

## A new partial diallel model adapted to analyze reciprocal effects in grain yield of maize

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Crop Breeding and Applied Biotechnology  
19: 22-30, 2019  
Brazilian Society of Plant Breeding.  
Printed in Brazil  
<http://dx.doi.org/10.1590/1984-70332019v19n1a04>

**Abstract:** Comparison between two distinct groups using a partial diallel and considering reciprocal effects has not been described in the scientific literature, limiting diallel analysis results. This study compared two groups of parents using a partial diallel, and analyzed the general and specific combining ability and reciprocal effects, divided into maternal and cytoplasmic. A partial diallel was established with nine maize hybrids, including the  $F_1$  and reciprocal hybrids for grain yield. For this application, the reciprocal effects were not significant. The proposed model would provide plant breeders with additional information to analyze partial diallel mating designs.

**Keywords:** Combining ability, cytoplasmic effects maternal effects.

### INTRODUCTION

Maize breeding programs increase the efficiency in planning crosses by evaluating the combining ability of genitors in diallel mating schemes. Usually, breeders design crosses among inbred lines or varieties that result in  $F_1$  hybrids, which may include the reciprocal  $F_1$ 's and their parents, resulting in a very large number of crosses. To control this problem, the partial diallel of parents from contrasting populations was proposed (Miranda Filho and Geraldi 1984, Geraldi and Miranda Filho 1988, Ferreira et al. 2008).

Diallel mating designs are mainly used to assess the general and specific combining abilities (GCA and SCA, respectively) (Griffing 1956), to partition the heterosis in different effects (Gardner and Eberhart 1966) and to study the genetic control of quantitative traits (Hayman 1954a, 1954b). However, the reciprocal effects (REC), which can be partitioned into maternal (MAT) and cytoplasmic or extrachromosomal effects (CIT), are also a study target.

The available models compare two groups of different parents evaluating the GCA and SCA effects (with heterosis evaluation); or evaluate the *per se* analysis of the parents but without considering reciprocal effects (Geraldi and Miranda Filho 1988, Griffing 1956), or evaluate the combining ability and reciprocal effects, which are partitioned into maternal and cytoplasmic effects. More specifically, the reciprocal crosses are included in Griffing's Method 1 and Method 3, by which the reciprocal effects as well as non-maternal effects (Zhang and Kang 1997, Zhang et al. 2005) can be calculated. However, to date, a comparison of two distinct heterotic groups in a partial diallel scheme and considering reciprocal effects has not been described, which limits diallel analysis

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**Received:** 04 April 2018

**Accepted:** 02 November 2018

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and the reciprocal effect over the most important traits in maize.

In maize, for instance, reciprocal effects have been demonstrated for quantitative traits such as grain dry-down (Magari et al. 1996) and resistance to kernel disease caused by *Aspergillus flavus* (Zhang et al. 1997). According to Fan et al. (2014), for several reasons, plant breeders may not always be able to include reciprocal crosses in experiments. Reciprocal crosses may fail or produce an insufficient seed quantity. In crops such as maize, where grain yield (GY) is largely determined by endosperm, reciprocal crosses are important and knowledge about the impact of the inclusion or non-inclusion of reciprocal  $F_1$  crosses in a diallel analysis on GY is essential. The results obtained by Fan et al. (2014) show that the inclusion of reciprocal crosses in a diallel greatly influences GY and the estimation of GCA and SCA effects.

The aims of this study were to: a) a comparison of a single model with fixed and then random effects, of two groups of parents in a partial diallel, as proposed by Geraldi and Miranda Filho (1988), and b) the analysis of the GCA, SCA and reciprocal effects and divided into maternal and cytoplasmic effects, as proposed by Cockerham and Weir (1977) on grain yield.

## MATERIAL AND METHODS

The proposed model was applied in a dataset obtained from a partial diallel cross scheme. The experiment was carried out with nine maize hybrids on a field of the experimental station of Iguatemi (lat 23° 25' S, long 51° 57' W, alt 510 m asl), of the State University of Maringá, Paraná, Brazil. The genotypes were divided in two groups; group 1 comprised the cultivars: 8330, CD3121-1, AG8080, Flash, and Dekalb 350 (denoted as 1,2,3,4, and 5), and group 2 the cultivars 30F80, Strike, Speed, and CD3121-2 (denoted as 6, 7, 8, and 9). The hybrids were obtained from a partial diallel scheme (two contrasting groups), resulting in 20  $F_1$  double hybrids and 20  $F_1$  reciprocal hybrids.

The 49 treatments that include 40 hybrids and 9 parents were evaluated in the growing season 2007/2008 (Table 1). The experiment was arranged in a complete block design with three replications. Each plot consisted of one 5-m row, spaced at 0.9 meters between rows and with plants spaced 0.2 m apart. Grain yield (GY; kg ha<sup>-1</sup>) was measured at harvest.

**Table 1.** The 49 maize treatments, including 40 hybrids and 9 parents evaluated in the growing season 2007/2008

Parents	Hybrids $F_1$ 's and reciprocals	
1 8330	1 x 6 (8330 x 30F80)	9 x 3 (CD3121-2 x AG8080)
2 CD3121-1	6 x 1 (30F80 x 8330)	4 x 6 (Flash x 30F80)
3 AG8080	1 x 7 (8330 x Strike)	6 x 4 (30F80 x Flash)
4 Flash	7 x 1 (Strike x 8330)	4 x 7 (Flash x Strike)
5 Dekalb 350	1 x 8 (8330 x Speed)	7 x 4 (Strike x Flash)
6 30F80	8 x 1 (Speed x 8330)	4 x 8 (Flash x Speed)
7 Strike	1 x 9 (8330 x CD3121-2)	8 x 4 (Speed x Flash)
8 Speed	9 x 1 (CD3121-2 x 8330)	4 x 9 (Flash x CD3121-2)
9 CD3121-2	2 x 6 (CD3121-1 x 30F80)	9 x 4 (CD3121-2 x Flash)
	6 x 2 (30F80 x CD3121-1)	5 x 6 (Dekalb 350 x 30F80)
	2 x 7 (CD3121-1 x Strike)	6 x 5 (30F80 x Dekalb 350)
	7 x 2 (Strike x CD3121-1)	5 x 7 (Dekalb 350 x Strike)
	2 x 8 (CD3121-1 x Speed)	7 x 5 (Strike x Dekalb 350)
	8 x 2 (Speed x CD3121-1)	5 x 8 (Dekalb 350 x Speed)
	2 x 9 (CD3121-1 x CD3121-2)	8 x 5 (Speed x Dekalb 350)
	9 x 2 (CD3121-2 x CD3121-1)	5 x 9 (Dekalb 350 x CD3121-2)
	3 x 6 (AG8080 x 30F80)	9 x 5 (CD3121-2 x Dekalb 350)
	6 x 3 (30F80 x AG8080)	
	3 x 7 (AG8080 x Strike)	
	7 x 3 (Strike x AG8080)	
	3 x 8 (AG8080 x Speed)	
	8 x 3 (Speed x AG8080)	
	3 x 9 (AG8080 x CD3121-2)	

correction to 13% moisture. Fertilizer and field management practices recommended for optimum maize production were used at each location (EMBRAPA 2006).

A partial diallel scheme, composed by the parents,  $F_1$  and reciprocal  $F_1$  crosses, was evaluated by the following statistical model:

$$y_{ijk} = \mu + b_k + G_{ij} + e_{ijk} \quad (1)$$

where:  $Y_{ijk}$  corresponds to the response variable (grain yield) obtained in the trial;  $\mu$  is the general mean;  $G_{ij}$  the  $ij$  diallel effect;  $b_k$  the  $k^{th}$  block effect  $k=1...u$  ( $u$  the number of blocks), and  $e_{ijk}$  the random error effect with distribution NID ( $0, \sigma^2$ ). The genetic effects were included in a diallel sub-model, as follows:

$$G_{ij} = 0.5(g_{r_1} + g_{r_2}) + g_i + g_j + s_{ij} + d_i - \quad (2)$$

with the restrictions:

$$s_{ij} = s_{ji}; r_{ij} = r_{ji} \quad (3)$$

Where  $G_{ij}$  is the diallel effect;  $g_{r_1}$  and  $g_{r_2}$  are the contrasting means between groups 1 and 2;  $g_i$  is the GCA effect of the  $i^{th}$  parent of group 1 with  $i=1,...,p$ ;  $g_j$  the GCA effect of the  $j^{th}$  parent in group 2 with  $j=6,...,q$ ;  $p$  and  $q$  are the number of parents in group 1 and 2, respectively;  $s_{ij}$  is the SCA effect between parent  $i$  and  $j$ , which represent group 1 and 2, respectively;  $d_i$  and  $d_j$  are the maternal effects of the  $i^{th}$  and  $j^{th}$  parent in group 1 and 2, respectively;  $r_{ij}$  is the cytoplasmic effect between the parents  $i$  and  $j$ ;  $d_i - d_j + r_{ij}$  represent the reciprocal variability in the diallel.

In matrix form, it was assumed that  $Y$ , or vector of the response variable have normal distribution  $N(X\beta, I\sigma^2)$  for the model with fixed effects and normal distribution  $N(J\mu, \Sigma)$  for model with random effects; where:  $X$  is the incidence matrix of fixed effects,  $\beta$  is the vector associated with the fixed effects,  $I$  is an identity matrix,  $J$  is a vector of 1s, and  $\Sigma$  is the matrix of variance-covariance associated with the data.

Considering the model with random effects,  $g$  and  $d$  have normal distribution  $N(0, \Sigma_{gd})$  for  $i$  and  $j$  individually,  $s$  and  $r$  have normal distribution with  $N(0, \sigma^2)$ , and  $\Sigma$  is the matrix of variance-covariance associated with the data. In the fixed model, the genetic effects were estimated by the least square method, and in the random model, the genetic effects were not estimated, since the focus is on variance components.

The system  $X'XB=X'y$  provides the normal equation, which with the appropriate restrictions, allows the establishment of the unique solutions:

$$\sum_{k=1}^u \hat{b}_k = 0; (1+q)\hat{g}_1 + q(1+p)\hat{g}_2 = 0; \sum_{i=1}^p \hat{g}_i = 0; \sum_{j=1}^q \hat{g}_j = 0; \hat{s}_i + \sum_{j=1}^q \hat{s}_j = 0; \hat{s}_j + \sum_{i=1}^p \hat{s}_i = 0; \sum_{i=1}^p \hat{d}_i + \sum_{j=1}^q \hat{d}_j = 0 \quad (4)$$

The solution of the normal equations provides the estimation of the parameters that represent the effects contemplated in the proposed fixed model:

$$\begin{aligned} \hat{\mu} &= \frac{Y_T}{N}; & \hat{g}_{r_1} &= \frac{1}{up(p+q+2)} [Y_{(1)} - Y_{(2)} - u(p-q)\hat{\mu}] & ; & & \hat{g}_{r_2} &= \frac{1}{uq(p+q+2)} [Y_{(2)} - Y_{(1)} + u(p-q)\hat{\mu}] \\ \hat{g}_i &= \frac{1}{u(4+2q)} [2Y_i + Y_i + Y_i - \frac{1}{q}(2Y_{(1)} + Y_H + Y_R)] & ; & & \hat{g}_j &= \frac{1}{u(4+2p)} [2Y_j + Y_j + Y_j - \frac{1}{q}(2Y_{(2)} + Y_H + Y_R)] \\ \hat{s}_i &= \frac{Y_i}{u} - \hat{r} + \hat{g}_{r_1} + 2\hat{g}_i & ; & & \hat{s}_j &= \frac{Y_j}{u} - \hat{r} + \hat{g}_{r_2} + 2\hat{g}_j & ; & & \hat{s}_i &= \frac{Y_i + Y_j}{u} - \hat{r} + \frac{1}{2}\hat{g}_{r_1} + \frac{1}{2}\hat{g}_{r_2} + \hat{g}_i + \hat{g}_j & ; & & \hat{d}_i &= \frac{Y_i - Y_j}{2uq} & ; \\ \hat{d}_j &= \frac{Y_j - Y_i}{2uq} & ; & & \hat{r}_i &= \frac{Y_i - Y_j}{u} - (\hat{d}_i - \hat{d}_j) \end{aligned} \quad (5)$$

If the number of parents are the same in both groups, the parameters  $\hat{d}_i, \hat{d}_j$  and  $\hat{r}_{ij}$  are estimates of the effects proposed in the model of Geraldi and Miranda Filho (1988) and Cockerham and Weir (1977).

The sum of squares (SS) for blocks ( $\hat{b}$ ), groups ( $\hat{gr}$ ), GCA within each group ( $GCAgr_1$  and  $GCAgr_2$ ), SCA, maternal effects within each group ( $MATgr_1$  and  $MATgr_2$ ) and cytoplasmic or extrachromosomal (CIT) effects were represented by:

$$SS(\hat{b}) = \frac{1}{N} (Y_{(1)k} + Y_{(2)k} + Y_{Hk} + Y_{Rk})^2 - \frac{(Y_T)^2}{uN} \tag{6}$$

$$SS(\hat{gr}) = \frac{[2q(1+p)Y_{(1)} - 2p(1+q)Y_{(2)} - (p-q)(Y_H + Y_R)]^2}{2uNpq(p+q+2)} \tag{7}$$

$$SS(GCAgr_1) = \frac{1}{u(4+2q)} \left[ \sum_{i=1}^p (2Y_{ii} + Y_i + Y_i) - \frac{1}{q} (2Y_{(1)} + Y_H + Y_R) \right] \quad SS(GCAgr_2) = \frac{1}{u(4+2p)} \left[ \sum_{j=1}^q (2Y_{jj} + Y_j + Y_j) - \frac{1}{p} (2Y_{(2)} + Y_H + Y_R) \right] \tag{8}$$

$$SS(MATgr_1) = \sum_{i=1}^p \frac{(Y_i - Y_i)^2}{2uq} - MS(D) \quad SS(MATgr_2) = \sum_{j=1}^q \frac{(Y_j - Y_j)^2}{2up} - MS(D) \tag{9}$$

$$SS(SCA) = \frac{1}{u} \sum_{i=1}^p Y_{ii}^2 + \frac{1}{u} \sum_{j=1}^q Y_{jj}^2 + \frac{1}{2u} \sum_{i=1}^p \sum_{j=1}^q (Y_{ij}^2 + Y_{ji}^2) - SS(\hat{\mu}) - SS(gr_1) - SS(GCAgr_1) - SS(GCAgr_2) \tag{10}$$

$$SS(CIT) = \frac{1}{2u} \sum_{i=1}^p \sum_{j=1}^q (Y_{ij} - Y_{ji})^2 - SS(MATgr_1) - SS(MATgr_2) - MS(D) \tag{11}$$

The  $SS(MATgr_1)$ ,  $SS(MATgr_2)$  and  $SS(CIT)$  are corrected by the mean square (MS) and by the mean square of the difference (MS(D)) between the sum of the  $F_1$ 's and the sum of the reciprocal  $F_1$ 's, as suggested by Cockerham and Weir (1977), which consider this as a noise in the estimation of the variance components of the effects  $d_1$  and  $d_2$ , as well as for the quadratic components of the same effects. The MS(D) used as correction was estimated as follows:

$$MS(D) = \frac{1}{2upq} (Y_H - Y_R)^2 \tag{12}$$

The mathematical expectations for variance analysis in a model with two approaches (fixed and random) in a complete block design are shown in Table 2. The environmental variance and quadratic components for fixed effects, which represent the variability of the genotypes, were estimated as follows:

**Table 2.** Mathematical expectations of the mean squares of the effects described by the fixed and random diallel models

Source variation	df	Sum of squares	E(LS)	
			Fixed	Random
Group	1	$SS(\hat{gr}_1)$	$\frac{upq(p+q+2)}{2N} \phi_{gr} + \sigma^2$	$a_1 u \sigma_{gr}^2 + a_2 u \sigma_{g1}^2 + a_3 u \sigma_{g2}^2 + a_4 u \sigma_s^2 + \sigma^2$
GCAgr <sub>1</sub>	p - 1	$SS(CGCgr_1)$	$(4+2q)u\phi_{g1} + \sigma^2$	$(4+2q)u\sigma_{g1}^2 + \frac{2(p+1)}{2+q} u\sigma_s^2 + \sigma^2$
GCAgr <sub>2</sub>	q - 1	$SS(CGCgr_2)$	$(4+2p)u\phi_{g2} + \sigma^2$	$(4+2p)u\sigma_{g2}^2 + \frac{2(p+1)}{2+q} u\sigma_s^2 + \sigma^2$
SCA	pq	$SS(SCA)$	$2u\phi_s + \sigma^2$	$a_5 u \sigma_s^2 + \sigma^2$
MATgr <sub>1</sub>	p - 1	$SS(MATgr_1)$	$2uq\phi_{d1} + \frac{2u(q-1)}{pq} \phi_r + \sigma^2$	$2qu\sigma_{d1}^2 + 2u\sigma_r^2 + \sigma^2$
MATgr <sub>2</sub>	q - 1	$SS(MATgr_2)$	$2up\phi_{d2} + \frac{2u(p-1)}{pq} \phi_r + \sigma^2$	$2pu\sigma_{d2}^2 + 2u\sigma_r^2 + \sigma^2$
CIT	pq - p - q + 1	$SS(CIT)$	$\frac{2u(2pq+1)}{pq} \phi_r + \sigma^2$	$2u\sigma_r^2 + \sigma^2$
Residual	N(u-1) - u + 1	SSR	$s^2$	$s^2$

$N = 2pq + p + q$  is the number of treatments (diallel number);  $k=1, \dots, u$  (being  $u$  the number of blocks per treatments) and  $\phi_x = \sum_v \frac{f_v^2}{g_l}$ ,  $x=gr, g1, g2, s, d1, d2$  and  $r$ .

$$a_1 = \frac{pq(p+q+2)}{N}; a_2 = \frac{2q(p+q+2)}{N}; a_3 = \frac{2p(p+q+2)}{N}; a_4 = \frac{2(p+q)(p+1)(q+1)}{N(p+q+2)} \text{ and } a_5 = \frac{2p^2q + 2pq^2 + 3p^2 + 3q^2 + 10pq + 11p + 11q + 12}{(2+q)(2+p)(p+q+2)}$$

$$\hat{\sigma}_{gr} = MSR ; \hat{\phi}_{gr} = \frac{2N}{upq(p+q+2)} [MS(GR) - MSR] ; \hat{\phi}_i = \frac{1}{2u} [MS(SCA) - MSR] ; \hat{\phi}_i = \frac{pq}{2u(p-1)(q-1)} [MS(CIT) - MSR] ;$$

$$\hat{\phi}_{g1} = \frac{1}{u(4+2q)} [MS(GCA_{gr1}) - MSR] ; \hat{\phi}_{d1} = \frac{1}{2uq} [MS(MAT_{gr1}) + \frac{q-1}{pq+1} MS(CIT) - \frac{q(p+1)}{pq+1} MSR] ; \hat{\phi}_{g2} = \frac{1}{u(4+2p)} [MS(GCA_{gr2}) - MSR] ;$$

$$\hat{\phi}_{d2} = \frac{1}{2up} [MS(MAT_{gr2}) + \frac{p-1}{pq+1} MS(CIT) - \frac{p(q+1)}{pq+1} MSR]$$

These quadratic components were estimated by the method of least squares, and may therefore result in negative values; in this situation, they should be considered equal to zero. Considering the fixed and random-effect models, the hypotheses to compare the effects analyzed in this study are shown in Table 3, with their respective statistics for the F-test and degrees of freedom. For the fixed effects, the variances of genetic effects were calculated as:

$$Var[\hat{\mu}] = \frac{1}{N} \sigma^2 ; Var[\hat{g}_{r1}] = \frac{2q(1+p)^2}{up(p+q+2)^2} \sigma^2 ; Var[\hat{g}_{r2}] = \frac{2p(1+q)^2}{uq(p+q+2)^2} \sigma^2 ; Var[\hat{g}_i] = \frac{p-1}{up(4+2q)} \sigma^2 ; Var[\hat{g}_j] = \frac{q-1}{uq(4+2p)} \sigma^2 ;$$

$$Var[\hat{s}_{ii}] = \frac{q(p+q+1)}{u(p+q+2)(2+q)} \sigma^2 ; Var[\hat{s}_{jj}] = \frac{p(p+q+1)}{u(p+q+2)(2+p)} \sigma^2 ; Var[\hat{s}_{ij}] = \frac{4pq+p^2q+3p^2+q^2+pq^2+3q+4}{2u(p+q+2)(q+2)(p+2)} \sigma^2 ; Var[\hat{d}_i] = \frac{1}{2uq} \sigma^2 ;$$

$$Var[\hat{d}_j] = \frac{1}{2up} \sigma^2 ; Var[\hat{f}_{ij}] = \frac{N}{2upq} \sigma^2 ; Var[\hat{g}_{r1} - \hat{g}_{r2}] = \frac{2N}{upq(p+q+2)} \sigma^2$$

For  $i \neq k$  with  $i = 1, 2, \dots, k-1, k+1, \dots, p$  and for  $j \neq k'$  with  $j = 1, 2, \dots, k'-1, k'+1, \dots, q$ . The variances for the effects of differences were estimated as follows:

$$Var[\hat{g}_i - \hat{g}_k] = \frac{1}{u(2+q)} \sigma^2 ; Var[\hat{g}_j - \hat{g}_{k'}] = \frac{1}{u(2+p)} \sigma^2 ; Var[\hat{s}_{ij} - \hat{s}_{k'k'}] = \frac{2p}{u(2+p)} \sigma^2 ; Var[\hat{s}_{ij} - \hat{s}_{kj}] = \frac{q+1}{u(2+q)} \sigma^2$$

$$Var[\hat{s}_{ij} - \hat{s}_{ik'}] = \frac{p+1}{u(2+p)} \sigma^2 ; Var[\hat{s}_{ij} - \hat{s}_{kk'}] = \frac{pq+p+q+2}{u(2+q)(2+p)} \sigma^2 ; Var[\hat{d}_i - \hat{d}_k] = \frac{1}{q} \sigma^2 ; Var[\hat{d}_j - \hat{d}_{k'}] = \frac{1}{up} \sigma^2$$

$$Var[\hat{f}_{ij} - \hat{f}_{kj}] = \frac{q+1}{uq} \sigma^2 ; Var[\hat{f}_{ij} - \hat{f}_{k'k'}] = \frac{p+1}{up} \sigma^2 ; Var[\hat{f}_{ij} - \hat{f}_{kk'}] = \frac{1}{u} \sigma^2$$

Before calculating the mean square expectations, the variance components of genetic effects were estimated as follows:

$$\hat{\sigma}_{gr}^2 = \frac{N}{upq(p+q+2)} [MS(GR) - \frac{q(p+q+2)}{N(2+q)} MS(GCA_{gr1}) - \frac{q(p+q+2)}{N(2+q)} MS(GCA_{gr2}) -$$

$$\frac{2pq(3p^3q+3pq^3+3p^3+3q^3+6p^2q^2+p^2q^3+p^3q^2+4q+4p+8pq+8p^2+8q^2+10p^2q+10pq^2)}{N(2+q)(2+p)(2p^2q+2pq^2+3p^2+3q^2+10pq+11p+11q+12)} MS(SCA) -$$

$$\frac{pq(2p^3q^2+2p^2q^3+3q^3+3p^3+20p^2q^2+49pq^2+49p^2q+29p^2+29q^2+114pq+6p^3q+6q^3p+72p+72q+48)}{N(2+q)(2+p)(2p^2q+2pq^2+3p^2+3q^2+10pq+11p+11q+12)} MSR]$$

$$\hat{\sigma}_{g1}^2 = \frac{1}{2u(2+q)} [MS(GCA_{gr1}) - \frac{2(q+1)(2+p)(p+q+2)}{2p^2q+2pq^2+3p^2+3q^2+10pq+11p+11q+12} MS(SCA) -$$

$$\frac{p^2-q+3p+4-q^2}{2p^2q+2pq^2+3p^2+3q^2+10pq+11p+11q+12} MSR]$$

$$\hat{\sigma}_{g2}^2 = \frac{1}{2u(2+p)} [MS(GCA_{gr2}) - \frac{2(p+1)(2+q)(p+q+2)}{2p^2q+2pq^2+3p^2+3q^2+10pq+11p+11q+12} MS(SCA) -$$

$$\frac{-p^2-p+3q+4+q^2}{2p^2q+2pq^2+3p^2+3q^2+10pq+11p+11q+12} MSR]$$

**Table 3.** Hypotheses, statistics for F-test and degrees of freedom for the parameters of fixed and random models

Source of variation	Hypotheses	F-Statistics	df
<b>Fixed effects model</b>			
Group	$H_0: g_{r_1}=g_{r_2}$	$MS(GR)/QMR$	$[1, N(u-1)-u+1]$
GCAgr <sub>1</sub>	$H_0: g_1=g_2=\dots=g_p=0$	$MS(GCAgr_1)/QMR$	$[(p-1), N(u-1)-u+1]$
GCAgr <sub>2</sub>	$H_0: g_1=g_2=\dots=g_q=0$	$MS(GCAgr_2)/QMR$	$[(q-1), N(u-1)-u+1]$
SCA	$H_0: s_{i0}=s_{0i}=s_{ij}=0$	$MS(SCA)/QMR$	$[pq, N(u-1)-u+1]$
MATgr <sub>1</sub>	$H_0: d_1=d_2=\dots=d_p$	$[MS(MATgr_1) + b_1MS(CIT)]/b_2QMR$	$[n_1^*, (p-1)(q-1)]$
MATgr <sub>2</sub>	$H_0: d_1=d_2=\dots=d_q$	$[MS(MATgr_2) + b_3MS(CIT)]/b_4QMR$	$[n_2^*, (p-1)(q-1)]$
CIT	$H_0: r_{ij}=0$	$MS(CIT)/QMR$	$[(p-1)(q-1), N(u-1)-u+1]$
<b>Random effects model</b>			
Group	$H_0: s^2_{gr} = 0$	$MS(GR)/[c_1MS(GCAgr_1)+c_2MS(GCAgr_2)+c_3MS(SCA)+c_4QMR]$	$[1, n_3^*]$
GCAgr <sub>1</sub>	$H_0: s^2_{g1} = 0$	$MS(GCAgr_1)/[d_1MS(SCA)+(1-d_1)QMR]$	$[(p-1), n_4^*]$
GCAgr <sub>2</sub>	$H_0: s^2_{g2} = 0$	$MS(GCAgr_2)/[d_2MS(SCA)+(1-d_2)QMR]$	$[(q-1), n_5^*]$
SCA	$H_0: s^2_s = 0$	$MS(SCA)/QMR$	$[pq, N(u-1)-u+1]$
MATgr <sub>1</sub>	$H_0: s^2_{d1} = 0$	$MS(MATgr_1)/MS(CIT)$	$[(p-1), (p-1)(q-1)]$
MATgr <sub>2</sub>	$H_0: s^2_{d2} = 0$	$MS(MATgr_2)/MS(CIT)$	$[(q-1), (p-1)(q-1)]$
CIT	$H_0: s^2_r = 0$	$MS(CIT)/QMR$	$[(p-1)(q-1), N(u-1)-u+1]$

\* The df of linear combinations of least squares associated to F-test was calculated using the Satterthwaite (1946) approximation, as suggested by Gaylor and Hopper (1969), and Sahai and Ojeda (2004).

The degrees of freedom (v1, v2, v3 and v4) were calculated as:

$$v_1 = \frac{[MS(MATgr_1) + b_1MS(CIT)]^2}{[MS(MATgr_1)]^2 + \frac{[b_1MS(CIT)]^2}{(p-1)(q-1)}}; \quad v_2 = \frac{[MS(MATgr_2) + b_3MS(CIT)]^2}{[MS(MATgr_2)]^2 + \frac{[b_3MS(CIT)]^2}{(p-1)(q-1)}}; \quad v_3 = \frac{[c_1MS(GCAgr_1) + c_2MS(GCAgr_2) + c_3MS(SCA) + c_4QMR]^2}{\frac{[c_1MS(GCAgr_1)]^2}{p-1} + \frac{[c_2MS(GCAgr_2)]^2}{q-1} + \frac{[c_3MS(SCA)]^2}{pq} + \frac{[c_4QMR]^2}{N(u-1)}}; \quad v_4 = \frac{[d_1MS(SCA) + (1-d_1)QMR]^2}{\frac{[d_1MS(SCA)]^2}{pq} + \frac{[(1-d_1)QMR]^2}{N(u-1)}}$$

$$v_5 = \frac{[d_2MS(SCA) + (1-d_2)QMR]^2}{\frac{[d_2MS(SCA)]^2}{pq} + \frac{[(1-d_2)QMR]^2}{N(u-1)}}$$

Where:  $b_1 = \frac{q-1}{p+1}; b_2 = \frac{q(p+1)}{p+1}; b_3 = \frac{p-1}{p+1}; b_4 = \frac{p(q+1)}{p+1}; c_1 = \frac{p(p+q+2)}{N(2+q)}; c_2 = \frac{q(p+q+2)}{N(2+p)};$

$$c_3 = \frac{2pq(3p^3q+3p^3+3q^3+6p^2q^2+p^2q^3+p^3q^2+4q+4p+8p^2+8p^2+8q^2+0)p^2q+0p^2}{N(2+q)(2+p)(2p^2q+2p^2+3p^2+3q^2+0)p+1p+1q+2};$$

$$d_1 = \frac{2(q+1)(2+p)(p+q+2)}{2p^2q+2p^2+3p^2+3q^2+0p+1p+1q+2}; \quad d_2 = \frac{2(p+1)(2+q)(p+q+2)}{2p^2q+2p^2+3p^2+3q^2+0p+1p+1q+2}$$

$$\hat{\sigma}_s^2 = \frac{(2+q)(2+p)(p+q+2)}{u(2p^2q+2pq^2+3p^2+3q^2+10pq+11p+11q+12)} [MS(SCA) - MSR] \tag{16}$$

$$\hat{\sigma}_r^2 = \frac{1}{2u} [MS(CIT) - MSR]; \quad \hat{\sigma}_{d1}^2 = \frac{1}{2uq} [MS(MATgr_1) - MS(CIT)]; \quad \hat{\sigma}_{d2}^2 = \frac{1}{2up} [MS(MATgr_2) - MS(CIT)]$$

## RESULTS

The observed variation, in both fixed and random effect models, was partitioned into GCAgr1, GCAgr2, SCA, REC, MATgr1, MATgr2, and CIT effects. The results of these parameters were similar, mainly because the analysis of variance is very similar in both models. In the fixed-effect model, GCAgr1 and SCA were significant, and in the random effect model, only SCA was statistically significant (Table 4).

In the fixed model, the treatment effect was statistically significant for grain yield, suggesting mean differences among some of the 20 F<sub>1</sub>'s, 20 reciprocals and 9 parents (Table 4). As the GCAgr1 and SCA effects were statistically significant

**Table 4.** Variance and diallel analysis for grain yield considering fixed and random effects

Fixed effects					
Source of Variation	df	Sum of Squares	Mean Square	F	P-value
Treatments	48	238306781	4964725	3.563	0.000000
Block	2	21608144	10804072	7.753	0.000756
Residual	96	41388973	431135		
Total	146	393696024			
Group	1	3995786	3995786	2.867	0.0936
GCAgr <sub>1</sub>	4	46605185	11651296	8.361	0.0000
GCAgr <sub>2</sub>	3	10761960	3587320	2.574	0.0584
SCA	20	162530585	8126529	5.832	0.0000
MATgr <sub>1</sub>	4	1379999	345000	0.277**	0.9375
MATgr <sub>2</sub>	3	4307305	1435768	0.943**	0.4530
CIT	12	8057475	671456	0.482	0.9209
Estimates of least square					
$\hat{\phi}_{gr} = 357875.39; \hat{\phi}_{g1} = 279602.55; \hat{\phi}_{g2} = 47659.89; \hat{\phi}_s = 1090154.12; \hat{\phi}_{d1} = 0; \hat{\phi}_{d2} = 0; \hat{\phi}_r = 0$					
Random effects					
Source of Variation	df	Sum of Squares	Mean Square	F	P-value
Group	1	3995785.71	3995785.71	0.7714***	0.3886
GCAgr <sub>1</sub>	4	46605184.68	11651296.17	1.4706***	0.2480
GCAgr <sub>2</sub>	3	10761959.97	3587319.99	0.4424***	0.7253
SCA	20	162530584.70	8126529.24	5.8315	0.0000
MATgr <sub>1</sub>	4	1379999.37	344999.85	0.5138	0.7271
MATgr <sub>2</sub>	3	4307304.57	1435768.20	2.1383	0.1486
CIT	12	8057475.27	671456.28	0.4818	0.9209
Residual	96	133781099.00	1393553.10		
Estimates of components of variance					
$\hat{\sigma}_{gr}^2 = 0; \hat{\sigma}_{g1}^2 = 103563.41; \hat{\sigma}_{g2}^2 = 0; \hat{\sigma}_s^2 = 2238672.16; \hat{\sigma}_{d1}^2 = 0; \hat{\sigma}_{d2}^2 = 25477.06; \hat{\sigma}_r^2 = 0$					

\* This value should be considered zero when negative. \*\* The df for linear combination of least squares in the numerator of F-test on fixed effects was estimated with the Satterthwaite approximation for maternal effect in the groups 1 and 2, with values of  $v_1=5.535$  and  $v_2=4.679$ , respectively. \*\*\* The df for linear combination of least squares in the denominator of F-test for random effects were estimated by the Satterthwaite approximation for Group with  $v_3=23.620$ , GCAgr<sub>1</sub> and GCAgr<sub>2</sub> with  $v_4=20.214$  and  $v_5=20.017$ , respectively.

for GY, this indicates the importance of genes whit both additive and non-additive effects controlling this trait. However, the quadratic components of the fixed model show that SCA was higher than GCA ( $[\phi g_1 + \phi g_2] / \phi s = 0.3005$ ), suggesting the predominance of non-additive gene effects on grain yield (Table 4).

The group effects (contrast between Group 1 v/s Group 2) and GCAgr2 showed non-statistical significance (Table 4). This result indicates that, for GY, the additive genetic effects are similar between Group 1 and Group 2.

In the random model, the variances between groups (P-value = 0.3886) and GCA in both groups (GCAgr1 and GCAgr2) were not statistically significant (P-value = 0.2480 and 0.7253, respectively). In contrast, the variance for SCA was significant (P-value <0.1), indicating that GY was influenced by non-additive effects. In both fixed and random effect models, maternal effects for both groups were not statistically significant (MATgr1 P-value = 0.9375; MATgr2 P-value = 0.4530 and CIT P-value = 0.9209), suggesting that GY was not controlled by reciprocal effects (Table 4).

The best parents for GY were the hybrids AG8080, Flash and Dekalb 350. Based on SCA effects, the best double and multiple-cross hybrids were the crosses CD3121-1 (gr1) x 30F80 (gr2) (SCAS26 = 1284.96) and Dekalb 350 (gr1) x CD3121-2 (gr2) (SCAS59 = 1135.12) (Table 5). Although these combinations have no practical commercial applications, they can be improved by interpopulational breeding strategies.

## DISCUSSION

In diallel analysis based on a fixed effect model, the comparison of the results is restricted to the least square means

of the set of parents used in the diallel analysis, whereas the results obtained through the random effect model the inference can be made from the population that these parents are derived, based on the components of variance (Baker 1978). In breeding programs, it is very usual to consider the treatments (e.g., genotypes) as random effect, mainly due to the interest in genetic components of variance, although considering them as fixed effect allows the comparison between the genotypes used in the crosses.

**Table 5.** Estimates of genetic parameters for fixed model

Group1		Group2	
Parameters	Estimates	Parameters	Estimates
$gr_1$	-377.27	$gr_2$	392.99
$SE[\hat{g}r_1 - \hat{g}r_2]$	454.88	-	-
g1	-616.69	g6	285.89
g2	-598.53	g7	-73.47
g3	611.25	g8	164.48
g4	300.84	g9	-376.90
g5	303.15	-	-
$SE[\hat{g}r_1 - \hat{g}r_2]$	278.24	$SE[\hat{g}r_j - \hat{g}r_k]$	257.60
S11	1745.39	S66	169.34
S22	2010.99	S77	1864.21
S33	151.65	S88	1742.24
S44	1708.79	S99	1024.58
S55	-816.45	-	-
$SE[\hat{s}_{j_0} - \hat{s}_{k_0}]$	786.99	-	-
d1	31.55	d6	-47.79
d2	30.81	d7	223.65
d3	153.81	d8	-214.64
d4	-75.48	d9	-259.78
d5	232.49	-	-
$SE[\hat{d}_i - \hat{d}_k]$	340.78	$SE[\hat{d}_j - \hat{d}_k]$	357.41
S16	-521.35	r16	-266.46
S17	-693.09	r17	142.21
S18	-637.44	r18	-157.89
S19	106.49	r19	-16.40
S26	1284.96	r26	-537.26
S27	-65.24	r27	-131.99
S28	119.95	r28	159.77
S29	-3350.67	r29	210.94
S36	-404.68	r36	87.24
S37	-260.35	r37	-255.71
S38	-86.03	r38	227.43
S39	599.41	r39	-357.51
S46	-592.35	r46	-49.57
S47	-651.56	r47	276.75
S48	-949.96	r48	-207.24
S49	485.08	r49	-318.49
S56	64.08	r56	392.86
S57	-193.97	r57	-404.44
S58	-188.77	r58	-395.25
S59	1135.12	r59	108.27
$SE[\hat{s}_{ij} - \hat{s}_{kj}]$	622.17	$SE[\hat{r}_{ij} - \hat{r}_{kj}]$	762.00
$SE[\hat{s}_{ij} - \hat{s}_{kk}]$	630.99	$SE[\hat{r}_{ij} - \hat{r}_{kk}]$	746.61
$SE[\hat{s}_{ij} - \hat{s}_{kk}]$	585.54	$SE[\hat{r}_{ij} - \hat{r}_{kk}]$	1180.49

SE: Standard Error.

The reciprocal and maternal effects are essential for the selection of inbred lines as female or male parents. In addition, reciprocal effects have been reported for a number of quantitative traits in maize (Fan et al. 2008, Yao et al. 2013, Fan et al. 2014). Commonly, plant breeders use diallel methods without estimates of MAT and REC effects (e.g., Griffing's Methods 2 and 4), which causes lack of information and may result in unexploited superior crosses (Yao et al. 2013). Thus, we proposed a new partial diallel model adapted to analyze reciprocal effects allowing the computation of reciprocal as well as maternal and cytoplasmic effects.

The results of this study suggest that GY was not controlled by reciprocal effects in either group (MATgr1 and MATgr2), in agreement with reports of Zare et al. (2011), who pointed out that reciprocal effects were not significant for GY. In contrast, other authors concluded that the interaction of cytoplasmic and nuclear genes affects significantly hybrid performance for GY and other important agronomic traits (Zhang et al. 2016). According to Yao et al. (2013), for example, reciprocal effects have a major impact on the determination of hybrid yield. More specifically, the results of Fan et al. (2014) showed that considering reciprocal crosses in a diallel model greatly impacted GY and estimates of GCA and SCA effects. In addition, Zhang et al. (2016) mentioned that these results indicate the need for a new hypothesis that can fully explain heterosis, taking the cytoplasmic genes and their interaction with nuclear genes into account.

As proposed by Fan et al. (2014), considering the impact of reciprocal crosses on GY and SCA estimation, the possible result would have a great impact on maize heterotic group classification. Another study recently reported how MAT influenced GCA effects and how REC affected SCA effects in Griffing's Method 1 and 3 (Mahgoub 2011). The current proposed model should be relevant to analyze a partial diallel mating design, using key genetic statistics that allow the computation of REC as well as maternal (MAT) and cytoplasmic effects (CIT). None of the above studies reported the impact of reciprocal crosses or REC on a partial diallel mating design.

The proposed model generates additional information about partitioning GCA and SCA effects to estimate maternal and reciprocal effects in a partial diallel mating design, and would help to identify each parent used as male or female parent and provide precise information about the nature of the interaction between the best parent combinations.

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