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# Combining ability of popcorn lines for resistance to the fungus *Puccinia polysora* (Pucciniaceae)

**K.F.M. Schmitt, V.J. Lima, A.T. do Amaral Júnior, J.S. Santos, G.S. Mafra, M. Vivas, S.H. Kamphorst, Y.P. Souza, F.T. Oliveira, F.R.A. Ferreira and J.M.S. Vivas**

Laboratório de Melhoramento Genético Vegetal, Centro de Ciências e Tecnologias Agropecuárias (CCTA), UENF, Campos dos Goytacazes, RJ, Brasil

Corresponding author: S.H. Kamphorst
E-mail: samuelkampho@hotmail.com

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**ABSTRACT.** The selection of southern rust-resistant genotypes caused by *Puccinia polysora* (Pucciniaceae) is considered an efficient way to control this disease, which causes high crop losses in popcorn. To help choose adequate cultivars, we examined the combining ability of lines and the agronomic performance of popcorn hybrids for rust resistance. Eight $S_7$ popcorn lines were used, which were crossed in a complete diallel mating scheme, resulting in 56 hybrids. The disease incidence on the whole plant (INC), severity on a leaf of the main ear (SEV), grain yield (GY), popping expansion (PE) and volume of expanded popcorn per hectare (PV) were evaluated. Analysis of variance was performed and the means were grouped by the Scott-Knott algorithm. The analysis diallel was performed by the method of Griffing, using the Diallel I method. The hybrids L76xP8, P8xL70, L77xP8, P8xP1 and L55xL76 stood out with a GY of >3000 kg.ha$^{-1}$ and PE of >30 mL.g$^{-1}$. For the traits GY and VP, the non-additive effects were predominant, and the heterosis effects high. For the trait expression of INC, SEV and PE, the additive effects were more relevant. The estimates of general combining ability of lines L70, L61, P1 and L76 were negative for INC and SEV. For commercial cultivation, L77xL76, L76xP1, L77xL70, L76xL70, L70xL76 and L77xP1 are recommended, in view of their excellent agronomic performance and superior resistance to rust.

**Key words:** *Zea mays* var. *everta*; *Puccinia polysora*; Diallel; Rust

## INTRODUCTION

Maize (*Zea mays*) is one of the primary commodities grown worldwide (Zabed et al., 2016). Popcorn (*Z. mays everta*) is a special maize type that differs from the others in that the grains expand when heated, thus giving rise to popped corn (Sawazaki, 2001). Although it is a very popular food in Brazil, popcorn grain yields fall short of those of field maize (Santos et al., 2017). One of the reasons for this low production is the higher pest and disease susceptibility of popcorn (Kurosawa et al., 2016).

Since the 1990s, the increasing frequency and severity of some fungal foliar diseases have led to a significant decline in maize yields and grain quality (Pinto et al., 2006; Chávez-Medina et al., 2007; Vieira et al., 2011). Southern polysora rust, induced by the fungus *Puccinia polysora* (Pucciniaceae), is considered one of the most aggressive diseases of this crop, causing field losses of up to 65% (Costa et al., 2012). It has been detected in some of the main maize producing areas of Brazil (Dudienas et al., 2013; Ramirez-Cabral et al., 2017).

Polysora rust was first observed in Africa in 1949, causing an epidemic (Pinho et al., 1999). This rust–inducing fungus reproduces abundantly; under ideal conditions, even a small amount of inoculum can trigger devastating epidemics (Godoy et al., 2000). The use of pathogen-resistant varieties has been indicated as one of the most efficient and economical control strategies (Colombo et al., 2014). However, the use of genetic resistance in popcorn, especially against *P. polyssora*, is still rare (Mafra et al., 2018). In this context, with a view to the introgression of leaf-disease resistance genes, the popcorn breeding program of the Northern Fluminense State University Darcy Ribeiro (UENF) has been working since 2013 to characterize the resistance of popcorn in the UENF genebank with regard to the complex of corn leaf and ear fungal diseases (Kurosawa et al., 2016; Santos et al., 2016; Schwantes et al., 2017; Kurosawa et al., 2018; Mafra et al., 2018), in order to breed improved hybrids.

Considering the economic losses that occur in popcorn as a result of the attack of the southern rust pathogen, as well as the genetic variability in the UENF genebank (Kurosawa et al., 2016; Santos et al., 2016; Schwantes et al., 2017; Kurosawa et al., 2018), which comprises accessions from various soil-climate regions, the selection of promising genotypes is highly relevant in breeding programs. We evaluated the combining ability and hybrid performance of popcorn lines in this genebank for the development of resistance to southern rust in popcorn.

## MATERIAL AND METHODS

To establish hybrids, crosses were made based on a complete diallel design with reciprocals, as proposed by Griffing (1956). To this end, eight popcorn lines were used, previously identified as of interest for introgression of southern rust resistance genes by

Kurosawa et al. (2016). The lines ($S_7$) belong to the UENF Popcorn Breeding Program and formed 56 hybrid combinations in paired crosses.

For the crosses resulting in the hybrids, each line was cultivated in ten 5 m rows, spaced 0.90 m apart. Three seeds were sown together every 0.20 m, at a depth of 0.05 m and thinned to two plants per pit after 30 days. At flowering, the lines were hand pollinated, to establish 28 hybrid and 28 reciprocal combinations. The crosses were carried out in the experimental area of the Agricultural State College Antônio Sarlo, in Campos dos Goytacazes, northern region of the State of Rio de Janeiro.

The plant evaluation trial of the 56 hybrids ($F_1$s and reciprocals) and 8 parents was arranged in randomized blocks, with four replications. The plots consisted of one 5 m row with 25 plants, at a spacing of 0.90 m between rows and 0.20 m between plants.

In both trials, fertilization was applied at sowing, composed of 60 $kg.ha^{-1}$ of $K_2O$, 30 $kg.ha^{-1}$ N and 60 $kg.ha^{-1}$ of $P_2O_5$, and the cover fertilization was 100 $kg.ha^{-1}$ N. sidedressing applied 30 to 45 days after emergence, consisting of N-P-K (20-0-2), using 300 $kg.ha^{-1}$ and 200 $kg.ha^{-1}$ of urea, respectively. Sprinkle irrigation as well as herbicide and insecticide were applied whenever needed. The experiment was carried out in the experimental area of the Agricultural State College Antônio Sarlo.

The disease-related traits were evaluated during flowering, in the pasty grain stage. Rust occurrence was evaluated once a week for three weeks. The incidence of southern rust (INC) was determined based on a grading scale proposed by Agroceres (1996), which determines the proportion of injured leaves on the whole plant. The severity of southern rust (SEV) was estimated on a diagrammatic scale proposed by Fantin (1997). According to the scale, the average portion of the adaxial surface of the leaf of the first ear was evaluated. The following agronomic traits were evaluated: grain yield (GR), determined by weighing the grains of a plot after removal of the cob and expressed in $kg.ha^{-1}$; expansion capacity of popped grain (PE) $mL.g^{-1}$, defined by the quotient between popcorn volume and mass of a 30-g grain sample; and volume of expanded popcorn per hectare (PV), by multiplying the mean yield per plot by popping expansion, generating the mean expanded popcorn volume per hectare, expressed in $m^3.ha^{-1}$.

When the effect of the source of genotypic variation was significant, the data were subjected to analysis of variance and the means grouped by the Scott-Knott (1974) test at 5% probability. The selection accuracy was calculated by the method of Resende and Duarte (2007).

The combining capacity was analyzed by the Diallel Method I, proposed by Griffing (1956), in which the $p^2$ combinations are included. The genotype effect was considered fixed. The genetic and statistical analyses were processed with software GENES (Cruz, 2013).

## RESULTS

Significant differences between genotypes ($P < 0.01$) for all evaluated traits were found (Table 1), indicating the existence of variability between hybrids and lines. This provides a favorable basis for genetic gains by selection, resulting in superior genotypes.

**Table 1.** Analysis of variance for two traits of southern rust resistance and three agronomic variables, evaluated in a complete diallel mating scheme of popcorn lines.

| SV | DF | Mean squares | | | | |
|---|---|---|---|---|---|---|
| | | INC | SEV | GY | PE | PV |
| Blocks | 3 | 4220.38 | 2042.88 | 7849813.53 | 0.50 | 6169.33 |
| Genotypes | 63 | 111.14** | 150.12** | 3662308.02** | 46.67** | 3211.65** |
| Residue | 189 | 59.69 | 44.76 | 710220.31 | 6.55 | 627.13 |
| Mean | | 28.18 | 13.82 | 3362.60 | 27.97 | 92.66 |
| AS | | 0.6804 | 0.8377 | 0.8978 | 0.9271 | 0.8971 |
| Genetic parameters | | | | | | |
| $\sigma^2 g$ | | 12.86 | 26.33 | 738021.92 | 10.02 | 646.13 |
| $\sigma^2 f$ | | 27.78 | 37.53 | 915577.00 | 11.66 | 802.91 |
| h² (%) | | 46.30 | 70.18 | 80.60 | 85.94 | 80.47 |

INC = polysora rust incidence; SEV = polysora rust severity; GY = grain yield (kg.ha$^{-1}$); PE = popping expansion (mL.g$^{-1}$); PV = popcorn volume (m³.ha$^{-1}$); $\sigma^2 g$: genotypic variance; $\sigma^2 f$: phenotypic variance, $h^2$: broad-sense heritability at the mean level, SA = selection accuracy; ** significant at 1% probability.

The selection accuracy can vary from 0.10 (low) to 0.99 (very high), which simultaneously takes the coefficient of variation, the number of replications and the coefficient of genotypic variation into consideration (Resende, 2002). According to Resende and Duarte (2007), a selection accuracy of >80% is desirable, and selection accuracy tests of <60% are little reliable. Therefore, only the INC had a percentage below 80%, although the value exceeded the minimum of 60%, indicating high experimental accuracy.

If a breeder knows the estimates of the genetic parameters, the best selection strategy for plant breeding can be defined (Cruz et al., 2012). In this aspect, all traits evaluated, except for INC, had consistent $\sigma^2 g$ values, resulting in a percentage of h² of >70%. For these traits, the chance of success in the selection of superior genotypes is greater (Freitas Júnior et al., 2009). The heritability value of INC was 46.30%, and could be lower to ensure reliability for a successful selection of resistant genotypes for this trait. However, Cruz et al. (2014) consider h² values of around 40% as mean, and which can still provide an effective selection, which indicates a perspective of success for INC.

The Scott-Knott (1974) test detected variation for resistance-related traits. The trait polysora rust incidence (INC) separated two groups (Table 2). In the group with lower incidence, 29 genotypes were allocated, mainly the hybrid combinations P1xL70, L61xL76, L70xL76, P8xL61, P1xL61 and L76xP1, with the lowest means. For the trait SEV, three groups were formed, and the group with the lowest severity consisted of 45 genotypes, of which the hybrid combinations L61xL76, L70xL76, P1xL70, P1xL76 and L76xP1 preformed best and had the lowest means (Table 2). It is worth mentioning that the hybrid combinations L61xL76, L70xL76, P1xL70 and L76xP1 had the lowest means, both for incidence and severity. At least one of the parents (L70, L61 and L76) participated in all these combinations with lowest means. This indicated their consistency to constitute promising combinations and to be used in breeding programs for introgression of southern rust tolerance genes.

**Table 2.** Means of five popcorn traits evaluated in 56 hybrids, with Scott-Knott (1974) grouping (a, b, c), at 5% probability.

| **Genotypes** | **INC** | | **SEV** | | **GY** | | **PE** | | **PV** | |
|---|---|---|---|---|---|---|---|---|---|---|
| L88xL76 | 29.22 | b | 11.12 | a | 4343.91 | a | 24.27 | c | 106.84 | a |
| P8xL76 | 25.43 | a | 12.11 | a | 3504.58 | b | 33.15 | a | 116.43 | a |
| L61xL76 | 19.25 | a | 5.02 | a | 3613.17 | a | 26.38 | c | 96.00 | b |
| L70xL76 | 19.60 | a | 5.49 | a | 3470.24 | b | 29.27 | b | 100.78 | a |
| L77xL76 | 26.72 | a | 9.56 | a | 4210.48 | a | 29.21 | b | 123.97 | a |
| L55xL76 | 30.87 | b | 13.63 | a | 3744.33 | a | 28.68 | b | 106.47 | a |
| P1xL76 | 24.15 | a | 7.34 | a | 4561.11 | a | 29.44 | b | 134.34 | a |
| L76xL88 | 31.38 | b | 13.72 | a | 3645.64 | a | 24.27 | c | 88.96 | b |
| P8xL88 | 33.38 | b | 25.13 | c | 4313.39 | a | 27.38 | b | 118.53 | a |
| L61xL88 | 29.11 | b | 14.14 | a | 4118.20 | a | 20.60 | c | 85.04 | b |
| L70xL88 | 23.83 | a | 15.05 | a | 4311.84 | a | 23.50 | c | 103.91 | a |
| L77xL88 | 35.01 | b | 15.13 | a | 4648.00 | a | 23.44 | c | 108.76 | a |
| L55xL88 | 39.18 | b | 20.25 | b | 3742.28 | a | 22.90 | c | 86.85 | b |
| P1xL88 | 30.39 | b | 15.74 | a | 4254.48 | a | 23.67 | c | 100.71 | a |
| L76xP8 | 34.35 | b | 17.61 | b | 4018.88 | a | 33.15 | a | 132.34 | a |
| L88xP8 | 37.53 | b | 27.94 | c | 3879.00 | a | 27.38 | b | 108.14 | a |
| L61xP8 | 22.59 | a | 9.35 | a | 3909.59 | a | 29.48 | b | 113.92 | a |
| L70xP8 | 27.27 | a | 13.28 | a | 3545.45 | a | 32.38 | a | 115.73 | a |
| L77xP8 | 31.13 | b | 23.98 | c | 3553.60 | a | 32.31 | a | 114.86 | a |
| L55xP8 | 41.56 | b | 28.24 | c | 2038.37 | b | 31.78 | a | 63.42 | b |
| P1xP8 | 23.88 | a | 12.60 | a | 3611.88 | a | 32.54 | a | 117.25 | a |
| L76xL61 | 29.21 | b | 9.89 | a | 4089.00 | a | 26.38 | c | 106.68 | a |
| L88xL61 | 26.23 | a | 10.56 | a | 3097.45 | b | 20.60 | c | 62.65 | b |
| P8xL61 | 20.28 | a | 9.61 | a | 3755.58 | a | 29.48 | b | 110.91 | a |
| L70xL61 | 28.72 | b | 9.71 | a | 2557.71 | b | 25.60 | c | 64.46 | b |
| L77xL61 | 22.14 | a | 10.50 | a | 3871.41 | a | 25.54 | c | 99.81 | a |
| L55xL61 | 27.07 | a | 10.54 | a | 3199.01 | b | 25.01 | c | 80.34 | b |
| P1xL61 | 20.55 | a | 10.10 | a | 3290.18 | b | 25.77 | c | 85.36 | b |
| L76xL70 | 24.83 | a | 7.92 | a | 3830.97 | a | 29.27 | b | 112.35 | a |
| L88xL70 | 28.08 | b | 9.74 | a | 4502.03 | a | 23.50 | c | 104.12 | a |
| P8xL70 | 28.88 | b | 13.98 | a | 3625.70 | a | 32.38 | a | 117.52 | a |
| L61xL70 | 23.37 | a | 9.19 | a | 2477.70 | b | 27.71 | b | 69.00 | b |
| L77xL70 | 23.24 | a | 9.44 | a | 3960.76 | a | 28.44 | b | 112.76 | a |
| L55xL70 | 27.21 | a | 15.02 | a | 3246.53 | b | 27.90 | b | 90.50 | b |
| P1xL70 | 17.92 | a | 6.70 | a | 3758.75 | a | 28.67 | b | 108.16 | a |
| L76xL77 | 31.11 | b | 9.49 | a | 4388.25 | a | 29.21 | b | 129.33 | a |
| L88xL77 | 32.19 | b | 14.88 | a | 4495.34 | a | 23.44 | c | 104.66 | a |
| P8xL77 | 25.96 | a | 16.61 | a | 4316.98 | a | 32.31 | a | 138.86 | a |
| L61xL77 | 24.84 | a | 11.47 | a | 3106.65 | b | 27.65 | b | 85.76 | b |
| L70xL77 | 24.38 | a | 7.89 | a | 4433.02 | a | 28.44 | b | 126.12 | a |
| L55xL77 | 31.23 | b | 17.74 | b | 2199.03 | b | 27.84 | b | 59.22 | b |
| P1xL77 | 25.51 | a | 13.23 | a | 3046.57 | b | 28.60 | b | 87.03 | b |
| L76xL55 | 28.86 | b | 14.67 | a | 3910.11 | a | 28.68 | b | 111.42 | a |
| L88xL55 | 29.88 | b | 18.69 | b | 3247.13 | b | 22.90 | c | 76.51 | b |
| P8xL55 | 38.35 | b | 28.65 | c | 2432.02 | b | 31.78 | a | 76.28 | b |
| L61xL55 | 23.53 | a | 11.01 | a | 2635.48 | b | 27.11 | b | 70.77 | b |
| L70xL55 | 30.05 | b | 11.37 | a | 3513.57 | b | 27.90 | b | 97.89 | a |
| L77xL55 | 37.18 | b | 21.69 | b | 3341.14 | b | 27.84 | b | 93.03 | b |
| P1xL55 | 26.07 | a | 14.68 | a | 3208.88 | b | 28.07 | b | 89.24 | b |
| L76xP1 | 20.59 | a | 7.40 | a | 4035.65 | a | 29.44 | b | 116.70 | a |
| L88xP1 | 26.42 | a | 11.47 | a | 4767.01 | a | 23.67 | c | 111.04 | a |
| P8xP1 | 29.58 | b | 19.29 | b | 3382.14 | b | 32.54 | a | 107.81 | a |
| L61xP1 | 26.11 | a | 11.11 | a | 3830.66 | a | 25.77 | c | 99.84 | a |
| L70xP1 | 22.38 | a | 10.27 | a | 2897.08 | b | 28.67 | b | 82.80 | b |
| L77xP1 | 28.12 | b | 12.46 | a | 3359.97 | b | 28.60 | b | 96.07 | b |
| L55xP1 | 30.55 | b | 15.06 | a | 3001.18 | b | 28.07 | b | 84.53 | b |

INC = polysora rust incidence; SEV = polysora rust severity; GY = grain yield (kg.ha$^{-1}$); PE = popping expansion (mL.g$^{-1}$); PV = popcorn volume (m$^3$.ha$^{-1}$). Values followed by the same letters in a column do not significantly differ from each other.

For grain yield (GY), means of >3640 kg.ha$^{-1}$ (experimental mean) were observed in 29 combinations and the hybrids had a good performance. Two groups were formed for this trait. In the higher-yielding group, the combinations with highest means were L88xP1; L77xL88; L88xL70; L70xL77; L76xL77 e P8xL77 (Table 2).

For popping expansion (PE), three groups (a, b & c) were formed (Table 2) based on average test applied. Among these, the group with the best performance stood out with 10 genotypes, for which means of >31.78 mL.g$^{-1}$ were estimated. It was observed that all hybrids of this group have line P8 as common parent. In this case, the good performance of these hybrids for PE can be explained by the additive action of genes originating from parent P8 (Hallauer et al., 2010).

With regard to PV, two groups were formed. In the best group, 34 hybrids were allocated, of which mainly P8xL77, P1xL76, L76xP8, L76xL77, L70xL77 and L77xL76 presented the highest PV means (138.86 - 123.97 m$^3$.ha$^{-1}$). Based on the separate GY and PE values, all of these six hybrids were allocated in the best group for grain yield, however, only hybrids P8xL77 and L76xP8 were in the best group for PE, and the others were assigned to the second best. According to Lima et al. (2016), a higher PV value is associated with a greater GY expression and, therefore, selection for PV should consider a minimum PE of 30 mL.g$^{-1}$, to avoid a loss in popcorn quality. Thus, of the 34 hybrids in the best PV group, seven (P8xL77, L76xP8, P8xL70, P1xP8, P8xL76, L70xP8 and L77xP8) had a PE of 30 mL.g$^{-1}$, all with yields of >3504.58 kg.ha$^{-1}$, which exceeds the recommended value of 3000 kg.ha$^{-1}$, proposed by Scapim et al. (2006) as minimum value for recommendation of popcorn hybrids.

A priority of popcorn breeding programs is to reconcile grain yield with grain quality, of which the latter is expressed, above all, by popping expansion. Thus, the seven above hybrids had satisfactory PV, GY and PE values and can be recommended as new cultivars. As hybrids with high agronomic means associated with disease resistance, the combinations P8xL77, P1xP8, L70xP8 and L77xP8 (Table 2) can be highlighted, with a satisfactory performance for all traits. Complementary to the mean grouping data results, the discrimination of the general and specific combining ability effects provides important information about the performance of the parents and hybrids under study, generating more precise bases for genotype selection and continuity of the breeding program (Hallauer et al. al., 2010).

The partitioning of the treatments in GCA (Table 3) detected significant effects for all traits evaluated. For SCA (Table 3), no significant difference was found for the traits INC, SEV and PE. Therefore, the additive gene effects were assumed as more important in the expression of these traits. According to Vieira et al. (2011) and Mafra et al. (2018), the additive effects are highly relevant in the expression of southern rust resistance. For PE, the existence of a greater expression of additive effects for the trait was confirmed (Cabral et al., 2016; Pereira and Amaral Junior, 2001). According to Mafra et al. (2018), the use of parents in intrapopulation breeding programs is the best alternative to obtain selection gains for PE. For the traits GY and PV, the non-additive effects were predominant and therefore, the heterosis effects should be taken into account to explore the hybrid vigor for the selection of superior genotypes.

**Table 3.** Variance analysis for general combining (GCA) and specific combining ability (SCA), reciprocal effect (ER) and mean squares of the effects for five traits assessed in a complete diallel of popcorn lines.

| **FV** | **DF** | **Mean squares** | | | | |
|---|---|---|---|---|---|---|
| | | **INC** | **SEV** | **GY** | **PE** | PV |
| Genotype | 63 | 111.11$^{**}$ | 149.98$^{**}$ | 3662310.21$^{**}$ | 46.65$^{**}$ | 3211.73$^{**}$ |
| GCA | 7 | 500.19$^{**}$ | 1037.76$^{**}$ | 5331110.64$^{**}$ | 350.38$^{**}$ | 6907.70$^{**}$ |
| SCA | 28 | 78.59$^{ns}$ | 57.67$^{ns}$ | 6354137.13$^{**}$ | 6.97$^{ns}$ | 5068.91$^{**}$ |
| Reciprocal | 28 | 46.35$^{ns}$ | 20.35$^{ns}$ | 553283.18$^{ns}$ | 10.41$^{*}$ | 430.56$^{ns}$ |
| Residue | 189 | 59.69 | 44.76 | 710220.31 | 6.55 | 627.13 |
| | | **Mean squares** | | | | |
| GCA | | 6.88 | 15.52 | 72201.41 | 5.37 | 98.13 |
| SCA | | 4.73 | 3.23 | 1410979.20 | 0.10 | 1110.44 |
| ER | | -1.67 | -3.05 | -19617.14 | 0.48 | -24.57 |

INC = polysora rust incidence; SEV = polysora rust severity; GY = grain yield (kg.ha$^{-1}$); PE = popping expansion (mL.g$^{-1}$); PV = popcorn volume (m$^3$.ha$^{-1}$). **significant at 1% probability, * significant at 5% probability, ns = non- significant. DF = degrees of freedom.

With regard to the reciprocal effect (ER), significance was only observed for PE. The ER can be divided into maternal effect - when the genes originate from the nucleus of the parent used as mother - and extrachromosomal effect - when the genes come from mitochondria and chloroplasts (Ramalho et al., 2012). However, since the popcorn comes from the endosperm, there is a double genetic load of the female parent in the formation of this structure, in other words, 2/3 of the endosperm comes from the female parent (Ramalho et al., 2012), which may cause a reciprocal effect on PE.

The concept of general combining ability proposed by Sprague and Tatum (1942), characterizes the ability of the parent to transmit its performance to the progenies. In this study, parents with high performance and positive GCA estimates are preferred for traits such as GY, PE and PV. On the other hand, parents with low estimates and negative GCA values are preferred for characteristics such as INC and SEV. The parents L70, L61, P1 and L76 stood out with negative GCA estimates for INC and SEV (Figure 1.a). Thus, these lines are recommended in crosses to reduce the disease levels.

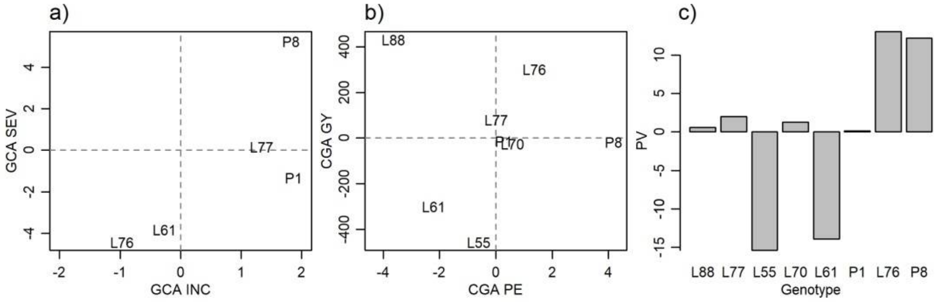

**Figure 1.** Estimate of the general combining ability, evaluated in a complete diallel with eight parents. a) relationship between the two traits of southern rust resistance; b) relationship between two agronomic traits in popcorn; and c) expanded popcorn volume per hectare. GCA = general combining ability, INC = polysora rust incidence, SEV = polysora rust severity, GY = grain yield (kg.ha$^{-1}$); PE = popping expansion (mL.g$^{-1}$); PV = popcorn volume (m$^3$.ha$^{-1}$).

Considering the positive GCA estimates for the agronomic traits, the best parents for grain yield were L76, L77 and L88. The parents L70, L76, L77, P1 and P8 stood out with positive GCA estimates for PE (Figure 1.b). In popcorn breeding programs, the selection of genotypes that combine favorable genes for GY and PE, which are the most economically important traits, is a priority. Line L88 - with the highest GCA for GY - expressed the lowest GCA estimates for PE, due to the negative correlation between GY and PE (Daros et al., 2004; Cabral et al., 2015). In spite of a negative correlation between GY and PE, genotypes can be selected for both traits, which is evident when the rankings in Figure 1.c of lines L76 and L77 are observed, particularly the first. Not coincidentally, L76 and P8 had the highest GCAs for PV (Figure 1.c). However, only for L76 the GCA estimates for GY and PE were positive, concomitantly; on the other hand, the effects of GCA for GY for parent P8 were negative.

For line L76, promising values for all analyzed traits were observed, with positive GCA for GY, PE and PV and negative estimates for INC and SEV. Therefore, this parent is characterized as the most appropriate to breed hybrids with high GY, PE and lower susceptibility to southern rust. On the other hand, the GCA for the agronomic traits of line L77 was also positive, while the performance for the two traits related to rust resistance was unsatisfactory. For INC and SEV, the GCA estimates of L77 were high and positive.

The significance of the SCA effects in genetic terms indicates that, in the trait inheritance, part of the genotypic variation was due to the expression of non-additive gene action (dominance and epistasis), interpreted as a deviation of a hybrid from what would be expected based only on the GCA of its parents (Gorgulho and Miranda Filho, 2001). With respect to the significance of the SCA effects in breeding programs for disease resistance, negative SCA estimates are sought for genotypes that contribute to a reduction of these traits (Aguiar et al. al., 2004). For the traits for southern rust resistance (INC, SEV), 19 of the 56 evaluated hybrid combinations stood out with negative SCA estimates, and the hybrids L61xP8, L76xL61, L76xP1, L77xL55 and P8xP1, with the lowest means for both traits (Tables 4). In all superior hybrids for INC and SEV, the GCA of at least one of the parents was also good.

For GY, 35 of the 56 evaluated hybrid combinations had positive SCA, particularly L61xP8, L70xL77, L88xP1 and L77xL88. For PE, the SCA estimates of 37 hybrid combinations were positive, mainly for P8xL77 and L88xL70. For PV, 36 hybrids had positive SCA estimates; and of these, the combinations L61xP8, L76xP1 and L70xL77 stood out with the highest SCA estimates (Table 3), and were also grouped with the highest-yielding hybrids.

Pinho et al. (1999), as well as Costa et al. (2012) and Ramirez-Cabral et al. (2017) reported a great reduction in maize yield caused mainly by southern rust infestation; therefore, the selection of resistant genotypes is extremely important. In this study, the best SCA was found for hybrid L61xP8, for the traits INC, SEV, GY and PV, and positive values for PE, with a mean performance of INC of 22.59, SEV of 9.33, GY of 3,909.59 kg.ha$^{-1}$, PE of 30.73 30 mL.g$^{-1}$, and PV of 119.82 m$^3$.ha$^{-1}$.

The SCA values are related to the deviation of the hybrid mean from the mean of its parents (Gorgulho and Miranda Filho, 2001). For this reason, the hybrids with the best means are often not those with the highest SCA (Conrado et al., 2014). Analyzing the correlation between mean values and SCA the best associations were found between the traits PV and GY. Hybrids L76xl77, L76xP1 and L77xL88, with highest mean PV, were also those with highest SCA. For GY, the hybrids L8xP1, L77xL88 and L70xL77 had the highest mean yields and SCA. These results show that the highest-yielding hybrids were those with the highest dominance deviations, i.e., highest heterosis values, which is in line with the greater importance of the non-additive effects for GY and PV (Table 1). For INC, SEV and PE the best-performing hybrids were different from those with highest SCA. In this case, since the additive effects were the most important for the three traits (Table 1), the dominance deviations are inexpressive because they are close to the parent means and there is no association between the mean values and SCA.

**Table 4.** Estimates of specific combining ability (SCA) evaluated in a complete diallel design with 56 popcorn hybrids for two characteristics of southern rust resistance and three related to agronomic aspects.

| | | | **Hybrids** | | | | | | **Reciprocals** | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | **INC** | **SEV** | **GY** | **PE** | PV | | **INC** | **SEV** | **GY** | **PE** | **PV** |
| L88/L77 | 0.39 | 4.52 | -39.86 | 0.35 | -0.70 | L77/L88 | -3.98 | -6.51 | -404.41 | 0.71 | -2.95 |
| L88/L55 | -4.92 | -6.04 | 30.67 | 0.06 | 27.91 | L55/L88 | -1.67 | -2.17 | -148.21 | 0.31 | -11.64 |
| L88/L70 | -2.10 | -2.99 | -543.07 | 1.46 | 4.65 | L70/L88 | -4.56 | -2.11 | 456.27 | -2.07 | 18.04 |
| L88/L61 | -2.10 | -1.73 | 208.25 | 0.97 | 32.71 | L61/L88 | 1.74 | 0.06 | 124.86 | -1.38 | 2.73 |
| L88/P1 | 2.50 | 2.30 | -497.35 | 0.10 | -18.12 | P1/L88 | -0.18 | -2.05 | 772.65 | -0.88 | 27.94 |
| L88/L76 | -1.38 | 0.80 | 206.60 | 0.15 | -19.96 | L76/L88 | -0.96 | -3.67 | 676.11 | 0.19 | 23.06 |
| L88/P8 | 5.02 | 2.59 | 85.34 | -0.90 | -3.83 | P8/L88 | -2.98 | -3.18 | 987.77 | -0.19 | 27.88 |
| L77/L55 | -2.69 | -2.58 | 43.58 | 0.29 | 16.38 | L55/L77 | -1.72 | 0.88 | 383.19 | -0.49 | -0.30 |
| L77/L70 | -0.09 | -1.30 | 548.32 | 0.53 | -1.36 | L70/L77 | 6.44 | 2.31 | 388.29 | -0.58 | 12.91 |
| L77/L61 | 3.71 | 2.89 | -537.31 | -2.54 | -18.45 | L61/L77 | 5.99 | 2.62 | 247.87 | -3.73 | 3.69 |
| L77/P1 | -3.01 | -2.43 | 27.15 | 0.03 | -9.40 | P1/L77 | 2.44 | 1.26 | 603.95 | 0.96 | 11.76 |
| L77/L76 | -1.42 | -1.22 | 194.53 | 1.20 | 7.81 | L76/L77 | 6.88 | 5.10 | -8.38 | 0.23 | 6.92 |
| L77/P8 | 5.43 | 3.60 | -251.44 | 0.23 | -7.44 | P8/L77 | 0.36 | 6.51 | 1403.56 | -0.69 | 42.20 |
| L55/L70 | 8.83 | 6.16 | -874.56 | 0.06 | -22.48 | L70/L55 | 7.25 | 8.85 | -580.32 | -0.96 | -10.46 |
| L55/L61 | -5.41 | -4.22 | -128.27 | 0.44 | -16.25 | L61/L55 | 2.98 | 2.95 | -73.44 | 1.02 | 7.08 |
| L55/P1 | 1.26 | -3.75 | 594.31 | 1.59 | 8.24 | P1/L55 | 0.18 | -2.39 | 89.45 | 0.42 | -1.44 |
| L55/L76 | 0.62 | -1.84 | 317.62 | -0.84 | -7.53 | L76/L55 | -0.09 | -0.45 | -834.78 | 0.33 | -25.08 |
| L55/P8 | -3.76 | 4.17 | 129.98 | -0.74 | -7.45 | P8/L55 | -4.51 | -11.52 | 1116.85 | 0.31 | 36.96 |
| L70/L61 | 1.24 | -2.52 | 469.70 | -0.08 | 7.90 | L61/L70 | -3.14 | -0.78 | -278.64 | -2.02 | -7.82 |
| L70/P1 | 0.78 | 0.82 | 643.01 | -1.17 | -1.21 | P1/L70 | -0.90 | -4.48 | 627.45 | 0.67 | 16.50 |
| L70/L76 | 3.09 | 6.42 | 62.98 | -0.58 | 17.57 | L76/L70 | -0.35 | -2.65 | 121.78 | 0.19 | 3.04 |
| L70/P8 | -6.40 | -6.09 | -276.98 | 0.45 | 1.29 | P8/L70 | 0.79 | 0.96 | 419.61 | 0.07 | 8.41 |
| L61/P1 | 3.13 | 8.60 | -177.40 | -0.29 | 11.82 | P1/L61 | -6.20 | -6.02 | 942.48 | 0.86 | 16.25 |
| L61/L76 | -1.48 | 0.43 | -292.61 | 0.42 | -28.52 | L76/L61 | -0.64 | 0.18 | -362.00 | 1.67 | 42.28 |
| L61/P8 | -3.71 | -6.46 | -77.46 | 0.73 | 10.97 | P8/L61 | -1.71 | -0.61 | 1855.08 | 0.19 | 49.76 |
| P1/L76 | -2.21 | -2.20 | -147.59 | -1.19 | 9.89 | L76/P1 | 3.84 | 0.55 | 308.24 | -0.88 | -0.78 |
| P1/P8 | 4.52 | 1.86 | 65.93 | 0.38 | -18.83 | P8/P1 | 1.40 | 2.71 | 1028.16 | 1.05 | 28.68 |
| L76/P8 | 1.04 | -5.00 | -139.20 | 0.54 | -15.49 | P8/L76 | 0.31 | 6.12 | 683.95 | -0.79 | 13.33 |

INC = *Puccinia polissora* incidence; SEV = *P. polissora* severity; GY = grain yield (kg.ha$^{-1}$); PE = popping expansion (mL.g$^{-1}$); PV = popcorn volume (m³.ha$^{-1}$).

## CONCLUSION

Parent L76 stood out as promising for future crosses with a view to higher grain yield and lower incidence and severity of southern rust. Lines L70 and L61 are the most indicated parents to be used in future crosses with a focus on increasing resistance to southern rust. For commercial cultivation, the hybrids L77xL76, L76xP1, L70xP8, L77xL70, P1xP8, L61xP8, L76xL70, P8xL76, L70xL76 and L77xP1 are recommended in view of their superior performance for all agronomic and southern rust resistance traits. For INC, SEV and PE, the additive gene effects were most important and, therefore, intrapopulation breeding methods are recommended for optimized gains. For GY and PV, non-additive effects were predominant, evidencing the effects of heterosis, and it is recommended to breed superior hybrids for these traits.

## CONFLICTS OF INTEREST

The authors declare no conflict of interest.

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