Partial diallel analysis of maize inbred lines for grain yield and resistance to gray leaf spot including reciprocal effects

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Keywords: *Combining ability, gene effects, reciprocal effects.*

Abstract

The use of diallel crosses for breeding of disease-resistant genotypes with high grain yield is a common practice in maize (*Zea mays* L.) breeding programs. The objective of this study was to evaluate the grain yield and resistance to gray leaf spot of maize inbred lines and hybrids, including reciprocals,using a new diallel model approach, described in a recent publication, to estimate the effects of general and specific combining abilities and reciprocal effects partitioned in maternal and cytoplasmic effects. For a simultaneous increase in grain yield and genetic resistance to gray leaf spot, D3 is the most promising inbred line for future combinations, in view of the positive GCA effects for grain yield and negative effects for *C. zeina* severity.The hybrid combinations D2 x F3, D3 x F5 and D4 x F3 should be used in future field trials. Based on the estimates of the reciprocal effects, D6 is recommended as female parent in hybrid combinations for resistance to *Cercospora zeina*

Introduction

Gray leaf spotof maize (*Zea mays* L.), caused by the pathogens *Cercospora zeae-maydis* and *Cercospora zeina*, is one of the main foliar diseases that affect maize, causing grain yield losses of up to 65% (Donahue et al, 1991; Ward and Nowell, 1998; Ward et al, 1999; Brito et al, 2007). The level of incidence and damage caused by gray leaf spot varies according to the soil management, plant density, climatic conditions and resistance level of the genotype. Fungicide applications and crop rotation are some of the management techniques that mitigate the damage caused by the disease (Shaner et al, 1998), although planting resistant genotypes is considered the most effective method of gray leaf spot control (Gevers et al, 1994; Ward et al, 1999; Lennon et al, 2016).

The species *Cercospora zeae-maydis* and *Cercospora zeina* were initially classified into two distinct groups of the species C. *zeae-maydis* (Wang et al, 1998). However determining the genetic diversity among the groups by molecular markers allowed the separation into two species with distinct geographical distribution: *C. zeina*, which is common in Brazil, the African continent and eastern United States, while *C. zeae-maydis* is predominant in a large part of the maize-producing regions of the United States (Meisel et al, 2009).

According to Crous et al (2006), *C. zeina* has short conidiophores and fusiform conidia, slower culture growth andproduces none of the purple pigment associated to the toxin cercosporin, which is typical of *C. zea-maydis*. In addition, the leaf spots (width 2-3 mm, length 5-40 mm) caused by *C. zeina* are confined between the leaf ribs, with light gray to straw brown colors, and blurred and chlorotic edges of the young lesions.

The nature of genetic resistance to gray leaf spot in maize is quantitative, with moderate to high heritability and predominantly additive gene effects, with high environmental influence (Gordon et al, 2006; Zwonitzer et al., 2010; Sibiya et al, 2012, Lennon et al., 2016). However, some authors identified the participation of non-additive gene effects that influence the resistance of maize hybrids (Derera et al., 2008; Vivek et al., 2010; Sibiya et al., 2011. Nedi et al., 2018). Partial resistance is usually expressed by a reduction in lesion number and size, as well as in a drop in the fungal sporulation rate (Menkir & Ayodele, 2005).

In plant breeding programs, the genetic effects that influence the traits of interest must be known in order to determine the most appropriate breeding method (Hallauer et al., 2010). Using diallel analysis, breeders can obtain estimates of general combining ability (GCA) and specific combining ability (SCA), which are associated, respectively, with additive and non-additive gene effects (Griffing, 1956).

Recently, Barata et al. (2019) developed a new methodology involving diallel crosses, since the literature contains no reports on a method of partial diallel mating that takes the reciprocal effects partitioned into maternal and cytoplasmic effects into account. This new methodology is based on the partial diallel model of Geraldi and Miranda Filho (1988), associated with the reciprocal effects of Cockerham and Weir (1977).

The purpose of this study was to evaluate grain yield and genetic resistance of maize inbred lines to *Cercospora zeina*, based on GCA and SCA estimates and the partitioning of the reciprocal effect (RE) in maternal and cytoplasmic effects for partial diallels, in order to select the most promising lines in a maize breeding program for superior genotypes.

Material and methods

Maize genotypes

Of the 11 maize inbred lines used in this study (Table 1), seven were provided by the International Center for Improvement of Maize and Wheat, (CIMMYT) and four derived from commercial hybrids, selfed at the Universidade Estadual de Maringá (UEM). All inbred lines were in the 8th selfing generation (S8).

Agronomic trials

The crosses for the hybrid combinations were performed in the late season of 2012, based on a partial diallel mating design with six lines of the dent (Group I) and five of the flint group (Group II), resulting in the F_1 crosses and reciprocals. The 11 parents, 30F_1 hybrid combinations and 30 reciprocal combinations resulted in a total of 71 treatments.

Two field trials were carried out. The first (field trial I) evaluated the grain yield of the genotypes, and the second (field trial II) the resistance of these genotypes in response to field inoculation with *Cercospora zeina*. Both experiments were evaluated at two locations in the main growing season (summer) of 2012/2013, on the Experimental farm of Iguatemi - FEI (23° 25' S; 51° 57' W, 510m asl), county of Maringá, Paraná, and at the Experimental Unit Sementes Balu (23° 19' S; 51° 33'W, 725m asl), county of Sabáudia, Paraná.

The field trial was arranged in a randomized complete block design, with three replications. In field trial I, the experimental units consisted of two 5-m rows, spaced 0.8 m apart, resulting in a total assessable area of 8 m^2. In field trial II, the units consisted of one 3-mrow, at a spacing of 0.8 m, with an assessable area of 2.4 m^2. Thinning was performed 25 days after seedling emergence, adjusting the final plant density to 55,555 plants ha^{-1}. Other cultural treatments were applied according to official technical recommendations for maize (Galvão and Miranda, 2004), without fungicide application.

Table 1 - Description of the parents used in the partial diallel of Geraldi and Miranda Filho (1988),along with the reciprocal effects of Cockerham and Weir (1977).

Lines	Code	Origin	Grain color	Grain type
CML 9	D1	CIMMYT	Yellow	Dent
CML 23	D2	CIMMYT	Orange	Dent
77H301	D3	DKB360/Dekalb	Orange	Dent
9H33	D4	AG8080/ Agroceres	Orange	Dent
88H47	D5	CD303/Coodetec	Orange	Dent
95H344	D6	2C599/Dow	Orange	Dent
CML 12	F1	CIMMYT	Yellow	Flint
CML 19	F2	CIMMYT	Yellow	Flint
CML 22	F3	CIMMYT	Orange	Flint
CML 18	F4	CIMMYT	Orange	Flint
CML 13	F5	CIMMYT	Yellow	Flint

Inoculation assays

Five *Cercospora zeina* isolates were used for inoculation in field trial II, provided by the Laboratory of Phytopathology, Universidade Estadual de Maringá. The isolates were transferred to potato-dextrose-agar culture medium (PDA - 200 g L^{-1} potato, 20 g L^{-1} dextrose, and 14 g L^{-1} agar)in Pyrex petri dishes, and left to stand for approximately seven days at 27 °C and a 12-h photoperiod. Then, to induce sporulation, the isolates were plated on seasoned tomato juice (STJ - 200 m L)culture medium in Pyrex petri dishes, at 25 °C and a 12-h photoperiod, for15 days.

The inoculum was prepared by transferring five discs of STJ culture medium colonized by the fungus andwith visible sporulation to125-mL Erlenmeyer flasks containing 20g sorghum seeds previously moistened with 16 mL water and sterilized twice by autoclaving for 20 min at 1 atm. The cultures were maintained at 25°Cand a 12/12h ambient light/dark photoperiod for 15 days, for pathogen colonization and sporulation onthe sorghum seeds.

The plants in field trial II were inoculated in development stage V6 by placing 10 sorghum seeds colonized by the pathogen in the leaf whorls of each plant. In the first five days after inoculation,the field trial was irrigated twice a day, in the morning and afternoon, for approximately 20 min.

Evaluated traits

In field trial I, for grain yield assessment, the two plant rows were harvested and the grain yield expressed in kg ha^{-1}, for a moisture content adjusted to 13%.

In field trial II, five plants per plot were evaluated 40 days after inoculation. For this purpose, the ear leaf of every plant was collected and assessed separately for disease severity. The severity levels of five leaves represented the plot mean. Disease severity was visually assessed in severity classes of 0, 2, 5, 10, 20, 35, and 50%, based on the diagrammatic scale proposed by Smith (1989).

Statistical analyses

The analyses were based on a mathematical-statistical model proposed by Barata et al. (2019) using software R (R Core Team, 2016). The model includes the reciprocal effects divided into maternal and cytoplasmic effects, as proposed by Cockerham and Weir (1977) and the analysis of the *per se* performance of the parents. It also allows for a comparison of two parent groups using a partial diallel, as proposed by Geraldi and Miranda Filho (1988):

$$Y_{ijk} = \mu + \frac{1}{2}\left(g_1 + g_2\right) + g_i + g_j + s_j + d_i - d_j + r_j + \varepsilon_{ijk}$$

with the restrictions:

$$s_{ij} = s_j, r_j = -r_j$$

where: Y_{ijk} corresponds to the k-th response of diallel ij, with k=1...u; μ is the overall mean; gr_1 and gr_2 are the contrasts involving means of group 1 and 2; g_i is the effect of the general combining ability of the i-th parent of group 1, with i=1...p; g_j is the effect of the general combining ability of the j-th parent of group 2, j=1...q; s_{ij} is the effect of the specific combining ability between the parents of order i and j, of group 1 and 2, respectively;d is the maternal effect of the i-th parent of group 1; d_j is the maternal effect of the j-th parent of group 2; r_{ij} is the cytoplasmic effect between the parents of order i and j; d_i + d_j - r_{ij} represent the reciprocal variability within the crosses; and is the randomerror effect ~ NID(0,σ^2).

Results and discussion

Analysis of variance

The summary of the combined analysis of variance for grain yield and severity of gray leaf spot (Table 2) indicated significance ($p<0.05$) of the treatment means for the two traits, evidencing the existence of genetic variability among the studied genotypes. The mean squares for the interaction between treatments and environments were significant ($p<0.05$) for grain yield, evidencing the differentiated behavior of the genotypes in the two environments. With regard to gray leaf spot severityin response to *C. zeina* inoculation, the genotype performance was similar in the tested environments, so that the analysis could be based on the average performance of the genotype inthe two environments.

Table 2 - Combined analysis of variance in 11 parents, 30 F$_1$hybrids and 30 reciprocal F$_1$ hybridsevaluated in Maringá-PR and Sabáudia-PR, in the main growing season of 2012/2013

Source of variation	DF	Least Squares	
		GY^1	*C. zeina*^{2}
Blocks/ Environments	4	437897	65
Environment	1	395712378*	224*
Treatments	70	18201591*	4581*
Treatments x Environments	70	3225396*	27^{ns}
Residue	280	67255	41
$\hat{r}_{gg}$		099	098

*Significant ($p<0.05$) by the F test^{ns} non-significant ($p>0.05$) by the F test ^{1}Grain Yield (GY - kg ha^{-1});^{2} Severity caused by C. *zeina*(%)

In a study with hybrids of tropical lines evaluated in six environments, Sibiya et al. (2011) found significant differences between the effects of the genotype- environment interaction on gray leaf spot severity, while Engelsing et al. (2011) also observed a significant interaction between grain yield and *C. zeina* severity. In both studies,inoculation with gray leaf spot occurred under natural conditions. In field trial II, the inoculum pressure was standardized, ensuring a similar expression of genotype resistance or susceptibility in the tested environments.

Selection accuracy $(\hat{r}_{gg})$ was used by Resende and Duarte (2007) as anevaluation parameter of the quality of the field trials. According to the same authors, the precision of the selection accuracy estimates for grain yield and *C. zeina* severity can be classified as high (Table 2).

Diallel analysis

In the diallel analyses for grain yield and *C. zeina* severity (Table 3), the GCA effect was significant ($p<0.05$) for group I (Dent) and group II (Flint), indicating differences between the inbred lines in the capacity of transmitting additive effect alleles, influencing the evaluated traits of the hybrids.

The SCA effect was also significant ($p<0.05$) for the two traits, indicating not only additivity but also the presen-

Table 3 - Estimates of GCA, SCA, MAT, and CYT for the traits grain yield and C. zeina severity (%) evaluated in Maringá-PR and Sabáudia-PR, in the main growing season of 2012/2013

Source of variation	DF	Mean squares	
		GY^1	*C. zeina*^{2}
Group	1	413042.61*	77.96*
GCAgr_I^3	5	23527384.77*	1641.09*
GCAgr_{II}^4	4	15699892.44*	4824.90*
SCA^5	30	36399900.40*	129.27*
MATgr_I^6	5	36630.64^{ns}	17.58*
MATgr_{II}^7	4	42505.10^{ns}	7.46*
CYT^8	20	45579.91^{ns}	22.36*
Group x environments	1	5207547.78*	0.00^{ns}
GCAgr_I x environments	5	6560131.31*	5.84^{ns}
GCAgr_{II} x environments	4	7066258.76*	5.99^{ns}
SCA x environments	30	5287541.52*	2.29^{ns}
MATgr_Ix environments	5	45315.00^{ns}	1.40^{ns}
MATgr_{II} x environments	4	15860.24^{ns}	3.09^{ns}
CYT x environments	20	26388.15^{ns}	1.23^{ns}
Residue	280	67255	4.1

*Significant ($p<0.05$) by the F test. ^{Ns} not significant ($p>0.05$) by the F test.^{1}Grain Yield (GY-kg ha^{-1}); 2Severity caused by C. *zeina* (%);^{3}GCAgr_I: General combining ability for group I; ^{4}GCAgr_{II}: General combining ability for group II; ^{5}SCA: Specific combining ability; ^{6}MATgr_I: maternal effects for group I; ^{7}MATgr_{II}: maternal effects for group II; ^{8}CYT: cytoplasmic effects.

ce of non-additive gene action. This result shows that the hybrid performance differs from the expected based on GCA estimates of the parents, mainly due to a possible gene complementation or genetic divergence in relation to the allele frequencies in the loci with non-additive effects (Cruz et al, 2012).

The GCA, SCA, maternal (MAT), and cytoplasmic (CYT) effects were estimated based on the significance of their interaction with the environments (Table 3). Considering the results of the combined analysis of variance (Table 2), the GCA and SCA effects for grain yield were estimated separately for each environment, while for *C. zeina* severity, the effects were estimated based on the environment mean. For MAT and CYT, the effects were only considered significant ($p<0.05$) forC. zeinaseverity, and the respective interactions with the environments were not considered significant for eithertrait.

In a comparison of resistant vs susceptible parent groups regarding gray leaf spot, Derera et al. (2008) and Engelsing et al. (2011) found no evidence of the maternal effect, indicating the absence of a significant influence of cytoplasmic genes. Nevertheless, Huff et al. (1998) detected significant reciprocal effects in a study onthe inheritance of gray leaf spot resistance in maize inbred lines. In a diallel analysis study, Schwantes et al. (2017) reported significant effects for grain yield, but not for resistance to *Fusarium verticillioides* ear rot. Moreover, Kiyyo et al. (2017) found significant reciprocal effects for maize lethal necrosis, evaluated in a 6x6 diallel, at three distinct locations.

Based on the proposeddiallel model, the quadratic components were calculated to determine the predominant gene effects. According to the results (Table 4), the non-additivewas more relevant than the additive effects for grain yield, while additive gene effects predominated for *C. zeina* severity.

With regard to the GCA effectsbetween the groups of lines, the effects of group I (Dent) were higher for grain yield in Maringá, while in Sabáudia, those of group II (Flint)were higher. For C. zeinaseverity,the GCA effects were more pronounced in group II, and the reciprocal effects indicated that the cytoplasmic effect prevailed over the maternal effect.

Several studies have reported the predominance of additiveovernon-additive gene effects for gray leaf spot resistance(Gevers et al. 1994; Derera et al.2008; Vieira et al.2012, Bekeko et al., 2018, Nedi et al, 2018).In a generation mean analysis, Britto et al (2012) reported higher predominance of additive effects, but also of dominance at a few small-effect loci. In another study, Li et al (2018) estimated general and specific combining abilities in a North Carolina Design II, with inbred lines and testers from different heterotic groups. These authors reported significant values of additive and also dominance effects for gray leaf spot resistance, sugge-

Table 4 - Estimates of the quadratic components in the partial diallel proposed by Geraldi and Miranda Filho (1988), and the reciprocal effects proposed by Cockerham and Weir (1977), for grain yield and C. zeina severity (%) evaluated in Maringá-PR and Sabáudia-PR, main growing season of 2012/2013

Estimators	RG - Maringá	RG - Sabáudia	C. zeina
$\hat{\phi}_g$	510914.57	154917.40	4.48
$\hat{\phi}_{g1}$	304604.12	408562.68	19.48
$\hat{\phi}_{g2}$	78294.66	393197.85	50.21
$\hat{\phi}_s$	2258703.82	4666784.82	10.42
$\hat{\phi}_{d1}$	0*	0*	0.26
$\hat{\phi}_{d2}$	0*	0*	0.08
$\hat{\phi}_r$	0*	0*	2.27

*Negative values, which are caused by the estimation method, should be considered zero.

Table 5 - Estimates of the effects of the GCA, MAT and standard deviations for grain yield and C. zeina severity (%) evaluated in Maringá-PR and Sabáudia-PR, main growing season of 2012/2013

Effects of $\hat{g}_i$ and $\hat{g}_j$	GY Maringá	GY Sabáudia	*C. zeina*	Effects $\hat{d}_i$ of and $\hat{d}_j$	*C. zeina*
M	5405.85	7333.44	14.45		-
Gr_1	-355.16	199.07	-1.07		-
Gr_2	365.31	-204.76	1.10		-
SD $(\hat{g}r_1 - \hat{g}r_2)$	83.26	96.91	0.50		
D1	-439.37	-437.16	2.12		-0.65
D2	569.03	-151.04	7.59		-0.26
D3	835.63	938.00	-1.82		-0.08
D4	-276.90	457.12	0.13		0.16
D5	-310.30	-863.09	-4.00		0.11
D6	-378.09	56.17	-4.03		1.26
SD $(\hat{g}_i - \hat{g}_k)$	52.15	60.70	0.31	SD $(\hat{d}_i - \hat{d}_k)$	0.38
F1	378.77	-21.51	-0.61		0.23
F2	-398.52	-812.99	-7.12		-0.01
F3	20.85	-312.15	2.40		0.54
F4	89.06	858.05	-5.40		0.78
F5	-90.17	288.60	10.73		0.10
SD $(\hat{g}_j - \hat{g}_{k'})$	48.78	56.78	0.29	SD $(\hat{d}_j - \hat{d}_{k'})$	0.33

sting that heterotic groups play an important role in the genetic architecture of a trait.

General and specific combining ability estimates

The estimates of GCA effects for the groups of lines and of SCA of hybrid combinations are listed in Tables 5 and 6, respectively.The GCA effects between two lines were considered different when the amplitude of variation of effects was higher than twice the standard deviation of the GCA (Cruz et al., 2012).

Considering grain yield, the inbred lines of the dentgroup D2 and D3 performed particularly well inMaringá, and lines D4 and D3 in Sabáudia (Table 5). For the heterotic group flint, inbred line F1 in Maringá and F4 and F5 in Sabáudia had the highest estimate, indicating a higher contribution of additive gene effects in crosses in which these inbred lines participated.

Negative and values are important for disease resistance, sincelines that contribute to a reduction in disease severity are desirable in maize breeding programs. In this sense, the lines D3, D5 and D6 of group I contributed most to a reduction in severity, while in group II, lines F2 and F4 contributed most to a reduction in C. zeinaseverity.

Considering the two traits simultaneously, only line D3(77.H30.1) contributed withpositive GCA effects to grain yield and negative effects to *C. zeina* severity, and is therefore the most promising inbred line for future hybrid combinations.

In relation to SCA estimates ( ) (Table 6), the best hybrid combinations for grain yield were D1 x F1, D2 x F2, D2 x F4, and D3 x F4 in Maringá and D1 x F1, D1 x F5, D2 x F3 in Sabáudia. In the mean of the years, the best hybrids for *C. zeina* severity were D1 x F5, D2 x F1, D2 x F3, D3 x F5, and D4 x F3.

The SCA estimates of the hybrids D2 x F3, D3 x F5 and D4 x F3 were significant for both studied traits (Table 6), indicating a different performance thanexpected based on the GCA of their parent lines. This confirms the statement that the deviations from the effects ex-

Table 6 - Specific combining ability and reciprocal effects for grain yield and C. zeina severity (%) evaluated in Maringá-PR and Sabáudia-PR, main growing season of 2012/2013.

$\hat{s}_{ij}$	*GY Maringá*	*GY Sabáudia*	*C. zeina*	$\hat{r}_{ij}$	*C. zeina*
D1XF1	991.02	1579.24	-0.68	D1XF1	0.08
D1XF2	288.48	-509.94	-0.81	D1XF2	-0.12
D1XF3	565.77	-71.61	2.16	D1XF3	2.95
D1XF4	179.73	814.68	3.13	D1XF4	-0.49
D1XF5	-547.71	1557.14	-3.57	D1XF5	-0.77
D2XF1	532.11	292.46	-2.95	D2XF1	1.27
D2XF2	1038,24	312.77	1.55	D2XF2	-0.98
D2XF3	354.03	1457,44	-4,78	D2XF3	1.88
D2XF4	1056.99	387.06	-0.38	D2XF4	0.25
D2XF5	748.38	1018.02	0.94	D2XF5	-0.77
D3XF1	583.85	1395.08	2.50	D3XF1	0.46
D3XF2	599.98	-265.78	-0.65	D3XF2	1.06
D3XF3	-877.57	1575,39	2.04	D3XF3	-1,18
D3XF4	1101.06	1151.68	0.45	D3XF4	0.34
D3XF5	1100.29	960.81	-10.69	D3XF5	1.65
D4XF1	98.54	-391.54	2.15	D4XF1	-1.65
D4XF2	348.67	2073.77	1.31	D4XF2	1.64
D4XF3	1683.79	216.11	-2.10	D4XF3	0.24
D4XF4	-817.25	965.56	-1.80	D4XF4	1.09
D4XF5	894.48	1471.86	0.87	D4XF5	0.33
D5XF1	1046.11	-355.16	0.55	D5XF1	1.91
D5XF2	1166.07	1770.65	-0.67	D5XF2	-0.89
D5XF3	1413.36	829.15	0.58	D5XF3	-0.89
D5XF4	-771.51	-181.06	0.00	D5XF4	0.09
D5XF5	-381.62	1230.07	1.34	D5XF5	1.44
D6XF1	1127.73	2476.24	-1,11	D6XF1	-0.09
D6XF2	90.36	-44.11	-0.61	D6XF2	1.27
D6XF3	564.48	586.56	-0.91	D6XF3	-1.01 -
D6XF4	697.94	1268.85	-1.67	D6XF4	1.38
D6XF5	471.67	-197.69	7.61	D6XF5	0.11
SD $(\hat{s}_{ij} - \hat{s}_{jk})$	127.75	148.69	0.76	SD $(\hat{r}_{ij} - \hat{r}_{jk})$	0.90
SD $(\hat{s}_{ij} - \hat{s}_{k'})$	129.08	150.23	0.77	SD $(\hat{r}_{ij} - \hat{r}_{k'})$	0.89
SD $(\hat{s}_{ij} - \hat{s}_{k'})$	120.92	140.73	0.72	SD $(\hat{r}_{ij} - \hat{r}_{k'})$	2.03

pected based on additivity,i.e., associated to dominance and/or epistasis, are highly relevant in the expression of grain yield and resistance to *C. zeina* (Gevers et al. 1994; Menkir& Ayodele 2005; Derera et al. 2008). Consequently, these hybrid combinations can be used in future trials in the maize breeding program.

Maternal and cytoplasmatic effects

The maternal and cytoplasmiceffects were only estimated for *C. zeina* severity. The significantmaternal effects were caused by genetic cytoplasmic factors, and the (non-maternal) cytoplasmic effects can be explained by the interaction between nuclear genes and cytoplasmic gene effects (Mukanga et al., 2010). The maternal effect ( ) of inbred line D6 was high and negative for *C. zeina* severity, indicating a effect of reduced disease severity in the hybrids in which this line participates as female parent. This maternal effect may persist for the next generations, indicating a great potential to be explored for breeding of allogamous species (Wu and Matheson, 2001).

In relation to the estimates of the cytoplasmic effect( ),no hybrids with reduced *C. zeina* severity were found (Table 6). However, when D1, D2 and D5 were used as female parents, *C. zeina* severity increased in the resulting hybrid combinations. Therefore, the presence of an interaction between the nuclear and cytoplasmatic DNA between the respective lines can be inferred, resulting in increased susceptibility to gray leaf spot.

For grain yield, the reciprocal effects were not considered significant (Table 3). These results are consistent with those of a study on maize germplasm in South Africaby Mukankusi et al (2008), where the authors concluded that the reciprocal effect is irrelevant for this trait. Non-significance for maternal and non-maternal effects for grain yield were also observed by Zare et al. (2011), in a diallel analysis between maize inbred lines derived from different heterotic groups. Reciprocal effects, which include maternal and cytoplasmatic effects (Zhang et al., 2016), have been reported for quantitative traits in maize (Fan et al., 2014; Yao et al., 2013), although, for disease resistance, the results wererather inconsistent and depended strongly on the pathogen and germplasm selected for the crosses.

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