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Combining ability between tropical and temperate popcorn lines for seed quality and agronomic traits

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Abstract

In popcorn, the involvement of tropical and temperate genotypes is critical for genetic gains in the key traits of grain yield and popping expansion. The present work is the first reported study of combining ability involving reciprocals and seed quality traits in popcorn. Forty-five single crosses and their 45 reciprocals resulting from a system of complete diallel crossing between ten popcorn lines(five temperate and five tropical) were evaluated in two distinct growing seasons (first and second cropping season) for seed quality [field emergence (FE), germination test (GT), modified cold test (MCT) and seedling dry matter (DM)] and agronomic traits [plant height (PH), ear height (EH), popping expansion (PE) and grain yield (GY)]. The results showed that there is a strong reciprocal effect for EH, GY and seed quality, showing the need for prior indication of the male and female parents in crosses. The L53 and L70 lines revealed, simultaneously, favorable estimates of a general combining ability (GCA) for increases in PE and GY in crops during the first harvest, and the L70 lines showed a similar result for crops in the second harvest. The best hybrids regarding PE and GY, during the first harvest, were P1×L70, P1×L76, P3×P7, P7×L54 and P8×L54. For the second harvest, the best hybrids were P1×L53, P1×L76, P8×L53, P8×L54 and P10×L53. P1×L76 and P8×L54 exhibited a good performance for both of the cropping season.

Keywords: Diallel; gene effect; grain yield; popping expansion; reciprocal effect; *Zea mays*.
Abbreviations: CS _ Crop season; DM _ seedling dry matter; EH _ ear height; FE _ field emergence; GCA _ general combining abilities; GT _ germination test; GY _ grain yield; H _ Hybrid; MCT _ modified cold test; PE _ popping expansion; PH _ plant height; RE _ reciprocal effects; SCA _ specific combining abilities; SD _ standard deviation.

Introduction

Among the so-called "special corns", popcorn has high profitability and great popular acceptance (Sweley et al., 2012). The popcorn crop is worth approximately half a billion dollars annually in the United States alone. In Brazil, the importance of this crop is even greater because popcorn has a strong participation in the informal economy (Viana et al., 2011; Rossato Junior et al., 2013).

In Brazil, there are currently 48 popcorn cultivars registered in the National Register of Cultivars of the Ministry of Agriculture, Livestock and Supply (Registro Nacional de Cultivares do Ministério da Agricultura, Pecuária e Abastecimento), with the majority belonging to packing companies that establish restricted access of use to partner producers. Barreto et al. (2012) reported that only three hybrids were available on the Brazilian seed market in the 2010/2011 harvest: IAC 112, IAC 125 and Zelia. This scenario reveals a major limitation of the domestic cultivars available to producers, thus requiring enhanced breeding of this crop to obtain and make available cultivars with high agronomic potential that are adapted to Brazilian edaphoclimatic conditions. The production of hybrids depends on the selection of parents, seeking good genetic complementation of favorable agronomic traits. Among the strategies that enable success for this purpose, diallel crosses and analyses are particularly important because they provide information regarding the general and specific combining ability of a set of genotypes, allowing reliable inference of the best hybrid combinations (Hallauer et al., 2010). Despite the advantages of diallel crossing strategies, there are few studies of popcorn, especially studies that focused on seed quality traits linked to grain yield, with Moterle et al. (2012) being the only study available.

Diallels in popcorn lines that are used as parents have been studied by Larish and Brewbaker (1999), Pajic et al. (2008), Silva et al. (2010), Viana et al. (2011), Vieira et al. (2011) and Moterle et al. (2012). Silva et al. (2010), for example, used ten lines – six tropical and four temperate – and found that the hybrid combinations $P_1 \times P_3$ and $P_3 \times P_7$ exhibited a high capacity for expansion and yield at both of the sites assessed, i.e., the municipalities of Campos dos Goytacazes and Itaocara, which are located in the North and Northwest regions of the State of Rio de Janeiro.

There are still no reports in the scientific literature regarding diallels and the reciprocal effect of seed quality traits in popcorn, and only studies on common corn have been identified involving the traits of germination speed and percentage of hybrid seedlings compared to seedlings from their progenitor lines (Sarkissian et al., 1964; Pesey, 1970; Eagles and Hardacre, 1978; Mino, 1980; Gomes et al., 2000). Pesey (1970) and Eagles and Hardacre (1978) reported the existence of a reciprocal effect on the degree of tolerance to low temperatures, germination and emergence rate in hybrid seedlings of common corn. Those studies indicated the possibility that such associations may also occur in popcorn due to its genealogical proximity to common corn, from which it may have been derived by selections of the "flint" type (Kantety et al., 1995).

Given the above context, the objective of this study was to evaluate the combining ability of 45 single crosses and their 45 reciprocals resulting from a system of complete diallel cross between ten popcorn lines, aiming to produce hybrids and identify parents with greater potential for seed quality and superior agronomic traits to meet the demands of crops in the first and second cropping season and to generate populations for use in breeding programs.

Results and Discussion

The sum of squares of hybrids was broken down into general (GCA) and specific (SCA) combining abilities and the reciprocal effect (RE) (Tables 2 and 3).

Diallel analysis for popcorn seed quality traits

The seed quality traits (FE, GT, MCT and DM) were statistically significant for GCA and SCA simultaneously (Table 2), indicating the existence of additive and non-additive effects in genetic control of these traits. Moreover, RE was significant for all the traits assessed, showing the existence of differences between each hybrid and its reciprocal. Working with diallel analysis in common corn lines for seed quality, Moterle et al. (2011) found significant effects of GCA, SCA and RE for the germination, seedling vigor, first count of seed germination, modified cold and seedling emergence rate tests in a sand seedbed.

The quadratic components associated with GCA effects were greater than those of SCA for the FE, MCT and DM tests, indicating a greater contribution of additive effects for these traits. For GT, the effects of SCA were greater than those of GCA, showing a greater contribution of non-additive effects to the genetic control. Similar results were obtained in common corn by Gomes et al. (2000) and Moterle et al. (2011) and in popcorn by Moterle et al. (2012).

Gomes et al. (2000) evaluated the combining ability of common corn lines for grain quality and reported greater contribution of non-additive effects for GT, a result that agrees with those obtained by Moterle et al. (2012). However, these results differ from those obtained by Antuna et al. (2003) and Ortiz et al. (2006), who found a greater contribution of additive genetic effects for GT. It is worth noting the difference in the methodology used by the latter authors, who used only the mean square associated with the GCA and SCA effects for each trait and not the estimate of mean squares of the fixed effects associated with the traits.

The mean squares of the fixed effects associated with RE of all the traits were greater than those associated with the SCA, indicating a difference in effect when using a line as the male or female parent in the same cross. These results agree with those obtained by Moterle et al. (2011) in common corn, who observed a greater magnitude of the effects of RE relative to the effects of SCA for a germination test, first count of seed germination and seedling emergence rate in a sand seedbed. However, these results differ from those obtained by Gomes et al. (2000), who evaluated the seed quality in common corn and found that estimates of SCA were greater, in most cases, than those associated with RE.

The mean percentage of normal seedlings germinated in the GT was higher than in the MCT and FE tests (Table 2), showing an overestimation of this parameter, especially regarding FE, and indicating that the result for GT should not be used to calculate the number of seeds to be sown in the field without assessing seed vigor. According to Johson and Wax (1978) and Marcos Filho et al. (1987), overestimation of GT compared to FE occurs because of the ideal conditions of humidity and temperature in the germination test, which do not occur under field conditions. The percentage of normal seedlings emerged in the MCT (73.15%) was very close to the percentage for the FE test (72.18%). Marcos Filho et al. (1987) explained that the cold test combines low temperature with high humidity, which allows only the most vigorous seeds to survive. This challenge explains the lower values obtained in MFT and FE, where seed vigor is evident as is their ability to germinate under ideal conditions.

Diallel analysis for the agronomic traits

Table 3 shows the sum of mean squares for the variation source hybrids (H) broken down into general (GCA) and specific (SCA) combining abilities and reciprocal effects (RE) as well as the H×CS interaction broken down into the interactions of GCA, SCA and RE with cropping season (CS) for agronomic traits in the first and second Cropping season. For plant (PH) and ear (EH) height, GCA was significant, while the SCA was not significant for both traits. That result indicates that only genes with additive effects are involved in the genetic control of these traits, a finding similar to the results obtained by Pfann et al. (2009). GCA and SCA were significant for popping expansion (PE) and grain yield (GY), demonstrating the existence of additive and non-additive effects in the genetic control of these traits, which were also observed by Pinto et al. (2001), Andrade et al. (2002), Malik et al. (2004), Rangel et al. (2008) and Silva et al. (2010).

The reciprocal effect (RE) was significant for EH and GY, showing a significant difference between hybrids and their reciprocals for these traits and that gains may be obtained by reversing the parents when crossing. Similar results were obtained by Andrade et al. (2002), who evaluated six popcorn varieties in a complete diallel with reciprocals and found a reciprocal effect for plant height and grain weight.

For the interaction between hybrids and cropping season (H×CS), the PH, EH, PE and GY traits were statistically significant, indicating a differential response of hybrids at the different cropping season (Table 3). According to Troyer (1996), the significant effects of interaction between the simple hybrids and sites are frequently tested because the narrow genetic base of simple hybrids allows for a stronger differential response to assessment sites than in the case of double hybrids or cultivars with a broader genetic base.

The interaction between the general combining ability and cropping season (GCA×CS) was significant for PH, PE and GY (Table 3), indicating the existence of specific progenitors for each cropping season. Similar results were reported by Rangel et al. (2007). Silva et al. (2010) evaluated a complete diallel without reciprocals among ten popcorn lines and found significant effects of GCA×CS for plant height, ear height, days to flowering and grain yield.

Table 1. Genealogy of 10 lines used as parents in diallel.

Lines	Genealogy
P1	Obtained from the triple hybrid 'Zelia', released by Pioneer Seeds, considered tropical and temperate.
P3	Obtained from the white grain composite 'CMS-42' released by Embrapa-Corn and Sorghum (Embrapa-Milho e Sorgo), considered tropical.
P6 P7	Obtained from the triple hybrid 'Zaeli', resulting from a cross between temperate lines.
P8 P10	Obtained from the modified hybrid 'IAC 112' adapted to tropical regions, consisting of lines derived from the South American Mushroom (SAM) population crossed with South American lines from the intervarietal "Guarani" x "Yellow" hybrid, considered tropical and temperate.
L53 L54	Obtained from open-pollinated non-selected 'Beija-flor' variety, belonging to the Federal University of Viçosa (Universidade Federal de Viçosa - UFV), considered tropical.
L70	Obtained from open-pollinated 'BRS Angela' variety, derived from the white grain composite 'CMS-43' released by Embrapa, considered tropical.
L76	Obtained from the open-pollinated Viçosa-Viçosa variety, derived from crosses of local varieties with North American hybrids, considered tropical and temperate.

Table 2. Mean squares of general (GCA) and specific (SCA) combining abilities, reciprocal effects (RE) and mean squares of fixed effects for popcorn seed quality traits.

Source of Variation	DF	Mean square of traits			
		FE	GT	MCT	DM
Hybrids	89	421.23**	312.04**	1265.57**	1556.87**
GCA	9	1157.19**	572.40**	4676.62**	5202.35**
SCA	35	217.34*	211.22**	611.63**	583.55**
RE	45	432.61**	338.39**	1091.99**	1584.8**
Estimates of quadratic components					
GCA		16.03	8.26	70.37	80.54
SCA		10.77	20.96	54.86	67.03
RE		37.67	36.85	114.91	192.19
CV (%)		15.86	7.34	7.96	8.47
Mean		72.18	89.88	73.15	81.06

FE: field emergence; GT: germination test; MCT: modified cold test and DM: dry matter. *, ** Significant at 5 and 1% based on the F-test, respectively.

Table 3. Mean squares of general (GCA) and specific (SCA) combining ability, the reciprocal effects (RE), their interaction with the planting time (T) and mean squares of the fixed effects for the agronomic traits of popcorn assessed during the first and second Cropping season.

Source of Variation	DF	Mean square of traits			
		PH	EH	PE	GY
Hybrids (H)	89	0.09^{**}	0.04^{**}	109.8^{**}	3152544^{**}
GCA	9	0.68^{**}	0.34^{**}	836.5^{**}	23911784^{**}
SCA	35	0.02^{ns}	0.01^{ns}	44.48^{**}	867736^{*}
RE	45	0.03^{ns}	0.02^{**}	15.32^{ns}	777768^{*}
H × Cropping season (CS)	1	0.02^{*}	0.01^{*}	17.55^{**}	559687^{**}
GCA × CS	9	0.04^{*}	0.01^{ns}	69.90^{**}	1444966^{**}
SCA × CS	35	0.01^{ns}	0.01^{*}	12.23^{ns}	497887^{**}
RE × CS	45	0.02^{ns}	0.01^{*}	11.21^{ns}	430697^{*}
Estimates of quadratic components					
GCA		0.005	0.003	6.34	182367
SCA		-0.001	0.001	1.24	18684
RE		0.000	0.001	-0.57	13061
CV (%)		7.28	9.48	10.26	18.65
Mean of first CS		2.00	1.04	34.03	3516
Mean of second CS		1.60	0.73	34.04	2210

PH: plant height; EH: ear height; PE: popping expansion, and GY: grain yield. ^{ns}, *, ** non-significant, significant at 5 and 1% based on the F-test, respectively.

The interaction between specific combining ability and cropping season (SCA×CS) was significant for EH and GY (Table 3), showing that the hybrid performance differed between cropping season for these traits. Silva et al. (2010) reported a significant effect of SCA×CS for EH and GY in popcorn. Pinto et al. (2001) reported a significant SCA×CS effect for grain yield in common corn. In contrast, Pfann et al. (2009) evaluated the combining ability of eleven simple hybrids of common corn and found that SCA×CS was not significant for grain yield or ear height.

The interaction between the reciprocal effect and cropping season (RE×CS) was significant for EH and GY, showing differences for these traits in the reciprocal effect of hybrids between cropping season. The mean squares for the fixed effects associated with the GCA for the PE trait were greater than those for the effects associated with SCA (Table 3). This result indicates greater predominance of additive effects in the genetic control of this trait, which is consistent with the results obtained by Pereira and Amaral Júnior (2001), Rangel et al. (2007) and Silva et al. (2010). Vieira et al. (2011) evaluated the combining ability of ten popcorn lines in a partial diallel and reported greater contribution of additive effects in controlling the PE.

For GY, the mean squares of the fixed effects associated with GCA were greater than those associated with SCA (Table 3), suggesting greater contribution of additive effects relative to non-additive effects in the genetic control of this trait. This result was not expected because greater contribution of the effects associated with SCA than those associated with GCA is commonly reported for grain yield. However, similar results were obtained by Gama et al. (1995), Pinto et al. (2001) and Vieira et al. (2011).

Sprague and Tatum (1942) showed that estimates of GCA and SCA are relative and depend on the particular set of genotypes included in the hybrid combinations being tested. Accordingly, when working with lines with a certain degree of kinship, i.e., from the same population, similarity of loci that control the trait may occur, and thus, one may not obtain genetic complementation in hybrids expressing the effects of gene dominance, which leads to a decreased effect of SCA. However, this limitation is not the case in the present study because the lines used are derived from distinct populations, as shown in Table 1.

The estimate of SCA is a deviation from estimates of GCA of the respective parents and of the overall mean. Accordingly, if the estimates of GCA and of the mean are high, then these factors may influence the decrease of SCA and lead to lower significance relative to GCA, which is a more plausible explanation for the results obtained. Ferrão et al. (1985) reported that, depending on the set of genotypes tested, high estimates of GCA can be obtained, which may result in low SCA estimates.

Plant (PH) and ear (EH) height were, on average, higher in the first than in the second cropping season. In the first cropping season, the mean PH and EH were 2.00 and 1.04 m, while the mean values in the second cropping season were 1.60 and 0.72 m, respectively (Table 3). These results can be explained by the better climate conditions observed during the first cropping season, in which there was increased production of photoassimilates and thus higher PH and EH.

The main features of a good popcorn cultivar include high popping expansion (PE) and grain yield (GY). PE showed no significant difference in mean values between the first (34.03 $ml.g^{-1}$) and second (34.04 $ml.g^{-1}$) cropping season. These results can be explained by the fact that this trait is governed by few genes (Lu et al., 2003; Li et al., 2007a), thus suffering less influence from environmental changes. The mean GY was 3516.00 kg ha^{-1} in the first cropping season and 2210.00 $kg.ha^{-1}$ in the second cropping season. This result was expected because grain yield is a quantitative trait governed by many genes and highly influenced by changes in the environment (Li et al., 2007b).

Estimate of the General Combining Ability

Estimates of the effects of general combining ability ($\hat{g}_i$) for seed quality (Table 4) differed among the lines and between the tests applied. This fact can be explained by differences in the principle of the tests used, causing lines to behave differently in the tests applied. The line with the greatest frequencies of favorable alleles for the trait in question would exhibit the greatest $\hat{g}_i$ (Hallauer et al., 2010). Lines P3 and L70 expressed positive values of high magnitude for all the traits related to seed quality (Table 4), indicating that these lines may contribute to increasing the quality of seeds when crossed. In contrast, line P1 showed negative values of high magnitude for all the traits, so this line should be avoided in crosses aimed at increasing seed quality.

For agronomic traits, the magnitude of the estimates $\hat{g}_i$ differed between the cropping season, but the lines retained the signs of the estimates (Table 4). This finding can be explained by the fact that these traits are of quantitative inheritance and highly influenced by the environment and that the lines contribute to the expression of the trait in the same direction, either positive or negative, regardless of the planting time.

In Campos dos Goytacazes, state of Rio de Janeiro, Brazil, there is a high incidence of strong winds, making it necessary to offer producers cultivars with greater resistance to lodging and breaking of plants. Thus, lines with lower estimates of $\hat{g}_i$ for PH and EH are desirable. In this context, lines P1, P6 and P7 had negative values of high magnitude for PH and EH for both of the cropping season (Table 4), demonstrating that these lines may contribute to decreasing plant and ear heights. In contrast, P3 and L70 showed high magnitude and positive $\hat{g}_i$ values and should not be used in crosses aimed at decreasing PH and EH.

The key traits for popcorn breeding are popping expansion (PE) and grain yield (GY). However, only line L70 contributed to increasing both of these traits simultaneously for both cropping season (Table 4). However, the magnitude of $\hat{g}_i$ of this line for PE in the first cropping season was low, i.e., the mean PE in crosses involving this line did not differ much from the overall mean of the diallel. Andrade et al. (2002) evaluated six popcorn populations in diallel crosses and found that only one population obtained favorable (although of low magnitude) estimates of $\hat{g}_i$ for PE and GY simultaneously.

Lines P1, P7 and P8 showed positive $\hat{g}_i$ values of high magnitude for PE in the first and second cropping season, but these lines had negative values of high magnitude for GY (Table 4). In contrast, lines P3 and L54 had negative $\hat{g}_i$ values of high magnitude for PE in both of the planting times and positive $\hat{g}_i$ values for GY. Thus, lines P1, P7 and P8 should be used in crosses to capitalize their PE. For grain yield, the lines with the highest $\hat{g}_i$ values in both the planting times were P3, L76, L70 and L54. Lines P1 and P7 had the most negative $\hat{g}_i$ values for GY. Thus, lines P3, L76, L70 and L54 should be used in crosses to increase GY in the progeny.

Due to the predominance of the of additive effects for PE and GY (Table 3), a strategy for obtaining popcorn populations with high yield and good PE is the synthesis of populations

Table 4. Estimates of the effects of general combining ability ($\hat{g}_i$) and standard deviations (SD) of the ten popcorn lines for seed quality and agronomic traits.

Lines	Seed quality				Agronomic traits							
	FE	GT	MCT	DM	PH		EH		PE		GY	
					CS1	CS2	CS1	CS2	CS1	CS2	CS1	CS2
P1	-8.68	-4.60	-18.17	-10.06	-0.15	-0.14	-0.12	-0.11	2.39	4.51	-528.3	-885.2
P3	4.52	3.29	9.70	22.33	0.05	0.06	0.04	0.07	-5.21	-5.22	436.4	609.3
P6	-4.07	-5.54	-8.66	1.04	-0.04	-0.05	-0.03	-0.03	-0.12	-0.80	-330.1	-461.3
P7	1.69	-1.28	-4.03	-3.12	-0.05	-0.05	-0.02	-0.02	1.46	1.18	-242.6	-229.4
P8	-2.79	0.48	-1.23	-5.47	0.05	0.03	0.05	0.03	3.10	1.68	-195.5	-395.4
P10	0.15	0.68	-0.38	-5.44	0.03	0.03	0.03	0.01	1.84	1.27	-313.5	-173.9
L53	3.87	0.35	6.70	-1.46	0.08	0.01	0.03	0.02	0.21	-0.29	189.7	71.40
L54	3.04	1.79	6.89	-5.44	0.01	-0.02	-0.02	-0.03	-1.47	-3.78	217.8	392.3
L70	3.67	2.90	6.31	4.28	0.08	0.14	0.06	0.06	0.09	1.84	191.3	545.7
L76	-1.40	1.94	2.86	3.35	-0.05	-0.01	-0.01	0.00	-2.29	-0.39	574.8	526.5
SD	1.35	0.78	1.55	8.15	0.01	0.01	0.01	0.01	0.43	0.39	66.89	59.35

FE: field emergence; GT: germination test; MCT: modified cold test; DM: dry matter test; PH: plant height; EH: ear height; PE: popping expansion; GY: grain yield; CS1: first cropping season; CS2: second cropping season; SD: standard deviation. PH: plant height; EH: ear height; PE: popping expansion; GY: grain yield; CS1: first cropping season; CS2: Second cropping season; SD: standard deviation.

for breeding programs that capitalize on additive effects, such as recurrent selection. Therefore, the choice of lines to form these populations should be based on GCA. Given the above, lines with high GCA for PE – P1, P7 and P8 – and high GCA for GY – P3, L76, L70 and L54 – are recommended.

Estimate of the Specific Combining Ability

Regarding SCA, the best hybrid combination for gains in seed quality is possible in P3×P8. However, this hybrid showed negative estimates $\hat{s}_{ij}$ for DM, although these estimates did not exceed the standard deviation of 2.14 (Table 5). The means of this hybrid were 83.3%, 96.7%, 88.5% and 77.3 mg (data not shown) for FE, GT, MCT and DM, respectively. Greater resistance to lodging and breaking of plants can be achieved by reducing PH and EH. Therefore, the most favorable hybrid combinations in both of the growing seasons were P6×P10 and P1×L76. However, the magnitude of $\hat{s}_{ij}$ in these hybrids does not exceed the standard deviation for most of the traits, i.e., the values do not differ much from the overall mean (Table 5).

The hybrids with the most favorable $\hat{s}_{ij}$ estimates for PE and GY simultaneously were P1×L70, P1×L76, P3×P7, P7×L54 and P8×L54 in the first harvest; P1×L76, P1×L53, P8×L53, P8×L54 and P10×L53 in the second harvest; and P1×L76 and P8×L54 in both of the growing seasons (Table 5). However, the magnitude of $\hat{s}_{ij}$ in at least one of those traits did not exceed the SD, i.e., did not differ much from the overall mean for the diallel. The mean PE and GY for these hybrids (data not shown) reveal that these hybrids are in the group with the best means for both of these traits, and only P7×P3 had a mean PE of 31.75 $mL.g^{-1}$, placing it in the group of the second-highest PE means. These results indicate that these hybrids are promising and should be tested in other experiments.

In the hybrid combinations with the best $\hat{s}_{ij}$ estimates for PE and GY simultaneously, lines of different origins are always involved, i.e., between temperate and tropical lines or between those with dual aptitude (tropical and temperate lines). Hybrids between temperate lines or between tropical lines only were not observed among the best combinations, showing that the best genetic complementation occurred between lines of different origins, which may have favored heterosis (Carena and Wicks, 2006).

The estimate of the effects of specific combining ability ($\hat{s}_{ij}$) indicates the best hybrid combination but does not reveal which should be the recipient parent and which should be the pollen donor. Therefore, it is necessary to evaluate the estimates of the reciprocal effect ($\hat{R}_{ij}$) among the hybrid combinations selected for those traits that showed significance for the reciprocal effect (RE) (Tables 2 and 3). Negative estimates of $\hat{R}_{ij}$ of high magnitude indicate that if the parents of the hybrid were reversed, there would be a significant increase in the expression of the trait.

For seed quality traits, the hybrid P3×P8 was selected, and among estimates of $\hat{s}_{ij}$ for that trait, only that for DM (14.14) surpassed the standard deviation of 2.45. Thus, because the sign is positive, this cross should be maintained to produce a superior hybrid. The hybrids selected for EH in both the Cropping season, according to $\hat{s}_{ij}$, were P6×P10 and L70×L76, which had $\hat{s}_i$ estimates of 0.04 and -0.02 in the first harvest and of -0.03 and -0.04 in the second harvest, respectively, with these values being very close to the SD for both of the planting times (0.03). However, comparing the means for the first harvest revealed a significant difference between P6×P10 (1.02 m) and P10×P6 (0.95 m) as well as between L70×L76 (0.98 m) and L76×L70 (1.07 m), and the hybrid with the lowest mean should always be used, i.e., P10×P6 and L70×L76.

The hybrids that exhibited the best $\hat{s}_{ij}$ for PE and GY, simultaneously, were P1×L70, P1×L76, P3×P7, P7×L54 and P8×L54 for the first cropping season and P1×L76, P1×L53, P8×L53, P8×L54 and P10×L53 for the second cropping season; however, a significant estimate of RE was only observed for GY. Thus, hybrids P1×L70, P1×L76 and P3×P7 showed negative estimates of $\hat{s}_{ij}$ in the first cropping season for GY, and the hybrids P7×L54 and P8×L54 showed positive values, but only hybrid P1×L76 showed estimates of $\hat{s}_{ij}$ (-263.03) greater than the SD (199.44). In this regard, due to the negative sign, the parents should be reversed to obtain greater gains for GY. In the second cropping season, the hybrids P1×L53 and P1×L76 exhibited $\hat{s}_{ij}$ estimates (-385.8 and -434.7, respectively) that surpassed the SD of 176.9. These negative estimates of $\hat{s}_{ij}$ indicate that the reciprocal performed better for GY. These results can be best observed by comparing the means: the hybrid P1×L76 had a value of 1137.0, and its reciprocal (L76×P1) had a value of 2913.7 $kg.ha^{-1}$. The hybrid P1×L53 had a value of 1415.2, and for L53×P1, the estimate was 2186.8 $kg.ha^{-1}$. This pattern

Table 5. Estimate of the effects of specific combining ability ($\hat{s}_{ij}$) and standard deviation (SD) of hybrids among the ten popcorn lines on the seed quality and agronomic traits.

Hybrids	Seed quality				Agronomic traits							
	FE	GT	MCT	DM	PH		EH		PE		GY	
					CS1	CS2	CS1	CS2	CS1	CS2	CS1	CS2
P1×P3	3.64	-6.44	13.57	-5.10	0.05	0.01	0.05	0.01	2.52	3.02	-161.2	-99.6
P1×P6	0.57	8.51	-10.32	6.65	-0.01	0.03	-0.02	0.04	-1.99	-0.73	379.5	-26.1
P1×P7	1.89	-2.76	-7.95	-1.03	-0.06	0.00	-0.05	0.00	-2.22	-1.94	86.2	229.7
P1×P8	-4.67	-7.26	-18.25	-8.02	0.04	-0.02	-0.02	-0.01	-2.74	-2.70	25.8	-194.2
P1×P10	-0.74	4.79	-1.86	5.90	-0.04	0.01	0.02	0.00	-3.44	-1.11	31.4	310.5
P1×L53	3.04	1.87	9.57	8.29	0.05	0.05	0.01	0.01	2.30	1.25	-357.5	401.7
P1×L54	-3.42	0.81	3.88	0.02	0.07	0.01	0.02	-0.03	0.88	2.19	-243.8	-241.0
P1×L70	2.62	3.20	7.96	-2.44	0.01	-0.05	0.04	-0.01	1.62	-1.07	102.4	-552.1
P1×L76	-2.93	-2.72	3.41	-4.27	-0.10	-0.04	-0.05	-0.01	3.08	1.10	136.9	171.0
P3×P6	4.24	4.99	6.80	-2.39	-0.02	0.00	0.00	-0.05	0.71	-0.13	30.7	-112.5
P3×P7	0.36	-5.15	-4.32	5.03	0.06	-0.01	-0.03	0.00	1.55	2.25	47.4	92.7
P3×P8	7.34	3.48	8.38	-1.95	0.03	0.03	0.05	0.01	-0.59	-0.41	330.1	-9.70
P3×P10	-2.06	1.78	9.02	9.76	-0.02	0.00	0.02	0.00	-1.12	-0.45	91.5	336.3
P3×L53	-9.95	1.73	-5.31	1.90	-0.07	-0.01	-0.04	0.01	1.00	0.98	-75.5	-3.50
P3×L54	-2.46	1.29	-9.50	11.04	-0.06	-0.01	-0.03	0.01	0.56	-2.52	-355.4	-18.7
P3×L70	-6.84	-2.07	-15.92	-4.60	0.06	-0.01	-0.02	-0.01	-2.34	-0.44	-45.1	-258.7
P3×L76	5.74	0.39	-2.72	-13.6	-0.02	-0.01	-0.02	0.01	-2.28	-2.29	137.4	73.8
P6×P7	-8.97	4.43	5.28	2.37	-0.10	-0.01	-0.07	0.01	-0.38	0.14	-646.9	-434.4
P6×P8	6.55	-0.94	6.74	12.71	0.00	-0.05	0.04	-0.01	0.69	1.60	-39.5	140.6
P6×P10	-2.01	0.23	-0.50	-0.35	-0.04	-0.04	-0.05	-0.02	0.91	0.46	103.0	-238.5
P6×L53	-8.86	-18.8	-11.45	-20.6	0.11	-0.04	0.02	-0.02	-1.96	-2.70	253.2	-460.2
P6×L54	-0.94	-3.13	8.11	-10.9	0.04	0.06	0.02	0.05	1.21	1.48	-208.0	160.1
P6×L70	9.67	2.51	-8.31	11.55	0.01	0.00	0.01	-0.03	-1.03	-0.28	173.3	592.4
P6×L76	-0.25	2.21	3.64	1.07	0.01	0.07	0.05	0.03	1.83	0.16	-45.4	378.6
P7×P8	-5.87	-1.58	-8.76	-21.0	0.04	0.02	0.00	-0.01	-0.74	0.24	234.5	379.1
P7×P10	5.36	3.46	5.75	2.12	0.02	-0.03	0.03	0.01	2.19	-1.15	-241.1	-400.2
P7×L53	0.38	-1.58	-3.07	4.11	-0.07	0.03	-0.03	0.01	1.41	-1.31	-73.1	-209.3
P7×L54	4.76	4.23	5.74	1.93	-0.02	0.03	0.02	0.01	0.85	0.87	116.9	188.6
P7×L70	0.38	-3.26	7.07	1.06	0.01	-0.04	0.03	-0.02	-1.90	-0.60	268.3	315.6
P7×L76	1.70	2.20	0.27	5.42	0.13	0.02	0.10	-0.01	-0.75	1.51	207.6	-161.8
P8×P10	-3.50	-1.16	-14.42	0.37	0.00	-0.08	0.01	-0.05	0.07	-2.85	-288.5	-745.2
P8×L53	2.78	3.79	4.13	10.08	-0.02	0.05	-0.02	0.04	-0.76	2.23	-52.9	203.3
P8×L54	-2.64	3.60	7.44	-0.48	-0.04	0.02	-0.04	0.02	2.46	1.44	94.2	181.0
P8×L70	5.27	1.62	11.27	-0.56	-0.07	0.05	-0.01	0.05	1.47	0.95	-269.2	182.4
P8×L76	-5.28	-1.55	3.47	8.86	0.01	-0.02	0.00	-0.03	0.13	-0.48	-34.5	-137.2
P10×L53	6.30	4.71	1.77	-0.08	0.01	0.01	-0.01	0.00	0.66	2.95	-116.4	341.2
P10×L54	2.96	-9.22	1.46	-9.24	0.06	0.06	0.00	0.01	-1.86	0.87	685.9	327.0
P10×L70	-6.01	-1.21	4.41	-7.23	0.04	0.04	0.02	0.02	0.88	0.73	-167.7	-105.2
P10×L76	-0.30	-3.38	-5.64	-1.25	-0.03	0.03	-0.04	0.03	1.71	0.55	-98.1	173.9
L53×L54	2.78	3.10	-0.75	6.60	-0.02	-0.07	0.03	-0.03	-2.38	-3.62	216.4	-318.6
L53×L70	2.56	1.12	-0.92	-6.68	0.04	0.03	0.03	0.00	-0.25	-1.14	226.2	61.4
L53×L76	0.97	4.07	6.03	-3.54	-0.01	-0.06	0.01	-0.02	-0.02	1.36	-20.4	-16.0
L54×L70	-4.52	-0.69	-6.73	1.29	-0.07	-0.06	-0.04	-0.02	1.77	1.54	-155.5	-15.9
L54×L76	3.47	0.01	-9.65	-0.22	0.04	-0.04	0.01	-0.02	-3.48	-2.23	-150.7	-262.3
L70×L76	-3.13	-1.22	1.18	7.60	-0.03	0.04	-0.06	0.03	-0.21	0.31	-132.7	-220.0
SD	3.57	2.05	4.09	2.14	0.04	0.04	0.03	0.03	1.15	1.03	175.8	156.0

FE: field emergence; GT: germination test; MCT: modified cold test; DM: dry matter.

conclusively shows that it is possible to achieve significant gains for both the seed quality traits and agronomically important traits, showing the success of the present study.

Materials and Methods

Plant materials

Forty-seven popcorn lines from generation S_7 of the Germplasm Bank at the State University of Norte Fluminense 'Darcy Ribeiro' (Universidade Estadual do Norte Fluminense Darcy Ribeiro) were tested for their popping expansion (PE), from which the best ten lines in terms of PE and with distinct genealogies were selected (Table 1). The ten lines were then used to obtain all possible hybrids by means of a complete diallel crossing scheme, and the hybrids were evaluated for seed quality and agronomic traits. The experimental design for studying both seed quality and agronomic traits was randomized blocks with four replicates.

Assessment of seed quality

Field emergence was evaluated in the experimental area of the 'Antônio Sarlo' State Agricultural College (Colégio Estadual Agrícola Antônio Sarlo) in Campos dos Goytacazes, state of Rio de Janeiro (RJ). For this purpose, 90 hybrids were sown in two 3.00 m long rows with 0.90 m spacing between rows and 0.20 m spacing between plants, using two seeds per hole at a depth of 0.05 m. The number of normal seedlings emerged (NSE) was counted in each plot at 14 days after sowing, and the results were expressed as percentages (Nakagawa, 1994).

The germination test was conducted with four replicates per treatment, with each replicate consisting of 50 seeds. The seeds were sown between three sheets of germitest paper moistened with distilled water, using an amount equivalent to 2.5 times the mass of the dry paper. The sheets were made into rolls that were transferred to a BOD incubator with alternating temperature of 20-30°C following Brasil (2009). After seven days, a final count was performed to assess the percentage of normal seedlings.

The modified cold test was carried out with four replicates of 50 seeds per treatment. Sowing was performed between three sheets of germitest paper previously moistened with distilled water at a ratio of 2.5 times the mass of the dry paper. The prepared rolls were wrapped in plastic bags, remaining in that condition for seven days in a BOD germination chamber in the dark and at a constant temperature of 10°C. At the end of that seven-day period, the rolls were transferred to the germinator with alternating temperature of 20-30°C for four days, following Brasil (2009). Subsequently, an evaluation was performed by calculating the percentage of normal seedlings.

To obtain the dry matter, seedlings considered normal in the germination test were placed in properly labeled paper bags and placed in an oven at 70°C for 48 hours. Then, the seedlings were weighed on a precision scale (0.0001 g), and the values were corrected for the mean per normal seedling and expressed in mg.

Assessment of agronomic traits

For this evaluation, the 90 diallel hybrids were tested in two seasons, the first (October-February) and second (February to June) Cropping season, at the 'Antônio Sarlo' State Agricultural College in Campos dos Goytacazes, northern region of the state of Rio de Janeiro, located at 21° 45' S latitude and 41° 20' W longitude and 11 m elevation.

Each experimental unit consisted of two three-meter-long rows, with row spacing of 0.9 m and 0.20 m spacing between plants. The seeds were sown at 0.05 m depth with three seeds per hole, and thinning was performed after 15 days, leaving only one plant per hole.

The following agronomic traits were assessed: Plant height (PH), measured in meters from ground level to the insertion of the flag leaf in ten competitive plants; ear height (EH), measured in meters from ground level to the insertion of the upper ear in ten competitive plants; popping expansion (PE), determined by measuring 30 g of grains and placing this amount in a microwave using a special plastic container for popping corn at 1000 W power for one minute and forty five seconds, then measuring the popcorn volume in a 2000-mL beaker, and finally dividing the popped volume by 30 (the grain mass) and expressing PE in $mL.g^{-1}$; grain yield (GY), determined by the total mass of grains in the plot and converted to $kg.ha^{-1}$. For GY, stand correction was performed using the ideal stand covariance method, as described by Schmildt et al. (2006), taking 30 plants as the ideal stand.

Statistical analyses

The results obtained were subjected to analysis of variance by the F-test. Based on the analysis of variance, the sums of squares of hybrids were broken down into general and specific combining ability and reciprocal effect. For this purpose, Griffing's Method 3 (Griffing, 1956) was used, where one set of F1 plants and reciprocals were included. All the analyses were performed using the Genes software (Cruz, 2013).

Conclusion

There was a marked reciprocal effect for ear height, grain yield and the seed quality traits in popcorn, requiring prior indication of the male and female parents in crosses. Lines L53 and L70 revealed, simultaneously, favorable estimates of general combining ability for increases in popping expansion and grain yield in crops during the first harvest, and the line L70 showed such results for crops in the second harvest. The best hybrids for popping expansion and grain yield during the first harvest were P1×L70, P1×L76, P3×P7, P7×L54 and P8×L54. For the second harvest, the best hybrids were P1×L53, P1×L76, P8×L53, P8×L54 and P10×L53. P1×L76 and P8×L54 showed a good performance for both of the growing seasons.

References

Andrade RA, Cruz CD, Scapim CA, Silverio L, Pinto RJB, Tonet A (2002) Análise dialélica da capacidade combinatória de variedades de milho pipoca. Acta Sci Agron. 24: 1197-1204.

Antuna OG, Sanches FR, Rio EG, Torres NAR, Garcia LB (2003) Componentes genéticos de caractertes agronómicos y de calidad fisiológica de semillas en líneas de maíz. Rev Fitotec Mex. 26: 11-17.

Barreto RR, Scapim CA, Amaral Júnior AT, Rodovalho MA, Vieira RA, Schuelter AR (2012) Avaliação da capacidade de combinação de famílias S2 de milho-pipoca por meio de diferentes testadores. Semin-Cienc Agrar. 33: 873-890.

Brasil, Ministério da Agricultura Agropecuária e Abastecimento. Secretaria de Defesa Agropecuária (2009) Regras para Análise de Sementes. Brasília. 398p.

Carena MJ, Wicks III ZW (2006) Maize early maturing hybrids: an exploitation of U.S. temperate public genetic diversity in reserve. Maydica. 51: 201-208.

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

Eagles HA, Hardacre AR (1978) Genetic variation in maize (*Zea mays* L.) for germination and emergence at 10°C. Euphytica. 28: 287-295.

Ferrão RG, Silva JC, Cruz CD (1985) Avaliação da capacidade combinatória de oito linhagens de milho em um sistema dialélico desbalanceado. Rev Ceres. 32: 283-292.

Gama EEG, Hallauer AR, Lopes MA, Parentoni SN, Santos MX, Guimarães PEO (1995) Combining ability among fifteen early cycle maize populations in Brazil. Braz J Genet. 18: 569-577.

Gomes MS, Von Pinho EVR, Von Pinho RG, Vieira MGGC (2000) Estimativas da capacidade de combinação de linhagens de milho tropical para qualidade fisiológica de sementes. Cienc Agrotec. 24: 41-49.

Griffing JB (1956) A generalized treatment of the use of diallel crosses in quantitative inheritance. Heredity. 10:31-50.

Hallauer AR, Miranda Filho JB, Carena MJ (2010) Quantitative genetics in maize breeding. 3rd Ed., Springer, New York.

Johnson RR, Wax LM (1978) Relationship of soybean germination and vigor tests to field performance. Agron J. 70: 273-278.

Kantety RV, Zeng X, Bennetzen J, Zehr BE (1995). Assessment of genetic diversity in dent and popcorn (*Zea mays* L.) inbred lines using inter-simple sequence repeat (ISSR) amplification. Mol Breed. 1: 365-373.

Larish LLB, Brewbaker JL (1999) Diallel analyses of temperate and tropical popcorns. Maydica. 44: 279-284.

Li YL, Dong YB, Niu SZ, Cui DQ (2007a) QTL for popping characteristics in popcorn. Plant Breeding. 126: 509-514.

Li YL, Niu SZ, Dong YB, Cui DQ, Wang YZ, Liu YY, Wei MG (2007b) Identification of trait-improving quantitative trait loci for grain yield components from a dent corn inbred line in an advanced backcross BC2F2 population and comparison with its F2:3 population in popcorn. Theor Appl Genet. 115: 129-140.

Lu HJ, Bernardo R, Ohm HW (2003) Mapping QTL for popping expansion volume in popcorn with simple sequence repeat markers. Theor Appl Genet. 106: 423-427.

Malik SI, Minhas NM, Munir M (2004) General and specific combining ability studies in maize diallel crosses. Int J Agr Biol. 6: 856–859.

Marcos Filho J, Cícero SM, Silva WR (1987) Avaliação da qualidade das sementes. FEALQ, Piracicaba. 230p.

Mino M (1980) Hybrid vigor found in some characters of maize seedlings. JPN J Breed. 30: 131-138.

Moterle LM, Braccini AL, Scapim CA, Pinto RJB, Gonçalves LSA, Rodrigues R, Amaral Júnior AT (2012) Combining ability of popcorn lines for seed quality and agronomic traits. Euphytica. 185: 337-347.

Moterle LM, Braccini AL, Scapim CA, Pinto RJB, Gonçalves LSA, Amaral Júnior AT, Silva TRC (2011) Combining ability of tropical maize lines for seed quality and agronomic traits. Genet Mol Res. 10: 2268-2278.

Nakagawa J (1994) Testes de vigor baseados na avaliação das plântulas. In: Vieira RD, Carvalho NM (Eds.) Testes de vigor em sementes. FUNEP, Jaboticabal. 48-85p.

Ortiz FC, Santos GG, Carballo-Carballo A, Bergvinson D, Crossa JL, Mendoz-Elos M, Moreno-Martinez E (2006) Análisis dialélico para caracteres de vigor de semilla y de plântula en genótipos de maíz tropical. Agric Téc Méx. 32: 77-87.

Pajic Z, Eric U, Srdic J, Mladenovic Drinic S, Filipovic M (2008) Popping volume and grain yield in diallel set of popcorn inbred lines. Genetika. 40: 249 -260.

Pereira MG, Amaral Júnior AT (2001) Estimation of genetic components in popcorn based on the nested design. Crop Breed Appl Biot. 1: 3-10.

Pesey NV (1970) Genetic factors affecting maize tolerance to low temperatures at emergence and germination. Theor Appl Genet. 40: 350-356.

Pfann AZ, Faria MV, Andrade AA, Nascimento IR, Faria CMDR, Bringhentti RM (2009) Capacidade combinatória entre híbridos simples de milho em dialelo circulante. Cienc Rural. 39: 635-641.

Pinto RMC, Garcia AAF, Souza Jr CL (2001) Alocação de linhagens de milho derivadas das populações BR-105 e BR-106 em grupos heteróticos. Sci Agri. 58: 541-548.

Rangel RM, Amaral Júnior AT, Scapim CA, Freitas Júnior SP, Pereira MG (2008) Genetic parameters in parents and hybrids of circulant diallel in popcorn. Genet Mol Res. 7: 1020-1030.

Rangel RM, Amaral Júnior AT, Viana AP, Freitas Júnior SP (2007) Prediction of popcorn hybrid and composite means. Crop Breed Appl Biot. 7: 287-295.

Rossato Junior JAS, Cazetta DA, Barbosa JC, Fornasieri Filho D (2013) Popping expansion and yield responses of popcorn cultivars under different row spacings and plant populations. Pesqui Agropecu Bras. 48: 1538-1545.

Sarkissian IV, Kessinger MA, Harris W (1964) Differential rate of developments of heterotic and nonheterotic young maize seedlings. Proc Natl Acad Sci USA. 51: 212-218.

Schmildt ER, Krause W, Cruz CD (2006) Melhoria na eficiência dos experimentos de indicação de cultivares de milho. Cienc agrotec. 30: 72-80.

Silva VQR, Amaral Júnior AT, Gonçalves LSA, Freitas Júnior SP, Candido LS, Vittorazzi C, Moterle LM, Vieira RA, Scapim CA (2010) Combining ability of tropical and temperate inbred lines of popcorn. Genet Mol Res. 9: 1742-1750.

Sprague GF, Tatum LA (1942) General vs specific combining ability in single crosses of corn. Agron J. 34: 923-932.

Sweley JC, Rose DJ, Jackson DS (2012) Hybrid and environment effects on popcorn kernel physiochemical properties and their relationship to microwave popping performance. J Cereal Sci. 55: 188-194.

Troyer AF (1996) Breeding widely adapted, popular maize hybrids. Euphytica. 92, 163-174.

Viana JMS, Valente MSF, Scapim CA, Resende MDV, Silva FF (2011) Genetic evaluation of tropical popcorn inbred lines using BLUP. Maydica. 56: 273-281.

Vieira RA, Scapim CA, Tessmann DJ, Hata FT (2011) Diallel analysis of yield, popping expansion, and southern rust resistance in popcorn lines. Rev Cienc Agron. 42: 774-780.