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Genetic variability in popcorn synthetic population

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ABSTRACT. The Brazilian popcorn has low genetic variability and the successful development of advanced lines, new popcorn cultivars with high grain yield (GY) and expansion volume (PE) is dependent on parental selection and precise determination of heterotic groups. The aim of this study was to evaluate genetic variability and identify heterotic groups in synthetic populations of popcorn, using diallel crosses. Thus, nine synthetic populations were crossed using complete diallel scheme. The GY and PE traits of 36 hybrids and reciprocals were evaluated in a randomized complete block design with 72 treatments and two replicates in two years. The effects of non-additive genes were the most important in the genetic control of these traits, indicating a favorable situation to produce hybrids. The reciprocal effect is mainly due to non-maternal effects for GY and PE. The highest GY values were obtained for the 02 x 08, 04 x 09, 05 x 09, and 01 x 09 crosses and the highest PE were obtained for the 07 x 01 and 03 x 04 crosses. The exploitation of synthetic populations from S_3 lines can be an alternative to increase the genetic variability for grain yield and popping expansion in popcorn breeding programs.

Keywords: *Zea mays*; general combining ability; specific combining ability; diallel.

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Introduction

Popcorn (*Zea mays* L.) has high market demand and high added value. However, its commercial plantation still does not compare with the cultivation of common corn. According to the Anuário Brasileiro do Milho (Carvalho, Kist, Santos, Muller, & Beling, 2015), the main producing areas in the country produced a total of approximately 255 thousand tons of grains, with an average yield of 4,425 kg ha^{-1}. This result is due, in particular, to the low quality of the popcorn available in the Brazilian market caused by the limited high-quality cultivars and inadequate production technology (Scapim, Pacheco, Tonet, Braccini, & Pinto, 2002). Among the main traits of interest of this crop, we highlight grain yield (GY) and popping expansion (PE). Thus, popcorn improvement should benefit both producers due to high productivity and consumers, since the high popping expansion implies in better flake texture and softness, which are linked to popcorn quality.

However, low genetic variability is observed for the expansion volume trait in Brazilian cultivars compared to foreign commercial cultivars. On the other hand, there is significant genetic variability for grain yield to be explored among the local varieties (Miranda et al., 2008; Amaral Junior et al., 2010). In this context, success in developing advanced lines and new cultivars of popcorn maize with high GY and PE is dependent on parental selection and accurate determination of heterotic groups (Munhoz, Prioli, Amaral Júnior, Scapim, & Simon, 2009; Resh et al., 2015). In the United States, success in increasing the germplasm genetic basis is especially due to the characterization of three distinct heterocyclic groups of popcorn, allowing the introduction of new elite materials from the selection of the best crosses (Goodman, 2005).

In Brazil, genetic divergence studies of temperate and tropical popcorn maize germplasm have been performed to generate important information on the genetic basis of the national popcorn and several methodologies have been used for this purpose. Gonçalves et al. (2014) evaluated the potential of nine popcorn cultivars of tropical climate using multivariate analyzes. Saavedra, Silva, Mora, and Scapim (2013) evaluated the structure of Brazilian popcorn germplasm using Bayesian inference. Miranda et al. (2008) evaluated the genetic variability and determined heterotic groups in local varieties and F2 populations using information from diallel analysis.

Diallelic analysis has been developed for the purpose of exploring information on the gene action controlling the traits and determining the heterotrophic groups (Griffing, 1956a). These analyses can be applied to open pollinated varieties for homozygous genotypes and can be used, without restriction, in the methodology proposed by Griffing (1956b). They allow determining the average performance of the parents at crosses, known as the general combining ability (GCA), and estimating the deviation of individual crosses from the media, known as specific combining ability (SCA). The effects of GCA are proportional to the frequency of favorable alleles present in the parents. On the other hand, the effects of SCA show that the parents differ significantly in the production of hybrids of superior or inferior performance.

Thus, the objective of this study was to evaluate, through diallel crosses, genetic variability and to identify in popcorn synthetic populations.

Material and methods

A total of 185 S_3 lines were obtained from nine commercial popcorn cultivars. The nine populations used in this study were formed by grouping the 185 lines according to origin (commercial cultivar) and by removing and mixed the same number of seeds from each line of the same group. These populations were crossed in the complete diallel scheme, method III (F1 and reciprocal), model II (random treatments) of Griffing (1956a), resulting in 72 diallel hybrids. For the evaluation of these genotypes, a randomized complete block design with 72 treatments and two replications was used. The study was conducted in Jaboticabal, SP (21°15'17"S, 48°19'20"W, and 605 m altitude). The experiments were evaluated in two years, crop 2013/2014 (crop13/14) and crop 2014/2015 (crop14/15). The experimental plots consisted of a 5 m line, with 0.8 m spacing between rows and 0.2 m between plants within each row. Crop management followed the requirements of the culture.

The grain yield (GY) and expansion volume (PE) traits were evaluated using all the corn ears of the plot. The grain weight data of the plot (g plot^{-1}) were corrected to 13% humidity, adjusted by stand using covariance and converted to kilogram per hectare (kg ha^{-1}). Grain samples were stored in a dry chamber for two weeks, and humidity was determined periodically using a pilot sample. The popping expansion analysis was performed when the samples reached 12% moisture content. Three 30-g samples, weighed in precision scale, from each treatment were used for each repetition, totaling six samples per treatment. The evaluated samples were placed in paper bags and popped in a microwave (Brastemp®, 30 liters, 0.8 KW h^{-1}, 800 w, 127 w, 30 x 53, 9 x 42 cm, 16 kg) during 2 min. and 30 s popping time to determine popping expansion.

The expansion volume was measured using a graduated 1,000 mL cylinder, with one inversion for each sample, and the PE (mL g^{-1}) was given by the ratio between total popped volume (mL) and original sample weight (g). The final sample PE was given by the average of the three replicates.

The obtained data were submitted to individual analyses of variance and the residues for each trait were compared to confirm the homogeneity of the variances (Hartley, 1950). The studied variables collected over two years of evaluation were combined for the analyses.

The data were fitted to the three linear models suggested by Wu and Matheson (2001). The first model was used to estimate the treatment effects:

$$Y_{lmijk} = u + l_l + r_{m(l)} + f_{ij} + lf_{lij} + rf_{mij(l)} + e_{lmijk} \quad [1]$$

where: Y_{lmijk} is the observation of ith, jth individual, u is the overall mean, l_l is the l^{th} year, $r_{m(l)}$ is the m^{th} repetition in the l^{th} year, f_{ij} is the ij^{th} effect of treatment, lf_{lij} is the interaction between the l^{th} year and the ij^{th} treatment, $rf_{mij(l)}$ is the interaction between the m^{th} repetition in the l^{th} year and ij^{th} treatment, and e_{lmijk} is the residual.

The second model, partitions the effect of treatment into GCA (g_i or g_j), where g_i and g_j are the effects of GCA of the i^{th} and j^{th} parent; SCA (s_{ij}) where s_{ij} are the crossings between parents of the i and j order; and reciprocal effect (rec_{ij}), rec_{ij} are the differences provided by parent i or j when used as male or female in the ij crossing and partitioning the interaction between years and treatments in GCA x years (lg_{li} + lg_{lj}), SCA x years (ls_{lij}), and REC x years ($lrec_{lij}$).

$$Y_{lmijk} = u + l_l + r_{m(l)} + g_i + g_j + s_{ij} + rec_{ij} + lg_{li} + ls_{lij} + lrec_{lij} + e_{lmijk} \quad [2]$$

The third model, partitions the reciprocal effect into maternal (MAT) (m_i) and non-maternal effects (NMAT) (nm_{ij}), and the effect of REC x years (lm_{li}+lm_{lj}) and the effect of NMAT x years interaction (lnm_{lij}).

$$Y_{lmijk} = u + l_l + r_{m(l)} + g_i + g_j + s_{ij} + m_i + m_j + nm_{ij} + lg_{li} + lg_{lj} + ls_{lij} + lm_{li} + lm_{lj} + lnm_{lij} + e_{lmijk} \quad [3]$$

The following assumptions were made to estimate the GCA, SCA, REC, MAT, and NMAT effects: $\Sigma g_i = 0, \Sigma s_{ij} = 0$ for each j with $s_{ij} = s_{ij}$, $rec_{ij} = -rec_{ji}$, $\sum m_i = 0$, $\sum nm_{i.} = \sum nm_{.j} = 0$ with $nm_{ij} = -nm_{ij}$. The additive and dominance effects involved in determining the traits were calculated by the ratio between the sum of squares of GCA and SCA, and for each trait, estimated by the Griffing method (1956a) according to the following equation proposed by Baker (1978):

$$GCA{:}\,SCA = SQ_{gca}/(SQ_{gca} + SQ_{sca}) \qquad [4],$$

where: SQ_{gca} = GCA sum of square; SQ_{sca} = SCA sum of square.

The average squares estimates for all effects were calculated using Statistical Analisys System (SAS, 2011) and the Diallel-05 macro proposed by Zhang et al. (2005).

Results and discussion

The evaluated traits indicated a significant difference between the genotypes and, therefore, variability in the diallel (F_1 hybrids and reciprocals), which is fundamental to obtain genetic gains in the hybrid combinations (Table 1). The low coefficients of variance (CV) obtained for the evaluated traits confirm the reliability of the results obtained for the two crops. In addition, the relative performance of the genotypes was different between the evaluated years as shown by the significant interaction between genotypes x years for all traits. These results suggest a differentiated performance in response to environmental changes. In the literature, studies with popcorn maize also report interaction between genotype and environment (Cabral et al., 2015). This interaction may explain the reason behind the fact that few national varieties adapted to different environments and regions (Amaral Júnior et al., 2013a).

Table 1. Analysis of combined variance and average grain yield (GY, kg ha^{-1}) and popping expansion (PE, mL g^{-1}) of popcorn hybrids.

SV	DF	MS	
		GY	PE
Rep(Years)	2	5536.60^{ns}	3.87^{ns}
Years	1	104171.20^{***}	380.03^{***}
Genotypes	71	4121208.90^{***}	512.23^{***}
Genotypes*Years	71	44827.80^{***}	32.46^{***}
Residual	-	6858.40	9.76
Average		1982.63	32.15
CV (%)		4.17	9.71
Harvest 13/14			
Average	-	1999.77	30.97
CV (%)	-	4.27	11.69
Harvest 14/15			
Average	-	1965.37	33.32
CV (%)	-	4.07	7.62

***: significant at $p < 0.0001$; SV: source of variation; DF: degrees of freedom; MS: mean square; GY: grain yield as kg ha^{-1}; PE: popping expansion as mL g^{-1}.

The interaction between genotypes x years indicates that partitioning the treatment effects into GCA, SCA and their interactions with the harvesting years is important and necessary for the complete genetic interpretation of the diallel (Wu & Matheson, 2001). It was observed that the genotype x year interaction was due especially to the SCA x year interaction effect (Table 2), since this effect was significant for GY and PE, while GCA x year interaction was significant only for PE. The effects of REC x year interaction were also significant for all traits due to the effect of NMAT x year interaction, indicating that gene segregation of parental populations caused the differences between the hybrids and their reciprocals in the evaluation years. It is well known that in hybrid breeding programs, the general objective is to select crosses that are adapted to all tested environments, or at least to most of them. In this regard, Mukanga, Derera, and Tongoona (2010) suggest that only the significant GCA x year interaction should be used to select parents in specific environments. The genetic study of traits and was based only on the joint data analysis due to the lower effect of GCA x year interaction on genotype x year compared to SCA x year.

The GCA and SCA estimates were simultaneously significant for grain yield, indicating that the additive and non-additive effects of the genes are present in the genetic control of this trait. However, only SCA was significant for the expansion volume, revealing that the non-additive effects are the most important in the inheritance of this trait. The GCA: SCA relationship for both traits, reinforces the existence of predominance of genes of dominant effect controlling these traits and that developing hybrids can lead to a significant increase of the mean (Bello & Olawuyi, 2015; Soni & Khanorkar, 2014).

Table 2. Analysis of variance of the specific combination ability (SCA), reciprocal effect (REC), maternal effect (MAT), and non-maternal effect (NMAT) for the traits, popping expansion and grain yield of diallel popcorn populations.

SV	DF	MS	
		GY	PE
GCA	8	8738660.33^{*}	409.54^{ns}
SCA	27	3602796.28^{***}	455.98^{***}
REC	36	3478157.86^{***}	569.61^{***}
MAT	8	3889706.00^{ns}	116.37^{ns}
NMAT	28	3357032.35^{***}	698.45^{***}
GCA x year	8	54696.32^{ns}	60.21^{**}
SCA x year	27	33254.51^{***}	20.59^{**}
REC x year	36	45666.02^{**}	30.37^{**}
MAT x year	8	46820.06^{ns}	22.22^{ns}
NMAT x year	28	44106.76^{***}	31.28^{***}
Residual	-	1198788.20	151.46
GCA: SCA		0.41	0.22
Harvest 13/14			
GCA	8	4426910.64^{***}	255.59^{***}
SCA	27	1893866.48^{***}	246.55^{***}
REC	36	1822581.71^{***}	242.20^{***}
MAT	8	1925275.42^{***}	106.39^{***}
NMAT	28	1539775.91^{***}	232.63^{***}
Harvest 14/15			
GCA	8	4366446.01^{***}	244.15^{***}
SCA	27	1742184.31^{***}	230.02^{***}
REC	36	1701242.17^{***}	357.77^{***}
MAT	8	1138960.88^{***}	81.06^{***}
NMAT	28	1296521.39^{***}	41.37^{***}

***: significant at $p < 0.0001$, **: significant at $p < 0.01$ and * significant at $p < 0.05$, ns: non-significant, respectively; SV: source of variation; DF: degrees of freedom; MS: mean square; CGC/GCA: general combining ability; CEC/SCA: specific combining ability; REC: reciprocal effect; MAT: maternal effect; NMAT: non-maternal effect; PG/GY: grain yield expressed as kg ha^{-1}; PE: Popping expansion, mL g^{-1}.

Gonçalves et al. (2014) evaluated 10 lines of popcorn maize from different origins and reported a significant effect of GCA and SCA for GY and PE. On the other hand, Moterle et al. (2012) evaluated GY and PE of nine lines of popcorn, eight of temperate and one of tropical climate, and found a significant effect of GCA and SCA only for GY. Scapim et al. (2002) recommended using populations with high GCA estimates to obtain new varieties with high GY and PE. However, according to Wu and Matheson (2001), only GCA and SCA estimates do not allow obtaining information on when parents are used as either male or female. Cabral, Amaral Júnior, Freitas, Ribeiro, and Silva (2016) reported reciprocal effect on popcorn for GY and recommended alternating the parents in the crosses. Andrade, Cruz, Scapim, Silverio, and Tonet (2008) reported a negligible reciprocal effect for the PE trait. Rodovalho et al. (2014), using Bayesian reference, reported predominance of non-additive effects for these two traits whereas Miranda et al. (2008) found additive effects only for PE.

There was a reciprocal effect (REC) for both traits considered. This effect is due to the significant difference between the hybrid and its reciprocal and may have implications in the estimation of genetic effects (Mukanga et al., 2010). Fan et al. (2014) reported that reciprocal effects increased the chances of obtaining productive hybrids and that the methods that contemplate this effect are crucial for classifying the heterotic groups. Yao et al. (2013) recommend including reciprocal crosses in the diallel, since REC directly influences the estimation of GCA and SCA. Wu and Matheson (2001) partitioned this effect into maternal (MAT) and non-maternal (NMAT) effects. Mukanga et al. (2010) stated that the maternal effect can be explained by the contribution of genes present in the cytoplasm and that the non-maternal effect would be explained by gene product involving nucleus and cytoplasm genes. Cabral et al. (2015) and Andrade et al. (2008) observed a reciprocal effect for GY in popcorn and attributed it to the maternal effect, suggesting that the parents should be rotated at crosses for higher GY gains. In this work, REC effects were found for GY and PE due to NMAT effects, indicating the existence of variability in the populations formed from S_3 lineages, thus increasing the possibility of selecting superior genotypes when used in breeding programs due to the appearance of new hybrid combinations.

The average grain yield and expansion volume values of the hybrids and reciprocals varied widely, ranging from 321.26 to 4,496.31 kg ha^{-1} and from 11.8 to 56.18 mL g^{-1}, respectively (Table 3). On average, the F_1 hybrid combinations had higher GY and PE compared to hybrid reciprocal combinations. It was also observed that most of the genotypes with GY higher than 4,000 kg ha^{-1} had the lowest expansion volume average. This result suggests a negative correlation between these two traits, underscoring the difficulty of selecting productive genotypes with high expansion volume.

Table 3. Estimates of the average^{+} for grain yield (GY, kg ha^{-1}) and popping expansion (PE, mL g^{-1}) of hybrids and its reciprocals.

Hybrids	GY	PE	Reciprocals	GY	PE
01 x 02	457.18	49.14	02 x 01	2339.72	21.95
01 x 03	535.33	27.92	03 x 01	2360.43	22.12
01 x 04	1538.79	49.18	04 x 01	1487.90	25.76
01 x 05	520.06	17.00	05 x 01	3846.56	15.98
01 x 06	595.50	30.85	06 x 01	581.32	52.57
01 x 07	1441.70	47.22	07 x 01	321.26	56.18
01 x 08	3562.67	25.75	08 x 01	1507.67	23.44
01 x 09	4103.50	27.14	09 x 01	1500.33	51.28
02 x 03	2330.61	46.91	03 x 02	1556.71	33.50
02 x 04	2734.20	40.38	04 x 02	1705.17	34.53
02 x 05	1458.21	50.53	05 x 02	495.40	30.62
02 x 06	1683.21	32.61	06 x 02	1672.95	24.77
02 x 07	1683.12	37.36	07 x 02	1899.87	30.95
02 x 08	4496.31	23.47	08 x 02	2931.89	32.35
02 x 09	2075.82	37.87	09 x 02	936.75	20.37
03 x 04	1867.47	53.30	04 x 03	322.01	26.24
03 x 05	1853.71	28.46	05 x 03	1235.41	49.18
03 x 06	584.31	20.33	06 x 03	1878.16	25.91
03 x 07	2076.36	17.88	07 x 03	1933.16	27.16
03 x 08	1329.25	24.36	08 x 03	1431.42	38.93
03 x 09	1906.65	46.52	09 x 03	2894.29	22.62
04 x 05	2673.39	22.79	05 x 04	1309.77	31.19
04 x 06	2698.39	50.13	06 x 04	1232.13	31.34
04 x 07	1782.18	43.48	07 x 04	1336.87	14.30
04 x 08	1556.48	23.23	08 x 04	964.26	37.70
04 x 09	4438.61	30.13	09 x 04	967.54	38.95
05 x 06	2608.33	44.63	06 x 05	3081.23	31.37
05 x 07	1676.70	35.71	07 x 05	1099.13	16.91
05 x 08	3889.31	25.39	08 x 05	3446.94	27.88
05 x 09	4257.27	11.89	09 x 05	3609.67	42.90
06 x 07	2049.14	43.62	07 x 06	1493.09	20.15
06 x 08	1648.06	26.25	08 x 06	2789.99	14.31
06 x 09	2013.09	21.62	09 x 06	2564.21	33.47
07 x 08	1791.38	31.73	08 x 07	2681.17	25.33
07 x 09	2303.53	47.16	09 x 07	2287.95	21.46
08 x 09	2500.06	25.98	09 x 08	2184.71	21.21
Amplitude	4039.13	41.41		3525.30	41.88
Average	2131.11	33.83		1830.19	29.86

+: average of joint analysis.

The parents 01, 02, and 04 had the highest GCA values for PE (Table 4) among all parents and, therefore, may be indicated when the objective of the breeding program is to obtain good PE, since GCA is the parameter that indicates best average parental cross-breeding performance, in the crossing block. However, the maternal effect in these parents should be taken into account. When genitor 04 is considered, for example, with a maternal effect of -2.14, methods based on progeny testing, focusing especially on progeny performance from plants used as a female (S_1 family selection), may be less effective in identifying and selecting superior parents, and consequently less effective to improve the population. However, significant and positive MAT effect in parent 02 indicates that gains with selection are expected when using this same method.

Parents 05 and 08 had significant negative GCA values, revealing that these parents contribute with an additive effect to reduce the PE trait. On the other hand, parent 08 may contribute with additive effects when used as female parent. Parents 03, 06, 07, and 09 did not have significant GCA values. Positive and significant GCA values for GY were observed for parents 05, 08, and 09 (Table 4). These parents may be used in breeding programs to increase GY with performance utilization *per se*, but the breeding method must be chosen carefully for these parents, especially for 08 and 09, due to the negative and significant pronounced maternal effect. Negative and significant GCA values were observed for 01, 02, 03, 04, 06, and 07, showing low parental performance for GY.

Table 4. Estimate of popping expansion (mL g^{-1}) and grain yield (kg ha^{-1}) regarding the general combining ability (GCA) and maternal effect (MAT), for all nine parents.

Parents	EV		GY	
	GCA	MAT	GCA	MAT
01	2.55***	0.06^{ns}	-356.50***	-66.15***
02	2.54***	1.92***	-88.13***	396.98***
03	0.17^{ns}	-0.83^{ns}	-399.42***	53.99***
04	2.96***	-2.14***	-219.71***	261.82***
05	-1.67***	-0.02^{ns}	383.55***	87.56***
06	-0.63^{ns}	0.59^{ns}	-179.83***	-47.85***
07	0.49^{ns}	-1.34***	-273.91***	-194.45***
08	-5.88***	1.29***	501.69***	-122.34***
09	-0.52^{ns}	0.48^{ns}	632.26***	-359.55***

***: significant at $p < 0.0001$, **: significant at $p < 0.01$, *significant at $p < 0.05$, and ns: non- significant, respectively.

It was observed that approximately 31 and 50% of the hybrid combinations (F_1) and reciprocal hybrid combinations for PE, respectively, had positive and significant SCA values (Table 5). Positive SCA show that the parents involved in the crosses are either complementary or are the most dissimilar regarding the frequency of the genes with dominance. However, even if SCA is used as the parameter for choosing the best hybrid combinations, it is not possible to predict the performance of crosses using the parents as male or female.

Table 5. Estimates of the specific combining ability (SCA) and reciprocal effect (REC) of the hybrids and their reciprocals regarding grain yield (GY, kg ha^{-1}) and popping expansion (PE, mL g^{-1}).

Hybrids	GY	EV	Reciprocals	GY	EV
01 x 02	-137.63**	-1.60	02 x 01	-941.26**	13.74**
01 x 03	223.47**	-9.72**	03 x 01	-912.59**	3.01*
01 x 04	108.91*	-0.18^{ns}	04 x 01	25.51^{ns}	11.45**
01 x 05	175.58**	-16.55**	05 x 01	-1663.19**	0.51^{ns}
01 x 06	-855.65**	7.67**	06 x 01	7.41^{ns}	-10.90**
01 x 07	-468.76**	18.59**	07 x 01	560.28**	-6.07**
01 x 08	409.25**	-3.75^{ns}	08 x 01	1027.50**	1.18^{ns}
01 x 09	544.83**	5.54**	09 x 01	1300.97**	-12.34**
02 x 03	450.52**	5.58**	03 x 02	386.91**	6.46**
02 x 04	546.82**	-0.18^{ns}	04 x 02	514.53**	2.91^{ns}
02 x 05	-1299.34**	8.50**	05 x 02	481.40**	10.27**
02 x 06	-34.67^{ns}	-5.25**	06 x 02	5.12^{ns}	4.05**
02 x 07	172.85**	-1.03**	07 x 02	-108.32*	3.21*
02 x 08	1319.99**	-0.90^{ns}	08 x 02	782.39**	-4.44**
02 x 09	-1018.55**	-5.11**	09 x 02	569.55**	8.56**
03 x 04	-266.83**	4.88**	04 x 03	772.73**	13.94**
03 x 05	-420.19**	8.87**	05 x 03	309.25**	-9.86**
03 x 06	-170.23**	-8.37**	06 x 03	-646.92**	-2.67^{ns}
03 x 07	697.36**	-10.35**	07 x 03	71.60^{ns}	-4.70*
03 x 08	-701.10**	6.10**	08 x 03	-52.64^{ns}	-6.81**
03 x 09	187.01*	3.02*	09 x 03	-493.70**	12.10**
04 x 05	-152.98**	-6.30**	05 x 04	681.81**	-4.05**
04 x 06	384.15**	6.62**	06 x 04	733.06**	9.66**
04 x 07	72.42^{ns}	-6.70**	07 x 04	222.65**	14.58**
04 x 08	-1002.31**	1.55^{ns}	08 x 04	296.09**	-7.03**
04 x 09	309.80**	0.32^{ns}	09 x 04	1735.53**	-4.14**
05 x 06	660.33**	8.17**	06 x 05	-236.45**	6.65**
05 x 07	-702.45**	-4.45**	07 x 05	288.78**	8.89**
05 x 08	802.14**	2.42^{ns}	08 x 05	221.18**	-1.64^{ns}
05 x 09	936.92**	-0.66^{ns}	09 x 05	323.80**	-17.22**
06 x 07	244.13**	-0.04^{ns}	07 x 06	278.02**	11.83**
06 x 08	-83.56^{ns}	-5.33**	08 x 06	-570.96**	6.02**
06 x 09	-144.50**	-3.47*	09 x 06	-275.56**	-5.79^{ns}
07 x 08	27.76^{ns}	1.76^{ns}	08 x 07	-444.89*	3.20*
07 x 09	-43.33^{ns}	2.21^{ns}	09 x 07	7.79^{ns}	12.48**
08 x 09	-772.18	-1.84^{ns}	09 x 08	157.55**	2.05^{ns}

***, **, *, and ns: significant at 0.001, 0.01, 0.05, and non-significant, respectively.

The crosses 01 x 07 and 07 x 04 had the highest increases in the PE average of the diallel, of 18.59 and 14.58 mL g^{-1}, respectively. On the other hand, parent 05 used as female in the crosses with the 01 and 09 had the lowest increase estimates in the diallel average for this same trait. These results suggest that popcorn breeding programs for the PE trait should test reciprocal crosses to increase the chances of encountering hybrids with high PE in certain crosses. However, it should be highlighted that when obtaining breeding lines or synthesis of base populations in breeding programs from reciprocal hybrids with high and positive REC values, the effects can be lost during the generations due to the presence of the NMAT effect in certain crosses (Wu & Matheson, 2001).

The PE is the most important trait of the popcorn hybrids, especially when the objective is to increase the competition between national and foreign cultivars, especially American ones. However, the low genetic variability among the national genotypes (Amaral Júnior et al., 2013b; Silva et al., 2015) strengthens the dependence on the use of foreign cultivars and increases the challenge of popcorn breeding programs in Brazil. In addition, although there is genetic variability in the local cultivars (Miranda et al., 2008), GY is another trait that deserves attention in breeding programs, mainly due to the negative genetic correlation with PE (Cabral et al., 2016). The crosses 09 x 01, 09 x 04, and 05 x 09 had significant SCA while the cross 09 x 04 had the highest SCA estimate for increasing the GY average of the diallel (Table 5).

The second highest SCA estimate for diallel mean increase was obtained for the cross 02 x 08 with significant gains in GY, in addition, it is common to observe that the highest SCA estimates do not originate from two parents with the highest and most positive GCA estimates of the diallel (Cruz & Vencovsky, 1989).

Developing synthetic populations from the mixture of lines from commercial cultivars may be an alternative to increase genetic variability for grain yield and popping expansion in popcorn breeding programs. These results create positive expectations regarding the tools available to increase genetic variability in popcorn breeding programs as to obtain progenies with high grain yield and good popping expansion.

Conclusion

The additive and non-additive gene effects are important in the genetic control of GY, whereas only the non-additive effects of the genes are important for PE.

The highest GY values were obtained for the crosses 02 x 08, 04 x 09, 05 x 09, and 01 x 09 while PE was higher for the crosses 07 x 01 and 03 x 04. Populations 01, 02, and 04 may be indicated for intra-population breeding programs to increase popping expansion, while populations 05, 08, and 09 may be used in intra-population breeding programs to increase grain yield.

Caution is suggested when choosing the breeding method for the significant and pronounced maternal effect. We recommend using the 08 and 09 parents for improving intrapopulation breeding programs.

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