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Genetic control and combining ability of agronomic attributes and northern leaf blight-related attributes in popcorn

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ABSTRACT. The present study was conducted to investigate the genetic control and to estimate the general and specific combining abilities of popcorn for agronomic attributes and attributes related to resistance to northern leaf blight (NLB). The 56 hybrids (F_1 and reciprocals), together with the eight parent lines and six controls, were evaluated in two harvests, in a randomized-block design with four replications. Dominance components were more expressive than the additive components for grain yield and expression of resistance, and hybridization was the most suitable option for obtaining resistant and productive genotypes. For grain yield, popping expansion, and resistance to NLB, there was no significance for reciprocal effects, which indicates that the direction in which the cross is performed does not interfere with the hybrid's performance. Then, the superior hybrids recommended for more profitable growth were P8 x L61, L61 x L76, and L61 x L77.

Key words: *Zea mays*; Genetic resistance; Leaf disease; Diallel analysis

INTRODUCTION

Popcorn (*Zea mays* L.) is a type of corn whose main characteristic is its hard and small kernels, which hold the ability to expand as a result of an internal pressure when heated (Hoseney et al., 1983; Silva et al., 1993). Typically, when compared with cultivars of common corn, popcorn plants display a greater susceptibility to the attack of pests and diseases (Hallauer, 2001; Arnhold, 2008; Leonello et al., 2009). Besides contributing to low yields, this fact elevates production risks. Therefore, producing genotypes resistant to the main leaf diseases should be considered a relevant aspect in breeding programs for this species (Arnhold, 2008).

Northern leaf blight (NLB), a disease caused by *Exserohilum turcicum* (Pass.) Leonard and Suggs (sin. *Helminthosporium turcicum* Pass.), is widespread all over the world and practically in all corn grown (Smith and White, 1988; Carson, 1995). In popcorn, in particular, it is considered one of the main leaf diseases (Fantin et al., 1991; Miranda et al., 2002; Sabato and Pinto, 2013). The pathogen causes losses that can exceed 40% of the grain yield under favorable climatic conditions and in susceptible genotypes. In Brazil, the greatest severities of diseases have occurred in off-season crops, when the pathogen infects the plants during the flowering period (Costa et al., 2009). Because of the growing participation of the off-season seasons for this species, it is even more important to control diseases of higher incidence during this growing season.

Several control measures are implemented to minimize the damage caused by NLB (spot blotch), e.g., the spraying of fungicides and the planting of resistant varieties. Furthermore, some practices are adopted, such as crop rotation, the use of the adequate planting density and spacing, and the use of balanced fertilization and elimination of crop residues (Bergamin Filho and Amorim, 2011). Of the recommended measures, the use of resistant cultivars is the most effective means of control (Ishfaq et al., 2014), as it decreases production costs and reduces the risks to the activity of man and the environment (Vieira et al., 2009).

According to Paterniani and Miranda Filho (1978) and Hallauer et al. (2010), the breeding of corn has two alternatives that can be implemented together: obtaining genetically improved populations or hybrids. In the first case, by using adequate selection methods, the frequency of favorable genes in the enriched population can be gradually increased. In the second scenario, the breeding strategy is aimed at producing inbred lines that, when in proper combinations, can produce hybrids superior to the populations of origin. In the conception of Cruz et al. (2012), in the case of hybrid production, the diallel analysis has been exploited successfully, as it provides an estimate of useful parameters in the selection of parents for hybridization in a simple manner, as well as information about promising combinations.

Despite the advantages of diallel-cross strategies, however, little research has been conducted with popcorn using this methodology. The studies undertaken by Larish and Brewbaker (1999), Pinto et al. (2007), Pajic et al. (2008), da Silva et al. (2010), Viana et al. (2011), Vieira et al. (2011), Moterle et al. (2012), and Cabral et al. (2015) are the few examples in which diallels were used in popcorn, in which lines are used as parents. In this group, Vieira et al. (2011) evaluated grain yield (GY), popping expansion (PE), and partial resistance to southern corn rust (*Puccinia polysora* Underw) in hybrids originating from crosses in a partial circulating diallel scheme among ten popcorn lines (IAC 112 line groups x 'Zaeli' line groups). The authors observed a significant effect of general combining ability (GCA) in the Zaelin group for GY, PE, and resistance to southern corn rust and concluded that there is a predominance of additive genes in the expression of resistance, and these recurrent selection methods are recommended for obtaining gains in these traits.

At the moment, there are no studies on resistance to NLB employing diallel analysis in popcorn, although different levels of resistance to the disease have been reported in evaluations of popcorn genotypes (Fantin et al., 1991; Miranda et al., 2002; Vieira et al., 2009). Given the considerations mentioned above, the present study aimed to evaluate the genetic effects and the combining ability of hybrids of popcorn lines for incidence and severity of NLB, as well as for GY and PE, via diallel analysis, in the first and second harvests.

MATERIAL AND METHODS

Single-cross hybrids were produced, and parents and F_1 hybrids with reciprocals were evaluated at the Antônio Sarlo State Agricultural College, located in Campos dos Goytacazes - RJ, Brazil. The parent lines and diallel hybrids were cultivated in the agricultural periods of the first harvest (October 2014 to January 2015) and the second harvest (May to August 2015). The trial consisted of 70 treatments, including 56 simple hybrids (F_1 and reciprocals), eight parents (S_7 lines), and six controls, which were selected according to their performance regarding agronomic attributes and resistance to spot blotch, aiming to compare these traits in the controls with the hybrids. The adopted controls were IAC 125, BRS Angela, UENF 14, UFV M2-Barão de Viçosa, and hybrids L70 x L54 and P8 x L54.

The trials were implemented in a randomized-block design with four replications. The lines were chosen at random and separated from the hybrids to prevent competition effects. Plots consisted of a 5.0-m planting row with 25 plants, with 0.90 m spacing between rows and 0.20 m between plants. Grains were seeded at a depth of 0.05 m, using three grains per furrow; 30 days later, the area was thinned, leaving one plant per furrow. Plots were fertilized at seeding with 60 kg/ha K_2O, 30 kg/ha N, and 60 kg/ha P_2O_5, in addition to 100 kg/ha N. Irrigation was applied by a sprinkling system, and herbicides and insecticides were applied whenever necessary.

To evaluate the incidence and severity of NLB, caused by *E. turcicum*, five plants were analyzed per plot. The assessments took place during the flowering period and the grain's dough stage. Three evaluations were carried out, once a week. To study the incidence of *E. turcicum* in the plant, the scores proposed by Agroceres (1996) were adopted, and then, the proportion of leaf area of the plant was evaluated, considering all leaves. The severity of the disease in the leaf was determined by using a diagrammatic scale proposed by Vieira et al. (2013). In the study of severity in the leaf, only the leaf of the uppermost cob of the plant was considered.

Further, GY and PE were evaluated. The former was determined by weighing the grains after eliminating the cob, relative to the area extrapolated to hectares, and was expressed as kg/ha. To determine the PE (mL/g), the weight of 30 g grains was heated in a microwave oven inside a special bag for popping at the power of 1000 W for 2 min and 20 s. The popcorn volume was quantified in a 2000-mL beaker, by dividing the popped volume by 30 (weight of grains).

The data obtained from the experimental plots were initially subjected to an individual analysis of variance for each location, and combined analysis of variance in a completely randomized block design. Whenever a significant effect was detected, treatment means were grouped by the Scott-Knott algorithm at the 5% probability level.

In the diallel analysis, we used Griffing's (1956) Method 1, Model B. The GCA effects ($\hat{g}_i$) of each parent and the specific combining ability (SCA) effect ($\hat{s}_{ij}$) from a set of parental (p) and [p (p - 1) / 2] F_1 hybrids with the reciprocals were estimated. All analyses were performed using the computer resources of the Genes software (Cruz, 2013).

RESULTS AND DISCUSSION

For both incidence and severity of *E. turcicum*, there were significant effects for all tested sources of variation (data not shown); it thus follows that there is variation between the treatments, which allows us to anticipate the opportunity to identify lines and hybrids of interest for obtaining selective gains. A significant effect of growing harvest was already expected, given that the development of the disease is influenced by environmental variations, e.g., temperature and relative humidity of the air (Agrios, 1988). Costa et al. (2009) reported that the disease is more severe in the conditions of the second harvest, which is in line with the results obtained in the present study.

Considering the occurrence of a significant treatment x harvest interaction effect, individual analyses were performed for each growing harvest. A significant effect of treatment was observed in both harvests, indicating the existence of genetic variation, and consequently, the possibility of selection of superior genotypes. The variation of treatments as observed by the F-test was also detected by the Scott-Knott algorithm, and then, three (for severity in the first harvest) and six (for incidence in the second harvest) groups were formed (Table 1).

The group of genotypes that showed the lowest mean values for incidence and severity in both growing harvests, and consequently, the highest resistance levels was formed by parent L76, control UFV M2-Barão de Viçosa, and the combinations L55 x L61, L55 x L70, L55 x L76, L55 x L88, L55 x P8, L61 x L76, L61 x L77, L70 x L55, L70 x L88, L76 x L77, L77 x L76, L88 x L77, L88 x L61, L88 x L70, L88 x L76, L88 x P8, P8 x L61, and P8 x L88 (Table 1). According to the genealogy of the hybrids mentioned above, it is observed that the 18 combinations included lines L88, L77, L55, and L76 in their constitution that were obtained from varieties Viçosa and Beija-Flor, and were considered potential sources of resistance to NLB caused by *E. turcicum* (Miranda et al., 2003). The same was true for lines L70 and L61, which originated from cultivar BRS Angela, which has been reported as moderately resistant to *E. turcicum* (Embrapa, 2008). In this case, it was inferred that the lines provided experimental hybrids with the genetic contribution that culminated in higher levels of resistance in hybrids originating from lines of variety Beija-Flor. Therefore, the use of these parents in crosses tends to benefit the introduction of resistance genes, thereby making them of interest for breeding.

For grain yield, the means of the genotypes in the first harvest were allocated into three groups, whereas four groups were formed in the second harvest. In the two growing harvests, good performance was shown by the hybrids, since the means expressed by the genotypes that made up the group with the highest yields exceeded the magnitude of 3000.0 kg/ha. Of the genotypes that showed, in the first harvest, the best performance for grain yield, hybrids P8 x L61, L61 x L88, L77 x L55, and L88 x L77 stood out with estimated yields of 4767.01, 4648.00, 4502.03, and 4495.34 kg/ha, respectively. We also observed that among the lowest magnitudes for grain yield were varieties BRS Angela and UFV-M2 Barão de Viçosa, with mean values of 2560.12 and 2685.74 kg/ha, respectively. Therefore, these controls did not adapt well to Campos dos Goytacazes in the first growing harvest. In the second harvest, 20 genotypes expressed mean values for grain yield between 4197.92 and 5411.23 kg/ha. The highest mean for this trait was obtained in the second harvest. The experimental hybrids with the highest means for grain yield were L77 x L55, L61 x L77, L61 x L55, L77 x P1, with estimated yields of 5411.23, 4969.94, 4946.64, and 4787.83 kg/ha, respectively.

Table 1. Means clustering test for incidence and severity of northern leaf blight (NLB) evaluated in 8 parents, 56 hybrids, and 6 controls in the first harvest (October 2014 to January 2015) and the second harvest (May to August 2015) in Campos dos Goytacazes, RJ, Brazil.

Genotypes	Incidence of NLB		Severity of NLB		Grain yield (kg/ha)		Popping expansion (mL/g)	
	1st harvest	2 nd harvest	1st harvest	2 nd harvest	1st harvest	2 nd harvest	1st harvest	2 nd harvest
L55xL61	11.85c	10.69f	11.85c	1.65d	4,343.91a	3,674.22b	26.34c	27.75a
L55xL70	9.56c	9.99f	9.56c	1.49d	3,504.58b	3,743.56b	26.13c	24.84b
L55xL76	6.77c	11.30f	6.77c	0.65d	3,613.17b	4,716.69a	30.17b	21.09c
L55xL77	13.76c	17.42e	13.76c	3.37d	3,470.24b	4,621.03a	26.25c	24.26b
L55xL88	13.26c	5.26f	13.26c	0.13d	4,210.48a	4,544.87a	24.71d	20.67c
L55xP1	10.44c	21.94e	10.44c	3.88d	3,744.33b	3,130.30c	25.59c	26.17b
L55xP8	9.64c	10.14f	9.64c	2.08d	4,561.11a	3,463.94b	30.63b	25.25b
L61xL55	18.95b	9.32f	18.95b	0.47d	3,645.64b	4,946.64a	27.17c	30.00a
L61xL70	16.37c	10.48f	16.37c	1.81d	4,313.39a	3,828.60b	25.46c	31.17a
L61xL76	7.58c	8.30f	7.58c	1.15d	4,118.21a	4,492.78a	26.71c	29.63a
L61xL77	12.93c	11.94f	12.93c	1.73d	4,311.84a	4,969.94a	27.25c	31.50a
L61xL88	18.36b	8.23f	18.36b	0.32d	4,648.00a	4,380.38a	21.88e	24.42b
L61xP1	21.73b	21.14e	21.73b	1.76d	3,742.28b	3,614.79b	25.54c	31.00a
L61xP8	14.87c	20.97e	14.87c	4.60d	4,254.48a	3,681.30b	30.73b	31.83a
L70xL55	7.57c	10.69f	7.57c	1.16d	4,018.89a	4,197.92a	27.46c	23.34b
L70xL61	17.22c	17.24e	17.22c	3.69d	3,879.00a	3,940.50b	27.38c	30.75a
L70xL76	8.29c	28.68e	8.29c	5.60d	3,909.59a	3,734.11b	30.46b	26.00b
L70xL88	13.42c	7.63f	3.10c	0.73d	3,553.60b	3,666.81b	28.46c	22.00c
L70xL77	10.88c	23.56e	4.87b	5.22d	3,545.45b	4,286.40a	26.50c	30.25a
L70xP1	19.92b	21.71e	9.52b	6.69c	2,038.37c	2,943.92c	28.46c	30.56a
L70xP8	14.98c	23.64e	5.29b	7.03c	3,611.88b	2,536.97c	33.87a	30.59a
L76xP1	10.93c	21.01e	2.70c	2.82d	4,089.00a	4,390.84a	30.96b	25.75b
L76xL55	11.60c	19.37e	1.32c	1.80d	3,097.46b	4,485.45a	28.08c	21.92c
L76xL61	8.22c	31.68e	1.10c	6.25c	3,755.58b	3,732.35b	26.09c	28.33a
L76xL70	22.20b	52.33c	4.18c	10.85b	2,557.71c	2,894.31c	30.33b	26.25b
L76xL77	7.08c	9.78f	1.59c	0.59d	3,871.41a	3,898.32b	29.92b	22.08c
L76xL88	14.76c	50.50c	3.58c	10.32b	3,199.02b	3,524.20b	25.00d	19.09d
L76xP8	8.62c	27.98e	1.38c	5.18d	3,290.18b	3,197.01c	34.46a	28.83a
L77xP1	11.30c	17.56e	3.84c	2.56d	3,830.97a	4,787.83a	30.37b	30.84a
L77xL55	12.03c	16.57e	1.40c	2.20d	4,502.03a	5,411.23a	27.96c	22.92b
L77xL61	10.53c	26.04e	1.91c	5.05d	3,625.70b	4,210.63a	25.21d	31.58a
L77xL70	14.81c	50.50c	3.29c	8.56c	2,477.70c	2,804.77c	30.54b	30.08a
L77xL76	7.74c	5.32f	1.21c	0.35d	3,960.76a	4,582.80a	30.29b	25.42b
L77xL88	11.21c	43.94d	3.69c	7.52c	3,246.53b	3,310.99b	26.71c	17.70d
L77xP8	10.75c	35.93d	1.63c	6.93c	3,758.75b	3,095.58c	33.38a	30.42a
L88xL55	12.19c	3.69f	4.86b	0.55d	4,388.25a	4,235.68a	22.96e	21.50c
L88xL61	15.01c	7.86f	3.15c	2.27d	4,316.98a	4,305.62a	22.50e	24.34b
L88xL70	7.54c	4.60f	0.84c	0.07d	3,106.65b	4,501.46a	24.33d	22.58b
L88xL76	9.57c	5.69f	1.97c	0.20d	4,433.02a	4,647.67a	24.63d	18.83d
L88xP1	18.79b	13.82f	9.18b	2.76d	2,199.03c	3,016.15c	24.96d	22.96b
L88xP8	12.91c	13.27f	3.09c	3.36d	3,046.57b	2,616.87c	29.58b	23.02b
P1xL55	13.38c	16.65e	2.53c	4.57d	3,910.11a	3,876.68b	27.34c	26.13b
P1xL70	19.79b	23.04e	5.16b	3.86d	3,247.13b	3,019.11c	28.08c	30.63a
P1x L77	12.88c	21.00e	5.84b	4.76d	2,432.02c	3,158.94c	27.04c	30.59a
P1xL61	15.56c	45.00d	5.51b	8.24c	2,635.48c	3,353.60b	24.88d	31.33a
P1xL76	16.05c	51.75c	5.72b	11.57b	3,513.57b	3,576.33b	29.38b	25.42b
P1xL88	16.70c	14.02f	5.37b	2.46d	3,341.14b	2,820.74c	24.58d	22.09c
P1xP8	14.26c	45.26d	6,92b	7.75c	3,208.88b	2,556.71c	33.42a	30.92a
P8xL55	12.22c	10.99f	6.55b	0.98d	4,035.65a	3,654.52b	32.54a	23.00b
P8xL61	13.50c	15.56f	1.53c	2.00d	4,767.01a	3,832.40b	29.75b	31.92a
P8xL70	16.23c	16.32e	6.51b	3.98d	3,382.14b	3,673.81b	32.71a	30.25a
P8xL76	6.45c	25.47e	3.79c	2.47d	3,830.66a	3,916.17b	33.08a	26.54b
P8xL77	15.73c	25.86e	8.61b	4.54d	2,897.08b	4,538.59a	25.92c	30.22a
P8xL88	13.02c	14.19f	4.38c	1.48d	3,359.97b	3,230.11c	28.17c	23.08b
P8xP1	13.54c	53.43c	6.25b	13.98a	3,001.18b	2,394.37b	33.87a	31.59a
L88	36.03a	25.81e	6.08b	3.69d	1,670.11d	2,031.41c	18.50f	15.75d
L77	28.29a	30.89e	5.43b	6.94c	1,071.87d	1,035.91d	28.38c	29.25a
L55	34.79a	75.78a	16.09a	17.40a	1,521.88d	730.83d	27.31c	20.50c
L70	21.65b	52.59c	5.14b	10.44b	1,638.48d	1,992.93c	28.50c	29.92a
L61	28.42a	61.33b	3.77c	8.21c	722.88d	475.26d	22.71e	33.71a
P1	20.53b	47.75c	5.44b	8.69c	1,284.83d	664.69d	28.83c	29.58a
L76	16.47c	9.14f	1.23c	1.46d	1,633.28d	1,998.29c	30.04b	23.00b
P8	20.52b	40.28d	4.00c	6.04c	1,814.40d	2,553.24c	36.25a	31.09a
IAC 125	14.53c	31.61e	5.74b	8.04c	3,215.19b	2,817.62c	34.71a	33.08a
L70xL54	19.70b	60.65b	9.30b	12.3b	3,797.68b	3,355.37b	34.79a	25.00b
P8xL54	14.24c	40.85d	4.29c	6.68c	3,762.86b	3,205.60c	32.79a	31.92a
UENF-14	16.90c	20.70e	4.21c	3.28d	3,191.20b	3,778.18b	33.50a	28.38a
B. Viçosa	15.07c	10.14f	3.84c	2.61d	2,685.74c	3,142.96c	33.71a	27.75a
BRS Angela	9.20c	17.13e	3.44c	5.01d	2,560.12c	2,768.61c	34.38a	28.83a

Means followed by the same letter in a column do not differ by the Scott-Knott test at a significance level of 5%.

For popping expansion in the first harvest, the genotypes were distributed into five groups, while four groups were formed in the second harvest. Within the groups formed in the first harvest, fifteen genotypes showed average estimates greater than 32.71 mL/g, composing the group with the best performance. Among these, parent P8 and controls L70 x L54 and IAC 125 had the best performance, with estimated popping expansion of 36.25, 34.79, and 34.71 mL/g, respectively. Regarding experimental hybrids, L76 x P8 expressed the highest popping expansion, 34.46 mL/g. However, the estimated grain yield was not sufficiently high: 3290.00 kg/ha; nevertheless, this magnitude exceeds by 9.67% the minimum recommended for a release, characterizing it as a hybrid that can be indicated for commercial crops.

In the second harvest, parents L61 and P8 had the best means composing the group of genotypes with the highest estimates for popping expansion: 33.71 and 31.09 mL/g, respectively. Controls IAC 125 and P8 x L54 had the best performance for this growing harvest, with estimates of 33.08 and 31.92 mL/g. These higher mean values of parent P8 in both growing harvests demonstrate its potential among the evaluated parents, characterizing it as promising to be used in breeding programs aimed at increasing the popping expansion. Experimental hybrids L61 x P8, P8 x P1, L77 x L61, and P1 x L77 had the best performances for popping expansion, with estimated values of 31.83, 31.59, 31.58, and 31.33 mL/g, respectively.

The mean squares for GCA and SCA, in the second harvest, were significant for incidence and severity of *E. turcicum*, as well as for GY and PE, which indicates the existence of variability resulting from the action of additive and non-additive effects in the control of the gene expressions of these traits (Table 2). By contrast, for the first harvest, a significant effect of GCA was only observed for severity of *E. turcicum*, GY, and PE; for SCA, only for the incidence of leaves with symptoms of NLB. As also shown in Table 2, there was no significant reciprocal effect for the evaluated traits, either relating to resistance to NLB or for agronomic

Table 2. Estimates of mean squares of treatments (parents, F_1, and reciprocals), general (GCA) and specific (SCA) combining abilities, reciprocal effects and residue, as well as of square means for the combining ability effects for six traits evaluated in a full diallel among eight parents, with the reciprocals, in the first harvest (October 2014 to January 2015) and the second harvest (May to August 2015) in Campos dos Goytacazes, RJ, Brazil.

SV	d.f.	Incidence of NLB		Severity of NLB	
		1st harvest	2 nd harvest	1st harvest	2 nd harvest
Genotype	63	27,454.8390**	218,117.5369**	4,468.2837**	4,367.1203**
GCA	7	60,583.8321$^{\dagger NS}$	1,203,867.4560**	18,258.8802**	23,109.1557**
SCA	28	41,796.5796**	179,669.4416**	3,623.0738^{NS}	3,277.1100**
Reciprocal	28	4,830.8501^{NS}	10,128.1523^{NS}	1,865.8445^{NS}	771.6218^{NS}
Residual	189	9,084.9527	15,824.1628	2,305.2210	517.0652
Mean squares of effects					
GCA		804.6700	18,563.1765	249.2759	353.0014
SCA		8,177.9067	40,961.3197	329.4632	690.0112
Reciprocal		-531.7628	-712.0013	-54.9221	31.8196
SV	d.f.	Grain yield		Popping expansion	
		1st harvest	2 nd harvest	1st harvest	2 nd harvest
Genotype	63	3,662,308.1049**	4,503,644.1416**	46.6543**	74.2646**
GCA	7	5,331,101.3828**	10,253,968.3452**	350.3801**	613.2601**
SCA	28	6,354,133.1696**	6,957,148.1128**	6.9675^{NS}	8.9460**
Reciprocal	28	553,284.7207^{NS}	612,559.1194^{NS}	10.4096^{NS}	4.8343^{NS}
Residual	189	710,220.2771	458,242.0666	6.5599	3.9158
Mean squares of effects					
GCA		72,201.2673	153,058.2231	5.3722	9.5210
SCA		1,410,978.2231	1,624,726.5115	0.1019	1.2576
Reciprocal		-19,616.9445	19,289.6316	0.4812	0.1148

NS, not significant at the 0.05 probability level. **Significant at the 0.01 probability level. SV: source of variation; d.f.: degrees of freedom.

attributes, which suggests that the performance of the parent as a pollen donor or receptor can be the same. Thus, resistance to NLB cannot be superior if the crosses are inverted, which is an important fact in breeding programs to prevent additional work and costs in potentiating variability through hybridization.

Non-additive genetic effects predominated in the evaluated traits (Table 2), except popping expansion, which determines that hybridization is the best alternative to obtain gains in breeding aimed at resistance to *E. turcicum* and grain yield. Results concerning the prominence of gene effects on resistance to *E. turcicum* in conventional corn have been controversial. Paterniani et al. (2000) and Vivek et al. (2010), for instance, found that the additive genes were the most important in the expression of resistance to *E. turcicum*; the opposite occurred in the study developed by Nihei and Ferreira (2012). These findings indicate that genetic control for this trait may vary across the different sources of resistance. In this case, it is up to breeding programs to characterize their sources of resistance to achieve maximum efficiency during the selection process (Lopes et al., 2007).

For grain yield, the mean squares of the effects associated with GCA were lower than those associated with SCA, demonstrating the higher importance of non-additive concerning additive effects in the genetic control of this trait. Analogously to these results, superior significant SCA effects concerning GCA were found by Pereira and Amaral Júnior (2001) and Freitas Jr et al. (2006) in popcorn.

As for popping expansion, the additive genetic effect was the most important; therefore, intrapopulation methods are the most recommended for obtaining gains in this trait. These results agree with those obtained by da Silva et al. (2010), Vieira et al. (2011), and Cabral et al. (2015).

In the first harvest, parents L76, L61, and L70 presented negative GCA estimates for incidence and severity of *E. turcicum* (Table 3), and are thus recommended for the generation of superior hybrids. In the second harvest, negative GCA estimates for incidence and severity of *E. turcicum* were expressed by parents L88, P8, L77, and L76. Only L76 displayed a negative estimate of GCA for incidence and severity of *E. turcicum* in both growing harvests (Table 3); moreover, according to the Scott-Knott test, L76 was allocated in the group with the greatest resistance to both variables related to NLB (Table 1). Therefore, L76 can be considered a line of interest for participation in breeding programs aimed at the production of segregants with resistance to NLB, especially in the composition of hybrids, given the greater evidence of dominance in the expression of resistance.

Table 3. Estimates of general combining ability, evaluated in a full diallel with eight parents, in the first harvest (October 2014 to January 2015) and the second harvest (May to August 2015) in Campos dos Goytacazes, RJ, Brazil.

Parents	Incidence of NLB		Severity of NLB		Grain yield		Popping expansion	
	1st harvest	2 nd Harvest	1st harvest	2 nd Harvest	1st harvest	2 nd harvest	1st harvest	2 nd harvest
L88	41.5590	-107.4250	-7.4022	-17.8440	431.5150	403.6550	-3.6400	-5.4520
P8	-12.3813	-33.1384	3.4578	-0.6050	-17.8590	67.3220	1.3740	2.2060
L61	-21.0606	118.0447	-17.9584	7.8530	-300.2580	-87.3050	0.0250	3.6650
L70	-9.7463	103.6778	-1.4622	12.8540	-24.5870	358.4060	0.5940	1.5500
L77	3.5888	-169.1720	-6.2791	-21.6050	79.5770	398.5200	4.1840	0.9600
L55	50.7094	194.2666	36.7572	31.0370	-456.1800	-639.4360	-2.2100	-2.7810
P1	-15.4450	52.5791	6.1866	9.7040	-14.1570	-516.9830	-0.6070	1.9250
L76	-37.2169	-158.8330	-13.2997	-21.3940	301.9490	37.44900	0.2790	-2.0720

Contrary to what has been considered for disease-related traits, in the evaluation of grain yield, higher positive estimates of GCA are preferred since the effects of allelic complementation are predominant in the generation of superior genotypes. For this trait, in the first harvest, the highest GCA estimates were observed in parent L88, followed L76 and L77. Of these, L88 and L76, together with L70, were the lines that stood out, also in the second harvest, for revealing high positive GCA estimates. Thus, for both growing harvests, L88 and L76 can be considered the parents of interest for obtaining gains in grain yield.

Regarding popping expansion, in the first harvest, the lines L61, P8, P1, and L70 showed the most significant positive estimates for GCA, whereas in the second harvest the lines L77, P8, and L70 were superior. For popcorn breeding programs, genotypes that conciliate favorable genes for GY and PE should be prioritized, because these are the characteristics of highest economic importance, besides other traits that may make the genotype superior, of course. In this context, most of the parents that were highlighted for GY were not for PE. In popcorn breeding, the existence of a negative correlation between PE and GY complicates the selection of genotypes for these two traits of economic value (Daros et al., 2004). For this reason, none of the parents that were superior for PE and GY could be simultaneously highlighted.

In the first harvest, 17 hybrid combinations were noteworthy for their negative SCA estimates, both incidence and severity of NLB. In the second harvest, however, 17 hybrids displayed negative SCA estimates for both traits related to resistance to NLB (Table 4). The superior hybrids - for showing negative estimates for incidence and severity of NLB - common for both growing harvests were L88 x L61, L88 x L70, L88 x L55, P8 x L70, L61 x L77, L61 x P1, L70 x L77, L77 x P1, and L55 x L76, which characterizes them as of interest when aiming at reduced attack of NLB in crops.

For grain yield, in both growing conditions, a high number of combinations with positive SCA estimates were obtained. The three combinations that most stood out in both harvests were L61 x L77, L61 x L76, and L77 x L76, whose means were higher than 3900.00 kg/ha.

The SCA for popping expansion in the first harvest revealed that 17 combinations presented positive magnitudes. However, combinations L76 x P8, P8 x P1, L70 x P8, P8 x L77, P8 x L55, P8 x L61, L76 x L70, and L77 x L76 can be considered promising for that trait, because in addition to revealing positive values for SCA they also showed satisfactory means for the trait (Table 1) and originated from at least one parent with the potential to increase popping expansion. This demonstrates that the desirable effect of the genetic accumulation of parents L70, L77, and P8 was translated into a satisfactory effect of genetic complementation in the combinations.

In the second harvest, 15 combinations expressed positive SCA estimates for popping expansion, in which P8 x L61, L77 x P8, L77 x L70, L61 x L77, L61 x L76, L70 x P8, and L61 x L70 were noteworthy. In this regard, P8 x L61 showed a higher SCA estimate than the other selected combinations, averaging 31.92 mL/g (Table 1), thus proving to be of great potential to increase PE. Despite the difficulty gathering high yields and good popping expansion in one hybrid, L61 x L77 managed to comprise quality with productivity and parent L61 had the highest GCA for popping expansion, while L77 expressed a good GCA estimate for grain yield. This denotes that the hybrid responded as expected based on the parental GCA. This was not true for the other combinations, whose hybrids, despite originating from GCA desirable for PE and GY, did not display good allelic complementation for both traits together.

Given the results, promising hybrids can be indicated to increase GY and PE and reduce incidence and severity of NLB. In this context, in the first harvest, combination P8

Table 4. Estimates of $\hat{s}_{ij}$ and $\hat{s}_{ii}$ effects in a full diallel with eight parents in the first harvest (October 2014 to January 2015) and the second harvest (May to August 2015) in Campos dos Goytacazes, RJ, Brazil.

Effects	Incidence of NLB		Severity of NLB		Grain yield		Popping expansion	
($\hat{s}_{ii}$) and ($\hat{s}_{ij}$)	1st harvest	2 nd harvest	1st harvest	2 nd harvest	1st harvest	2 nd harvest	1st harvest	2 nd harvest
L88 x L88	215.0313	257.5809	38.0791	34.3783	-2,555.5260	-2,275.2420	-2.2000	0.1320
L88 x P8	-1.1456	5.3247	28.0791	6.2695	319.9320	-85.7690	-0.8980	-0.0370
L88 x L61	-92.7863	-109.096	-11.9997	-13.8836	113.9720	673.4230	0.9710	-1.5140
L88 x L70	-62.2206	-113.0770	-19.8709	-15.4448	637.4010	929.1820	1.4610	-0.3290
L88 x L77	-15.6306	36.1484	-5.8841	2.6739	697.9720	301.2370	0.3510	-0.2260
L88 x L55	-0.8013	-108.5050	-2.6953	-25.2373	156.7640	53.3890	0.3510	-0.2260
L88 x P1	-37.7619	-13.4978	-24.6947	1.2708	730.7810	370.8370	0.1030	2.7970
L88 x L76	-4.6850	81.1841	-1.0134	9.9733	-101.2950	32.9430	0.1510	-0.4700
P8 x P8	79.5575	288.9984	-10.3509	14.4808	-1,512.4900	-1,080.7460	-0.6860	0.6240
P8 x L61	-50.0981	12.4703	-6.0397	6,7227	788.0950	253.8720	0.1850	1.6700
P8 x L70	-32.1875	-48.3228	-7.2459	-5.9486	265.4140	323.4450	0.0650	-0.1250
P8 x L77	0.1975	-22.6628	-8.4891	-2.1348	510.9650	379.7000	-0.6900	-1.1450
P8 x L55	0.5769	-177.2770	8.9347	-18.4211	-653.3730	124.2020	0.3100	0.6500
P8 x P1	39.9713	-60.9691	13.1853	3.4470	166.4190	55.7100	1.0450	-0.4150
P8 x L76	-36.8719	2.4378	-18.0734	-4.4155	115.0380	29.5870	-0.7900	-0.1650
L61 x L61	214.7563	308.2822	27.4616	19.1445	-2,039.2110	-2,849.4710	0.3520	0.8100
L61 x L70	86.5219	166.8991	16.3003	30.3233	-520.0560	-920.9020	-2.0200	0.0850
L61 x L77	-81.1131	-180.5360	-11.0328	-21.6680	347.1040	748.0020	-3.7300	-0.1000
L61 x L55	-14.3988	28.1853	-10.7241	7.4708	311.0810	666.3000	1.0200	-0.0400
L61 x P1	-53.5494	-128.1520	-6.6784	-19.9561	512.2280	661.5370	-0.2920	-1.1100
L61 x L76	-9.3325	-61.9903	2.7128	-8.1536	486.7870	767.2390	0.4220	1.3090
L70 x L70	112.5275	218.8959	24.6791	31.9420	-1,674.9520	-2,223.2230	-0.6670	0.3000
L70 x L77	-73.2275	-187.8740	-21.9941	-26.8542	779.2940	717.6360	-0.5800	-0.1700
L70 x L55	-52.2681	33.9322	-26.5653	2.1545	498.2100	225.3480	-0.9600	0.2100
L70 x P1	8.8563	-47.9003	13.6653	-13.0373	4.0520	476.3210	-1.1710	-1.2000
L70 x L76	11.9981	-22.5534	21.0316	-3.1348	10.6370	472.1930	-0.5820	0.5990
L77 x L77	176.4175	480.7459	27.5328	68.9695	-2,449.8910	-2,543.1350	-0.0970	0.1560
L77 x L55	-7.5481	-155.9180	8.7216	-25.4217	-215.9190	18.6680	02860	-0.5170
L77 x P1	-7.4138	-24.8153	-6.1428	-3.5486	-224.7570	-98.7200	0.0290	-1.8210
L77 x L76	8.3181	54.9116	17.2884	7.9839	555.2320	476.5920	1.2030	0.6020
L55 x L55	173.1763	361.7584	75.6003	52.7870	-928.3670	-1,489.6400	-0.8500	-0.1400
L55 x P1	-46.2844	113.4259	-13.6641	16.9052	212.7600	132.6180	1.5930	1.4700
L55 x L76	-52.4525	-95.6022	-39.6078	-10.2373	618.8440	269.0950	-0.8390	-0.9460
P1 x P1	99.8650	233.5934	-1.8184	26.9633	-2,049.4630	-1,800.6850	0.5450	-0.4590
P1 x L76	-3.6831	-71.6847	26.1478	-12.0442	647.9810	202.3820	-1.1860	0.4850
L76 x L76	86.7088	113.2972	-8.4859	20.0283	-2,333.2250	-2,250.0310	0.2930	-0.7920
Reciprocal								
L61 x L88	24.5400	75.1600	3.8450	3.2750	-510.3750	-3.6650	-1.3750	2.8150
L70 x L88	-10.8600	34.6050	-1.1700	3.8550	95.0950	220.6450	-2.0650	0.2900
L77 x L88	-11.2850	-29.1700	2.7100	-1.1950	-76.3300	-136.2950	0.7050	-0.0300
L55 x L88	-14.5250	20.4750	-6.5350	10.3050	-247.5750	-297.8400	0,3100	-0.0400
P1 x L88	-3.6300	-38.5450	-3.7250	-12.7600	256.2650	75.5500	-0.8750	0.4150
L76 x L88	-45.7850	17.4550	-10.2500	4.8150	349.1350	-636.2100	0.1900	0.4350
L61 x P8	-4.8150	7.0450	-13.7750	3.5400	-77.0050	-0.8800	0.7280	-1.6580
L70 x P8	-2.7100	14.2150	-19.5150	0.5700	40.1250	-37.8850	0.4480	0.1270
L77 x P8	15.9700	0.3950	1.9950	7.6950	381.6900	319.4050	0.2330	1.0300
L55 x P8	-55.2400	5.9500	-25.9850	-10.5500	196.8250	107.5100	-0.7430	0.8670
P1 x P8	3.0200	-61.5100	4.1850	-16.4050	-114.8700	568.4200	0.3800	-0.1630
L76 x P8	17.3650	4.5950	4.6400	2.4450	-257.1550	-227.1800	0.5380	-0.7890
L70 x L61	-62.4300	5.2500	-8.1050	-11.4000	-40.0050	-44.1700	-0.0780	1.1350
L77 x L61	8.4000	-35.7850	-3.3750	-2.3600	-382.3800	301.5700	-2.5380	0.6330
L55 x L61	6.8250	-55.1250	11.3000	-13.5000	-281.7700	-85.3000	0.4360	0.3950
P1 x L61	-14.8300	-17.9400	12.2250	-15.2500	270.2400	359.5800	0.8550	-0.6700
L76 x L61	-32.3750	-64.0500	-11.8800	-9.7050	-237.9150	162.9250	1.6650	0.1250
L77 x L70	12.1200	1.7500	5.4600	-0.7350	236.1300	32.4350	0.5330	0.1430
L55 x L70	38.6300	53.2450	15.7350	14.1450	133.5200	132.6700	0.0560	-0.7750
P1 x L70	36.7500	-65.9750	48.7050	-11.4400	-430.8350	721.5050	0.6650	-0.7500
L76 x L70	18.9100	-9.4100	4.6450	4.1350	-180.3650	-83,4000	0.1900	-0.0350
L55 x L77	-21.4350	-1.4450	-22.8850	0.7300	571.0550	-97.7050	-0.4900	0.0450
P1 x L77	-8.1850	9.1400	8.4100	-10.2300	156.0700	306.6200	0.9550	-1.1250
L76 x L77	2.0550	7.3950	-18.0350	-2.7550	-88.8850	154.5950	0.2250	0.3350
P1 x L55	-12.4050	44.1900	-1.3350	26.6050	-103.8500	-81.1700	0.4150	1.1250
L76 x L55	-22.3550	32.5500	-1.3650	-4.5450	-82.8900	-373.1900	0.3300	-0.1650
L76 x P1	-13.4900	-10.5900	-30.2500	5.7150	262.7300	-95.2900	-0.8750	0.0200

x L61 expressed the highest estimate for both traits together, whereas in the second harvest, combinations L61 x L76 and L61 x L77 stood out for the elevated negative SCA estimates for incidence and severity of NLB as well as high positive estimates for GY and PE.

Conflicts of interest

The authors declare no conflict of interest.

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