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RESEARCH ARTICLE

Selection of common bean parents and segregating populations targeting fusarium wilt resistance and grain yield

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ABSTRACT

The present work aimed to select populations for the breeding of common bean targeting fusarium wilt resistance and grain yield. Twelve carioca bean lines, which mainly differ in fusarium wilt resistance and grain yield, were crossed in a 6x6 partial diallel scheme. The parents and their 36 F1’s hybrids were evaluated for fusarium wilt severity caused by FOP isolate UFV 01 (FWS), and grain yield (YIELD). 34 F4’s populations, 12 parents and three other lines were also evaluated for grain yield per plant. The data of F1's parents and hybrids were submitted to diallel analysis. Using the grain yield data per plant, the potential of the 34 F4’s populations was predicted by the Jinks and Pooni method (1976). In the diallel analysis, BRSMG Talismã, CVIII 8511, BRS Pérola, VC 25 and VC 13 stood out in terms of the frequency of favorable alleles for FWS. Except for BRSMG Uai and IAC Formoso, these lines presented the most dominant genes associated in Fusarium wilt resistance. For YIELD, there was a predominance of dominant genes determining higher yield. The 20 F4’s populations with the highest potential included the best 12 of the 20 populations, based on diallel analysis for YIELD. Thus, the 12 populations received the addition of four that were highlighted only by the methodology of Jinks and Pooni (1976), and four based on diallel analysis, which totaled 20 populations. The use of information from more advanced inbreeding generations in complementarity with those of diallel is a promising strategy.

Keywords: *Phaseolus vulgaris* L., *Fusarium oxysporum f. sp. phaseoli*, diallel analysis, recurrent selection, disease resistance, parental selection, genetic diversity.

INTRODUCTION

Common bean (*Phaseolus vulgaris L.*) is one of the most important legume for human consumption in various countries worldwide (Hnatuszko-Konka et al., 2014). Common bean is the most consumed species of the Phaseolus genus due to its good nutritional values and its socioeconomic importance (Broughton et al., 2003; Companhia Nacional de Abastecimento [CONAB], 2019; Chimenez-Franzon et al., 2022). Brazil is one of the world's largest consumers and producers of dry beans (Food and Agriculture Organization of the United Nations [FAO], 2020). A factor that most affect dry bean yield is the presence of more than 45 types of plant diseases all across Brazilian producing regions (Paulino et al., 2021).

P. vulgaris L. is host to several fungi of aerial part and radical system, and the Fusarium wilt is one of the main current diseases that affect the species (Pastor-Corrales and Abawi, 1987. Fusarium wilt in common bean is caused by a soil fungus, *Fusarium oxysporum f. sp. phaseoli* (FOP), which colonizes the vascular system of the plant and, depending on the climatic conditions, inoculum concentration and stress conditions, can cause losses that range from 30 to 80% in grain yield (Cramer et al., 2003). The chemical control is inefficient and not recommended against Fusarium wilt. The development of resistant cultivars is the most efficient and recommended control alternative.

In common bean breeding programs, several studies (Rocha et al., 2014; Kurek et al., 2001; Moura et al., 2016; Silva et al., 2013) have reported efficiency in the selection of parents using diallel crosses, especially partial crosses (Moura et al., 2016; Silva et al., 2013). The effects of the general and specific combining ability of the parents involved in the diallel are estimated based on diallel analyses, which provide information, respectively, on the frequency of favorable alleles present in the parents and their genetic diversity. According to Cruz, Regazzi and Carneiro (2012), the general combining ability (GCA) is a function of the additive effects of the genes involved in the genetic control of the trait under analysis, and the specific combining ability (SCA) is a group of measures of the non-additive gene effects, estimated as the hybrid behavior deviation from that expected, based on the GCA of its parents.

It is noteworthy that the genetic diversity estimated by SCA is a function only of the loci with genes that exhibit dominance. Furthermore, if both genes with positive dominance deviations and others with negative deviations (bidirectional dominance) are involved in the control of the trait under analysis, and the frequency of alleles at each locus in the diallel is different from 0.5, the GCA estimates may be biased, depending on these dominance deviations, in this case as well (Cruz & Vencovsky, 1989). This also compromises the SCA estimates, since it is estimated as the deviation of the hybrid behavior from that expected based on the GCA, and, consequently, the accurate selection of parents to obtain segregating populations with the potential to be used in recurring selection programs.

The selection of segregating populations in advanced inbreeding generations by the methodology of Jinks and Pooni (1976) has been used in the improvement of common beans (Abreu, Ramalho, & Santos, 2002; Carneiro et al., 2002; Mendonça, Santos, & Ramalho, 2002; Rocha et al., 2013). Jinks and Pooni's (1976) methodology estimate the probability of obtaining lines in F_∞ that surpass a certain standard, based on the performance and variability of segregating populations.

In this context, segregating populations obtained from diallel crosses, evaluated in more advanced inbreeding generations, can provide auxiliary information to diallels for the selection of the right parents in breeding programs, since, in these populations, the variability of both genes with deviations from Positive, negative and null dominance can be better quantified.

Due to the scarcity of reports about the use of recurrent selection for the breeding of common bean targeting resistance to Fusarium wilt, it is emphasized the need to establish a recurrent selection program to obtain superior individuals, regarding the productivity of grain yield and Fusarium wilt resistance.

MATERIAL AND METHODS

Genetic material

In this work, 12 carioca bean lines were used, which differ mainly in terms of resistance to Fusarium wilt and grain yield (Table 1). These parents were crossed in a 6x6 partial diallel scheme. The six parents (MAI 1813, BRS Estilo, VC 13, VC 28, VC 25 and IAC Formoso) composed group 1, while the other six lineages (BRSMG Talismã, RC-I-8, BRSMG Uai, CVIII 8511, CNFC 11965, BRS Pérola) formed group 2 (Table 1).

Table 1. Origin and main characters of interest of the twelve common bean parents used in the partial diallel.

Parents	Origin	Feature of Interest
Group 1		
BRSMG Talismã	UFLA[1]	FOP Resistance
RC I-8	UFLA	FOP Resistance
BRSMG UAI	UFLA	Grain yield and FOP Resistance
CVIII 8511	UFLA	FOP Resistance
CNFC 11965	Embrapa[2]	FOP Resistance
BRS Pérola	Embrapa	FOP Resistance
Group 2		
MAI 1813	UFLA	Bean angular leaf spot resistance
BRS Estilo	Embrapa	Grain yield
VC 13	UFV[3]	Grain yield
VC 28	UFV	Grain yield
VC 25	UFV	Grain yield
IAC Formoso	IAC[4]	Grain yield

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The hybridizations were carried out in a greenhouse belonging to the Department of Agronomy of the Federal University of Viçosa (UFV), in 2013, and monitored as F1 seeds. These seeds were used in the two following experiments.

For the first experiment, seeds from parents and 36 hybrid combinations, totaling 48 treatments, were sown in the field in the dry season/2014, at the Coimbra experimental station, in Coimbra-MG, belonging to the Department of Plant Science at UFV, located at 690 meters of altitude, 20°45'S of latitude and 42°51'W of longitude. It was used a randomized block design with three replications. The plots consisted of two lines with 1.5 meters (m) in length, planting density of 12 seeds per meter and spacing between rows of 0.50 m. The cultural treatments adopted were those recommended for bean cultivation in the region. In this experiment, the grain yield (YIELD) was evaluated. The harvest was carried out manually. Then, the plots were threshed and weighed, and the grain yield was obtained, in kg ha^{-1}.

The remaining F1's seeds, together with the 12 parents, were evaluated in a greenhouse for the reaction to Fusarium wilt, also totaling 48 treatments. In this case, the experiment was arranged in a completely randomized design, with three replications, and plots of one pot with three plants. The inoculation methodology used was the immersion of roots in conidia suspension, as proposed by Pastor-Corrales and Abawi (1987). Fusarium wilt severity (FWS) was assessed at 21 days after inoculation (DAI), according to the grading scale proposed by Pastor-Corrales and Abawi (1987). Score 1: No visible symptoms, Score 3: 1 to 10% of symptomatic leaves, Score 5: 11 to 25% of symptomatic leaves, Score 7: 26 to 50% of symptomatic leaves and Score 9: dead or severely infected plant.

The seeds of the F1's plants harvested in the field experiment were multiplied and, subsequently, 34 of the 36 F2 populations were advanced in bulk until the F4 generation. These 34 populations, the 12 parents and 3 other lines, one of them a susceptible cultivar from the black commercial group (Meia-noite), totaling 49 treatments, were evaluated in a 7x7 triple lattice design. The experiment was conducted at the Experimental Station of the Federal University of Viçosa, in Coimbra, MG, in the winter/2017. Plots constituted by four rows of four meters, spaced at 0.50m and with planting density of 15 seeds per meter were used. The management and cultural treatments, such as fertilization and pest control, were in accordance with the technical recommendations for bean cultivation in the region.

After the harvest, data were obtained from thirty (30) individual plants randomly taken from one of the two central lines of each plot, which were individually threshed for the measurement of the grain yield per plant (PY), in grams (g plant^{-1}). Grain yield (YIELD), in kg ha^{-1}, was obtained from data from the two central lines of each plot.

Diallel analysis

The Genes software Cruz (2013) was used for a diallel analysis of fusarium wilt severity (FWS) and grain yield (YIELD) of the F1's parents and hybrids. According to Griffing (1956), the model 2 adapted for partial diallels by Geraldi and Miranda Filho (1988) was used, according to the following model:

$$Y_{ij} = \mu + \frac{1}{2}(d_1 + d_2) + g_i + g'_j + S_{ij} + \bar{\varepsilon}_{ij}$$

Where: Y_{ij}: average of the cross involving the ith parent of grup 1 and the jth parent of group 2; Y_{i0}: mean of the i-th parent of group 1 (i = 0,1,...p); Y_{0j}: average of the jth parent of group 2 (j = 0,1,...q); μ: general diallel mean; d_1, d_2: contrasts involving means of groups 1 and 2 and the general mean; g_i: effect of the general combining ability of the ith parent of group 1; g'_j: effect of the general combining ability of the jth parent of group 2; S_{ij}: effect of the specific combining ability between parents of order i and j, of groups 1 and 2, respectively; $\bar{\varepsilon}_{ij}$: mean experimental error.

The significance of the effects present in the diallel model was verified by the student's t test at 5% of probability.

Potential of F4 segregating populations

The grain yield data per plot (YIELD) of the 34 F4 populations and three lines were analyzed for the potential of segregating populations, using the model described below, with the effects of blocks and error treated as random and the effects of mean, repetition and treatment treated as fixed.

$$Y_{ijk} = \mu + \beta_j + \tau_i + b_{k(j)} + e_{ijk}$$

Where: Y_{ijk}:observation referring to treatment i, in repetition j and in block k; μ: is a general constant; β_j: effect of repetition j (j = 1, 2 and 3); τ_i: treatment effect i (i = 1.2,...,49); $b_{k(j)}$: effect of block k (k = 1,2,...,7) within repetition j; e_{ijk}: mean experimental error associated with observation Y_{ijk}.

Individual data from 90 plants from each segregating population in F4 were used to predict the potential of segregating populations using Jinks and Pooni's (1976) methodology. This method estimates the probability of the population in question, originating lines that exceed a certain standard, which in this case was the cultivar BRS Pérola. The phenotypic values of F_∞ lines derived from homozygous biparental crosses follow a normal distribution, according to Jinks and Pooni (1976). Thus, based on the mean and variance of the segregating populations, it is possible to estimate the probability of each population producing lines that exceed the standard (P%). This probability corresponds to the area to the right of a given value of μ on the abscissa of the normal distribution. This area is calculated by estimating the variable Z, using the properties of a standardized normal distribution:

$$Z = \frac{\mu - F_{ni}}{Si}$$

Where μ corresponds to the average of the standard cultivar (BRS Pérola) plus 20%. F_{ni} is the average of the plants of each F4 population, which, in a non-dominance model, corresponds to the average of all possible lineages in the F_∞ generation, once conducted in the absence of selection. In this procedure, the genetic variance($\hat{\sigma}^2_G$) of a given population "i" is estimated by the following expression:

$$\hat{\sigma}^2_{G\,i} = \hat{\sigma}^2_{F\,i} - \hat{\sigma}^2_E$$

Where $\hat{\sigma}^2_{G\,i}$is the genetic variance present in population i; $\hat{\sigma}^2_{F\,i}$ is the phenotypic variance observed in population i, obtained by the arithmetic mean of the variances of the populations in the three replications; and $\hat{\sigma}^2_E$ is the environmental variance, obtained by the arithmetic mean of the phenotypic variance of one or more strains present in the experiment. In this case, the black bean cultivar line Meia-Noite present in the experiment was used. It was considered that the environmental variance within populations is similar to the environmental variance between plants within the controls. Si is the estimate of the phenotypic standard deviation between the lines of the F_∞ generation, estimated by the equation:

$$Si = \sqrt{1{,}143\sigma^2_{F4} - 0{,}143\sigma^2_e}$$

Considering the extent of inbreeding in the analyzed plants (F4 generation), the variability across populations accounts for 85.7 percent of the overall genetic variability, which means that 14.3 percent is left for variability within populations. Pearson's correlation coefficient was used to examine the relationships between the average grain yield of populations in the F4 generation and F1 hybrids.

RESULTS AND DISCUSSION

Diallel analysis

Table 2 summarizes the analysis of variance for the traits Fusarium wilt (FWS) severity and grain yield of the 12 lines and their 36 hybrids derived from the 6x6 partial diallel (YIELD). The estimates of experimental variation coefficients (VC) ranged from 12.21 percent to 13.23 percent, which reveals that the two trials were precise (Table 2). Similar results have been found in studies employing these traits in the common bean crop (Moura et al., 2016; Pereira, Ramalho, & Abreu, 2011; Pereira, Ramalho, & Abreu, 2008).

Table 2. Summary of analysis of variance for fusarium wilt severity (FWS) and grain yield (YIELD). Viçosa, MG, 2018.

Sources of variation	dl	Mean Square	
		FWS	YIELD
Treatments	47	27.8069**	892709.2525**
GCA_1	5	121.2975**	262456.7203^{ns}
GCA_2	5	68.794**	579850.4854*
SCA	36	9.9002**	999105.2835**
Groups	1	0.0625^{ns}	1778008.6297**
Residual	94	0.2334	241644.1468
VC (%)		12.21	13.23
Parental averages		3.96	3715.41
Average of Group 1		3.92	3493.18
Average of Group 2		4.00	3937.65

**, *, ^{ns}Significant at 1%, 5% and not significant, respectively. GCA1 = general combining ability of group 1 parents; GCA2 = general combining ability of group 2 parents.

The F test exhibited a significant effect for treatment ($p<0.01$) on the two traits, which indicates variability between the genotypes examined for YIELD and FWS (Table 2). The effects of general combining ability of the parents of groups 1 and 2 (GCA1 and GCA2), specific combining ability of the parents' hybrids (SCA) and the effect of Groups were separated as the sources of treatment variation.

The variation source Groups had a significant ($p<0.01$) effect on YIELD and a non-significant effect on FWS (Table 2). A significant group effect indicates a difference in means between groups 1 and 2. In terms of grain yield, the parents BRSMG Talismã, RC I-8, BRSMG Uai, CVIII 8511, CNFC 11965 and BRS Pérola from group I performed worse than the parents MAI 1813, BRS Estilo, VC13, VC28, VC25 and IAC Formoso from group 2.

GCA had a significant ($p<0.05$) effect on FWS in both groups and YIELD in group

2. The effect of GCA was non-significant only for YIELD in group 1. (Table 2). The occurrence of a general combining ability with significant effect implies that the frequency of desirable alleles involved in the control of the trait under study varies between strains. The effects of SCA were significant ($p<0.01$) for the characters FWS and YIELD, which indicates variation among the cross parents of these characters. It should be highlighted that SCA-based parental diversity is only relative to dominant genes.

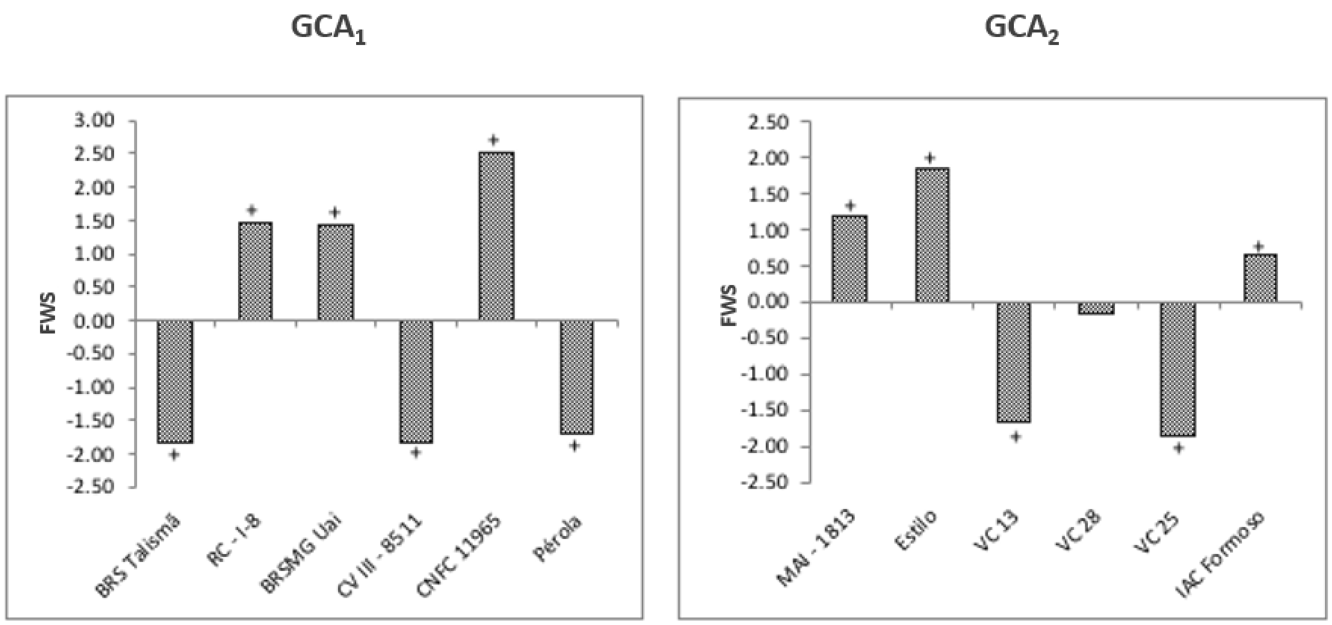
For the severity of fusarium wilt caused by FOP UFV 01 (FWS), the sum of the $\hat{s}_{ii}$, or $\hat{s}_{jj}$, presented a positive value (3.84) (Table 3), which reveals a predominance of genes with negative dominance deviations involved in the genetic control of this trait, that is, most dominant alleles determine the lowest values for FWS (plants more resistant to fusarium wilt). Thus, in terms of the frequency of desirable alleles for FWS, the BRSMG Talismã, CVIII-8511 and BRS Pérola strains from group 1 stand out, with the lowest and most significant estimations of $\hat{g}_i$, whereas the VC25 and VC13 strains from group 2 stand out by the same criterion (Table 3 and Figure 1). Lower values of $\hat{g}_i$ and $\hat{g}_j$ (negative values) suggest lines with a higher frequency of desirable alleles implicated in the control of fusarium wilt resistance, since lower scores relate to plants with greater resistance. It is worth noting that the severity scores of the BRSMG Talismã, CVIII-8511, VC 25 and VC 13 strains were all equal to one, due to the absence of severe symptoms in FOP UFV 01 (Table 4).

Table 3. Estimates of the general and specific combining ability of 12 common bean parents based on the severity score of Fusarium wilt, tested in a 6x6 partial diallel scheme. Viçosa, MG, 2018.

$G_1 \setminus G_2$	MAI 1813	BRS Estilo	VC 13	VC 28	VC 25	IAC Formoso	$\hat{g}_i$	$\hat{s}_{ii}$
BRSMG Talismã	-1,65*^{a}	-2,31*	1,19*	-0.32	1,39*	-1,12*	-1,84*	1,41*
RC I-8	1,08*	1,08*	-2,11*	0.04	-1,92*	0.24	1,46*	0,80*
BRSMG Uai	2,45*	2,09*	-0,1	-1,42*	-1,87*	2,41*	1,42*	-1,78*
CVIII 8511	-1,65*	-2,31*	1,19*	-0,32	1,39*	-1,12*	-1,84*	1,41*
CNFC 11965	1,66*	1,33*	-3,17*	0,26	-2,97*	2,52*	2,52*	0,19
BRS Pérola	-1,78*	-2,45*	1,06*	-0,46	1,26*	-1,26*	-1,71*	1,81*
$\hat{g}_j$	1,18*	1,84*	-1,66*	-0,15	-1,86*	0,65*	$\Sigma\hat{g}_i=\Sigma\hat{g}_j=0$	$\Sigma\hat{s}_{ii}=3,84$
$\hat{s}_{jj}$	-0.05	1,29*	0,97*	1,11*	1,36*	-0,83*	$\Sigma\hat{s}_{jj}=3,85$	

*Significant by t test at 5% probability level.

G_1: group 1 parents; G_2: group 2 parents; ^{a} estimates of the specific combining ability of the 36 hybrids ($\hat{s}_{ij}$); $\hat{g}_i$ and $\hat{g}_j$: estimates of the general combining ability of parents in groups 1 and 2, respectively; $\hat{s}_{ii}$ and $\hat{s}_{jj}$: specific ability of the parent to combine with itself for groups 1 and 2, respectively.



$^{+}$ significant at 5% probability by the t test.

Figure 1. Estimates of the general combining ability of group 1 (GCA1) and group 2 (GCA2) parents for Fusarium wilt severity (FWS).

FWS has a significant ($p<0.01$) specific combining ability (SCA), with 19 negative estimations, 15 of which were significant, ranging from -3.17 to -1.12 (Table 3). This suggests that the performance of some hybrids is better than expected, based on GCA estimations, which reveals the presence of dominant alleles in the parents involved in these crosses and determines resistance to fusarium wilt induced by the FOP UFV 01 strain (Table 4).

In this order, the 15 hybrids with the lowest and most significant SCA estimates are: CNFC 11965 / VC 13, CNFC 11965 / VC 25, BRS Pérola / BRS Estilo, BRSMG Talismã / BRS Estilo, CVIII 8511 / BRS Estilo, RC I-8 / VC 13, RC I-8 / VC 25, BRSMG Uai / VC 25, BRS Pérola / MAI 1813, BRSMG Talismã / MAI 1813, CVIII 8511 / MAI 1813, BRSMG Uai / VC 28, BRS Pérola / IAC Formoso, BRSMG Talismã / IAC Formoso and CVIII 8511 / IAC Formoso.

As previously stated, the impacts of SCA are estimated as the hybrid behavior deviation from what is expected, based on the GCA of the parents. However, with the exception of the hybrid between VC 13 and BRSMG Uai, which obtained a score of 2.97, no indications of Fusarium wilt were observed in any of the hybrids in which the lines BRSMG Talismã, CVIII-8511, VC 25, VC 13, and BRS Pérola participated as parents.

These results indicate that only a few genes are involved in the genetic control of resistance to fusarium wilt caused by the FOP UFV 01 isolate, and that the expected variability in segregating populations from these hybrids will be due to the presence of dominant alleles fixed in resistant parents and recessive for the same locus fixed in susceptibles, rather than the complementarity of dominant alleles from different loci involved in the control of resistance of fusarium wilt. Some studies on the genetic control of common bean fusarium wilt have identified the action of a few dominant genes implicated in resistance (Batista et al., 2017; Cândida et al., 2009; Cross et al., 2000; Fall et al., 2001; Pereira et al., 2011; Ribeiro & Hagedorn, 1979).

Table 4. FWS averages for 12 common bean lines and hybrids obtained from a 6x6 partial diallel. Viçosa, MG, 2018.

$G_1 \setminus G_2$	MAI 1813	BRS Estilo	VC 13	VC 28	VC 25	IAC Formoso	$\overline{G_1}$
BRSMG Talismã	1	1	1	1	1	1	1
RC I-8	7.03	7.7	1	4.67	1	5.67	7
BRSMG Uai	8.37	8.67	2.97	3.17	1	7.8	4.33
CVIII 8511	1	1	1	1	1	1	1
CNFC 11965	8.67	9	1	5.94	1	9	8.5
BRS Pérola	1	1	1	1	1	1	1.67
$\overline{G_2}$	5.67	8.33	1	4.17	1	3.83	
Average of parents in group 1							3.92
Average of parents in group 2							4.00
Average of all parents							3.96
Average of hybrids							3.10

G_1: group 1 parents; G_2: group 2 parents; $\overline{G_1}$: mean of each parent in group 1; $\overline{G_2}$: mean of each parent in group 2.

As already stated, SCA calculations are ineffective in indicating crosses with diversity that are of interest to the breeder intending to enhance Fusarium wilt resistance. As a result, the selection of crossings should be based solely on estimates of the effects of $\hat{g}_i$ and $\hat{g}_j$, which emphasize the presence of desirable dominant alleles in the parents. Cruz and Vencovsky (1989) have demonstrated that the best diallel hybrid is not always produced by a hybrid obtained by a cross between a parent selected based on the GCA, with frequency of favorable alleles higher than that of the population average and significant divergence from the variety with which it is crossed.

Positive and significant values were observed for the estimates of $\hat{s}_{ii}$ and $\hat{s}_{jj}$ referring to the parents with the highest general combining ability ($\hat{g}_i$) or frequency of favorable alleles involved in resistance to FOP UFV 01 (BRSMG Talismã, CVIII 8511 and BRS Pérola, from group 1, and VC 13 and CV 25, from group 2). These findings indicate the presence of genes with negative dominance shifts in these FWS-controlling parents, which implies that dominant alleles are associated with lower scores (greater resistance to Fusarium wilt).

However, the BRSMG Uai (group 1) has a positive and significant estimate of $\hat{g}_i$ (1.42) and a negative and significant estimate of $\hat{s}_{ii}$ (-1.78). The IAC Formoso (group 2) has a positive and significant estimate of $\hat{g}_j$ (0.65) and a negative and significant estimate of $\hat{s}_{jj}$ (-0.83). The latter result indicates the presence of one or more genes in these parents with negative dominance deviations, that is, recessive allele(s) involved in fusarium wilt resistance. Similar results were found for the MAI 1813 of group 2, but its $\hat{s}_{jj}$ value, despite negative, was not significant, which indicates the low frequency of these recessive alleles in this parent.

The BRSMG Uai strain has a fusarium wilt severity score of 4.33 (Table 4), which indicates moderate resistance. Ramalho et al. (2016) observed similar results for this strain under field conditions, where it was regarded moderately resistant. It is worth noting that crossings between this line and MAI 1813, BRS Estilo and IAC Formoso produced hybrids with scores higher than 7.8 (considered susceptible). These findings support the presence of a recessive allele implicated in fusarium wilt resistance in this parent. When the IAC Formoso strain was crossed with CNFC 11965 and RCI-8, a similar result was obtained, which corroborates the presence of recessive allele(s) participating in the resistance of IAC Formoso strain to fusarium wilt. Recessive genes have also been found to confer resistance to bacterial blight in common bean (*Pseudomonas syringae pv. phaseolicola*) (DUNCAN et al., 2014).

Regarding the grain yield characteristic, the estimates of the SCA sum of squares were higher than the estimates of the sum of squares of the GCA of groups 1 and 2, which indicates the predominance of genes with non-additive effects (dominance effects) engaged in the control of the characteristic. Silva et al. (2013) evaluated 14 common bean lines and their hybrids in partial diallel (8x6) and observed the prevalence of positive dominance deviation genes implicated in grain yield genetic regulation. Machado et al. (2002) corroborated this event in F2 populations derived from a full diallel conducted between 12 common bean lines. However, some research works indicate that additive effects predominate in the genetic control of grain yield in common bean. In an evaluation of partial diallel, Moura et al. (2016), Kurek et al. (2001) and Santos, Vencovsky and Ramalho (1985) obtained results that reveal the preponderance of additive genetic effects in the genetic control of grain yield.

Considering the specific ability of the parents to combine with themselves ($\hat{s}_{ii}$ and $\hat{s}_{jj}$) for the YIELD trait, it was discovered that the sum of the $\hat{s}_{ii}$, or $\hat{s}_{jj}$, presented a negative value (-4021.34) (Table 5), which indicates the predominance of genes with positive dominance deviations involved in the genetic control of this trait, that is, most dominant alleles determine the highest values for YIELD. Except for the RCI-8 and CVIII 8511 strains in group 1, which presented negative but not significant estimates of $\hat{s}_{ii}$ and $\hat{s}_{jj}$, all strains presented negative and significant estimates of $\hat{s}_{ii}$ and $\hat{s}_{jj}$. The negative and significant estimates of $\hat{s}_{ii}$ or $\hat{s}_{jj}$ for the great majority of lineages demonstrate that genes with positive dominance deviations involved in the genetic control of YIELD also prevail in each of the lineages, which implies that dominant genes raise the value of the trait.

Regarding the frequency of YIELD-friendly alleles ($\hat{g}_i$ effects), the VC 25 lineage from group 2 stands out, for presenting the highest and most significant estimate of general combining ability ($\hat{g}_j$) (Table 5 and Figure 2). In this scenario, positive values of $\hat{g}_i$ are relevant, since the highest averages for grain yield are of interest. Given that the estimates of $\hat{g}_j$ indicate the frequency of favorable alleles involved in the control of the trait under consideration, it is concluded that the VC 25 strain has the highest genetic value of the group 2 strains and should be used in crosses to produce populations with potential to improve grain yield. GCA had no effect on group 1 (Table 2), which demonstrates that the lines do not differ in the frequency of beneficial alleles implicated in YIELD control.

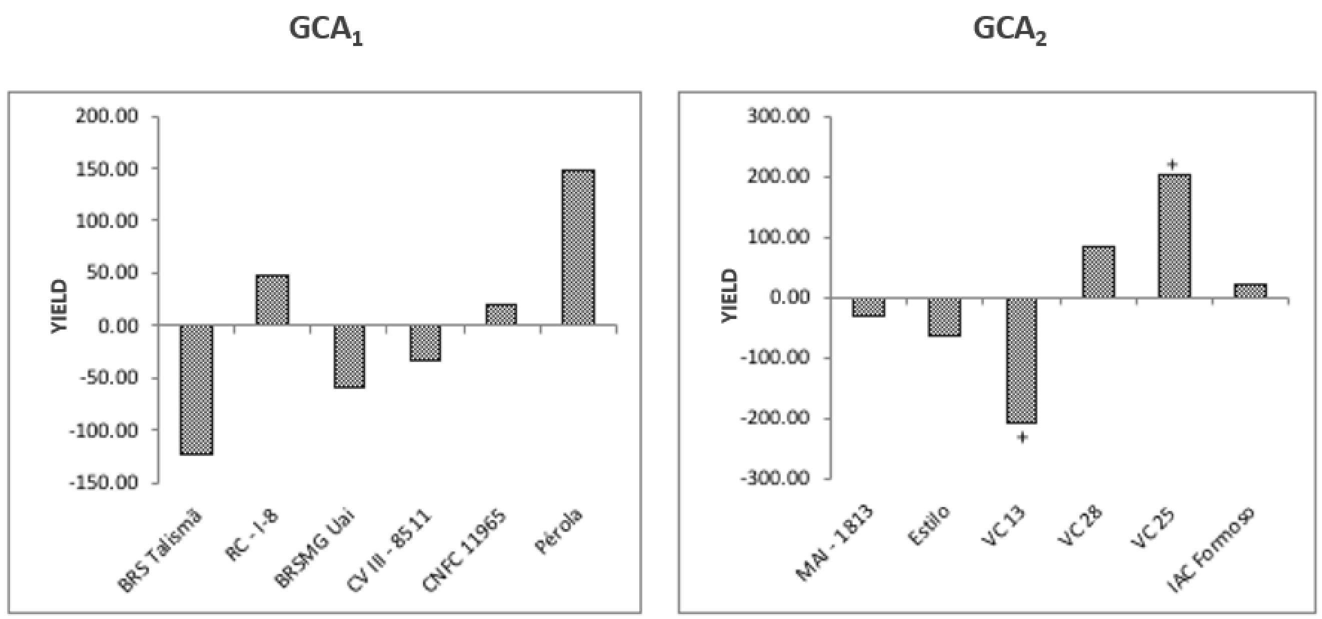
Lines MAI 1813, BRS Estilo and IAC Formoso present the most negative and significant estimates of $\hat{s}_{jj}$ and the least significant estimations of $\hat{g}_j$. This reveals that these strains have genes with mostly positive dominance deviations in the control of YIELD; however, the low estimate of $\hat{g}_j$ indicates the low frequency of these alleles, which could be owing to the existence of both dominant and recessive alleles in the trait regulation. Bidirectional dominance influences SCA estimates, and genes with negative dominance shifts with diallel frequencies higher than 0.5 influence $\hat{g}_i$ estimates as well. As a result, skewed estimates of GCA and SCA make it difficult to select parents in order to obtain segregating populations with increased possibility of superior lineage extraction. In contrast, the RC I-8 lineage includes non-significant estimations of $\hat{s}_{ii}$ and $\hat{g}_i$. This suggests that in this line, there is no majority of genes with positive or negative dominance shifts in YIELD control.

Table 5. Estimates of the general and specific combining ability of 12 bean parents, based on grain yield in a 6x6 partial diallel scheme. Viçosa, MG, 2018.

$G_1 \setminus G_2$	MAI 1813	BRS Estilo	VC 13	VC 28	VC 25	IAC Formoso	$\hat{g}_i$	$\hat{s}_{ii}$
BRSMG Talismã	899.34*[a]	-68.00	-87.04	104.03	-37.18	439.11	-122.27	-625.13*
RC I-8	-109.75	634.32*	297.31	-25.21	-127.38	52.70	46.92	-360.99
BRSMG Uai	339.63	192.90	619.38*	241.46	212.57	140.58	-58.59	-873.26*
CVIII 8511	48.01	418.25	136.28	145.92	-169.61	-13.91	-33.08	-282.47
CNFC 11965	778.20*	-555.77*	151.39	510.63*	606.22*	92.19	19.79	-791.43*
BRS Pérola	-390.50	841.95*	85.29	234.59	479.57	925.21*	147.22	-1088.06*
$\hat{g}_j$	-31.97	-62.36	-209.94*	82.22	201.15*	20.90	$\Sigma\hat{g}_i=\Sigma\hat{g}_j=0$	$\Sigma\hat{s}_{ii}= -4021.34$
$\hat{s}_{jj}$	-782.46*	-731.82*	-601.30*	-605.72*	-482.09*	-817.95*	$\Sigma\hat{s}_{jj}= -4021.34$	

*Significant by t test, at 5% probability level.

G_1: group 1 parents; G_2: group 2 parents; [a] estimate of the specific combining ability of the 36 hybrids ($\hat{s}_{ij}$); $\hat{g}_i$ and $\hat{g}_j$: estimates of the general combining ability of parents in group 1 and 2, respectively; $\hat{s}_{ii}$ and $\hat{s}_{jj}$: specific ability of the parent to combine with itself, for groups 1 and 2, respectively.



+ significant at 5% probability by the t test.

Figure 2. Estimates of the general combining ability of group 1 (GCA1) and group 2 (GCA2) parents for grain yield.

There were 26 positive estimates for the effects of the unique combining ability

($\hat{s}_{ij}$) of the hybrids, 8 of which were significant (Table 5). This suggests that the performance of some hybrids is better than expected, based on GCA estimates, which is due to parental diversity for loci that exhibit dominance. BRS Pérola / IAC Formoso, BRSMG Talismã / MAI 1813, BRS Pérola / BRS Estilo, CNFC 11965 / MAI 1813, RC I-8 / BRS Estilo, BRSMG Uai / VC 13, CNFC 11965 / VC 25 and CNFC 11965 / VC 28 are the eight hybrids with the highest and most significant SCA estimations.

As the means of the lines, BRSMG Talismã, RC I-8, BRSMG Uai, CVIII 8511 and CNF 11965 did not differ significantly from the mean of the cultivar BRS Pérola (reference standard of carioca bean), by Dunnett's test, at 5% probability. It can be concluded that in crosses with group 2 lines, any of these lines can be used to obtain populations with potential for superior line extraction. Thus, populations derived from hybrids that presented positive and significant estimations of SCA are the most promising for YIELD improvement.

The VC 25 line demonstrated both a positive and significant $\hat{g}_j$ impact as well as a negative and significant $\hat{s}_{jj}$ effect. This finding implies that the VC 25 has high frequency of YIELD -friendly favorable alleles, the majority of which are dominant. Similarly, VC13 presented a negative and significant estimate of $\hat{s}_{jj}$, but it also had a negative and substantial $\hat{g}_j$ impact (Table 5). These findings indicate that this line has dominant genes linked with higher grain yield values, although less often than other lines in group 2.

The means of the 12 lines and 36 hybrids for YIELD are shown in Table 6. It is worth noting that, among the 36, the hybrid with the highest average (5478.97) and the highest estimate of $\hat{s}_{ij}$ (925.21) is the outcome of the BRS Pérola / IAC Formoso combination. Since they have the lowest estimates of $\hat{s}_{ii}$ and $\hat{s}_{jj}$, these parents are the most divergent for genes with positive dominance deviations involved in YIELD regulation. High values of $\hat{s}_{ij}$ imply that the parents involved in the crosses have high genetic divergence when positive dominance deviations predominate (CRUZ and VENCOVSKY, 1989). With the exception of three hybrids, which are the outcome of crosses CVIII 8511 x VC 25, RC I-8 x VC 25 and BRSMG Talismã x VC 25, most hybrids presented averages higher than those of their parent with the highest average, which proves the presence of heterobeltiosis. These findings, along with those previously presented in terms of $\hat{s}_{ij}$, indicate the great complementarity between the parents of the two diallel groups for the grain yield trait.

Potential of F4 segregating populations

The analysis of variance of grain yield data (YIELD) per plot, in kg ha^{-1}, of the 34 populations tested in the F4 generation in the 2017 winter crop reveals a significant influence of populations, thus indicating variability between the means of these populations in relation to YIELD.

Then, the potential of each group was quantified by considering both its average performance and variability. Table 7 shows the estimations of the probabilities of obtaining superior lines to the cultivar BRS Pérola in 20 percent (P%) of each population, using the approach described by Jinks and Pooni (1976). The estimates range from 13% for population 9 (RC I-8 / VC 13) to 43% for population 1 (BRSMG Talismã / MAI 1813). The top 20 populations for estimating P% are, in descending order, 1, 24, 13, 17, 7, 2, 12, 10, 30, 8, 27, 18, 29, 36, 34, 28, 16, 11, 6 and 19.

Table 6. Grain yield averages for 12 common bean lines and hybrids obtained from a 6x6 partial diallel. 2018 Viçosa, MG.

$G_1 \setminus G_2$	MAI 1813	BRS Estilo	VC 13	VC 28	VC 25	IAC Formoso	$\overline{G}_1$
BRSMG Talismã	5130.74	4133.01	3966.39	4449.63	4427.34	4723.39	3293.74
RC I-8	4290.84	5004.52	4519.93	4489.57	4506.33	4506.16	3896.26
BRSMG Uai	4634.72	4457.59	4736.49	4650.73	4740.77	4488.54	3172.97
CVIII 8511	4368.60	4708.45	4278.9	4580.70	4384.10	4359.55	3814.77
CNFC 11965	5151.66	3787.30	4346.89	4998.28	5212.80	4518.53	3411.55
BRS Pérola	4110.39	5312.45	4408.22	4849.67	5213.58	5478.97	3369.78
$\overline{G}_2$	3761.47	3751.33	3586.70	4166.60	4528.08	3831.73	
Average of parents in group 1							3493.18
Average of parents in group 2							3937.65
Average of all parents							3715.41
Average of hybrids							4609.05

G_1: group 1 parents; G_2: group 2 parents; $\overline{G}_1$: mean of each parent in group 1; $\overline{G}_2$: mean of each parent in group 2.

According to Jinks and Pooni's (1976) methodology, the parents of group 1, BRSMG Talismã, RC I-8, BRSMG Uai, CVIII 8511, CNFC 11965 and BRS Pérola, were present in 3, 5, 4, 2, 4 and 2 of the crosses, respectively. In group 2, the parents MAI 1813, BRS Estilo, VC 13, VC 28, VC 25 and IAC Formoso were present in 4, 2, 1, 4, 3 and 6 of the crosses, respectively.

According to Jinks and Pooni's analysis, the parents RC I-8 and IAC Formoso were present in the highest number of crossings, when evaluating the genealogy of the 20 populations with the greatest potential (1976). However, based on the diallel analysis, the RC I-8 lineage exhibits non-significant estimates of $\hat{s}_i$ and $\hat{g}_i$ (Table 5), which indicates low frequency of beneficial alleles in this lineage, as well as limited diversity in comparison to the group 2 lines.

The existence of both genes with positive and negative deviation in the YIELD control found in this strain may explain the contradictory results. Similar results were obtained for the MAI 1813, BRS Estilo, VC 28 and IAC Formoso strains, which presented negative and significant estimates of $\hat{s}_{jj}$ and non-significant estimates of $\hat{g}_j$, possibly due to the existence of genes with positive and negative deviations. YIELD control is negative and affects $\hat{g}_j$ estimations. These findings suggest that information from populations with more advanced generations of inbreeding can compensate for the inadequacies in diallel analysis, in the selection of populations with higher potential for lineage extraction.

When the average performance of F4 populations (Table 7) and F1 hybrids (Table 6) was compared to the performance of the parents involved in their genealogies, it was discovered that the number of F4 populations exhibiting heterobeltiosis (14 in this case) was significantly lower than that of F1 hybrids (33 out of the 36 evaluated). This finding verifies the presence of genes with positive dominance shifts involved in YIELD control, discovered by means of diallel analysis.

Table 7. Average grain yield (kg ha^{-1}) of parents and F4 populations, as well as P% values (probability of exceeding the standard - BRS Pérola) of each F4 population. Viçosa, MG, 2018.

Order	Nº Pop	Population	Grain yield average (kg ha^{-1})			P(%)
					Pop (F4)	
1	**1**	BRSMG Talismã / MAI 1813	4669	4406	4996	43.0
2	**24**	CVIII 8511 / IAC Formoso	4767	4660	4949	42.9
3	**13**	BRSMG Uai / MAI 1813	4552	4406	4486	36.0
4	**17**	BRSMG Uai / VC 25	4552	4048	4718	34.9
5	**7**	RC I-8 / MAI 1813	4844	4406	5034	33.8
6	**2**	BRSMG Talismã / BRS Estilo	4669	4540	4535	33.0
7	**12**	RC I-8 / IAC Formoso	4844	4660	5113	31.7
8	**10**	RC I-8 / VC 28	4844	4286	4604	31.3
9	**30**	CNFC 11965 / IAC Formoso	4299	4660	4623	30.5
10	**8**	RC I-8 / BRS Estilo	4844	4540	5153	30.4
11	**27**	CNFC 11965 / VC 13	4299	4466	4467	30.1
12	**18**	BRSMG Uai / IAC Formoso	4552	4660	5221	29.9
13	**29**	CNFC 11965 / VC 25	4299	4048	4258	29.4
14	**36**	BRS Pérola / IAC Formoso	5214	4660	4387	29.1
15	**34**	BRS Pérola / VC 28	5214	4286	4314	29.0
16	**28**	CNFC 11965 / VC 28	4299	4286	5007	27.6
17	**16**	BRSMG Uai / VC 28	4552	4286	4417	27.4
18	**11**	RC I-8 / VC 25	4844	4048	4432	26.4
19	**6**	BRSMG Talismã / IAC Formoso	4669	4660	4589	25.7
20	**19**	CVIII 8511 / MAI 1813	4767	4406	4852	25.6
21	**14**	BRSMG Uai / BRS Estilo	4552	4540	4792	25.6
22	**33**	BRS Pérola / VC 13	5214	4466	4158	23.7
23	**15**	BRSMG Uai / VC 13	4552	4466	4677	23.2
24	**25**	CNFC 11965 / MAI 1813	4299	4406	4563	23.0
25	**31**	BRS Pérola / MAI 1813	5214	4406	4337	22.8
26	**4**	BRSMG Talismã / VC 28	4669	4286	4372	22.4
27	**20**	CVIII 8511 / BRS Estilo	4767	4540	4435	22.4
28	**21**	CVIII 8511 / VC 13	4767	4466	4616	22.2
29	**3**	BRSMG Talismã / VC 13	4669	4466	4016	20.6
30	**22**	CVIII 8511 / VC 28	4767	4286	4579	20.5
31	**32**	BRS Pérola / BRS Estilo	5214	4540	4092	19.0
32	**5**	BRSMG Talismã / VC 25	4669	4048	4269	17.8
33	**26**	CNFC 11965 / BRS Estilo	4299	4540	4049	14.7
34	**9**	RC I-8 / VC 13	4844	4466	4314	13.1

G_1: mean of each parent in group 1; G_2: mean of each parent in group 2.

Pearson's correlation coefficient was estimated to be 0.09 between the average grain yield of populations in the F4 generation and F1 hybrids (Tables 6 and 7). Since the F1 hybrids were tested in the dry season of 2014, and the F4 populations, in the winter season of 2017, this low correlation estimate implies the presence of genotype x environment interaction (GxE). According to Cruz, Regazzi, and Carneiro (2012), the lack of connection between genotype performance is a determining factor in the occurrence of GxE interactions, particularly for the complicated ones. Considering solely the parents, there was a low estimate of Pearson's correlation coefficient (-0.34), considering their performances in the drought/2014 and winter/2017 harvests, which corroborates the occurrence of GxE interaction in grain yield characteristics. Faria et al. (2013) and Barili et al. (2015) also found genotype x environment interactions in common bean grain yield.

Considering the 20 populations with the highest potential for YIELD, based on the diallel analysis, that is, those with the highest SCA estimations (Table 5), it was observed that 12 of them were common (Table 8) to those picked based on the F4 generation by the Jinks and Pooni (1976) method (Table 7). This discrepancy may be related to the effect of the GxE interaction on grain yield, as well as the existence of both positive and negative dominance shift genes involved in the genetic control of YIELD in some of the parents.

Table 8. Classification of the 20 best segregating populations that outperform the cultivar BRS Pérola (P%) and the 20 F1 hybrids with greater and positive SCA estimations. Viçosa, MG, 2018.

Order	populations			
	P(%)		SCA	
1	**1***	BRSMG Talismã / MAI 1813	**36***	BRS Pérola / IAC Formoso
2	**24**	CVIII 8511 / IAC Formoso	**1***	BRSMG Talismã / MAI 1813
3	**13***	BRSMG Uai / MAI 1813	**32**	BRS Pérola / BRS Estilo
4	**17***	BRSMG Uai / VC 25	**25**	CNFC 11965 / MAI 1813
5	**7**	RC I-8 / MAI 1813	**8***	RC I-8 / BRS Estilo
6	**2**	BRSMG Talismã / BRS Estilo	**15**	BRSMG Uai / VC 13
7	**12**	RC I-8 / IAC Formoso	**29***	CNFC 11965 / VC 25
8	**10**	RC I-8 / VC 28	**28***	CNFC 11965 / VC 28
9	**30**	CNFC 11965 / IAC Formoso	**6***	BRSMG Talismã / IAC Formoso
10	**8***	RC I-8 / BRS Estilo	**20**	CVIII 8511 / BRS Estilo
11	**27***	CNFC 11965 / VC 13	**13***	BRSMG Uai / MAI 1813
12	**18***	BRSMG Uai / IAC Formoso	**9**	RC I-8 / VC 13
13	**29***	CNFC 11965 / VC 25	**16***	BRSMG Uai / VC 28
14	**36***	BRS Pérola / IAC Formoso	**34***	BRS Pérola / VC 28
15	**34***	BRS Pérola / VC 28	**17***	BRSMG Uai / VC 25
16	**28***	CNFC 11965 / VC 28	**14**	BRSMG Uai / BRS Estilo
17	**16***	BRSMG Uai / VC 28	**27***	CNFC 11965 / VC 13
18	**11**	RC I-8 / VC 25	**22**	CVIII 8511 / VC 28
19	**6***	BRSMG Talismã / IAC Formoso	**18***	BRSMG Uai / IAC Formoso
20	**19**	CVIII 8511 / MAI 1813	**21**	CVIII 8511 / VC 13

*Best classified by the two methodologies.

The population from the cross between CVIII 8511 and IAC Formoso, which was ranked second by Jinks and Pooni (1976), was not reflected by the SCA estimate. As previously stated, this result could be attributed to genes with positive and negative dominance shifts implicated in YIELD regulation that are present in this strain. One strategy to capitalize on the impact of the GxE interaction on grain yield is to test the diallel in more extreme environmental conditions. The difficulty in collecting a significant number of F1 seeds for this strategy, on the other hand, may be a limiting factor. Thus, in addition to diallel analysis, the use of information from populations in more advanced inbreeding generations can be a promising option, aiming at a more precise selection of those populations with greater potential.

The populations from the crosses BRS Pérola / BRS Estilo, CNFC 11965 / MAI 1813 and BRSMG Uai / VC 13 were categorized among the six with the highest potential by diallel analysis, but not among the 20 with the highest potential by Jinks and Pooni (1976). These populations presented high and substantial SCA estimates, which indicates that the cross parents were highly complementary. With the advancement of the inbreeding of these populations, the sample size may not have been sufficient to maintain all of their variability, which may have reduced the mean and variance of these populations in the F4 generation. Even the sample of 90 plants may not have been sufficient to quantify the average performance and variability of these populations in the F4 generation.

When compared to populations with a higher degree of inbreeding, the parameter estimates produced via diallel analysis are more accurate in terms of sample size and residual variance. It is also crucial to note that for populations with a higher degree of inbreeding, individual plants within populations must be evaluated to give an estimate of diversity within populations. However, evaluating segregating populations in different environments can be useful in the selection of populations with greater potential, since, as inbreeding progresses, the effects of genes with negative dominance deviation (recessive alleles increasing the value of the trait) and advantageous epistatic interactions are captured, thus increasing the likelihood of successful breeding.

In order to select the 20 populations with the greatest potential to start the breeding program by recurrent selection, the 12 populations common to both methodologies are recommended, plus four populations (CVIII 8511 / IAC Formoso, RC I-8 / MAI 1813 , BRSMG Talismã / BRS Estilo and RC I-8 / IAC Formoso) that stood out only by the methodology of Jinks and Pooni (1976) and four populations (BRS Pérola / BRS Estilo, CNFC 11965 / MAI 1813, BRSMG Uai / VC 13 and CVIII 8511 / BRS Estilo) that stood out only based on information from the diallel analysis. It is important to note that all of the parents which stood out for resistance to fusarium wilt by diallel analysis are included in the genealogy of these 20 selected populations (1, 2, 6, 7, 8, 12, 13, 15, 16, 17, 18, 20, 24, 25, 27, 28, 29, 32, 34 and 36). Thus, a recurrent selection breeding program based on these 20 populations can be formed, with the potential to improve resistance to fusarium wilt as well as grain yield.

CONCLUSIONS

BRSMG Talismã, CVIII 8511, BRS Pérola, VC 25 and VC 13 were the lines with the highest frequency of beneficial alleles for fusarium wilt resistance. Except for BRSMG Uai and IAC Formoso, which contain a majority of recessive genes, these strains present predominance of dominant genes involved in fusarium wilt resistance. It was observed the prevalence of dominant genes, which indicates more productive plants for grain yield, particularly the VC 25 strain. This strain also stands out in terms of the frequency of beneficial alleles for fusarium wilt resistance.

In the occurrence of bidirectional dominance involved in the genetic control of the trait of interest, the use of information from populations in more advanced generations of inbreeding in complementarity with those of diallel analysis is a promising strategy, aiming at a more accurate selection of those populations with the highest potential.

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