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ARTICLE

Analysis of heterosis components and prediction of hybrid means based on intergroup topcrosses in maize

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Abstract: *Diallel designs are widely used in plant breeding to select parents and to study trait inheritance. The present work aimed to present a method to evaluate two divergent groups of parents, in which one group is used as a tester of the contrasting group. Each parent is crossed with a balanced mixture of seeds from the parents of the other group, and the parents and topcrosses are experimentally evaluated. Two groups of ten inbred maize lines were used to obtain intergroup topcrosses and biparental crosses in a diallel scheme. The data were subjected to analysis of variance and parameter estimation using the two models. The results showed the reliability of the method for the evaluation of lines and prediction of means of hybrid populations and can be recommended when the number of parents to be evaluated is large, making it difficult to evaluate biparental crosses in a diallel scheme.*

Keywords: *Testcross, heterosis, combining ability, maize, synthetic*

INTRODUCTION

Diallel crosses are widely used in plant breeding programs to select parents for the synthesis of hybrids with a high frequency of desired alleles, in addition to being a useful method for determining the genetic basis of trait inheritance (Hallauer et al. 2010, Aslam et al. 2017, Coelho et al. 2020). The partial diallel strategy, in which groups of divergent parents are crossed to maximize heterosis, is interesting for breeding programs, as it guarantees the optimization of financial resources and increases the chances of identifying promising crosses (Silva et al. 2021).

A successful maize breeding program is dependent on known heterotic groups of lines or populations (Oyetunde et al. 2020). Miranda-Filho and Geraldi (1984) presented a method for partial diallel analysis adapted from the model by Gardner and Eberhart (1966), in which two divergent groups of varieties or lines are evaluated, allowing economy in the estimation of genetic parameters. However, for large numbers of parents, great effort remains necessary for obtaining, evaluating and manipulating data, especially when the goal is to predict the performance of composite or synthetic populations, in which a set of n parents can generate $N_c = 2^n - n - 1$ composites or synthetics (Miranda-Filho and Chaves 1991).

To evaluate genotypes from a smaller number of crosses, breeders have used topcrosses (or testcrosses), in which the lines are crossed with common testers

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(Hallauer et al. 2010). The selection of genotypes is based on estimates of general combining ability effects, and the most promising are evaluated in the diallel scheme (Miranda-Filho 2018). However, although there are several studies aiming to define the best tester to be used in the evaluation of maize genotypes (Guimarães et al. 2012, Rodrigues et al. 2016, Rosa et al. 2020, Rosa et al. 2021), there is still no consensus on which tester best discriminates the genotypes under evaluation.

Aiming to promote a more practical and simplified selection of parents and reduce costs with evaluations, Chaves and Miranda-Filho (1997) proposed the use of intragroup topcrosses using a mixture of seeds from all parents as a tester. The analysis is based on an adaptation of the model by Gardner and Eberhart (1966), in which the evaluation of parents and their crosses allows the estimation of useful genetic parameters for the selection and discarding of genotypes. Furthermore, the method allows the prediction of means of composites and hybrids between composites without significant loss of precision compared to usual procedures.

The intragroup topcrosses method used to evaluate the performance of popcorn populations showed that there was efficient discrimination of the evaluated populations, enabling the identification of superior genotypes (Souza et al. 2012). The evaluation of populations of maize landraces through intragroup topcrosses showed that the populations with the highest estimates of general combining ability participated in the best predictions of composite means, proving the effectiveness of the methodology in the selection of genotypes (Ferreira et al. 2009).

Aiming at greater economy of crosses and maximization of the heterotic response, the present work aims to adapt the methodology proposed by Chaves and Miranda-Filho (1997) to the interpopulation level to evaluate two divergent groups of maize lines, in which one group is used as a tester of the contrasting group. For this, the heterosis component analysis procedure is presented, and the results are compared with those of the partial intergroup diallel with the same set of parents.

MATERIAL AND METHODS

For two groups of parents 1 and 2, with m and n parents, respectively, the intergroup reciprocal topcross scheme consists of crossing each parent of a group with a balanced mixture of pollen from all parents of the contrasting group. The $m + n$ topcrosses and the parents are evaluated in a trial with replications, totaling $2(m + n)$ treatments. The scheme consists of an adaptation to the interpopulation level of the intragroup topcrosses scheme proposed by Chaves and Miranda-Filho (1997). Conventional analysis of variance of experimental data provides treatment means in addition to an estimate of the experimental error.

The analysis of variance of the topcross design was performed based on adaptations of the intragroup model proposed by Chaves and Miranda-Filho (1997) and the parameters of the partial intergroup diallel model proposed by Miranda-Filho and Geraldi (1984). In this model, diallel analysis uses the method adapted from the Gardner and Eberhart (1966) model, in which the average of a cross involving one parent i (i = 1, 2, 3, ... , m) and one parent j (j = 1, 2, 3, ... , n) from two distinct groups (groups 1 and 2) is given by:

$$Y_{ij} = \mu + \alpha d + \frac{1}{2}(v_i + v_j) + \theta(\overline{h} + h_i + h_j + s_{ij}) + \overline{\varepsilon}_{ij},$$

where μ is the midpoint between the means of the two parent groups; d is the deviation of the mean of each group from the mean of the two groups; v_i and v_j are the parent effects relative to groups 1 and 2, respectively; $\overline{h}$ is the average heterosis of all crosses; h_i and h_j are the heterosis effects of parents of groups 1 and 2, respectively; s_{ij} is the specific heterosis of the cross between parents i and j; and $\overline{\varepsilon}_{ij}$ is the average experimental error associated with the observed means Y_{ij}, assumed with normal distribution, null mean and constant variance. The indicator variables α and θ assume the values: $\alpha = 0$ and $\theta = 1$, for hybrids; $\alpha = 1$ and $\theta = 0$, for the parents of group 1, with $Y_{ij} = Y_{ii}$; or $\alpha = -1$ and $\theta = 0$, for parents of group 2, with $Y_{ij} = Y_{jj}$.

All parameters of the intergroup partial diallel model, with the exception of specific heterosis, can be estimated from the means of each row and each column of the diallel table. The assumption for the analysis of the topcross scheme is that the mean of the crosses of a parent provided by the diallel table ($\overline{Y}_{i.}$ and $\overline{Y}_{.j}$, for groups 1 and 2, respectively) is equivalent to the mean of the cross of this parent with a mixture of the parents of the contrasting group, that is, the topcrosses T_i and T_j, for groups 1 and 2, respectively, provided that there is a balanced contribution of all pollinators,

so that $\overline{Y}_{i.} = T_i$, for parents of group 1 and $\overline{Y}_{i.} = T_j$, for parents of group 2. The models for analysis of the data table are:

$T_i = \mu - c + \overline{h} + \frac{1}{2}v_i + h_i$, for topcrosses of group 1;

$T_j = \mu - c + \overline{h} + \frac{1}{2}v_j + h_j$, for topcrosses of group 2;

$V_i = \mu - d + v_i$, for parents of group 1;

$V_j = \mu - d + v_j$, for parents of group 2;

where T_i and T_j are the values of the topcrosses of groups 1 and 2, respectively; V_i and V_j are the values of the parents of groups 1 and 2, respectively; d is the deviation of the mean of parents of each group from the mean of the two groups; and c is the deviation of the mean of each group of topcrosses from the mean of the two groups. The other parameters are equivalent to those of the partial intergroup diallel.

The formulas for estimating the parameters and obtaining the sums of squares for the analysis of variance of the intergroup reciprocal topcrosses model were developed using the least squares procedure from the normal equations $Y = X\beta + \varepsilon$, where Y is the vector of observed treatment means, X is the matrix of incidence of the parameters, β is the vector of parameters and ε is the vector of errors associated with the treatment means. Parameter estimates are obtained by $\hat{\beta} = (X'X)^{-1} X'Y$ and the sums of squares by $SQ = \hat{\beta}' (X'Y)$ for the complete model and sequentially reduced models. To solve the normal equations, the following parametric restrictions were assumed:

$\sum_i v_i = \sum_j v_j = \sum_i h_i = \sum_j h_j = 0$.

For the evaluation of the topcrosses method and comparison with the diallel method, 20 maize lines in the fourth generation of inbreeding (S_4) were used. The lines were derived from three populations of the breeding program carried out at the research unit of the company Sementes Agroceres S.A., at Inhumas, Goiás, Brazil. To establish distinct heterotic groups, the lines were divided into two groups according to the type of grain: group 1 with ten flint grain lines and group 2 with ten dent grain lines.

To obtain the biparental hybrids, the lines were crossed in a partial intergroup diallel scheme, according to Miranda-Filho and Geraldi (1984), obtaining 100 F_1 hybrids. Of this total, only one hybrid did not have enough seeds to be evaluated. To obtain the twenty intergroup topcrosses, the ten lines of each group were sown in rows interspersed by rows of the tester composed of a balanced mixture of seeds from the lines of the contrasting group. The lines and tester of each group were sown in isolated blocks and spaced approximately 500 meters apart to avoid pollen contamination. At the time of flowering, the female rows (lines) were detasseled so that they were pollinated only by the male rows (tester mixture).

The parental lines, the hybrids and the reciprocal intergroup topcrosses were evaluated in the experimental area of the company Sementes Agroceres at Araçu, Goiás, Brazil. The soil of the experimental area is a Dark Red Latosol (Embrapa 2018). The climate in the region is Aw, according to Köppen's classification, with a rainy season from October to April and a dry season from May to September (Kottek et al. 2006). Fertilization and cultural practices were carried out in accordance with the recommendations for maize crop. The experiment was carried out in a randomized complete block design with four replications. The experimental plots were composed of rows of 4.0 meters in length, spaced 0.2 meters between plants and 0.8 meters between rows. The treatments were divided into six trials, four for hybrids, one for parent lines and one for topcrosses. In each trial, the commercial hybrids BR 201 and AG 510 were used as controls. The traits evaluated were female flowering (days), plant height (cm) and grain yield (kg ha^{-1}) after adjustment for 13% grain moisture.

For the diallel model, the sums of squares and parameter estimates were obtained according to Miranda-Filho and Geraldi (1984), using Genes software (Cruz 2013). For the topcrosses model, the formulas developed in this study were applied using Microsoft Excel™ spreadsheet. The general combining ability of each parent (g_i and g_j) was also estimated for groups 1 and 2, respectively, in the two models, corresponding to method 4 of Griffing (1956), using the expressions: $\hat{g}_i = \frac{1}{2}\hat{v}_i + \hat{h}_i$, for parental lines of group 1, and $\hat{g}_j = \frac{1}{2}\hat{v}_j + \hat{h}_j$, for parental lines of group 2. The estimates of the general combining ability obtained by the two methods were compared using the Pearson correlation coefficient, whose significance was evaluated using the parametric bootstrap procedure, with 10,000 resamplings.

The predictions of means of crosses between synthetics were performed based on the adaptation of the model

proposed by Chaves and Miranda-Filho (1997) for the interpopulation level. Due to the high number of combinations of crosses between possible synthetics, predictions were made with the same number of lines in both groups ($k_1 = k_2$) to obtain all possible combinations considering $k_1 = k_2 = 2, 3, \ldots, 9$. Mean predictions were made for the main trait, grain yield. The predicted means of the crosses between synthetics obtained using data from the partial diallel table were correlated with the means predicted from the topcrosses using the Spearman's rank correlation.

RESULTS AND DISCUSSION

Parameter estimators and analysis of variance

The estimators of parameters and contrasts between estimates for the topcross model with their associated variances are shown in Table 1. The estimators of μ, d, v_i and v_j, as well as the variances of the estimates, are the same as for the partial intergroup diallel. For the heterosis components ($\bar{h}$, h_i and h_j), the estimators are different for the two models, with smaller variances of the estimates by the diallel model, supposing the same residual variance. Therefore, considering the same number of parents in each group, there is a loss of precision in the estimates by the topcross model. However, as the topcross design allows the evaluation of a greater number of parents with the same experimental effort, this loss of precision can be compensated by the experimental gain, which must be evaluated on a case-by-case basis. The parameters μ, v_i, v_j, $\bar{h}$, h_i and h_j can be genetically interpreted in the same way as presented by Gardner and Eberhart (1966). Thus, μ represents the midpoint between the means of the two groups of parents; $v_i = a_i + d_i$ represents the sum of the contributions of the homozygous (a_i) and heterozygous (d_i) loci to the mean of parent i; $\bar{h}$ represents the average expected heterosis of all biparental crosses between parents from groups 1 and 2; h_i represents the contribution of parent i to total heterosis, measured in relation to the average heterosis. The parameters v_i and h_i are interpreted similarly to v_j and h_j for the second group of parents. The parameter d corresponds to the deviation of the mean of each group of parents in relation to μ, with $\mu + d$ being the mean of the parents of group 1 and $\mu - d$ the mean of the parents of group 2 (Miranda-Filho and Geraldi 1984).

Table 1. Parameter estimators or contrasts and associated variances from the intergroup reciprocal topcrosses complete model

Parameter or contrast	Variance
$\hat{\mu} = \frac{1}{2}[\bar{V}_{.(1)} + \bar{V}_{.(2)}]$	$\left(\frac{n+m}{4nm}\right)\sigma^2$
$\hat{d} = \frac{1}{2}[\bar{V}_{.(1)} - \bar{V}_{.(2)}]$	$\left(\frac{n+m}{4nm}\right)\sigma^2$
$\hat{v}_i = V_i - \bar{V}_{.(1)}$	$\left(\frac{n-1}{n}\right)\sigma^2$
$\hat{v}_j = V_j - \bar{V}_{.(2)}$	$\left(\frac{m-1}{m}\right)\sigma^2$
$\hat{\bar{h}} = \frac{1}{2}\{[\bar{T}_{.(1)} + \bar{T}_{.(2)}] - [\bar{V}_{.(1)} + \bar{V}_{.(2)}]$	$\left(\frac{n+m}{2nm}\right)\sigma^2$
$\hat{h}_i = T_i - \bar{T}_{.(1)} - \frac{1}{2}[V_i - \bar{V}_{.(1)}]$	$\left[\frac{5(n-1)}{4n}\right]\sigma^2$
$\hat{h}_j = T_j - \bar{T}_{.(2)} - \frac{1}{2}[V_j - \bar{V}_{.(2)}]$	$\left[\frac{5(m-1)}{4m}\right]\sigma^2$
$\hat{c} = \frac{1}{2}[\bar{T}_{.(1)} - \bar{T}_{.(2)}]$	$\left(\frac{n+m}{4nm}\right)\sigma^2$
$v_i - v_{i'}$	$2\sigma^2$
$v_j - v_{j'}$	$2\sigma^2$
$h_i - h_{i'}$	$\frac{5}{2}\sigma^2$
$h_j - h_{j'}$	$\frac{5}{2}\sigma^2$

$\bar{V}_{.(1)}$ and $\bar{V}_{.(2)}$: means of parents from groups 1 and 2, respectively; $\bar{T}_{.(1)}$ and $\bar{T}_{.(2)}$: means of topcrosses from groups 1 and 2, respectively.

The parameter c represents a deviation of the mean of each group of topcrosses from the mean of the two groups. In the absence of reciprocal effects in the cross between parents, a null value for parameter c is expected. Thus, the significance of this parameter is an indication of possible reciprocal effects, assuming a balance in the contribution of pollen by the parents for the formation of topcrosses. The non-significance for this effect, however, could not be interpreted as the absence of reciprocal effects, since the occurrence of these effects in opposite directions in different hybrids can result in values close to zero in the mean of the effects. When there is no control of pollination in the formation of topcrosses, as in the case of maize, with detachment of male inflorescences of female rows and random pollination, there may be an imbalance in the contribution of pollen by the parents. In this case, there will be a confounding of the reciprocal effects and the unbalance in the formation of parameter c. The non-significance of this parameter is, therefore, indicative of the absence of significant imbalances in the formation of topcrosses, which provides a test for the basic assumption of the present model.

The analysis of variance scheme and the sum of squares estimators for the different sources of variation can be obtained sequentially using matrix operations, which results in the formulas shown in Table 2. The data analysis showed agreement between the significance of mean squares for the common effects obtained using the diallel model (Miranda-Filho and Geraldi 1984) and those obtained by the intergroup reciprocal topcross model for the three evaluated traits (Table 3).

The effects of lines from groups 1 and 2 (v_i and v_j) were significant ($p \leq 0.01$) for all traits by the two methods (Table 3) and explained 55.33%, 27.96%, and 8.95% of the total variation, considering the traits female flowering, plant height and grain yield, respectively, from the partial diallel analysis. For the intergroup reciprocal topcross model, the percentages of representativeness in the total variation for the line effects were 51.17%, 12.05% and 3.94% for the same traits, respectively, with the remaining variation explained by heterosis. The results obtained by both methods indicate low, medium and high importance of the dominance effects for flowering, plant height and grain yield, respectively, as observed by other authors (Begum et al. 2018, Coelho et al. 2020).

Specific heterosis, according to the partial diallel analysis, showed significant differences ($p \leq 0.01$) for all traits (Table 3), evidencing the presence of pairs of parents with exclusive allelic complementation, which contributes to the better performance of particular hybrids. For all traits, the sum of squares partition of total heterosis revealed a greater contribution of specific heterosis. Considering the main trait, grain yield, heterosis was responsible for 91.04% of the total variation, and of these, 20.43% was due to average heterosis, 1.06% to heterosis of lines of group 1, 1.26% to heterosis of lines of group 2 and 68.29% to specific heterosis.

For the intergroup reciprocal topcross scheme, specific crosses between pairs of lines are not performed; therefore, it is not possible to obtain information about the specific combining ability of particular hybrids (Chaves and Miranda-Filho 1997). Thus, the method proposed here is recommended for the intermediate phase of evaluation of lines, which is generally carried out after three or four self-pollinations, in which there is greater interest in the general combining ability. Generally, during this phase of breeding programs, lines have been crossed with one or more standard testers as a way to estimate the effects of general combining ability and to support the selection of promising lines (Miranda-Filho 2018). However, doubts still persist about the choice of testers to be used in the pre-evaluations of lines, since

Table 2. Analysis of variance according to the intergroup reciprocal topcross model

Source of variation	df	Sum of squares
Populations	$2(m+n)-1$	$\sum_{i=1}^{m} T_i^2 + \sum_{i=1}^{m} V_i^2 + \sum_{j=1}^{n} T_j^2 + \sum_{j=1}^{n} V_j^2 - \frac{Y_{..}^2}{2(m+n)}$
Varieties (1)	$m-1$	$\frac{4}{5}\sum_{i=1}^{m}\{[V_i - \overline{V}_{.(1)}] + \frac{1}{2}[T_i - \overline{T}_{.(1)}]\}^2$
Varieties (2)	$n-1$	$\frac{4}{5}\sum_{j=1}^{n}\{[V_j - \overline{V}_{.(2)}] + \frac{1}{2}[T_j - \overline{T}_{.(2)}]\}^2$
V (1) vs V (2)	1	$\frac{mn}{m+n}(\overline{V}_{.(1)} - \overline{V}_{.(2)})^2$
Average heterosis	1	$\frac{1}{2(m+n)}\{[T_{.(1)} + T_{.(2)}] - [V_{.(1)} + V_{.(2)}]\}^2$
Varieties heterosis (1)	$m-1$	$\frac{4}{5}\sum_{i=1}^{m}\{[T_i - \overline{T}_{.(1)}] - \frac{1}{2}[V_i - \overline{V}_{.(1)}]\}^2$
Varieties heterosis (2)	$n-1$	$\frac{4}{5}\sum_{j=1}^{n}\{[T_j - \overline{T}_{.(2)}] - \frac{1}{2}[V_j - \overline{V}_{.(2)}]\}^2$
TC (1) vs TC (2)	1	$\frac{mn}{m+n}(\overline{T}_{.(1)} - \overline{T}_{.(2)})^2$
Error	df_e	SS_e

$\overline{V}_{.(1)} = \frac{1}{n}\sum_{i=1}^{n} V_i$; $\overline{V}_{.(2)} = \frac{1}{m}\sum_{i=1}^{m} V_j$; $\overline{T}_{.(1)} = \frac{1}{n}\sum_{i=1}^{n} T_i$; $\overline{T}_{.(2)} = \frac{1}{m}\sum_{i=1}^{m} T_j$; $Y_{..} = \sum_{i=1}^{n} V_i + \sum_{i=1}^{m} V_j + \sum_{i=1}^{n} T_i + \sum_{i=1}^{m} T_j$; m and n: number of parents from groups 1 and 2, respectively; r: number of replications. The error mean square must be divided by the number of replications.

Table 3. Analysis of variance according to the partial diallel model and intergroup reciprocal topcross model for parents from groups G1 (flint) and G2 (dent); FF: female flowering (days), PH: plant height (cm), GY: grain yield (kg ha^{-1}), TC1 and TC2: topcrosses from groups 1 and 2, respectively

Source of variation	df	FF	PH	GY
Partial diallel				
Populations	118	30.296**	3742.151*	13.1581**
Parents group 1 (G1)	9	56.608**	8607.559**	8.4989**
Parents group 2 (G2)	9	145.521**	4684.066**	6.7861**
G1 vs G2	1	151.250**	3125.000**	0.2289
Heterosis	99	16.207**	3220.447**	14.2915**
Average heterosis	1	285.315**	57859.437**	314.5897**
Parent heterosis (G1)	9	5.159**	5208.223**	1.8128**
Parent heterosis (G2)	9	15.013**	851.048**	2.1618**
Specific heterosis	80	14.045**	2548.536**	13.1419**
Error	372	0.144	12.133	0.1382
Intergroup reciprocal topcrosses				
Populations	39	11.33**	1578.83**	5.10955**
Parents group 1 (G1)	9	4.20**	184.50**	0.46634**
Parents group 2 (G2)	9	16.72**	553.38**	0.39885**
G1 vs G2	1	37.81**	781.25**	0.05722
Average heterosis	1	160.00**	51480.62**	178.94723**
Parent heterosis (G1)	9	1.87**	143.83**	0.49121**
Parent heterosis (G2)	9	2.90**	125.77**	0.89124**
TC1 vs TC2	1	12.80**	245.00**	0.03929
Error	126	0.148	17.379	0.12812

*, **: significant at the 5% and 1% probability levels, respectively, by *F* test.

the tester should not mask the true genetic value of the lines under test (Ismail et al. 2020, Rosa et al. 2020, Rosa et al. 2021). Thus, the method of intragroup topcross can be an alternative to minimize the genetic interference of testers. Furthermore, when lines are obtained using the double haploid technique, a great number of homozygote lines are available (Chaikam et al. 2019), and the method proposed here could be used to reduce the number of lines to be crossed in the diallel scheme or to be genotyped for genomic selection.

In this context, the use of topcrosses with reciprocal intergroup testers is advantageous as a way to expose the values of genotypes when crossing, facilitating the prediction of hybrid means and means of crosses between synthetics, which could be used *per se* or as base populations in interpopulation recurrent selection programs. In addition, the method makes it possible to evaluate a smaller number of crosses in relation to complete or partial diallel, which could be carried out in the final phases of breeding programs, in which the specific combining ability assumes great importance.

The contrast between topcrosses of groups 1 and 2 (Table 3) was significant ($p \leq 0.01$) for female flowering and plant height and not significant for grain yield. The expectation for this parameter would be the absence of significance, as occurred for grain yield, which would indicate similar means between the contrasting groups. One of the possible causes of the significance found for some traits for this parameter may be an imbalance in pollination during the obtainment of topcrosses.

General combining ability

The general combining ability is associated with a higher frequency of favorable alleles in the population and its potential for the production of composites or synthetics (Miranda-Filho and Chaves 1991). This parameter is associated with additive effects, is useful for plant selection and discarding (Fasahat et al. 2016) and is widely used as a selection criterion in diallel models. According to Cruz and Vencovsky (1989), the general combining ability is the best parameter used in the choice of parents, being efficient even in cases where there is overdominance between the alleles.

The correlation coefficients between the estimates of general combining ability obtained for each group from the partial diallel and the intergroup reciprocal topcrosses are shown in Table 4. There was significance ($p \leq 0.01$) for the

Table 4. Estimates of the general combining ability using the partial diallel model (PD) and the intergroup reciprocal topcrosses model (TC) for Flint (F1 to F10) and Dent (D1 to D10) lines; r_1 and r_2: Pearson correlation coefficient between models, for groups 1 and 2, respectively, FF: female flowering (days), PH: plant height (cm), GY: grain yield (kg ha^{-1})

Lines	FF		PH		GY	
	PD	TC	PD	TC	PD	TC
F1	1.51	-0.37	20.83	6.5	481.09	128.91
F2	0.41	2.62	1.83	1.5	231.18	489.54
F3	0.38	1.62	7.83	1.5	-683.34	-333.36
F4	-1.06	-1.62	-0.66	-18.5	42.62	283.55
F5	-1.83	-1.62	-2.97	-13.5	-64.61	-1205.13
F6	-1.48	-0.62	19.33	21.5	-295.48	1282.29
F7	0.53	0.37	18.33	6.5	527.14	-536.31
F8	0.91	2.62	-7.16	16.5	-849.81	-1494.64
F9	-0.28	-2.62	-34.16	-13.5	22.65	1087.96
F10	0.91	-0.37	-23.16	-8.5	588.56	297.19
r_1	0.535**		0.586**		0.324^{ns}	
D1	0.68	-0.22	14.33	19.5	898.92	1981.57
D2	1.28	1.02	7.33	9.5	-14.95	620.22
D3	2.28	2.02	6.02	14.5	-102.96	1306.64
D4	-0.11	-2.97	9.33	14.5	-110.55	-485.91
D5	0.48	0.77	6.83	4.5	68.21	-197.12
D6	0.28	2.77	-10.66	-10.5	-437.35	-422.69
D7	-0.98	-2.22	-10.16	-20.5	358.8	95.08
D8	-3.61	-3.22	-8.66	-15.5	-366.14	-1845.65
D9	0.41	1.02	-8.16	-15.5	-677.72	-505.31
D10	-0.73	1.02	-6.16	-0.5	383.73	-546.8
r_2	0.745**		0.964**		0.608**	

**: Significant at the1% probability level using 10,000 bootstrap resamplings; ^{ns}: nonsignificant.

correlation coefficient for the three traits, with the exception of grain yield, in the Flint group. These results indicate the existence of a good correspondence between the estimates of the general combining ability obtained by the two models, which suggests that the proposed model can be used reliably in the estimation of these parameters in a more practical and economical way.

The intergroup reciprocal topcross model can also be applied to the selection of noninbred genotypes, in which specific heterosis values tend to be lower, with a predominance of the general combining ability. Due to having worked with endogamous lines, the values of heterosis were high, especially the average heterosis. However, as seen from the results (Table 4), the estimates of general combining ability obtained by the two models showed significant correlations in most cases. Importantly, the estimates of general combining ability and heterosis components are relative to the groups of genotypes evaluated, and the estimated values are valid for these particular groups of lines.

Prediction of means

The predicted mean of a biparental hybrid from parents of groups 1 and 2 ($\hat{C}_{ij}$), disregarding the effect of specific heterosis, can be obtained by:

$$\hat{C}_{ij} = T_i + T_j - \frac{1}{2}\left[\overline{T}_{.(1)} + \overline{T}_{.(2)}\right]$$

where T_i and T_j are the values of the topcrosses of groups 1 and 2, respectively, and $\overline{T}_{.(1)}$ and $\overline{T}_{.(2)}$ are the general means of all topcrosses of groups 1 and 2, respectively.

The predicted mean of the cross between two synthetics composed of subsets of parents of each group [$\widehat{MS}_{(i...i' \times j...j')}$] corresponds to:

$$\widehat{MS}_{(i...i' \times j...j')} = \frac{1}{k_1}\sum_{i=1}^{K_1} T_i + \frac{1}{k_2}\sum_{j=1}^{K_2} T_j - \frac{1}{2}\left[\overline{T}_{.(1)} + \overline{T}_{.(2)}\right]$$

where k_1 and k_2 are the number of lines that compose the synthetics from groups 1 and 2, respectively.

The estimates of parameters from the partial diallel can be used to predict the means of hybrids and other crosses (Hallauer et al. 2010). In the intergroup reciprocal topcross method, the prediction of hybrids between synthetics is facilitated, since parental data are not needed and, in crosses with multiple parents, the predicted mean without the inclusion of specific heterosis does not differ considerably from the predicted mean with this inclusion, as its sum tends to zero with the increase in the number of parents.

The Spearman's rank correlation coefficients comparing the predicted means of crosses between synthetics by the partial diallel and by the intergroup reciprocal topcrosses method were significant ($p \leq 0.01$) for all sizes of synthetics and varied increasingly from 0.408 to 0.468 for synthetics of sizes two to nine, which suggests the feasibility of the proposed method in predicting the means of these crosses. However, the results indicate that the remaining parameters, mainly specific heterosis, are responsible for a large part of the model's variation. It is necessary to emphasize that the data used for prediction by the two methods result from different experiments, and part of the lack of correlation between the predicted values is due to environmental factors associated with the treatment means.

It is probable that, when working with non-endogamous parents, the expected values of average heterosis and specific heterosis have smaller magnitudes, as observed by authors when evaluating populations and landraces (Vancetovic et al. 2015, Rovaris et al. 2017, Zhang et al. 2017), which would provide more realistic predicted means of crosses between synthetics (or composites) using the proposed method.

The results of the present study indicate that the proposed method is useful for evaluating the combining ability and heterosis components of parents from different heterotic groups compared to diallel analysis. The loss of information about specific crosses can be compensated with the gain in experimental effort, particularly when the number of parents to be evaluated is large, in the intermediary phases of hybrid breeding programs. Furthermore, the method allows evaluating the potential of lines to form base populations for reciprocal recurrent selection.

REFERENCES

Aslam M, Sohail Q, Maqbool MA, Ahmad S and Shahzad R (2017) Combining ability analysis for yield traits in diallel crosses of maize. **The Journal of Animal and Plant Science 27**: 136-143.

Begum S, Alam SS, Omy SH, Amiruzzaman M and Rohman MM (2018) Inheritance and combining ability in maize using a 7 x 7 diallel cross. **Journal of Plant Breeding and Crop Science 10**: 239-248.

Chaikam V, Molenaar W., Melchinger AE and Boddupalli PM (2019) Doubled haploid technology for line development in maize: technical advances and prospects. **Theorical and Applied Genetics 132**: 3227-3243.

Chaves LJ and Miranda-Filho JB (1997) Predicting variety composite means without diallel crossing. **Brazilian Journal of Genetics 20**: 501-506.

Coelho IF, Alves RS, Rocha JRASC, Peixoto MA, Teodoro LPR, Teodoro PE, Pinto JFN, Reis EF and Bhering LL (2020) Multi-trait multi-environment diallel analyses for maize breeding. **Euphytica 216**: 1-17.

Cruz CD and Vencovsky R (1989) Comparação de alguns métodos de análise dialélica. **Revista Brasileira de Genética 12**: 425-438.

Cruz CD (2013) GENES - a software package for analysis in experimental statistics and quantitative genetics. **Acta Scientiarum. Agronomy 35**: 271-276.

Embrapa – Empresa Brasileira de Pesquisa Agropecuária (2018) **Sistema brasileiro de classificação de solos**. Embrapa, Brasília, 356p.

Fasahat P, Rajabi A, Rad JM and Derera J (2016) Principles and utilization of combining ability in plant breeding. **Biometrics & Biostatistics International Journal 4**: 00085.

Ferreira JM, Moreira RMP and Hidalgo JAF (2009) Capacidade combinatória e heterose em populações de milho crioulo. **Ciência Rural 39**: 332-339.

Gardner CO and Eberhart SA (1966) Analysis and interpretation of the variety cross diallel and related populations. **Biometrics 22**: 439-452.

Griffing B (1956) Concept of general and specific combining ability in relation to diallel crossing systems. **Australian Journal of Biological Sciences 9**: 463-493.

Guimarães LJM, Miranda GV, DeLima RO, Maia C, Oliveira LR and Souza LV (2012) Performance of testers with different genetic structure for evaluation of maize inbred lines. **Ciência Rural 42**: 770-776.

Hallauer AR, Carena MJ and Miranda-Filho JB (2010) **Quantitative genetics in maize breeding**. Springer, New York, 664p.

Ismail MR, El-Hosary AA and El-Badawy MEM (2020) Comparison among three different testers for the evaluation of new maize inbred lines (*Zea mays* L.). **Maydica 65**: 1-6.

Kottek M, Grieser J, Beck C, Rudolf B and Rubel F (2006) World map of the Köppen-Geiger climate classification updated. **Meteorologische Zeitschrift 15**: 259-263.

Miranda-Filho JB (2018) Testadores e dialelos. In Lima R and Borém A (eds) **Melhoramento de milho**. Editora UFV, Viçosa, p. 130-158.

Miranda-Filho JB and Chaves LJ (1991) Procedures for selecting composites based on prediction methods. **Theoretical and Applied Genetics 81**: 265-271.

Miranda-Filho JB and Geraldi IO (1984) An adapted model for the analysis of partial diallel crosses. **Revista Brasileira de Genética 7**: 677-688.

Oyetunde OA, Badu-Apraku B, Ariyo OJ and Alake CO (2020) Efficiencies of heterotic grouping methods for classifying early maturing maize inbred lines. **Agronomy 10:** 1198.

Rodrigues CS, Pacheco CAP, Guedes ML, Pinho RGV and Castro CR (2016) Selection of inbred maize (*Zea mays* L.) progenies by topcrosses conducted in contrasting environments. **Genetics and Molecular Research 15**: gmr.15038827.

Rosa JC, Faria MV, Zaluski WL, Gava E, Andreoli PHW and Sagae VS (2020) Forage potential of S_3 corn progenies in topcrosses and selection of testers of different genetic bases. **Pesquisa Agropecuária Brasileira 55**: e01283.

Rosa JC, Faria MV, Zaluski WL, Uhdre RS, Andreoli PHW and Sagae VS (2021) Combining ability and genetic divergence in the selection of testers regarding grain yield and forage potential in maize topcrosses. **Revista Ciência Agronômica 52**: e20207174.

Rovaris SRS, Araújo PM, Garbuglio DD, Azevedo CVG and Prete CEC (2017) Genetic characterization of the 28 maize landraces in Paraná State. **Ciências Agrárias 38**: 1715-1726.

Silva EHC, Candido WS and Braz LT (2021) Obtaining okra hybrids through partial diallel analysis. **Crop Breeding and Applied Biotechnology 21**: e37192141.

Souza SGH, Carpentieri-Pípolo V, Garbúglio DD, Fonseca Júnior NS, Ruas CF and Ruas PM (2012) Genetic distance estimated by RAPD markers and performance of topcross hybrids in popcorn. **American Journal of Plant Sciences 3**: 1666-1673.

Vancetovic J, Bozinovic S, Ignjatovic-Micic D, Delic N, Kravic N and Nikolic A (2015) A diallel cross among drought tolerant maize populations. **Euphytica 205**: 1-16.

Zhang X, Yong H, Zhou Z, Zhang C, Lu M, Sun Q, Zhang L, Li M, Zhang D, Weng J, Hao Z, Zhang S, Wang Z and Li X (2017) Heterosis and combining ability of seven maize germplasm populations. **Euphytica 213**: 1-11.