unbiased predictor (BLUP)

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ABSTRACT

A major obstacle in corn (*Zea mays* L.) breeding programs is how to obtain strains which, when combined, ensure increased productivity in all crop characteristics. Therefore, the objective of this study was to evaluate the prediction efficiency of hybrid maize using diallel analysis and the best linear unbiased predictor (BLUP). Eight synthetic varieties were sown in a diallel scheme and the hybrid and their parents were then evaluated in three separate environments; both combining ability and predicted breeding values (BLUPs) were estimated. Correlations between the BLUP and combining abilities were also obtained. Combining ability analysis revealed that both additive and non-additive types of gene action were important in the studied traits. There was a moderate to high correlation between the mean square of the combining ability and the predicted breeding values. This shows that BLUP can be used to select the best parents for different traits, especially for ear height and ear position, which had the highest correlations. The parent VAR-01 had significant general combining ability (GCA) values, and it can be used in crosses to reduce plant height, ear height, and ear position while the parent VAR-06 can participate in crosses to increase ear height, plant height, and ear position. The result obtained for combining ability was moderately to highly consistent with BLUP results, but selection must be carefully undertaken.

Key words: GCA, mixed models, SCA, *Zea mays*.

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INTRODUCTION

A major difficulty in corn (*Zea mays* L.) breeding programs is finding strains which, when combined, ensure high gains in all crop characteristics, as well as reduced ability to evaluate large numbers of field crosses (Guo et al., 2013). Furthermore, the availability of variability is critical to successful selection.

There are several methodologies for selecting lines with high favorable allele frequency, for example, reciprocal recurrent selection (Faria et al., 2009). These methods require evaluating lines in multiple cycles of hybrid combinations, which is a slow and costly process. The diallel cross method is used to facilitate genotype selection, especially because of the crossing combining ability of these genotypes. In these crosses, a mathematical model is used to select parents and determine heterotic groups (Griffing, 1956). Even though genetic factors can be considered random, they are usually included in the fixed-effects coincidence matrix; this therefore excludes the use of mixed models, which allow, for example, unbalanced data analysis (Henderson, 1975).

The mixed model methodology has some advantages, such as predicting unrealized crosses (Cruz Baldissera et al., 2012; Gowda et al., 2013a), obtaining unbiased linear predictions, the best linear unbiased prediction (BLUP) for the random effects (genetic), and the best linear unbiased estimate (BLUE) for the fixed effects, associated with the estimated variance components for restricted maximum likelihood (REML). The use of this tool in breeding programs reduces time and costs by directly testing only the most promising crosses.

Using BLUP as a selection tool and predictor of unknown crosses is very effective (Gowda et al., 2013b). Efficient strain selection of unknown crosses depends on knowing the degree of the parents' relationship (Bernardo, 1995).

Thus, the aim of this study was to evaluate and predict the accuracy of maize crosses using diallel analysis and best linear unbiased predictor (BLUP).

MATERIALS AND METHODS

The procedure to obtain the varieties and intervarietal hybrids consisted in separating 158 inbred maize genotypes from different origins into eight groups according to origin and time to maturity. These genotypes were sown to achieve the "sib" (self in brothers) chain intersection scheme. All possible crossing combinations were made among the same genotype group. After harvesting, each group's seeds were sown in eight isolated plots for recombination.

Isolation was performed with a minimum distance of 300 m from any maize crop and/or 30-d temporal isolation when necessary. At harvest, the ears of all plants in each plot were collected and seeds were mixed, resulting in the eight varieties for this study.

Subsequently, the eight synthetic varieties were seeded in a diallel cross scheme where each array had been artificially crossed with all other possible combinations, except reciprocal combinations. A total of 28 intervarietal hybrids were evaluated along with the parental strains in three different environments. The experiment was conducted in the 2009-2010 crop year in three environments. The first crop (first environment) and second crop (second environment) were grown at the experimental farm at the Universidade Estadual Paulista 'Julio de Mesquita Filho' (UNESP), Jaboticabal (21°15'17" S, 48°19'20" W; 605 m a.s.l.) in São Paulo, Brazil, and a second crop (third environment) was grown in Campo Alegre de Goiás (17°37'59" S, 47°46'42" W; 877 m a.s.l.) in Goiás, Brazil. The climate in both locations is considered as tropical Aw (Koppen classification) with average rainfall of 60 mm in the driest month and average temperature of 18 °C in the coldest month of the year. The average temperature is 29 °C in the rainy seasons. Soil types in both locations are classified as Eutrophic Red Latosol and Dystrophic Red Latosol, respectively (Embrapa, 2006).

The experiment was conducted with a randomized block design and three replicates. The plots consisted of four 5-m long rows with a spacing of 20 cm between plants and 90 cm between rows; this resulted in a population of 55 555 plants per hectare. Only the two central rows of each plot were used for seed collection. The crops were JAB09/10 (first crop, Jaboticabal 2009-2010), SJAB10 (second crop, Jaboticabal 2010), and SGO10 (second crop, Goiás 2010).

To evaluate varieties and intervarietal hybrids, the studied variables were ear height (EH, cm), plant height (PH, cm), ear position (EP), EH:PH ratio t, and grain yield (GY, kg ha⁻¹). Plot production data were corrected to 13% moisture and adjusted based on the covariance method and converted into kg ha⁻¹ (Silva et al., 2014).

Data were subjected to statistical analysis. A homogeneity test of the data was applied according to Bartlett's test (Bartlett, 1937) and a combined ANOVA was then performed on the three environments.

The diallel analyses were performed with the Diallel-05 package of the SAS program (Zhang et al., 2005), which takes into account the Griffing (1956) diallel model II (random effect), method 2, and analyzes the crosses and parents without reciprocal crosses. The general combining ability (GCA) and specific combining ability (SCA) were estimated. The model proposed by Griffing (1956) analyzes the diallel table by decomposing the average v_{ij} in the following equation:

$$v_{ij} = \mu + g_i + g_j + s_{ij} + \frac{1}{b} \sum_k b_k + \frac{1}{b} \sum_k (bv)_{ijk} + \frac{1}{bc} \sum_k \sum_l e_{ijkl} \quad [1]$$

where v_{ij} is the average phenotypic value observed in the plot for the i^{th} and j^{th} genotypes; μ is the average general effect; $g_i + g_j$ is the effect of GCA associated with the i^{th} and j^{th}

parents, respectively; s_{ij} is the effect of SCA as $s_{ij} = s_{ji}$; k is the number of varying plots 1, ..., b ; bv is the effect of the block \times genotype interaction; $c = p^2 - p + 1$ when p is the number of progenitors; and e_{ijkl} is the average random error associated with the observations $ijkl$.

In this model, it is assumed that both $\sum_i g_i = 0$ and $\sum_{i \neq j} s_{ij} = 0$ (for each j) are imposed on the effects of combining ability. The relative additive effects involved in determining the characteristics assumed the absence of epistasis and calculated GCA and SCA in each studied characteristic by the ratio of the mean squares:

$$\%GGA = \frac{GCA}{GCA + SCA} \times 100 \quad [2]$$

We also estimated BLUP for parents and their crosses with the experimental data. The BLUP, GCA, and SCA estimates of the genotypes were correlated. The BLUP and correlation coefficients were provided by the PROC MIXED and PROC COR function, respectively, of SAS 9.3 (SAS Institute, Cary, North Carolina, USA).

RESULTS AND DISCUSSION

There were significant differences ($P < 0.01$) among genotypes for all analyzed variables (Table 1) and there was variability among tested materials. This is of paramount importance for obtaining genetic gains in terms of hybrid crosses among populations since the success of the breeding program depends on variability to optimize the selection process (Machado, 2014). For all analyzed variables, the variation coefficients were at or below the ideal described by Hallauer et al. (2010) and Fritsche-Neto et al. (2012) and revealed high experimental precision.

The sum of squares for treatments was arranged in GCA and SCA. Significant GCA effects were observed for PH, EH, and EP, thus revealing significant differences between parents, or at least the existence of a superior parent, among all those evaluated related to their mean performance in hybrid combinations. The presence of a significant GCA indicates the importance of additive genetic effects on the expression of the evaluated characteristic. For a set of parents, this directly involves the artificial selection of plants with desirable characteristics that also produce progeny with increased or favorable performance (Rocha et al., 2014). However, for GY, a high frequency of non-additive effects of alleles was found because only 27.80% was due to additive effects (Table 1).

In the diallel analysis, additive effects explained more than 65% of the variation, except for GY (Table 1). This superiority of GCA over SCA is also observed in other maize studies (Vivek et al., 2010; Rocha et al., 2014). Even with a high and significant effect of GCA, one cannot ignore dominance effects. Rangel et al. (2007) obtained predominantly non-additive effects for PH, which is different from what we observed in the present study. Furthermore, as seen in a simple top-crossing using only one tester, combining ability is calculated as the difference between the top-crossed hybrid and population mean;

Table 1. Summary of ANOVA for general combining ability (GCA) and specific combining ability (SCA).

Source or variation	Degree of freedom	MS			
		GY	PH	EH	+EP
Genotype	35	3679754.60**	355535.00**	315942.00**	24.96**
GCA	7	1547330.10 ^{ns}	790.42**	1003.52**	81.14**
SCA	28	4016914.30**	237.29*	140.06*	12.32 ^{ns}
Environment	2	85657388.50**	384506.80**	627489.00**	31.24*
G×E	70	1033409.6**	256022.00**	144257.00**	9.82*
GCA×E	14	1388328.47 ^{ns}	132.40 ^{ns}	99.72 ^{ns}	9.38 ^{ns}
SCA×E	56	1037458.32**	285.37**	146.52**	8.87 ^{ns}
Residual	287	1198788.20	151.46	83.59	8.19
GCA, %		27.80	76.91	69.11	86.82
CV, %		11.83	4.28	6.56	4.73
Average		5766.18	201.41	114.08	0.56
Quadratic components					
JAB09/10 Environment					
GCA		2016265.93**	251.29**	313.64**	30.5294**
SCA		1646011.00**	250.46**	147.08**	7.8084**
SJAB10 Environment					
GCA		641740.86 ^{ns}	417.23**	604.26**	50.6644**
SCA		1432310.08**	280.79**	147.98**	8.7931 ^{ns}
SGO10 Environment					
GCA		1665980.25**	386.69**	285.05**	18.7272 ^{ns}
SCA		3013509.90**	276.80**	138.05**	13.4611 ^{ns}

*, **Significant at the 0.05 and 0.01 probability levels, respectively,

^{ns}nonsignificant.

MS: Mean square; GY: grain yield variables (kg ha⁻¹); PH: plant height (cm); EH: ear height (cm); EP: ear position.

+Value multiplied by 10 000.

both the deviation of the heterozygote related to the mean and frequency of favorable alleles on the tester directly participate in estimating GCA. Since it has been proven that the *locus* influences the effect of GCA dominance, we can say that the predominance of GCA for the variable under study does not necessarily imply a lack of dominance. This would be possible only if the *loci* involved in the character's expression had a frequency of 0.5 (Ribeiro et al., 2014).

The SCA showed a significant effect on all the variables, except for EP which indicated different complementarity between parents, thus enabling the production of high-yielding hybrids. The significance of SCA for productivity reflects a high divergence of the involved parents and indicates that these parents have a higher number of heterozygous *loci*; the formed population will therefore have a greater range of variation and be favorable for selection (Vencovsky, 1972). Breeding programs generally want hybrid combinations with high SCA estimates that involve at least one parent with high GCA (Cruz Baldissera et al., 2012).

Significant Genotype × Environment interactions (G × E) were observed for all traits. When this type of interaction exists, it presupposes that there is a variation between the same genotypes in different environments and is directed toward a particular selection. In this case, it probably resulted from the significant effect of SCA × E; assuming that the hybrids showed greater differences than the parents in the evaluated environments, an individual GCA and SCA analysis is therefore required for each environment (Werle et al., 2014).

There was no difference in the mean performance between parents according to environmental variations

revealed by the nonsignificance of the GCA × E source of variation. This type of interaction for parents is very important for using diallel components in breeding programs (Júnior et al., 2006). According to the quadratic components, there was a slight difference in performance (yield) between parents only in the SJAB10 environment (Table 1). The individual analysis for parents' combining ability showed high and significant GCA, except for the SJAB10 environment. This means that parents can be used for intra-population breeding programs aimed at establishing generations with higher productivity gains.

Contrasts show that there was variability between parents (Table 2). The existence of variability between parents participating in crossings shows the importance of obtaining genetic variability and subsequent selection of promising genotypes in segregating generations (Cruz Baldissera et al., 2012). Selection should be performed so that values can be reproduced in the assessment of subsequent generations, especially for long-term breeding programs aimed at maximizing the distance between parents to explore heterosis.

Attaining genetic gains for every characteristic is always the target of breeding programs when the goal is to release cultivars. These characteristics are usually PH, EH, and GY among others. For example, Ribeiro et al. (2014) found that selecting for tassel size significantly affects grain production due to nutrient targeting. Oliboni et al. (2013), who used diallel analysis, obtained parents with the potential to segregate populations for inter-population improvement because of the increased ability for EH and husked ear productivity. Aguiar et al. (2004) selected promising maize lines for GY, PH, and EH by complete diallel analysis in four environments. Machado et al. (2009) obtained lines with

Table 2. Mean between eight maize varieties and their crosses.

Parent	Mean phenotype			
	GY	PH	EH	EP
VAR-01	5554.75	198.15	107.73	0.54
VAR-02	5367.64	196.48	111.16	0.57
VAR-03	5391.28	199.91	115.09	0.57
VAR-04	5502.69	203.98	114.58	0.55
VAR-05	4681.00	202.36	117.73	0.58
VAR-06	4634.01	214.54	123.28	0.57
VAR-07	3888.92	209.31	123.25	0.59
VAR-08	4522.25	214.72	123.52	0.57
General mean	4942.82	204.93	117.04	0.57
Contrast	1665.83	18.24	15.79	0.05
Hybrids				
C1X2	5923.86	187.59	98.22	0.52
C1X3	6040.67	194.07	107.96	0.55
C1X4	5594.37	192.59	103.61	0.54
C1X5	5861.12	199.63	108.24	0.54
C1X6	6439.54	190.37	108.06	0.57
C1X7	5954.81	196.11	112.59	0.57
C1X8	6042.47	197.04	106.02	0.54
C2X3	6301.00	199.72	111.11	0.56
C2X4	6061.16	201.39	111.48	0.55
C2X5	5756.54	202.59	115.00	0.57
C2X6	6462.13	210.37	119.81	0.56
C2X7	5746.83	203.61	109.91	0.54
C2X8	7152.05	209.63	117.50	0.56
C3X4	5903.12	193.89	111.02	0.57
C3X5	5679.18	196.39	111.85	0.57
C3X6	6596.02	205.46	119.54	0.58
C3X7	5888.68	202.78	118.43	0.58
C3X8	5226.01	198.43	112.41	0.56
C4X5	6031.16	203.98	113.33	0.55
C4X6	6031.36	203.06	117.41	0.57
C4X7	6273.43	204.60	113.89	0.55
C4X8	5842.30	205.40	119.26	0.58
C5X6	6369.76	206.85	120.37	0.58
C5X7	6522.87	203.79	120.18	0.59
C5X8	5781.21	195.18	110.28	0.56
C6X7	5051.40	199.08	115.00	0.57
C6X8	5822.13	199.44	114.44	0.57
C7X8	5684.86	208.24	123.88	0.59
General mean	6001.43	200.40	113.24	0.56
Contrast	2100.65	22.78	25.66	0.07

GY: Grain yield (kg ha⁻¹); PH: plant height (cm); EH: ear height (cm); EP: ear position.

high favorable allele frequencies for GY evaluated in 12 environments.

However, this can only be predicted for hybrid production and evaluation because along with parent means, estimates can be affected (Guo et al., 2013). *Per se*, parent means are not reliable parameters to predict hybrids. There were, however, promising hybrid crosses even when parents exhibited low means in some characteristics, such as between VAR-05 × VAR-06. This is due to the complementarity of favorable *loci* among these varieties, which directly reflects heterotic crosses.

For parent prediction means through diallels, the methodology by Griffing (1956) requires hybrid combinations. A method that can predict the best possible hybrid combinations allows obtaining hybrids in breeding programs faster and more economically.

The BLUP, although not yet widely used for annual plants, has shown great potential for more relevant genetic progress (Bernardo, 1996; Lorenzana and Bernardo, 2009;

Jesus Freitas et al., 2014). Employing variance component estimates by REML and predicting breeding values by BLUP can be efficiently used (Resende and Sturion, 2001). The breeder could therefore predict progeny values by focusing only on the most promising combinations.

In the present study, correlations between estimated GCA and SCA and BLUP values were moderate to high (Table 3). This shows that you can use BLUP to select the best parents for the traits, especially for EH and EP which had the highest correlations. This was not observed for SCA which had low to moderate correlations, particularly for GY and EH. According to Cruz Baldissera et al. (2012), care should be taken in selecting and interpreting results when comparing combining ability estimates and BLUP.

When studying the parents for GCA, selection for progeny can be made for a specific performance trait. For example, parent VAR-01 has significant GCA values ($P < 0.05$) and can be used in crosses to reduce PH, EH, and EP while parent VAR-06 can participate in crosses to increase EH, PH, and EP. The genotypes VAR-01, VAR-02, VAR-03, VAR-04, and VAR-06 showed high and positive GCA values for GY (Table 3), revealing the existence of favorable alleles for this character in these parents.

For intervarietal hybrids, the best combinations were C2X8 and C5X7 and both had high GY estimates. The C2X8 combination was selected to increase PH and the C5X7 combination was selected to reduce it. These combinations revealed the crosses that complemented mean production the most and revealed the importance of complementarity and divergence between parents to exploit heterotic and genetic gains (Gowda et al., 2013a).

The predicted breeding value correlations with SCA for GY were moderate, generating opposite results in some combinations. While the SCA estimates showed a decrease in C1X2 combinations of -230.19 kg ha⁻¹, BLUP estimated a productivity complement of 113.40 kg ha⁻¹ and the SCA estimates showed a decrease of -230.19 kg ha⁻¹; however, both parents showed positive GCA values, which was contradictory. This can be explained only by low complementarity between these parents. With BLUP estimators, both parents contribute to mean productivity, which is confirmed in the cross.

For both BLUP and combining ability, it was possible to identify C2X8 as the best hybrid combination, originated from completely contrasting parents. When observing the C2X7 combination, we found contrasting parents; involving the best parent in the cross (VAR-02) did not achieve significant productivity according to BLUP and GCA. This is probably because the methods were not sufficiently sensitive to separately identify contrasting parents for the characteristics under consideration. According to Bernardo (1995), BLUP can effectively predict when the degree of relationship between parents is known. Guo et al. (2013) corroborated this when they predicted hybrid corn from inbred lines and concluded that genetic architecture determines the accuracy of prediction.

Table 3. Correlation between predicted breeding values (BLUPs) both general combining ability (GCA) for varieties and specific combining ability (SCA) for hybrids.

Parent	GY		PH		EH		EP	
	GCA	BLUP	GCA	BLUP	GCA	BLUP	GCA	BLUP
VAR-01	57.34	866.05	-6.52*	-5.73	-7.16*	-8.42	-0.017**	-0.010
VAR-02	227.29	695.19	0.45	-7.11	-1.94*	-5.65	-0.011**	0.001
VAR-03	7.00	716.78	-2.14	-4.60	-0.29	-2.53	0.004	0.005
VAR-04	50.82	818.39	0.14	-1.31	-0.64	-2.89	-0.003	-0.003
VAR-05	-35.89	68.50	0.38	-2.61	0.90	-0.39	0.003	0.009
VAR-06	54.55	25.82	2.68	6.74	3.52**	4.14	0.010**	0.005
VAR-07	-244.77	-654.30	2.47	2.84	3.42**	4.14	0.010	0.014
VAR-08	-109.94	-76.29	2.54	7.26	2.19*	4.14	0.003	0.005
Correlation	0.79**		0.71**		0.94**		0.86**	
Hybrid	SCA	BLUP	SCA	BLUP	SCA	BLUP	SCA	BLUP
C1X2	-230.19	113.40	-7.31*	-3.87	-6.39**	-8.62	-0.013	-0.025
C1X3	104.77	197.40	1.77	-2.05	1.70	-3.33	0.003	-0.005
C1X4	-365.78	-123.56	-1.99	-2.47	-2.29	-5.69	-0.006	-0.017
C1X5	-31.88	682.75	4.80	-0.49	0.78	-3.18	-0.009	-0.015
C1X6	456.09	484.25	-6.75*	-3.09	-2.02	-3.28	0.010	0.001
C1X7	270.68	135.65	-0.81	-1.48	2.61	-0.81	0.015*	0.005
C1X8	225.65	198.69	0.05	-1.22	-2.73	-4.39	-0.014	-0.017
C2X3	195.15	384.62	0.44	-0.47	-0.37	-1.62	-0.003	-0.005
C2X4	-68.95	212.13	-0.18	-0.01	0.35	-1.42	0.002	-0.008
C2X5	-306.41	-69.31	0.79	0.33	2.32	0.49	0.008	0.001
C2X6	308.73	500.50	6.27	2.50	4.52	3.11	0.005	0.002
C2X7	-107.25	-139.17	-0.29	0.62	-5.29*	-2.27	-0.025**	-0.016
C2X8	1165.29	996.67	5.66	2.30	3.53	0.54	0.002	-0.003
C3X4	-8.82	984.82	-5.08	-2.11	-1.76	-1.67	0.006	0.004
C3X5	-165.62	-625.67	-2.82	-1.41	-2.48	-1.21	-0.004	0.002
C3X6	660.78	596.79	3.95	1.13	2.58	2.96	0.002	0.009
C3X7	252.76	880.98	1.47	0.38	1.58	2.36	0.004	0.011
C3X8	-542.59	-388.47	-2.94	-0.84	-3.21	0.27	-0.008	0.0001
C4X5	162.09	190.56	2.49	0.72	-0.64	-0.41	-0.009	-0.006
C4X6	71.86	190.70	-0.73	0.46	0.81	1.80	0.006	0.007
C4X7	613.25	364.80	1.04	0.90	-2.61	-0.11	-0.015	-0.005
C4X8	49.43	547.38	1.72	1.12	3.99	1.98	0.015	0.009
C5X6	477.41	434.07	2.83	1.52	2.23	3.41	0.002	0.009
C5X7	929.83	544.18	-0.03	0.67	2.14	3.31	0.010	0.014
C5X8	55.49	108.08	-8.70**	-1.70	-6.54**	4.99	-0.007	-0.001
C6X7	-632.07	-514.05	-7.04*	-0.65	-5.66	0.49	-0.008	0.006
C6X8	5.98	402.38	-6.74*	-0.55	-4.99	4.97	-0.005	0.005
C7X8	168.02	-584.85	2.26	1.91	4.55	5.32	0.015	0.017
Correlation	0.63**		0.74**		0.35*		0.70**	

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

GY: Grain yield (kg ha⁻¹); PH: plant height (cm); EH: ear height (cm); EP: ear position; BLUP: best linear unbiased prediction.

CONCLUSION

There was a difference between diallel analysis and best linear unbiased prediction (BLUP) methods in terms of predicting efficiency. In addition, the ideal situation is that breeders use combining ability analysis together with breeding value (BLUP) estimates to identify promising genotypes more efficiently and promote the rapid development of new cultivars. Finally, if breeders choose to use only one methodology, BLUP was more efficient in determining parents related to higher earnings.

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