Combining ability of S₃ progenies for key agronomic traits in popcorn: comparison of testers in top-crosses

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ABSTRACT. The successful development of hybrid cultivars depends on the reliability of estimated combining ability of the parent lines. The objectives of this study were to assess the combining ability of partially inbred S₃ families of popcorn derived from the open-pollinated variety UENF 14, via top-crosses with four testers, and to compare the testers for their ability to discriminate the S₃ progenies. The experiment was conducted in the 2015/2016 crop season, in an incomplete-block (Lattice) design with three replications. The following agronomic traits were evaluated: average plant height, grain yield (GY), popping expansion (PE), and expanded popcorn volume per hectare. The top-cross hybrid, originating from the BRS-Angela *vs* S₃ progeny 10

combination, was indicated as promising, showing high values for specific combining ability for GY and PE. For the S_3 progenies that showed high and positive GCA values for GY and PE, the continuity of the breeding program is recommended, with the advance of self-pollination generations. Fasoulas' differentiation index discriminated the BRS-Angela tester as the most suitable for identifying the superior progenies.

Key words: Popcorn; *Zea mays* L.; General ability; Specific ability; Partial diallel; Hybrid

INTRODUCTION

Popcorn is a special type of corn mainly used as food by humans and is highly appreciated, worldwide. Growing this crop is an attractive option for the producer, given its high profitability, and for the popcorn seller, it is a product with wide acceptance (Matta and Viana, 2001; Amaral Júnior et al., 2013). In Brazil, the production area of this crop has increased progressively owing to the growing demand for popcorn in its natural or industrially processed form (Von Pinho et al., 2003; Moterle et al., 2006; Freitas Júnior et al., 2009). However, the growing demand is not being met because of the frequent unavailability of the cultivars registered with the Brazilian Ministry of Agricultural, Livestock, and Food Supply (Ministério da Agricultura, Pecuária e Abastecimento Agrário). Especially, the inability of the public research institutions working on this plant to supply the required number of cultivars is a big obstacle for the expansion of popcorn cultivation (Seifert et al., 2006; Ematné et al., 2012). In this regard, the development of hybrid cultivars deserves special attention from popcorn breeders.

The first stage in obtaining superior hybrids involves the selection of base populations from which the hybrid lines will be produced (Oliboni et al., 2013). The base populations should feature desirable agronomic traits and have their performance tested under different environments. They should also accumulate a high proportion of alleles associated with superior yields (Amorim and Souza, 2005) in addition to other traits of interest, such as popping expansion (PE), which is of special importance in popcorn. The popcorn cultivar UENF 14, adapted and recommended for the North and Northwest regions of Rio de Janeiro State, Brazil, is a good example of a base population possessing the above-mentioned traits (Amaral Júnior et al., 2013).

In a breeding program aimed at generating superior hybrid combinations, the production of hybrid lines begins with artificial self-pollination of hundreds of plants. The main consequence of this process is inbreeding depression and the consequent expressive gains in the exploitation of heterosis with hybrid production (Simon et al., 2004). The evaluation and selection of the generated hybrid takes into consideration both the behavior *per se* and in the hybrid combinations (Ferreira et al., 2009). The selection of superior lines based on traits that undergo inbreeding depression is limited due to the low correlation between their performance *per se* and of their subsequent hybrid combinations (Lima et al., 1984; Simon et al., 2004). Considering the high number of lines generated in a breeding program, as well as the need for identifying the genotypic superiority already existing in earlier generations (S_3, for instance), a preliminary assessment based on their combining ability is required (Carvalho et al., 2003; Marcondes et al., 2015).

A feasible option for evaluation of lines is the top-cross method, proposed by Davis (1927). This method involves evaluation of the crosses between lines, with one or more testers, using their combining ability. The combining ability can be defined as the performance of a genotype when used in hybrid combinations (Sprague and Tatum, 1942; Hallauer et al., 2010). The combining ability is distinguished into general (GCA) and specific (SCA) combining ability (Cruz and Venconvsky, 1989). GCA is the measurement of behavior related to a certain genotype in a number of crosses that generate the hybrids. It is associated with the additive effects of alleles and additive-type epistatic actions. On the other hand, SCA represents the positive or negative deviation of hybridization relative to the mean GCA of the parents, through the effects of dominance and epistasis involving dominance.

The main difference between the general and specific combining abilities is attributed to the genetic basis of the tester, which can be broad or narrow. This distinction occurs because of the difference in the allele frequencies of the tester (Hallauer et al., 2010). When the tester from a broad genetic base is considered, the allele frequencies assume values between 0 and 1. In contrast, for allele frequencies of narrow-base testers, the values are limited to 0 or 1 (Cruz and Carneiro, 2006). In this context, the broad genetic base testers are used for discriminating the predominance of additive effects, whereas the narrow genetic base testers are used to measure the predominance of the dominance effects (Hallauer et al., 2010). Either way, the choice of the tester is paramount to the success of the top-cross methodology. A good tester shows efficiency in the discrimination of genotypes according to the purposes of selection, is easy to manipulate, and provides information about the relative genetic value of the lines (Hallauer, 1975; Hallauer et al., 2010). There are several methods that estimate the GCA and SCA effects to evaluate the combining ability, among which the one proposed by Griffing (1956) is the most commonly adopted.

In the case of popcorn breeding, knowledge about the genetic control of the main genetically important traits is noteworthy; these traits could be the grain yield (GY) or PE. Studies demonstrate the primacy of the gene effects of dominance in the expression of GY, whereas the additive effects prevail for PE (Larish and Brewbaker, 1999; Pereira and Amaral Júnior, 2001). In popcorn breeding, a negative correlation has been reported between the GY and PE (Hallauer, 2001; Daros et al., 2004; Hallauer et al., 2010; Cabral et al., 2016). To overcome this obstacle, the use of expanded popcorn volume per hectare (PV) super trait has been suggested. This variable is obtained as the product between the average yield of a plot and the PE, and is expressed as m^3/ha. PV is becoming an important selection criterion in popcorn, since it would be combining the two main traits of economic importance, which characterizes it as the basis for identification of superior genotypes.

The objectives of this study were to assess the combining ability of partially inbred S$_3$ families of popcorn, together with four testers, and to compare the testers as to the discriminatory ability of S$_3$ progenies by using the main traits of economic importance of the crop – PE and GY - associated with discrimination based on the PV super trait.

MATERIAL AND METHODS

Forty-three partially inbred S$_3$ families developed from the open-pollinated variety UENF 14 through three self-pollination generations were used in the experiment. The variety UENF 14 originated from a cross between an indigenous compound and a North-American variety that, after massal selection processes, backcrosses, and five recurrent intrapopulation

selection cycles, was recommended for the North and Northwest regions of Rio de Janeiro State, Brazil (Pereira and Amaral Júnior, 2001; Amaral Júnior et al., 2013).

The S_3 progenies were crossed with four testers, namely the open-pollinated variety BRS-Angela (Tester 1), top-cross hybrid IAC-125 (Tester 2), S_7 line P2 (Tester 3), and open-pollinated variety UENF 14 (Tester 4), in a partial diallel scheme. Among the four testers, three - UENF 14, BRS-Angela, and IAC-125 - are classified as having a broad genetic base, and one - P2 - has a narrow genetic base. BRS-Angela originated from five recurrent intrapopulation selection cycles of the popcorn compound CMS43 from Embrapa Maize and Sorghum (Pacheco et al., 2001). IAC 125 is a top-cross hybrid (simple hybrid *vs* variety) resulting from the cross between modified single-cross hybrid IAC 112 and a synthetic population, obtained from a North-American hybrid. Line P2, named so by the Popcorn Breeding Program of Universidade Estadual do Norte Fluminense (UENF), was obtained after seven self-pollination (S_7) cycles of the CMS-42 compound, belonging to the Germplasm of Embrapa Maize and Sorghum.

To obtain the top-cross hybrids, a proportion of four plots of each S_3 progeny was used for one plot of the testers; each experimental plot was 6.00 m long, spaced 1.00 m from each other, and plants were spaced 0.40 m apart. At the phenological stage of flowering, the crosses were made manually. The S_3 progenies were used as the female parents, and testers as the male parents. The crosses were performed with the mixture of the pollen from viable plants of each tester, and then the S_3 progenies whose stigmas were receptive were pollinated. Forty-three hybrid combinations were produced for each tester, totaling 172 top-cross hybrids. The crosses were performed in the months of June and July, 2015, at the Antonio Sarlo State College of Agriculture, located in Campos dos Goytacazes, RJ, Brazil. At the same location, the top-cross hybrids were evaluated in the 2015/2016 harvest, and planting took place on September 15, 2016. The experiment was arranged in an incomplete block (Lattice) design with three replications. Each experimental unit consisted of a 4.20-m long row, spaced 0.60-m apart, with plants spaced 0.30-m from each other, totaling 16 plants in the plot. Base fertilization was applied with 30 kg/ha N (in the form of urea), 60 kg/ha P_2O_5 (triple superphosphate), and 60 kg/ha K_2O (potassium chloride). The area was top-dressed 30 days after seeding, using 100 kg/ha N (in the form of urea). The cultivation treatments followed the recommendations for the popcorn crop (Amaral Júnior et al., 2013).

For assessment purposes, the average plant height (PH; m) was measured from the soil to the flag leaf. The values were obtained on the basis of the average of five plants from the usable area of the plot and measured in the grain-filling phenological stage. After the harvest, GY was assessed by weighing the grains produced in each plot, after threshing, and was expressed in kg/ha. PE was measured by placing 30 g of grains in a microwave oven (model NN-S65B, Panasonic, Manaus, AM, Brazil), inside a special bag for popping, at 1000 W, for 2.25 min. The popcorn volume was measured in a 2000-mL graduated beaker. PE, estimated using two samples per plot, was determined as the ratio between the expanded popcorn volume and the weight of 30 g of grains, expressed in mL/g. PV was estimated by multiplying the average yield of the plot by PE, expressed in m^3/ha.

The data were subjected to analysis of variance by the F test and significance at the 5% and 1% probability levels was evaluated. Subsequently, the treatment (S_3 progenies) was decomposed for the effects of testers and contrasts between the testers using the SAS software (Statistical Analysis System, SAS Institute Inc., 2003). To evaluate the efficiency of the testers, the differentiation test (D%) proposed by Fasoulas (1983) and based on the

Duncan test of means, was adopted. The analysis of variance of the partial diallel scheme was performed using the Genes software (Cruz, 2013), and was based on the results. The sums of squares of treatments were decomposed into GCA and SCA, adopting the means of the adjusted treatments, based on the model proposed by Griffing (1956), and adapted by Geraldi and Miranda Filho (1988).

RESULTS AND DISCUSSION

There was a significant difference between treatments for the traits (Table 1) at 1% probability level by the F test, providing evidence for genetic variability between S$_3$ progenies and testers, which indicates the need for decomposing the treatments for the inference of the effects of testers.

Table 1. Analysis of variance of traits of economic importance, based on estimates of top-cross hybrids of S$_3$ progenies from UENF 14 with four testers.

SV	d.f.	Mean square			
		PH	GY	PE	PV
Repetition	2	0.07	1,233,604.70	159.25	2,632.69
Block (Repetition)	42	0.14	1,372,648.30	12,13	1,486.33
Treatment	214	0.12**	2,687,545.10**	50.98**	2,632.04**
Tester 1	42	0.03**	968,833.54**	17.53^{ns}	972.47^{ns}
Tester 2	42	0.04^{ns}	904,758.11*	28.21**	1,127.92*
Tester 3	42	0.02*	1,658,915.47**	45.18**	1,550.56**
Tester 4	42	0.04^{ns}	612,135.07**	19.41**	722.90*
Tester 1 *vs* Tester 2	1	0.34*	26,825,438.28**	8.82^{ns}	23,279.32**
Tester 1 *vs* Tester 3	1	0.98**	1,720,993.48*	1,486.90**	24,301.48**
Tester 1 *vs* Tester 4	1	0.03^{ns}	15,609,498.65**	79.95**	11,194.21**
Tester 2 *vs* Tester 3	1	0.19^{ns}	14,618,986.22**	1,807.56**	58.09^{ns}
Tester 2 *vs* Tester 4	1	0.17^{ns}	1,391,941.19^{ns}	34.16^{ns}	2,033.54*
Tester 3 *vs* Tester 4	1	0.73**	6,850,394.09**	2,360.61**	2,912.00*
Residual	386	0.06	394,290.60	10.88	463.03
CV (%)		12.20	26.74	10.92	30.14
Average		2.05	2,348.53	30.20	71.38

SV = source of variation. d.f. = degrees of freedom. CV = coefficient of variation. PH = average plant height. GY = grain yield. PE = popping expansion. PV = expanded popcorn volume per hectare. **Significant at 1% probability level by the F test. *Significant at the 5% probability level by the F test. ^{ns}Not significant at 5% probability level by the F test. Tester 1: BRS-Angela; Tester 2: IAC-125; Tester 3: S$_7$ P2; Tester 4: UENF 14.

The decomposition of treatments (testers) showed significance at 5% probability level by the F test for the hybrids originating from the intercross between S$_3$ progenies and Tester 1 (BRS-Angela) for traits GY and PV, as well as Tester 3 (P2) for the PH trait, and, lastly, Tester 4 (UENF 14), for the PV trait. However, at 1% probability level by the F test, there were significant differences between the hybrid combinations of S$_3$ progenies and Tester 1 for the traits PH and GY, as well as with Tester 2 for the trait PE, in addition to Tester 3 for GY, PE, and PV, and Tester 4 for the traits GY and PE. These results demonstrate the distinct response of the testers in combination with S$_3$ progenies for the different traits evaluated. A lack of significant difference by the F test was noted with regard to the hybrids obtained with Tester 1 (BRS-Angela) for traits PE and PV. This was also the case for the PH trait, with hybrids from Testers 2 (IAC 125) and 4 (UENF 14) (Table 1).

Considering the differences between the testers (Table 1), Tester 1 *vs* Tester 3 and Tester 3 *vs* Tester 4 exhibited significance for all the traits. Thus, it can be inferred that there was a distinction of the produced hybrids between the above-mentioned testers for these evaluated

traits. The comparisons Tester 1 *vs* Tester 2 and Tester 1 *vs* Tester 4 revealed no significant differences at 5% probability levels for the traits PE and PH, in this order. This was also the case for Tester 2 *vs* Tester 3 for the traits PH and PV, and Tester 2 *vs* Tester 4 for most of the evaluated traits, except PV (P < 0.05). The lack of significant (P > 0.05) in the comparisons between the testers indicates that there was no amplitude of means, obtained by the hybrid combination with S_3 progenies, that could enable the distinction between the testers for the said traits.

In popcorn breeding programs, the key traits of this crop are GY and PE (Pereira and Amaral Júnior, 2001); for this reason, the analysis of the statistical significance of the comparisons between the testers is important because it directs the choice of testers to be used. In this regard, when two or more testers display a similar behavior, their use is not justified; this was the case for Tester 2 *vs* Tester 4, where the means did not show a significant difference.

There was a significant difference at 1% probability level in the GCA effect within the set of S_3 progenies (Group I) and testers (Group II) for all the evaluated traits (Table 2). The magnitude of the additive variance, expressed by the mean squares of GCA of the groups, indicates the occurrence of marked additive effects (Vencovsky and Barriga, 1992). Comparatively, Group II displayed a greater predominance of additive effects relative to Group I. The observation that Group II shows high mean squares for GCA is due to the broad genetic background of the testers (testers 1, 2, and 4), with a predominance of additive alleles.

Table 2. Estimates of mean squares (parents and F_{1s}) of general combining ability (GCA) and specific combining ability (SCA) and of the experimental residue for traits of economic importance evaluated in top-crosses of S_3 progenies from UENF 14 with four testers.

SV	d.f.	Mean square			
		PH	GY	PE	PV
Treatment	218	0.14**	3,521,063.07**	57.37**	3,394.78**
Groups	1	6.30**	326,535,119.62**	212.05**	321,530.34**
GCA Group I	42	0.35**	2,653,568.01**	106.58**	2,365.92**
GCA Group II	3	0.31**	11,758,717.71**	1,321.59**	14,543.50**
SCA I x II	172	0.05^{ns}	1,711,224.53**	22.40**	1,601.94**
Residual	436	0.07	487,341.26	10.96	562.35

SV = source of variation. d.f. = degree of freedom. MS = mean square. GCA = general combining ability. SCA = specific combining ability. Group I = S_3 progenies. Group II = testers. PH = average plant height. GY = grain yield. PE = popping expansion. PV = expanded popcorn volume per hectare. **Significant at 1% probability level by the F test. ^{ns}Not significant at 5% probability level by the F test.

In the SCA analysis (Table 2), only the PH trait did not display a significant effect, thus indicating a lack of gene action of dominance. The lack of significance of SCA for this trait denotes that the studied crosses did not present a satisfactory degree of complementation, concerning the allele frequencies, in the loci with some dominance (Vencovsky and Barriga, 1992). For the other evaluated traits, significant results were observed at 1% probability level for GCA and SCA, indicating the presence of a gene action of additivity and dominance, respectively (Table 2). The significant difference for SCA permits the demonstration of different degrees of complementation between the evaluated groups (S_3 progenies and testers), indicating hybrid combinations with a phenotypic performance different from that expected based only on the effects of GCA (Pinto et al., 2007).

The GCA estimates of the S_3 progenies *per se* (Group I) and of the testers (Group II) for each trait evaluated (Table 3) revealed that of the 43 S_3 progenies evaluated, 21 expressed negative estimates, suggesting a decrease in the size of the hybrids from these progenies. Among the testers, only P2 showed positive values; BRS-Angela, IAC 125, and UENF 14, in

turn, provided negative GCA estimates for PH, and were thus considered of interest for a reduction of PH, which is advantageous for cultivation in the North of Rio de Janeiro State, given the strong winds affecting the region (Freitas et al., 2014). According to Miranda et al. (2007), for PH not to be affected by the incidence of winds, plants shorter than 2.00 m should be preferred.

Table 3. Estimates of general combining ability (GCA) effects associated with S$_3$ progenies of popcorn (Group I) and testers (Group II) for the traits plant height (PH), grain yield (GY), popping expansion (PE), and expanded popcorn volume (PV), evaluated in a partial diallel scheme.

		Estimates of CGC effects associated/Group I - Progenies S$_3$						
S$_3$	Trait				S$_3$	Trait		
	PH	GY	PE	PV		PH	GY	PE	PV
1	0.02	80.43	3.19	8.86	23	0.01	-344.94	-3.47	-13.79
2	0.10	233.02	3.71	14.85	24	-0.23	-386.80	0.87	-7.81
3	0.32	347.47	-1.60	6.44	25	-0.01	-563.28	-1.53	-18.76
4	0.02	-429.95	-0.45	-12.13	26	0.13	337.83	-3.06	3.03
5	0.00	147.84	2.90	10.09	27	0.01	-59.02	-0.22	0.02
6	0.03	-144.02	2.29	0.75	28	0.02	-80.50	1.97	1.77
7	0.15	24.50	0.20	-0.49	29	0.43	136.72	0.10	4.16
8	-0.05	661.17	-2.53	14.03	30	-0.04	257.09	-5.06	-0.47
9	-0.02	282.65	0.45	7.01	31	0.06	-282.91	1.57	-7.00
10	0.07	204.13	-2.88	3.27	32	-0.15	-168.83	-4.10	-11.05
11	-0.07	287.83	2.34	13.67	33	0.09	219.32	0.66	7.96
12	0.00	-179.20	-0.10	-3.53	34	0.05	-709.94	-0.19	-21.80
13	0.06	-496.98	-0.60	-16.77	35	-0.14	102.65	-0.25	0.23
14	-0.09	634.87	-1.15	16.06	36	-0.02	32.09	0.92	0.65
15	-0.14	44.13	-0.34	0.87	37	-0.01	138.57	0.31	5.33
16	0.01	-205.31	1.81	-4.25	38	-0.17	-70.87	2.03	1.92
17	-0.05	586.35	-1.14	11.44	39	-0.09	-239.95	-0.83	-9.62
18	-0.06	253.76	0.67	10.46	40	0.00	145.43	0.09	5.39
19	-0.11	-337.35	-3.76	-14.89	41	-0.16	-336.98	3.39	-5.63
20	-0.06	-44.02	1.62	0.97	42	-0.04	10.61	3.01	6.14
21	-0.07	-672.54	0.16	-20.17	43	0.17	159.32	0.35	3.36
22	0.03	425.61	-1.35	9.42					
SE (Ĝi)	0.05	140.83	0.67	4.78					
		GCA effects associated/Group II - Testers						
Tester	Trait				Tester	Trait		
	PH	GY	PE	PV		PH	GY	PE	PV
BRS Angela	-0.04	350.21	1.04	13.60	P2	0.06	88.52	-4.55	-9.32
IAC-125	0.01	-327.68	1.50	-5.90	UENF-14	-0.03	-111.04	2.01	1.62
SE (Ĝi)	0.02	50.91	0.24	1.72					

GCA = general combining ability. PH = average plant height. GY = grain yield. PE = popping expansion. PV = expanded popcorn volume per hectare. SE = Standard error.

For the GY trait, 19 S$_3$ progenies showed negative GCA estimates, which is undesirable. This means that, when used as parents in crosses, these progenies will tend to reduce the average GY. The most expressive values for the GY trait were obtained by S$_3$ progenies 8, 14, 17, 22, 3, and 26. However, when these S$_3$ progenies were evaluated for PE, the observed values were negative, which is explained by the negative genetic correlation between GY and PE observed in the crop (Pereira and Amaral Júnior, 2001; Rangel et al., 2011). This correlation hinders the production of superior genotypes, i.e., those simultaneously showing high GY and PE (Zinsly and Machado, 1987; Andrade et al., 2002).

The PE trait provided 23 S$_3$ progenies with positive estimates (Table 3), among which the S$_3$ 2, 41, 1, 42, and 5 stood out with the respective values of 3.71, 3.39, 3.19, 3.01, and 2.90. This outcome indicates that these are hybrids with a higher concentration of favorable alleles for a trait with predominance of action of additive gene effects (Larish and Brewbaker, 1999; Pereira and Amaral Júnior, 2001). With regard to the testers, they displayed

a good performance, overall, and only the P2 line showed a negative estimate. The negative GCA present in this tester may be due to its narrow genetic base, and consequently the lower frequency of alleles with additive effects (Pena et al., 2016). Considering the GY and PE traits simultaneously, S_3 progenies 2 and 11 as well as Tester BRS-Angela were noteworthy, with positive and superior GCA values. That said, promising top-cross hybrids can be produced from the cross between BRS-Angela and S_3 progenies 2 and 11, with elevated yields and PE.

Considering the difficulty to obtain hybrids with high GY and PE estimates, at the same time, due to the negative genetic correlation between these traits (Zinsly and Machado, 1987; Daros et al., 2004; Rangel et al., 2011), we have proposed the use of the PV trait, which is considered a super trait. The PV is the product between PE and GY, and its use has allowed for simultaneous gains in the main traits of economic importance for the crop. The GCA estimates for PV discriminated 27 S_3 progenies and the testers BRS-Angela and UENF14 with positive values. Among these S_3 progenies, ten expressed, separately, negative values for PE. The positive and high PV estimates are explained by the higher forcefulness of the expression of GY achieved by these S_3 progenies. However, high PV values, influenced mostly by GY, should be interpreted with caution. It is, thus, necessary to make a comparison between PV and the individual values of GY and PE of each genotype, especially when the overall mean of the PE of a genotype is below 30.00 mL/g, which is the minimum value recommended for the cultivar. This is because since GY and PE are the traits of highest economic importance, neither of them should be excluded in the selection process.

BRS-Angela in combination with S_3 progenies provided superior hybrids for GY and PE, in which the combination with S_3 progeny 10 stood out with SCA estimates of 1274.03 and 4.43, respectively (Table 4). This hybrid was highlighted for having the highest SCA estimate for PV, which is in line with the individual results for GY and PE, ratifying the use of PV as an adequate alternative for the selection of superior genotypes, concomitantly, for the main economic traits of this crop. Analogously, S_3 progenies 8 and 14 were also promising with Tester BRS-Angela for the traits GY and PE, separately, with SCA estimates of 1202.18 and 910.46 for GY, and of 0.30 and 0.66 for PE, respectively, and for PV, when expressing, in this order, the second and third most expressive SCA values.

Regarding the tester with narrow genetic base - line P2 - its favorable allele concentration resulted in high genetic complementation for GY, with the combinations originating from the crosses with S_3 progenies 1, 17, 27, and 30 standing out (Table 4); the SCA estimates in these were greater than 1000. Of these hybrids, S_3 progeny 27 x P2 was highlighted for its high estimate for GY, of 1169.27, and consequently an expressive PE estimate of 1.69. This was, by no accident, the combination with the highest SCA estimate of PV, with an expressed value of 35.75.

For Tester IAC 125, there was no agreement between the SCA estimates of GY and PE; the hybrids that expressed the highest positive SCA magnitudes for GY displayed negative SCA values for PE. For instance, of all the combinations assessed, the hybrid between S_3 progeny 9 and Tester IAC 125 showed the most expressive GY estimate: 1587.58; however the SCA estimate of PE for this combination was negative (-3.31; Table 4). It should be stressed that both Tester IAC 125 and the S_3 progeny from which hybrid 9 originated did not present elevated GCA estimates for GY. The high SCA estimate of S_3 hybrid 9 x IAC 125 indicates the occurrence of high complementarity between its parents for the GY trait.

A small extent of expressive SCA estimates for GY occurred in the hybrids between UENF 14 and S_3 progenies, and this was expected because these combinations have a common genealogy and consequently little expressive heterosis, resulting from crosses between the parents with reduced genetic distances.

Table 4. Estimates of specific combining ability (SCA) effects between the S$_3$ progenies (Group I) and four testers (Group II) for the traits PH, GY, PE, and PV, evaluated in test crosses with popcorn in a partial diallel.

S$_3$		SCA effects			S$_3$				
	BRS-Angela					IAC-125			
	PH	GY	PE	PV		PH	GY	PE	PV
1	0.02	-160.79	0.14	-1.87	1	-0.02	-81.41	1.51	1.06
2	0.14	720.70	-3.73	13.23	2	0.17	646.00	0.54	25.64
3	-0.25	-253.01	3.48	2.73	3	-0.28	229.33	0.85	8.90
4	0.10	-263.75	2.33	-6.02	4	0.05	-134.01	-1.14	-9.04
5	-0.04	11.81	-0.30	2.96	5	-0.02	97.10	-0.15	1.95
6	0.14	505.15	2.59	27.74	6	0.06	6.74	0.91	4.13
7	-0.16	1095.14	-3.77	21.07	7	0.01	211.55	0.66	9.91
8	0.10	1202.18	0.30	34.41	8	0.05	843.03	0.94	27.05
9	0.14	172.66	-2.59	1.34	9	0.05	1587.58	-3.21	28.12
10	0.12	1274.03	4.43	48.97	10	-0.06	553.40	1.69	18.06
11	-0.02	405.15	2.60	27.98	11	0.11	540.80	-1.87	17.32
12	0.17	95.88	1.93	5.59	12	0.01	98.22	2.57	6.43
13	0.08	567.74	-0.91	13.20	13	0.03	-656.60	-5.49	-27.35
14	-0.05	910.46	0.66	32.83	14	0.01	-152.26	-2.96	-16.25
15	0.04	658.69	-1.52	10.60	15	-0.04	-53.37	0.17	0.89
16	0.10	133.85	0.63	9.38	16	0.05	38.40	3.44	10.62
17	0.11	835.52	-3.14	15.75	17	-0.03	1012.66	-1.11	29.57
18	0.03	436.25	0.38	15.56	18	-0.02	157.11	0.25	3.79
19	-0.05	-314.86	0.81	-13.16	19	-0.04	-114.01	0.01	-8.26
20	-0.01	-45.22	-1.51	-3.74	20	0.03	410.44	0.97	16.94
21	0.01	-124.85	-1.00	-6.75	21	0.06	-694.38	-4.19	-28.14
22	0.07	68.85	1.04	6.21	22	-0.01	-79.93	1.09	-0.48
23	0.04	-209.49	-0.81	-14.32	23	-0.02	361.74	2.62	13.06
24	0.21	170.14	5.46	19.04	24	-0.03	-55.68	3.38	0.78
25	0.08	-373.38	0.91	-11.83	25	0.07	301.55	0.57	7.10
26	-0.07	11.44	-1.94	-5.66	26	-0.05	-1180.31	-4.53	-41.42
27	-0.01	378.66	2.05	16.37	27	-0.03	-158.26	1.59	-4.53
28	-0.01	142.37	-2.32	4.98	28	-0.06	73.59	0.06	3.12
29	-0.40	46.63	1.73	7.67	29	-0.34	-282.89	-2.73	-15.33
30	0.09	370.70	1.72	7.41	30	-0.01	310.80	2.09	9.21
31	-0.05	-286.33	-2.96	-14.35	31	0.00	-129.93	1.58	-1.09
32	0.09	144.77	2.99	7.21	32	0.06	200.44	-0.03	1.94
33	0.02	155.65	1.47	9.31	33	0.00	284.03	-0.94	6.85
34	0.03	-593.17	-2.13	-16.10	34	0.01	-991.16	0.80	-29.65
35	-0.03	-242.26	-0.14	-6.10	35	0.02	272.66	-2.17	4.33
36	0.08	179.41	-7.09	-13.59	36	-0.05	-47.89	1.83	4.77
37	0.01	106.99	-1.32	-1.69	37	0.06	580.44	4.55	30.02
38	-0.06	-237.63	0.80	-4.02	38	0.05	530.63	-1.23	13.14
39	-0.01	455.88	-2.95	2.46	39	0.15	-315.12	-2.92	-15.25
40	0.04	909.03	0.74	30.95	40	0.00	-264.93	-0.18	-9.61
41	-0.06	-469.30	1.99	-7.43	41	0.04	-499.56	0.70	-15.68
42	0.08	501.63	0.21	20.97	42	-0.08	880.26	-0.70	28.53
43	0.02	41.80	-1.08	0.28	43	0.08	648.59	-2.93	13.55
S$_3$		P2			S$_3$		UENF 14		
	PH	GY	PE	PV		PH	GY	PE	PV
1	0.00	-307.98	5.03	4.53	1	0.04	288.61	-0.89	6.23
2	0.03	-26.94	0.91	3.66	2	0.02	194.24	6.43	27.42
3	-0.20	710.90	0.63	15.40	3	-0.21	486.76	-4.39	-1.22
4	-0.02	-520.58	1.92	-9.97	4	-0.03	369.35	0.47	12.53
5	0.00	-416.87	3.18	-4.44	5	0.00	-163.98	2.06	1.95
6	0.04	45.35	1.96	7.28	6	-0.04	-72.13	-1.93	-6.84
7	-0.05	527.21	-0.07	14.31	7	0.00	-1157.69	2.04	-32.15
8	-0.03	213.50	1.23	4.71	8	0.01	-256.57	-2.51	-16.74
9	0.05	133.80	0.29	9.29	9	-0.02	505.14	1.16	24.03
10	0.03	-185.76	-1.37	-15.89	10	0.13	55.27	0.23	-3.07
11	0.17	1161.64	-1.53	26.79	11	-0.08	-543.98	0.01	-15.74
12	-0.05	-392.06	2.79	-6.70	12	0.12	142.32	1.50	5.38

Table 4. Continued.								
				SCA effects				
S₃		BRS-Angela			S₃		IAC-125		

S₃	PH	GY	PE	PV	S₃	PH	GY	PE	PV
13	-0.02	-394.28	-2.43	-11.94	13	0.07	-126.58	2.17	-1.20
14	0.02	457.48	3.56	26.34	14	-0.04	704.98	-0.82	9.89
15	-0.04	-270.65	-0.87	-10.42	15	0.04	165.26	3.92	13.37
16	-0.11	109.61	-9.23	-18.18	16	0.38	529.91	2.55	27.06
17	0.10	1014.23	-3.33	10.24	17	-0.05	-199.54	0.55	-1.73
18	0.06	579.43	5.86	32.18	18	0.13	331.57	-1.27	6.94
19	0.03	-1267.98	-5.67	-36.57	19	-0.07	463.43	1.44	13.23
20	0.08	-562.80	-0.65	-15.26	20	0.03	943.42	-1.61	27.45
21	-0.01	-556.51	-0.74	-14.23	21	-0.03	99.35	3.41	8.47
22	0.05	683.13	-0.40	12.65	22	0.02	-21.02	1.81	5.81
23	-0.01	-691.50	-4.67	-26.68	23	-0.09	75.46	4.26	7.10
24	0.03	-245.21	3.05	-0.43	24	0.01	243.24	-2.25	-1.49
25	0.12	-683.54	1.00	-16.48	25	-0.01	-42.50	-3.67	-10.64
26	-0.07	-677.99	2.26	-10.43	26	-0.07	96.39	0.13	2.57
27	0.04	1169.23	1.69	35.75	27	0.00	-69.72	1.51	-0.72
28	0.07	-30.02	2.23	5.01	28	0.04	-457.13	1.10	-11.01
29	-0.42	-195.39	6.20	5.27	29	-0.25	561.20	-2.20	9.89
30	0.16	1364.24	-1.08	15.27	30	0.02	473.43	1.75	13.49
31	0.00	-389.10	-1.82	-11.62	31	-0.01	100.83	-0.21	4.23
32	-0.04	442.02	0.63	6.53	32	0.05	-309.53	-3.61	-19.66
33	0.16	-36.60	-0.25	-2.09	33	0.04	341.28	0.98	12.36
34	0.04	-215.49	0.72	-7.40	34	0.06	107.13	-1.74	-1.28
35	0.07	955.72	-3.67	12.08	35	0.06	47.13	0.49	5.52
36	0.11	786.27	1.11	30.03	36	0.15	114.72	-1.57	2.66
37	0.05	131.64	-0.11	3.23	37	0.04	-474.72	-3.35	-19.70
38	-0.02	868.49	3.05	34.95	38	0.11	-108.24	1.98	1.31
39	0.06	-112.06	-1.66	-5.68	39	0.09	638.61	2.46	27.18
40	0.08	662.57	1.33	20.16	40	-0.06	7.32	1.31	2.11
41	0.11	162.76	-2.14	3.30	41	0.02	18.61	1.07	4.68
42	0.13	86.27	2.91	12.15	42	0.03	-136.39	0.34	-2.55
43	-0.04	884.24	0.40	25.67	43	-0.03	-157.68	-1.67	-6.92

SCA = specific combining ability. PH = average plant height. GY = grain yield; PE = popping expansion; PV = expanded popcorn volume per hectare.

Likewise, the SCA estimates for PV were also inexpressive (Table 4), denoting again the preponderance of GY in the expression of PV. The higher influence of GY on PV is better understood when we analyze the four highest SCA estimates for PV (Table 4): S_3 20, S_3 2, S_3 39, and S_3 16, in this order, for which there was coincidence in the ranking of the first and fourth most expressive values, with respective magnitudes of 943.42 and 638.61 for the S_3 20 and S_3 116 hybrids. Besides, the fourth ranking of SCA for PV referred to the fifth hierarchical order of SCA for GY, with estimates of 27.06 and 529.91 for the hybrid of the order of 16. Moreover, among the positive SCA for PV, 35 were also positive for GY, whereas for SCA this quantum was 27 positive estimates (Table 4).

Contrasting the low SCA values for GY, the hybrid obtained between S_3 progeny 2 x UENF 14 showed the highest SCA for PE, with an estimate of 6.43. This is due to the action of the additive effects that predominate for popping expansion (Larish and Brewbaker, 1999; Pereira and Amaral Júnior, 2001). It should be mentioned that cultivar UENF 14 originated from the recurrent intrapopulation selection cycles, and was released as a new cultivar in the fifth cycle (Amaral Júnior et al., 2013), which provided an accumulation of favorable alleles in the improved population (Hallauer et al., 2010).

Fasoulas' differentiation index (D%; Fasoulas, 1983) discriminated the testers P2 and

BRS-Angela as superior for GY, with respective estimates of 12.00 and 11.81% (Table 5). This is in line with the GCA estimates, which had positive values only for these two testers (Table 3). Testers IAC 125 and UENF 14, however, expressed comparatively lower values, with D% estimates of 3.02 and 3.79%, respectively.

Table 5. Discriminatory ability of testers, according to Fasoulas' differentiation index (Fasoulas, 1983), of top-cross hybrids, based on Duncan's (0.05) mean comparison test.

Tester	GY (%)	PE (%)	PV (%)
BRS-Angela	11.83	11.95	12.60
IAC-125	3.02	14.02	4.98
P2	12.00	3.93	4.72
UENF 14	3.79	15.34	5.47

GY = grain yield. PE = popping expansion. PV = expanded popcorn volume per hectare.

For PE, D% discriminated testers UENF 14, IAC 125, and BRS-Angela, in this order, as superior, with estimates of 15.34, 14.02, and 11.95%, whereas P2 provided the lowest percentage, 3.93% (Table 5). Thus, D% differentiated Tester P2 as the least interesting in the discrimination of progenies from crosses with S$_3$. For the PV trait, Tester BRS-Angela stood out with the highest estimate (D% = 12.60%), indicating that it was the best Tester in the discrimination of S$_3$ progenies for the super trait that comprises valuation for the GY and PE. Tester BRS-Angela was also the only one to show a high GCA estimate for PV (Table 3). The other testers - UENF 14, IAC 125, and P2 - expressed lower D% estimates, in a hierarchical order of 5.47, 4.98, and 4.72% (Table 5).

Considering the main traits of economic importance for the popcorn crop together - GY, PE, and PV - Tester BRS-Angela stood out revealing the most expressive estimates of the differentiation index, which indicates that it is the most suitable for discriminating S$_3$ progenies. Additionally, testers IAC 125 and UENF 14 can be highlighted for revealing similar values for the three traits, which agrees with the analysis of variance of the contrasts between these testers, in which most of the traits considered here did not show significance at 5% probability level by the F test (Table 1).

In the identification of the tester to differentiate superior S$_3$ progenies, the coincidence of the order of their top-crosses with the classification of the combining ability of the tested progenies was used as an additional criterion (Scapim et al., 2008). Considering the GY trait (Table 6), Tester BRS-Angela was most distinct, as it allowed for the classification of the first three S$_3$ progenies - 8, 14, and 17 - among their six combinations, ranked second, fourth, and sixth. Tester IAC 125, in turn, identified two superior combinations; among these, S$_3$ progeny 8 was in the fourth place and S$_3$ progeny 17 was ranked second, whereas for testers P2 and UENF 14, only one progeny from each of these testers was identified as superior: progeny 17, ranking fourth, and progeny 14, ranking second, respectively.

With regard to PE, none of the testers provided good similarity in the classification of the best hybrids. Scapim et al. (2008) compared three testers of distinct genetic bases in the discrimination of 36 popcorn S2 families and found similar results, in which testers did not show a good classification for the families that expressed the best combining abilities. It is noteworthy that of the eight best hybrid combinations between S$_3$ progenies and Tester P2, seven showed S$_3$ parents with positive GCA for PE. In fact, because Tester P2 showed a negative GCA (Table 3) for PE, the positive values of its hybrids were mostly due to the combining abilities of the S$_3$ progenies.

Table 6. Ranking of S$_3$ progenies concerning the general combining ability (GCA) values and their top-crosses with four testers.

S$_3$	GY					S$_3$	PE					S$_3$	PV				
	GCA	T1	T2	T3	T4		GCA	T1	T2	T3	T4		GCA	T1	T2	T3	T4
1						1	3°			3°		1	9°				
2		7°	6°			2	1°				1°	2	2°		6°		2°
3	5°			9°	7°	3			3°			3				9°	
4					10°	4			7°			4					9°
5						5	5°			5°	8°	5	7°				
6		10°				6	7°	6°				6			6°		
7		3°				7					9°	7			7°		
8	1°	2°	4°			8						8	3°	2°	5°		
9	8°		1°		6°	9						9			4°		5°
10		1°	8°			10		2°	8°			10		1°	7°		
11	7°		9°	3°		11	6°	5°				11	4°	5°	8°	5°	
12						12		10°	5°	9°		12					
13		9°				13					7°	13					
14	2°	4°			2°	14				4°		14	1°	3°		6°	
15		8°				15				3°		15					7°
16					5°	16	10°		2°		5°	16					4°
17	3°	6°	2°	4°		17						17	5°		2°		
18	10°					18			2°			18	6°			3°	
19				9°		19						19					8°
20				1°		20						20			9°		1°
21						21				4°		21					
22	4°			10°		22						22	8°				
23						23			4°		2°	23					
24						24		1°	3°	7°		24			9°		
25						25						25					
26	6°					26				10°		26					
27			2°			27		8°	9°			27			10°	1°	
28						28	9°					28					
29				4°		29				1°		29					
30	9°			1°	8°	30			6°			30				10°	6°
31						31			10°			31					
32						32		4°				32					
33						33						33	10°				10°
34						34						34					
35			5°			35						35					
36			8°			36			7°			36				4°	
37		7°				37			1°			37			1°		
38		10°	7°			38	8°			6°	10°	38			2°		
39				3°		39					6°	39					3°
40	5°					40						40		4°		8°	
41						41	2°	9°				41					
42		3°				42	4°			8°		42		8°	3°		
43		5°	6°			43						43			10°	7°	

GCA = general combining ability. T1 = BRS-Angela; T2 = IAC 125; T3 = P2; T4 = UENF 14. GY = grain yield. PE = popping expansion. PV = expanded popcorn volume per hectare.

When all hybrid combinations were considered of the testers in which the S$_3$ progenies expressed positive values for both GCA (Table 3) and SCA (Table 4), three S$_3$ progenies were identified in a hybrid combination with testers BRS-Angela, P2, and UENF 14, whereas Tester IAC 125 expressed eleven combinations.

Among the five best S$_3$ progenies in terms of GCA for PV - 14, 2, 8, 11, 17, in this order - genealogies 14, 8, and 17 stood out for the highest GCA estimates also for GY (Table 3). Additionally, progeny 2 had the highest GCA estimate for PE, whereas progeny 11 expressed a good classification for parental GCA for both the traits: GY and PE. For PV, Tester BRS-Angela was again highlighted as it classified three of the five best progenies: 14, 8, and 11, among its best combinations, besides the fact that combinations 2 and 11 also showed high

values when crossed with this tester. With regard to Tester IAC 125, good classifications for PV were identified (Table 6); however, progeny 14 was the only one to be identified, with the best GCA but with a negative SCA of -16.25. P2 and UENF 14, in turn, were not good testers, as they classified only one of the five best S$_3$ progenies for GCA among their best hybrid combinations (Table 6).

Based on D%, along with the classification criteria using the combining abilities of progenies and top-cross hybrids, Tester BRS-Angela should be discriminated, as it expresses high estimates for GY and PE in combinations with S$_3$ progenies.

CONCLUSIONS

The top-cross was efficient in the discrimination *per se* of the popcorn S$_3$ progenies and testers, as well as of the SCA effects on the hybrids. BRS-Angela *vs* S$_3$ progeny 10 stood out for the conditions of the North Rio de Janeiro State, for both grain yield and popping expansion. BRS-Angela was the best suited tester to discriminate the best S$_3$ progenies. It is recommended to use the PV trait in the identification of superior genotypes.

Conflicts of interest

The authors declare no conflict of interest.

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