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SHORT COMMUNICATION

Diallel analysis of resistance to *Fusarium* ear rot in Brazilian popcorn genotypes

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Abstract Among the ear rot pathogens, species of *Fusarium* cause significant economic losses to popcorn production. To generate popcorn genotypes resistant to *Fusarium* ear rot, the combining ability of popcorn lines in diallel crosses were assessed during two cropping years: the first from Mar to Sep 2015 and the second from Sep 2015 to Jan 2016. The traits analyzed were: average ear weight (AEW, kg ha^{-1}); grain yield (GY, kg ha^{-1}); popping expansion (PE, g mL^{-1}), *Fusarium* incidence on ears (EIF_U, %); *Fusarium* ear rot severity index (FSI, %), percentage of fungal-infected kernels (KIF), and percentage of *Fusarium*-infected kernels (KIF_U). Non-additive genetic effects prevailed in the expression of resistance to *Fusarium* ear rot and grain yield, while additive effects were the most prominent in the expression of popping expansion. Among 56 hybrids, seven showed outstanding grain yield, desirable popping expansion, and resistance to *Fusarium* ear rot. The less susceptible hybrids to ear rot produced high grain yield and popping expansion. Two disease-related traits, KIFu and EIFu, allowed to best differentiate among the genotypes.

Keywords *Fusarium verticillioides* · Additivity · Combining ability · Dominance · Griffing method

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Popcorn is a highly profitable crop for Brazilian farmers with a national production averaging 255,000 tons in recent years (GCEA/IBGE 2015). Among the limiting factors that affect popcorn yield and quality, infection by fungi directly affects the integrity of the pericarp and endosperm of the kernels. Among several fungi, *F. verticillioides* and *F. graminearum*, which cause *Fusarium* ear rot and *Gibberell*a ear rot, respectively (Munkvold 2003) are key contributors to damage in yield. These ear rots occur in all popcorn-producing areas of Brazil but their relative prevalence is associated with climatic conditions that prevail in the regions (Ramos et al. 2010; Stumpf et al. 2013). *Fusarium* ear rot is most commonly found in regions with hotter and drier climates; the optimal temperatures and altitudes for the pathogen are close to 30 °C and below 700 m, respectively (Munkvold 2003). The disease is favored by dry conditions at the beginning of the crop cycle, which results in lower solubility and availability of nutrients to plants. After pollination, warm temperatures (28 to 30 °C) and high humidity favor infection by the *Fusarium* ear rot pathogen (Munkvold 2003), although it may also occur in subtropical southern Brazilian regions in combination with *Gibberella* ear rot pathogens (Kuhnem et al. 2013; Stumpf et al. 2013).

Breeding efforts to improve resistance to ear rots are essential to reducing the dependence of fungicides and the import of popcorn seeds (Leonello et al. 2009). Among the breeding methods available, diallel analysis is an interesting approach due to its broad information coverage that allows selecting the most promising parents based on the general combining ability, as well as hybrid selection considering their heterotic potential (Griffing 1956). Moreover, combining ability estimates obtained by diallel crosses are important for the understanding of genetic effects involved in the assessment of traits (Hallauer et al. 2010; Cruz et al. 2014), and such information can be efficiently employed in studies on host genetic resistance to diseases (Njoroge and Gichuru 2013). While genetic analysis of resistance to *Fusarium* ear rot is available for common corn (Zila et al. 2014), no information exists for popcorn. Therefore, the objective of this study was to gain knowledge about the heterosis and genetic control of traits related to resistance to *Fusarium* ear rot, but also to grain yield and quality, via diallel analysis. Additionally, we assessed which *Fusarium* ear rot-variable allowed to best detect differences among the genotypes.

Diallel crosses were performed during two crop years: first, during the 2015 harvest year (Mar to Sep) and during the second harvest period of 2015/2016 (Sep to Jan). The experiments were conducted in Campos dos Goytacazes, RJ, Brazil (21° 42′ 48″ S latitude, 41° 20′ 38″ W longitude, 14 m a.s.l.) According to the Köppen Climate Classification System, the climate of the region is classified as a humid tropical type with hot summers and dry winters. To obtain the hybrids, eight S_7 lines of popcorn possessing levels of resistance to *Fusarium*, previously selected by Kurosawa (2015) (Table 1), were grown in rows and were crossed in a full diallel arrangement with the reciprocals, generating 56 hybrid combinations.

The diallel analysis trials were composed of 70 genotypes, consisting of 56 F_1 hybrids (including the reciprocals) and eight parents, plus six controls: IAC 125, BRS Angela, UENF 14, Barão de Viçosa, hybrid L70×L54, and hybrid P8×L54. The experimental design was arranged in randomized blocks with four replications. Lines were allocated separately from hybrids to avoid a competition effect. The experimental units consisted of a 5 m row with 0.90 m spacing between rows and 0.2 m between plants, totaling 25 plants per plot. The sowing depth was 0.05 m, with three seeds per furrow; thinning was performed after 30 days, leaving one plant per furrow. Base fertilization consisted of 30 kg ha^{-1} N, 60 kg ha^{-1} P_2O_5, and 60 kg ha^{-1} K_2O. Topdressing was applied 30 days after seeding, at 100 kg ha^{-1}. Overhead sprinkler irrigation, herbicides and insecticides were applied whenever needed.

Table 1 Information on the origin, reaction to Fusarium ear rot and climatic adaptation of popcorn S_7 lines used in the production of simple hybrids

Line	Origin	Reaction	Climatic adaptation
L 88	M2-Barão de Viçosa: UFV	Susceptible	Temperate/Tropical
L 70	BRS Angela: EMBRAPA	Resistant	Tropical
L 77	M2-Barão de Viçosa: UFV	Resistant	Temperate/Tropical
L 76	Beija-flor: UFV	Resistant	Temperate/Tropical
L 55	Beija-flor: UFV	Susceptible	Temperate/Tropical
L 61	BRS Angela: EMBRAPA	Intermediate	Tropical
P 1	Zélia	Resistant	Temperate/Tropical
P 8	IAC 112	Susceptible	Temperate/Tropical

The traits evaluated at both, the plot and ear levels were: 1) average ear weight (AEW, kg ha^{-1}); grain yield (GY, kg ha^{-1}); 2) popping expansion (PE, g mL^{-1}), obtained by measuring the mass of 30 g of kernels and heating them inside a special paper bag in a microwave oven operating at 1000 W for 1min45s. The popcorn volume was quantified using a 2000 mL beaker. PE was expressed as the ratio between the popped volume and 30 g of kernels; 3) incidence of ears infected by *Fusarium* (EIF_U, %), or the percentage of ears infected per plot; and 4) *Fusarium* ear rot severity index (FSI, %), estimated visually at the ear level with the aid of an ordinal (1–5) scale (CIMMYT 1985), where: 1 = 0% visually symptomatic kernels; 2 = 10%; 3 = 20%; 4 = 30%; and 5 ≥ 40%.

A sample of harvested kernels of all genotypes was assessed for the presence of fungi using the filter paper method (Neergaard 1979). The kernels were briefly surface-disinfested in 1% chlorine (sodium hypochlorite) solution to eradicate saprophytic and fast growing fungi. Later, they were placed on the top of two layers of filter paper moistened periodically inside a plastic box, at a rate of 25 seeds per box. The seeds were kept at ± 25 °C for a period of seven days under a regime of 12 h dark–light cycle. After the incubation, fungal colonies were inspected using stereoscopic microscope (60× magnification). One hundred seeds were evaluated per replicate of treatment, totaling 400 seeds per genotype for each experiment. The recorded variables were: percentage of kernels infected by fungi (KIF), and percentage of kernel infected by *Fusarium* spp. (KIF_U).

The combining ability analysis was performed according to Griffing's method I (1956), employing Model B, which considers the fixed effect of genotypes. $\mathbf{p^2}$ combinations corresponding to parents and their F_1 hybrids were evaluated, including the reciprocals. Afterwards, the treatment effects were estimated in general (GCA) and specific (SCA) combining abilities, and the following model was considered: $Y_{ij} = m + g_i + g_j + s_{ij} + r_{ij} + \bar{\varepsilon}$, where Y_{ij} = mean value of the hybrid combination (i ≠ j) or parent (i = j); m = overall mean of all treatments; g_i = effect of general combining ability of parent i; g_j = effect of general combining ability of parent j; s_{ij} = effect of specific combining ability for the crosses between parents i and j; r_{ij} = reciprocal effect, which quantifies the differences provided by parent i, or j, when used as a male or female in the cross; and $\bar{\varepsilon}_{ij}$ = mean experimental error. GENES software (Cruz 2013) was used for the genetic-statistical analysis.

Genotype, GCA, and SCA significantly affected ($P < 0.01$) AEW, GY, KIF, KIF_U, and EIF_U. FSI was significantly affected by GCA ($P < 0.01$). Only Genotype and GCA significantly

Table 2 Estimates of mean squares of popcorn genotypes (Parents, F_1, and reciprocals) for general and specific combining ability (GCA and SCA), and for the residual, as well as mean squares of combining ability effects for eight traits evaluated in a full diallel in the 1st (03/2015) and 2nd (09/2015) harvests

Mean squares of effects							
Sources of variation	AEW	GY	PE	KIF	KIF_U	EIF_U	FSI
Genotype	5264693.2[b]	3680620.8[b]	40.6[b]	120.3[b]	112.7[b]	154.8[b]	2.1[a]
GCA	8486362.8[b]	6664789.7[b]	338.2[b]	287.7[b]	310.8[b]	756.2[b]	8.9[b]
SCA	9380925.2[b]	6363999.7[b]	3.8[a]	154.4[b]	137.9[b]	136.1[b]	1.2[a]
RE	343043.7[a]	251199.7[a]	3.0[a]	44.3[a]	37.9[a]	23.2[a]	1.2[a]
Residual	915944.7	584229.7	5.2	45.5	34.3	49.5	1.8
Mean squares							
GCA	118287.7	95008.7	5.2	1.7	4.3	11.0	0.1
SCA	2116245.1	1444942.5	−0.3	20.4	25.3	21.6	−0.1
RE	−71612.6	−41628.7	−0.2	−0.1	0.4	−3.2	−0.0

AEW average ear weight, *GY* grain yield, *PE* popping expansion, *KIF* kernels infected by fungi (%), KIF_U kernels infected by *Fusarium* (%), EIF_U ears infected by *Fusarium* (%), *FSI Fusarium* ear rot severity index, and *RE* reciprocal effect

[a] Not significant at 5% probability level by the F test

[b] significant at 1% probability level by the F test

affected PE ($P < 0.001$) (Table 2). The mean reciprocal effect was not significant for any of the traits (Table 2). Based on the mean squares of the effects, the estimates of quadratic components of SCA were superior to those of GCA for the traits AEW, GY, KIF, KIF_U, and EIF_U. (Table 2). Estimated mean square for PE was much higher for the GCA effects than for SCA ones (Table 2).

Lines L88, L70, L61, and P8 stood out for AEW and GY, due to their positive mean $\hat{g}_i$ magnitudes (Table 3). Parent P1, in turn, displayed the most expressive negative results for GCA (Table 3). For PE, five lines showed positive $\hat{g}_i$ values, with an emphasis on parents L70 and L61, which also showed positive $\hat{g}_i$ estimates for GY and AEW, concomitantly (Table 3).

For the traits related to health condition against *Fusarium* ear rot, estimates based on the blotter test revealed that, in the case of KIF and KIFu, parents L77, L70, L61, and P8 stood out, expressing negative $\hat{g}_i$ values for both traits, with parents L70 and L61 also having favorable $\hat{g}_i$ results for GY, AEW, and PE traits (Table 3). Parents L55, L88, L76, and P1 showed positive estimates for KIF and KIF_U traits, characterizing them as unable to contribute to increase health on the seasons average. Of these lines, P1 is negatively remarked, as it also has unfavorable $\hat{g}_i$ values for PE and GY (Table 3). For the traits EIF_U and FSI, parents L55, L70, L61, and P8 were superior, since they showed negative $\hat{g}_i$ values associated with reduced ear rot intensity. In particular, P8, L70, and L61 also evidenced reduced KIF and KIF_U. Line L70 provided favorable $\hat{g}_i$ estimate values for all traits evaluated. Parents L76, P1, L77, and L88, however, expressed unfavorable $\hat{g}_i$ values, with higher values found in P1 and L76. Of these two lines, P1, as opposed to L70, had unfavorable results for all traits (Table 3).

The specific combining ability (SCA) effects were significant ($P < 0.01$) for AEW, GY, KIF, KIF_U, and EIF_U traits but not significant for PE or FSI (Table 4). For the traits AEW and GY, ten hybrids were noteworthy, as they provided the most expressive positive $\hat{s}_{ij}$ values and because they originated from at least one parent with $\hat{g}_i$ favorable to GY and AEW (Tables 3 and 4). The analysis of traits KIF and KIF_U indicates that eleven combinations provided favorable results. Of these hybrids, only L61 × L76 and L61 × P1 did not express favorable SCA results for GY (Table 4). The trait EIF_U had ten pairs with relevant negative values for $\hat{s}_{ij}$, with at least one parent

Table 3 Estimates of effects of general combining ability ($\hat{g}_i$) for eight traits evaluated in eight popcorn parents in a full diallel scheme with the reciprocal evaluated in the 1st (03/2015) and 2nd (09/2015) harvests

Line	Evaluated trait						
	AEW	GY	PE	KIF	KIF_U	EIF_U	FSI
L88	378.31	417.57	−4.54	0.94	1.33	0.92	0.15
L77	−24.00	24.72	3.19	−1.39	−1.35	0.60	0.10
L55	−153.00	−193.77	0.72	0.89	0.69	−3.81	−0.41
L70	293.41	166.90	1.07	−1.28	−1.49	−3.33	−0.15
L61	92.98	59.72	0.49	−2.27	−2.35	−2.43	−0.36
P1	−686.95	−547.81	−1.69	1.45	1.35	5.18	0.48
L76	−258.46	−265.56	1.10	3.78	3.96	4.51	0.52
P8	357.32	338.22	−0.34	−2.13	−2.13	−1.64	−0.34

AEW average ear weight, *GY* grain yield, *PE* popping expansion, *KIF* kernels infected by fungi (%), KIF_U kernels infected by *Fusarium* (%), EIF_U ears infected by *Fusarium* (%), and *FSI Fusarium* ear rot severity index

Table 4 Estimates of specific combining ability ($\hat{s}_{ii}$ and $\hat{s}_{ij}$) effects for eight traits evaluated in a full diallel among eight popcorn lines for the 1st (03/2015) and 2nd (09/2015) harvests

$\hat{s}_{ii} \times \hat{s}_{ij}$	n×n	Trait variable						
		AEW	GY	PE	KIF	KIF_U	EIF_U	FSI
L88	1 1	−2713.92	−2415.38	0.33	8.16	7.79	17.58	0.63
L88 × L77	1 2	169.28	117.09	0.13	−0.77	−1.29	−0.44	0.33
L88 × L55	1 3	452.59	393.69	−0.88	2.56	3.10	−0.30	−0.00
L88 × L70	1 4	782.62	783.29	0.72	−0.36	−0.37	−0.72	0.30
L88 × L61	1 5	517.15	499.59	−0.23	−1.42	−1.14	−3.71	−0.40
L88 × P1	1 6	174.76	105.07	0.31	−3.85	−3.35	−7.62	−0.24
L88 × L76	1 7	723.52	550.80	−0.15	−5.00	−5.16	−6.57	−0.83
L88 × P8	1 8	−106.03	−34.17	−0.22	0.69	0.43	1.80	0.20
L77	2 2	−1779.55	−1296.63	−0.37	4.68	5.01	1.63	0.34
L77 × L55	2 3	641.05	520.99	−1.91	−2.95	−2.63	−1.42	0.00
L77 × L70	2 4	397.43	294.41	−0.08	0.35	−0.06	−2.15	−0.64
L77 × L61	2 5	636.26	445.31	0.28	0.81	1.21	−0.93	0.10
L77 × P1	2 6	−237.27	−264.57	−0.91	0.73	−0.41	4.42	0.18
L77 × L76	2 7	66.70	111.07	−0.37	−3.76	−3.08	−0.22	−0.13
L77 × P8	2 8	106.07	72.32	0.49	0.90	1.27	−0.87	−0.19
L55	3 3	−3103.74	−2444.33	0.77	0.25	1.56	−0.19	−1.24
L55 × L70	3 4	−905.28	−720.48	0.08	0.51	−1.44	2.25	0.09
L55 × L61	3 5	676.87	547.56	0.48	0.54	−0.30	1.37	0.43
L55 × P1	3 6	699.70	488.67	−0.96	0.37	1.33	−0.81	0.52
L55 × L76	3 7	773.29	586.87	−0.04	1.66	0.47	−1.78	0.27
L55 × P8	3 8	765.50	627.02	0.07	−2.95	−2.10	0.89	−0.08
L70	4 4	−2386.87	−1949.09	−0.03	5.11	5.95	3.90	0.62
L70 × L61	4 5	1025.95	748.48	0.09	0.72	1.48	2.55	0.02
L70 × P1	4 6	448.56	361.77	0.89	−1.32	−1.40	−4.26	−0.34
L70 × L76	4 7	287.94	240.19	0.92	−3.43	−2.76	−1.76	0.13
L70 × P8	4 8	349.61	241.41	−0.42	−1.58	−1.38	0.19	−0.19
L61	5 5	−3054.91	−2496.54	0.31	6.38	5.16	4.69	−0.04
L61 × P1	5 6	−127.62	−98.57	−0.47	−2.46	−1.96	−2.79	−0.05
L61 × L76	5 7	−255.19	−161.75	0.86	−4.41	−4.10	0.23	0.22
L61 × P8	5 8	581.49	515.91	−0.46	−0.16	−0.35	−1.41	−0.28
P1	6 6	−1669.74	−1209.01	0.04	7.38	6.00	6.51	0.17
P1 × L76	6 7	190.54	172.68	−0.35	−1.32	−0.73	7.34	0.06
P1 × P8	6 8	521.05	443.95	0.10	0.47	0.54	−2.78	−0.29
L76	7 7	−2187.22	−1925.06	−0.24	21.87	20.92	4.66	0.44
L76 × P8	7 8	400.41	425.15	−0.12	−5.59	−5.54	−1.88	−0.16
P8	8 8	−2618.14	−2291.62	−0.03	8.22	7.13	4.07	1.02

Campos dos Goytacazes, RJ, Brazil

AEW average ear weight, *GY* grain yield, *PE* popping expansion, *KIF* kernels infected by fungi (%), KIF_U kernels infected by *Fusarium* (%), EIF_U ears infected by *Fusarium* (%), and *FSI Fusarium* ear rot severity index

containing favorable values for $\hat{g}_i$. Of these pairs, six were also classified among the best for the traits KIF and KIF_U (Table 4). All the traits were also analyzed separately for the 1st and 2nd seasons (supplementary file: Tables 1, 2, 3 and 4).

In summary, for the average of the two seasons, ten hybrid combinations showed the best results for GY and for the traits related to health condition against *Fusarium* ear rot. Parent L88 was present in three combinations and presented expressive favorable $\hat{g}_i$ results for GY. However, it had the most expressive unfavorable results for the trait PE (Tables 3 and 4). For this reason, when including the variable PE, the best hybrid combinations for the 1st and 2nd harvest environments are summarized by seven pairs (Tables 3 and 4).

For the traits AEW, GY, KIF, KIF_U, and EIF_U the results indicate the existence of additive and non-additive effects in the gene control of these traits. For FSI the results indicated that additive effects controlled it. It is thus inferred that, for the evaluated traits, there was genetic variability among the components of the diallel, which makes it possible to select promising hybrids. The mean reciprocal effect results reveal a lack of differences between the hybrids and their reciprocals and that no gains will be obtained if the parents are inverted in the crosses, meaning this task would only encumber the production of hybrids.

The mean square effect results of GCA and SCA suggested that for the variables analyzed, the exploitation of hybrids aiming at making use of heterosis is the best strategy to partially achieve the objectives of this study, which consists of obtaining superiority for productivity and resistance to *Fusarium* ear rot. The prevalence of dominance effects for grain yield and its components found in the present study is in line with previous studies (Larish and Brewbaker 1999; Pereira and Amaral Júnior 2001; Scapim et al. 2006). For the disease-resistance traits, although there are no analogous studies on *Fusarium* spp. causing ear rots in popcorn, dominance effects were reported in other pathosystems such as with *Fusarium solani* in soyben (Fronza (2003); *Giberella zeae* in common corn (Butron et al. 2006); *Physopella zeae* in popcorn (Sanches et al. 2011); *E. turcicum*, *Physopella. zeae*, and *Puccinia polysora* in corn (Nihei and Ferreira (2012). However, for the variable PE, the best strategy will be intrapopulation breeding methods. Those results are in agreement with results by Larish and Brewbaker (1999), Pereira and Amaral Júnior (2001), and Scapim et al. (2006) studies that reported superiority of additive genetic effects for PE.

When considering GCA for the variables AEW and GY the results showed that the best parents to provide increases in grain yield and in average ear weight for both planting seasons are L88 and P8, while P1 proved to be the worst. For the variable PE five lines presented favorable values, concomitantly with GY and AEW. According to Scapim et al. (2010), although high yield is the primary target of crop breeding programs, the grain quality should also be a concern to popcorn breeders, and, therefore, the popping expansion is a trait that must be evaluated in breeding programs for this crop. Thus, genotypes having favorable $\hat{g}_i$ values for both traits are suitable genetic materials that should be prioritized in selection procedures.

The disease-resistance traits results showed that there is variability among the genotypes of the UENF germplasm collection with some exhibiting genetic gains for resistance to *Fusarium* spp. According to Stumpf et al. (2013), *Fusarium verticillioides* found in Brazil are typical producers of fumonisin, which poses a hazard to the health of consumers. Thus, the use of hybrid combinations with lower kernel infection and favorable $\hat{g}_i$ results for GY and PE may help to reduce the risk of mycotoxins. By these analyses, the line L70 stood out providing favorable $\hat{g}_i$ estimate values for all traits.

According to Cruz et al. (2014), high $\hat{s}_{ij}$ values, either positive or negative, denote that the response of a certain hybrid is relatively better or worse than the one expected based on the GCA of the parents, whereas low absolute $\hat{s}_{ij}$ values indicate that F_1 hybrids behave as expected based on the GCA of the parents. Hence, for a cross to be recommended it must evidence a high phenotypic mean and SCA estimate (Cruz et al. 2014); additionally, at least one of the genotypes must show a high GCA estimate.

The SCA results for the traits KIF and KIF_U showed that nine combinations were noteworthy, as they provided expressive favorable $\hat{s}_{ij}$ for KIF, KIFU, GY and AEW. It can be concluded that hybrids exhibiting low levels of ear rot are the most productive ones in grain yield. When including the trait $EIF_{U,}$ six of these nine combinations provided expressive favorable ŝij values for the traits KIF, KIFU, GY and AEW. Therefore, these six hybrids may be of use in popcorn breeding when aiming to exploit the dominance effects for enhancing resistance against *Fusarium* ear rot.

The results indicate that ten hybrid combinations showed the best results for GY and for the traits related to health condition against *Fusarium* ear rot. Of these combinations, just seven stood out for PE. Several authors have observed negative correlations between GY and PE (Brunson 1937; Lima et al. 1971; Dofing et al. 1990; Daros et al. 2004). It should be noted that, in popcorn, the traits PE and GY are of great interest to breeding, as they meet the needs of both consumers and producers. Therefore, hybrid combinations that provide gains in GY and health condition against *Fusarium* ear rot should be prioritized, but also those with additive effects for PE. Therefore, the best hybrid combinations for the 1st and 2nd harvest environments are summarized by the following pairs: L55 × P8, L77 × L55, L61 × P8, L76 × P8, L70 × P1, L70 × P8, and L70 × L76. These pairs offer a considerable range of options to be directly used by producers.

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