

Combining ability of tropical and temperate inbred lines of popcorn

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ABSTRACT. In Brazil, using combining ability of popcorn genotypes to achieve superior hybrids has been unsuccessful because the local genotypes are all members of the same heterotic group. To overcome this constraint, 10 lines (P_1 to P_{10}) with different adaptations to tropical or temperate edaphoclimatic environments were used to obtain 45 F_1 hybrids in a complete diallel. These hybrids and three controls were evaluated in two environments in Rio de Janeiro State. Grain yield (GY), popping expansion (PE), plant height (PH), ear height (EH), and days to silking (FL) were evaluated in randomized complete blocks with three replications. Significant differences between genotypes ($P \leq 0.05$) were detected for GY, PE and EH. General combining ability was significant for EH, PH, PE, and GY, and specific combining ability was significant only for PE and GY. The most promising inbred lines that improved GY were P_3 and P_4 , unlike P_8 , P_9 and P_{10} , which improved PE, and P_2 , which improved both PE and GY. The additive effects were much more important for PE than for GY. The hybrid combinations

gave positive estimates of heterosis for GY but not for PE.

Key words: *Zea mays*; Edaphoclimatic adaptation; Gene effects; Diallel; Inheritance

INTRODUCTION

The development of popcorn hybrids depends on parental selection and the identification of heterotic groups (Melani and Carena, 2005). Genitor discrepancies and good gene complementation is necessary to achieve favorable agronomic characteristics (Hallauer and Miranda Filho, 1995). Diallel analysis is a breeding strategy to obtain superior genotypes because it provides consistent results over the years (Amaral Júnior et al., 1999; Cavalcanti et al., 2000; Gouis et al., 2002; Silva et al., 2004; Jaramillo et al., 2005; Marin et al., 2006; Bison et al., 2007). In Brazil, many popcorn studies have been conducted to determine genetic divergence (Pereira et al., 2006, 2008; Dandolini et al., 2008; Vilela et al., 2008; Silva et al., 2009; Trindade et al., 2010) in conjunction with the additional efforts in cytogenetics (Ricci et al., 2007), seed quality (Moterle et al., 2008), agronomic responses (Vendruscolo et al., 2001; Scapim et al., 2010), plant pathology (Vieira et al., 2009a), and the evaluation of breeding methods (Rangel et al., 2007, 2008; Arnhold et al., 2009; Freitas Júnior et al., 2009; Amaral Júnior et al., 2010).

Burnham Larish and Brewbaker (1999) were the first researchers to report the diallels of both temperate and tropical lines. Using Griffing's method (1956), these authors evaluated the combining ability for both grain yield and popping expansion through two diallels, in which the first one had six varieties and the other had five North American lines. This classical experiment indicated that popcorn breeders should work with the heterotic groups 'SuperGold' and 'Japanese Hulless' under tropical conditions. The same authors also found that the dominant genes were important for improving the crop yield and the components of seed production, and that the additive effects were important for improving popping expansion.

In Brazil, diallel experiments with popcorn are still incipient, and they are based on varieties from heterotic groups with tropical adaptations (Andrade et al., 2002; Freitas Júnior et al., 2006; Scapim et al., 2002, 2006; Miranda et al., 2008; Rangel et al., 2008; Vieira et al., 2009b; Silva et al., 2010). Miranda et al. (2008) reported that the small genetic variability for popping expansion has made it difficult to obtain superior hybrids from the national varieties. Therefore, there is an enormous need for lines from heterotic groups adapted to different environments to investigate the gene effects on grain yield and popping expansion, and to produce hybrids with a high degree of genetic diversity.

The objective of the present study was to evaluate the combining ability of 10 popcorn lines from tropical, temperate and semi-temperate germplasms by diallel crossing.

MATERIAL AND METHODS

Hybrid combinations

In March 2007, 10 pre-selected lines from tropical, temperate and semi-temperate lines were crossed in a complete diallel without reciprocals to obtain 45 F₁ hybrids (Table 1).

Plants of inbred lines were spaced 0.40 m apart and established in rows 0.90 m apart. Kraft paper bags were used to collect the pollen grains to pollinate each pair of inbred lines.

Table 1. The origin of the inbred lines.

Parental inbred lines	Description of the population from which the inbred lines were obtained
P ₁ (PR 023)	From the three-way hybrid 'Zélia', released by Pioneer Seeds; it consists of temperate and tropical inbred lines.
P ₂ (PR 024)	From the composite with yellow grains 'CMS-42', released by Embrapa-Maize and Sorghum; it consists of tropical inbred lines.
P ₃ (PR 036)	From the composite with white grains 'CMS-42', released by Embrapa-Maize and Sorghum; it consists of tropical inbred lines.
P ₄ (UEM J1)	From South American races in tropical regions.
P ₅ (PR 045-1) P ₆ (PR 045-2) P ₇ (PR 045-3)	From the three-way hybrid 'Zaeli', which consists of temperate inbred lines.
P ₈ (PR 087-1) P ₉ (PR 087-2) P ₁₀ (PR 087-3)	From the modified one-way hybrid 'IAC112', adapted to tropical regions; it consists of inbred lines from the open pollinated variety 'South American Mushroom' crossed with inbred lines from the South American intervarietal hybrid 'Guarani' x 'Amarela'.

Evaluation of hybrids, parents and control treatments

In November 2007, the first trial was established at the Colégio Estadual Agrícola 'Antônio Sarlo', Campos dos Goytacazes municipality, Northern Rio de Janeiro, Brazil (21°45' S, 41°20' W and altitude of 11 m), and the second trial was established at the PESAGRO-RIO, Itaocara municipality, Northwestern Rio de Janeiro State, Brazil (21°39' S, 42°04' W and altitude of 60 m).

Under both environmental conditions, the trials were conducted in randomized complete blocks with three replications in which the treatments with 45 F₁ hybrids from the 10 lines were compared with three commercial popcorn hybrids that have high potential for crop yield and popping expansion [(IAC112, IAC125 (released by the Agriculture Institute at Campinas, SP, Brazil), and Zélia (released by Pioneer)]. The experimental plots had rows 10.0 m long, spaced 0.90 m apart, and every plant in a row was set 0.20 m apart.

Agronomic traits

Grain yield (GY) in kg/ha was evaluated after hand-harvesting the ears with a moisture content of about 17%, which were then dried to 15%. The moisture content was determined according to the standard method of the International Seed Testing Association, which recommends the use of a circulating air oven at 105 ± 3°C for 24 h with three replications. Popping expansion (PE) was reported as mL/g, and determined from six 30.0 g samples per treatment, popped in a Panasonic microwave oven Model NN-S65B at 1000 W for 3 min. The grain volume for popping expansion was collected from the mid portion of every ear. Grain samples weighing 1.0 kg and with moisture content of 14% were safely stored. The average plant height (PH) was measured from the ground level to the flag leaf collar. The ear height (EH) was measured from the ground level to the uppermost ear-bearing node. The data were collected from six competitive plants per plot. Finally, we determined the number of days to silking (FL).

Statistical analysis

Levene's test and Kolmogorov-Smirnov's method were used to assess the homogeneity of variances and the normal distribution of errors, respectively. Data transformation was not necessary. The presence of homogeneity in the residual variances between the environments was examined by the F-maximum test at 5% of probability. Thereafter, the data from both sites were evaluated by combined analysis of variance (ANOVA) from which the sum of squares for the treatments was decomposed into general (GCA) and specific combining abilities (SCA). Treatments and environments were analyzed as random effects. Interactions with the environments were estimated by Griffing's method (Model II). The genetic-statistical analyses were carried out by the Genes program (Cruz, 2006).

RESULTS

Mean values of traits and the significance of statistical procedures

For all traits, the F-test did not disclose heterogeneity ($P < 0.05$) for the mean square of errors estimated by the individual analyses, and this fact permitted the combined analysis of environments. Significant differences from the mean squares of genotypes ($P \leq 0.01$) were detected for GY, PE and EH (Table 2), but not for PH and FL ($P > 0.05$). The GCA was significant for EH, PH, PE, and GY, and the SCA was significant only for PE and GY. All interactions GCA versus environments and SCA versus environments were significant for all traits, except for PE.

Table 2. Combined analysis of Griffing's diallel by method IV, model II, for five traits from 45 popcorn hybrids and their parental inbred lines in Campos dos Goytacazes and Itaocara, for growing season 2007/2008, Rio de Janeiro, Brazil.

Source of variation	d.f.	Mean square of traits				
		EH	PH	FL	PE	GY
Genotypes (G)	54	0.12**	0.27 ^{ns}	136.52 ^{ns}	5.90**	3294180.71**
GCA	9	0.27**	0.47*	57.99 ^{ns}	31.80**	8013432.68**
SCA	45	0.09 ^{ns}	0.24 ^{ns}	152.23 ^{ns}	0.72**	2350330.32**
Environments (E)	1	2.19**	14.90**	84.51**	0.03**	7015604.62**
G versus E	54	0.06**	0.18**	112.83**	0.09 ^{ns}	457732.67**
GCA versus E	9	0.05**	0.14**	121.86**	0.07 ^{ns}	608957.12**
SCA versus E	45	0.07*	0.18**	111.02**	0.10 ^{ns}	427487.79**
Error	216	0.01	0.03	4.51	0.35	83668.84

GCA = general combining ability; SCA = specific combining ability; d.f. = degrees of freedom; EH = ear height; PH = plant height; FL = days to silking; PE = popping expansion; GY = grain yield; ns = not significant ($P > 0.05$); **significant at $P \leq 0.01$; *significant at $P \leq 0.05$.

Grain yield for the inbred lines varied from 1,110.00 kg/ha (P_1) to 1,996.67 kg/ha (P_3), and for the hybrid combinations it varied from 1,223.33 kg/ha ($P_5 \times P_7$) to 3,493.33 kg/ha ($P_2 \times P_4$). The hybrid combinations $P_2 \times P_4$ (3,493.33 kg/ha), $P_1 \times P_3$ (3,360.00 kg/ha), $P_2 \times P_9$ (3,166.67 kg/ha), $P_2 \times P_3$ (3,033.33 kg/ha), $P_4 \times P_8$ (2,976.67 kg/ha), $P_1 \times P_4$ (2,973.33 kg/ha), and $P_3 \times P_{10}$ (2,915.00 kg/ha) demonstrated higher grain yields compared to the control treatments for which Zélia yielded 2,335.00 kg/ha, IAC112 yielded 1,970.00 kg/ha, and IAC125 yielded 1,880.00 kg/ha.

Popping expansion of the inbred lines varied from 31.90 (P_7) to 35.67 mL/g (P_8), and the hybrid combinations varied from 31.43 ($P_3 \times P_7$) to 34.83 mL/g ($P_8 \times P_{10}$). These responses are in contrast to the control treatments in which the popping expansion of IAC112 was 25.90, Zélia was 25.53 and IAC125 was 24.84 mL/g. In summary, the inbred lines and their hybrid combinations had the highest indices of PE.

The inbred lines had estimates of EH ranging from 0.74 (P_1) to 1.13 m (P_4), PH ranging from 1.30 (P_1) to 1.86 m (P_4) and FL ranging from 58.33 (P_9) to 62.67 days (P_6). The hybrid combinations had estimates of EH ranging from 0.88 ($P_1 \times P_7$) to 1.27 m ($P_4 \times P_9$), PH ranging from 1.06 ($P_5 \times P_6$) to 2.07 m ($P_7 \times P_9$) and FL ranging from 41.67 ($P_1 \times P_4$) to 60.67 days ($P_6 \times P_8$).

Average effects of the general combining ability

Three inbred lines (P_2 , P_3 and P_4) were the most outstanding for GY (Table 3) because of higher estimates of \hat{g}_i . Therefore, these inbred lines can be used in the development of high-yield hybrids unlike P_6 , P_7 and P_9 , which had negative estimates of \hat{g}_i , and negative estimates mean poor hybrid responses. The positive estimates of \hat{g}_i from P_2 , P_3 and P_4 were expected because these inbred lines had the best responses in both environments.

Table 3. Average effects of the general combining ability (\hat{g}_i) for five traits evaluated in 10 parental inbred lines of popcorn, in a complete diallel without reciprocals in the two environments of Campos dos Goytacazes and Itaocara, for growing season 2007/2008, Rio de Janeiro, Brazil.

Parental inbred line	\hat{g}_i of traits				
	GY	PH	EH	FL	PE
P_1 (PR 023)	-216.2670	-0.1400	-0.1250	1.2940	-0.2460
P_2 (PR 024)	405.2610	0.1080	0.0420	-0.2060	0.5350
P_3 (PR 036)	513.5390	-0.0200	0.0220	-0.4140	-0.6280
P_4 (UEM J1)	484.2890	0.1160	0.0980	-0.3860	-0.3650
P_5 (PR 045-1)	-132.1690	0.0190	0.0180	1.1420	-0.6910
P_6 (PR 045-2)	-335.2250	-0.0890	-0.0320	-1.1640	-0.4610
P_7 (PR 045-3)	-232.9190	-0.0370	-0.0510	0.2940	-0.5450
P_8 (PR 087-1)	-34.7390	0.0570	0.0430	0.6970	1.0990
P_9 (PR 087-2)	-276.1970	-0.0210	-0.0110	-1.4000	0.4800
P_{10} (PR 087-3)	-175.5720	0.0070	-0.0040	0.1420	0.8220

GY = grain yield; PH = plant height; EH = ear height; FL = days to silking; PE = popping expansion.

The estimates of \hat{g}_i for PE indicated that P_2 , P_8 , P_9 , and P_{10} were the most suitable inbred lines for producing hybrids with high popping expansion (Table 3), even though P_8 had been the most outstanding inbred line. Negative values of \hat{g}_i for PH and EH were found for P_1 , P_6 , P_7 , and P_9 , which meant that these inbred lines tended to reduce the plant height. P_3 had a negative estimate of \hat{g}_i for PH only, and P_6 and P_9 were the most promising inbred lines for reducing the number of FL.

Average effects of the specific combining ability

Two hybrid combinations $P_2 \times P_9$ and $P_3 \times P_7$ displayed positive estimates of \hat{s}_{ij} for GY. These hybrids had at least one superior inbred line with a high GCA. The hybrid combinations $P_1 \times P_9$, $P_1 \times P_{10}$, $P_2 \times P_4$, and $P_8 \times P_{10}$ had positive estimates of \hat{s}_{ij} for PE. Two hybrid combinations ($P_6 \times P_9$ [PH = -0.9860 and EH = -0.5620] and $P_5 \times P_8$ [PH = -0.1290 and EH = 0.0820]) may be selected to reduce the plant and ear heights (Table 4). Negative estimates of \hat{s}_{ij} for FL were found for $P_2 \times P_6$,

$P_1 \times P_8$, $P_2 \times P_8$, $P_4 \times P_6$, and $P_7 \times P_8$ (Table 4).

Table 4. Estimates of the effects of specific combining ability (\hat{s}_{ii} and \hat{s}_{ij}) for five traits evaluated in two environments by a complete diallel.

Effects (\hat{s}_{ii} and \hat{s}_{ij})	Traits evaluated				
	GY	PH	EH	FL	PE
$P_1 \times P_1$	-1247.0000	-0.3990	-0.2040	4.0720	0.1810
$P_1 \times P_2$	231.4400	0.1260	0.0420	-1.2600	-0.1570
$P_1 \times P_3$	651.4900	0.1410	0.0800	-2.2200	0.2870
$P_1 \times P_4$	260.7400	-0.0220	-0.0120	-7.0800	0.1950
$P_1 \times P_5$	353.8700	0.0660	0.0090	-0.1090	0.0830
$P_1 \times P_6$	153.5900	0.1290	0.0620	2.8630	-0.6980
$P_1 \times P_7$	-362.0000	-0.0440	-0.0410	0.0720	0.0700
$P_1 \times P_8$	44.7750	0.1150	0.0320	-3.3300	-0.0070
$P_1 \times P_9$	671.2300	0.1550	0.1010	0.1000	0.4380
$P_1 \times P_{10}$	222.2700	-0.0970	0.0020	-2.7700	0.3030
$P_2 \times P_2$	-1385.0000	-0.2100	-0.1670	5.5720	0.4920
$P_2 \times P_3$	-18.3600	-0.0120	-0.0370	-1.5500	-0.7610
$P_2 \times P_4$	409.2200	-0.0500	-0.0660	-0.9140	0.2920
$P_2 \times P_5$	46.5110	0.0110	-0.0150	-2.9400	0.0850
$P_2 \times P_6$	177.0600	0.1070	0.0530	-3.3000	-0.0620
$P_2 \times P_7$	313.9200	-0.0230	-0.0160	-2.5900	0.1220
$P_2 \times P_8$	83.2470	-0.2080	-0.0090	-3.3300	-0.3380
$P_2 \times P_9$	908.0300	0.1880	0.1650	0.9330	-0.0360
$P_2 \times P_{10}$	352.4100	0.0520	0.0830	-1.7700	-0.1280
$P_3 \times P_3$	-1579.0000	-0.1950	-0.1200	5.8220	0.5850
$P_3 \times P_4$	-77.3900	-0.0220	-0.0260	-1.8700	0.0720
$P_3 \times P_5$	64.0670	-0.0310	-0.0280	-2.5600	-0.3180
$P_3 \times P_6$	472.1200	0.0830	0.0690	0.4050	0.1350
$P_3 \times P_7$	1014.1000	-0.0210	0.0180	-2.7200	-0.1390
$P_3 \times P_8$	194.9700	0.0190	-0.0290	-3.1200	-0.3920
$P_3 \times P_9$	379.7610	0.0300	0.0310	-1.0200	-0.0220
$P_3 \times P_{10}$	212.4700	-0.0260	0.0290	-2.5600	-0.0310
$P_4 \times P_4$	-1593.9000	-0.2020	-0.1760	5.4330	0.3350
$P_4 \times P_5$	230.8170	-0.1700	0.0560	-1.7600	-0.1480
$P_4 \times P_6$	443.0390	0.1960	0.0830	-3.7800	-0.1540
$P_4 \times P_7$	484.0670	0.0740	0.0580	-2.2400	-0.1430
$P_4 \times P_8$	369.2200	0.0870	0.0330	0.8490	-0.7050
$P_4 \times P_9$	503.1780	0.1380	0.1310	2.4470	-0.0520
$P_4 \times P_{10}$	298.3860	-0.0560	-0.0390	-2.0900	-0.0280
$P_5 \times P_5$	-304.3900	-0.0070	-0.0220	2.8770	0.4880
$P_5 \times P_6$	-771.3300	-0.1260	-0.1000	1.8490	0.1810
$P_5 \times P_7$	-144.4700	-0.0600	-0.0130	-1.2700	-0.0550
$P_5 \times P_8$	110.6780	-0.1290	-0.0820	-1.3400	-0.1620
$P_5 \times P_9$	365.4700	0.1230	0.0410	-2.0800	-0.3900
$P_5 \times P_{10}$	86.5110	0.1010	0.0430	-1.1200	-0.2520
$P_6 \times P_6$	-236.6100	0.0020	-0.0340	8.6550	0.2170
$P_6 \times P_7$	378.5810	0.0610	0.0890	-1.4700	-0.0150
$P_6 \times P_8$	218.7330	0.1810	0.1770	3.4610	0.1580
$P_6 \times P_9$	-906.4700	-0.9860	-0.5620	-24.2000	0.0930
$P_6 \times P_{10}$	41.2330	0.1210	0.0650	1.3490	-0.0720
$P_7 \times P_7$	-777.8900	-0.1510	-0.1210	4.2380	0.1860
$P_7 \times P_8$	66.4280	-0.0170	-0.0290	-3.6600	0.0420
$P_7 \times P_9$	-498.7800	0.0610	0.0450	2.9330	-0.1390
$P_7 \times P_{10}$	37.2610	0.0410	-0.0030	-3.1000	-0.1150
$P_8 \times P_8$	-664.2500	-0.0930	-0.0940	3.4330	0.6310
$P_8 \times P_9$	-131.9600	0.0460	0.0200	0.6970	-0.1160
$P_8 \times P_{10}$	105.7470	-0.1380	-0.0590	-2.6700	0.2580
$P_9 \times P_9$	-553.0000	0.0140	-0.0300	7.4610	0.7860
$P_9 \times P_{10}$	-451.1200	-0.0130	-0.0450	-0.2480	-0.4730
$P_{10} \times P_{10}$	-585.9190	-0.1070	-0.1050	4.7110	0.2690

P_1 = PR 023; P_2 = PR 024; P_3 = PR 036; P_4 = UEM J1; P_5 = PR 045-1; P_6 = PR 045-2; P_7 = PR 045-3; P_8 = PR 087-1; P_9 = PR 087-2; P_{10} = PR 087-3; GY = grain yield; PH = plant height; EH = ear height; PE = popping expansion; FL = days to silking.

The genitors P_1 , P_2 , P_3 , and P_4 had higher and negative \hat{s}_{ii} , which indicated high genetic divergence for GY, PH and EH in comparison to the other inbred lines.

DISCUSSION

Genetic variability between genotypes was detected for GY and PE, and the variability from inbred lines (data not shown) permitted the selection and formation of promising hybrids. In the present experiment, all hybrids performed better than the commercial genotypes. Studies in South and South-eastern Brazil also demonstrated high GY differences between sites for Zélia (Sawazaki et al., 2000) and IAC112 (Freitas Júnior et al., 2006; Rangel et al., 2007, 2008). These authors showed that GY is a trait highly influenced by environmental conditions, confirming the importance of regional-breeding programs.

Although some variation in agronomic characteristics is based on the significance of genotypes versus environments, there are no constraints in recommending hybrids for both sites because the $P_1 \times P_3$ and $P_3 \times P_7$ were the best hybrids at both locations. Additionally, P_2 demonstrated a desirable response at both sites, which made it possible to infer about other combinations with the potential of releasing commercial genotypes because the combination $P_2 \times P_4$, for example, produced 3,667.00 kg/ha and had a PE of 33.22 mL/g.

Hybrids and lines had a PH with important indices because North and Northwestern Rio de Janeiro have high incidence of winds capable of dislodging the plants, and dislodging reduces crop yield. Popcorn plants are more prone to dislodging than is common maize. Ear height is important because this trait is also highly related to plant dislodging (Ji et al., 2006).

The \hat{s}_{ij} for PE were low and close to the general mean. Therefore, additive effects were predominant for PE, although several researchers have reported the presence of bi-directional dominance (Andrade et al., 2002; Viana and Matta, 2003; Simon et al., 2004; Freitas Júnior et al., 2006; Scapim et al., 2006; Miranda et al., 2008). The inheritance of bi-directional dominance also explains the low heterosis for PE in the national population.

The inbred lines P_8 , P_{10} , P_2 , and P_9 , which had superior PE in both environments, could be recommended to produce hybrids with phenotypic stability. The hybrid $P_1 \times P_3$ could be recommended because of the positive estimates for GY and PE. The hybrid $P_2 \times P_4$ had a positive estimate of \hat{s}_{ij} for PE, but had a poor estimate for GY, which puts it in the eighth order of the GY ranking. $P_3 \times P_7$ had a positive estimate of \hat{s}_{ij} for GY, but negative estimate for PE (-0.1390), which means negative heterosis. In this case, the hybrid recommendation should be based on the average values (Scapim et al., 2006). Therefore, the best hybrids for improving GY and PE were $P_1 \times P_3$ and $P_2 \times P_4$, which had GYs and PEs of 3,316.67 kg/ha and 32.17 mL/g, and 3,662.67 kg/ha and 31.44 mL/g, respectively. They had positive values of s_{ij} for GY and PE. These hybrids could also be recommended to increase GY and PE by reciprocal recurrent selection.

Although the number of parameters in Griffing's method (model II) is small, it is as efficient as the Gardner and Eberhart model (1966), not only because $\hat{g}_i = \frac{1}{2} \hat{v}_i + \hat{h}_i$, but also because of the underlying information in the \hat{s}_{ii} effects. For example, the magnitude of \hat{s}_{ii} indicates variety heterosis, and a larger \hat{s}_{ii} indicates a greater distance between genitor i and the average frequency from the other participants in the diallel. Therefore, the greater the divergence between genitor i and the other parents, the greater are the heterotic effects of varieties on their hybrids (Cruz et al., 2004). Furthermore, the sign of the \hat{s}_{ii} may indicate the presence

of unidirectional dominance. For example, a negative \hat{s}_{ii} indicates positive deviation of the dominance; therefore, the dominant genes contributed to increase the trait estimate, unlike the presence of both negative and positive signs, which indicates bi-directional dominance (Cruz and Vencovsky, 1989; Cruz et al., 2004). In summary, except for the P_6 line, the negative sign of GY indicated unidirectional dominance; therefore, the dominant genes contributed to the increase in productivity. Second, a similar unidirectional dominance was detected for PE, but the estimate of this trait was reduced by the genes. Third, positive heterosis for GY dominated the hybrid combinations in contrast to the responses for PE. Finally, higher estimates for GY but not for PE indicated that the genitors were more divergent for crop yield than for popping expansion.

Therefore, high crop yield and proper popping expansion may be achieved through lines with satisfactory allelic complementation as evaluated by Griffing's method, and even when there is positive unidirectional dominance for PE. Similarly, there are other responses from open-pollinated varieties (Vieira et al., 2009b) or hybrids (Vieira et al., 2009c) from popcorn lines.

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