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Diallel analysis for soybean resistance to the fungal pathogen *Sclerotinia sclerotiorum*

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ABSTRACT. Sclerotinia stem rot is a common soybean disease caused by the fungus *Sclerotinia sclerotiorum*, resulting in economic losses in Brazil and worldwide. The development of resistant cultivars is a good option for the management of this disease; however, it has been difficult, largely due to the variability found in the fungus. We assayed for the genetic resistance (vertical and horizontal) of soybean cultivars inoculated with various isolates of *S. sclerotiorum*. Twenty soybean cultivars were selected and tested; 10 were relatively resistant and 10 relatively susceptible to the pathogen. The cultivars were inoculated with mycelium from four fungal isolates: Mauá da Serra, Ingaí, and Nazareno, collected from soybean production areas and UFLA 24, an isolate normally used by the Lavras University Laboratory of Plant Resistance to Diseases team, for assays with the detached-leaf method. The experiment was conducted in a completely randomized design. Detached-leaves at V2 trefoil were placed on an agar disk containing the mycelium and each leaflet was considered a replicate. After 72 hours, the leaflets were evaluated using a scoring scale ranging from 0 (no symptoms) to 5 (susceptible). Statistical analyses were performed using the diallel method (Griffing IV model), which provided information on the vertical and horizontal resistance of the cultivars, as well as the

aggressiveness of the isolates. The soybean cultivars BRS Baliza RR, M-SOY 8001, Emgopa 316 and M-SOY 8329 showed horizontal resistance; BRS Favorita RR, Emgopa 315, MG/BR 46 (Conquista), 7166RSF IPRO, BRS Silvânia RR and BRS Milena presented specific resistance to most isolates The UFLA 24 and Ingaí fungal isolates were the most aggressive, indicating that these isolates should be preferred for evaluating the level of resistance of soybean genotypes.

Key words: Sclerotinia stem rot; *Glycine max*; General and specific resistance capacity

INTRODUCTION

White mold is a disease caused by the fungus *Sclerotinia sclerotiorum*. This fungus is a necrotrophic ascomycete that infects more than 400 species of plants, including important crops such as cotton, bean, sunflower, and soybean (Boland and Hall., 1994). In soybeans, the disease is also called stem rot and causes considerable damage to grain production and quality. Under favorable conditions, such as high humidity and mild temperatures, production losses of up to 40% may occur (Henneberg et al., 2012; Peltier et al., 2012; Jaccoud Filho et al., 2014). The fungus produces a resistant structure called a sclerotium that can survive in the soil for more than five years (Steadman et al., 2005).

In Brazil, before 2004, the disease occurred sporadically in soybean crops and did not cause significant production losses. However, since the 2003/2004 harvest, the disease has been increasing in incidence in many parts of the Southeast, South, and Central-West regions of the country (Silva et al., 2009). Close to 28% of the Brazilian soybean production area is estimated to be infested by this pathogen, totaling approximately 10 million hectares that require the adoption of integrated disease control measures (Meyer et al., 2019).

Disease control is conducted through agricultural practices such as no-till, the use of certified seeds, and rotation with nonhost crops. However, under conditions favorable to pathogen development, such practices are insufficient. Fungicide use has low efficiency since the penetration in the canopy is low and the distribution uneven. This pattern occurs because when the fungicide is applied, the plant canopy is already formed, as the infection begins at the plant reproductive stage. In addition, the use of fungicides is a costly strategy for producers.

Therefore, the use of resistant cultivars is the best alternative for controlling stem rot. However, genetic resistance to *S. sclerotiorum* is complex and has low heritability, with only a few cultivars showing some degree of resistance (Kim et al., 2000; Juliatti et al., 2014; Zhao et al., 2015; Pereira et al., 2019). In addition, plants have escape mechanisms that make it difficult to evaluate the disease in the field, such as flowering date, height, and architecture (Cunha et al., 2010).

To date, no soybean cultivars resistant to stem rot are known. Although differences in susceptibility do exist among cultivars and a few inoculation methods have been described, many are impractical and have inconsistent results (Chen et al., 2005; Huller et al., 2016). Despite variability in soybean reaction to *S. sclerotiorum*, little knowledge regarding the behavior of Brazilian cultivars exists.

According to Vanderplank (1963), resistance can be classified as vertical or horizontal, according to its efficacy against pathogen isolates. In addition, the type of resistance can be identified by the significance of the cultivar x isolate interaction. This situation is observed when different isolates of a pathogen are inoculated in different cultivars. Under these conditions, a highly significant cultivar x isolate interaction suggests that the reaction of each cultivar is specific to a specific isolate, indicating that the resistance is vertical. For nonsignificant interactions, the cultivars respond similarly to all isolates, and in these cases, the existence of horizontal resistance can be inferred.

Melo et al. (1999) developed an efficient method that is able to provide information regarding the host's vertical and horizontal resistance and the aggressiveness of the pathogen isolates. This method has been used in several studies (Silva et al., 2014; Pereira et al., 2015; Valdo et al., 2016; Leite et al., 2017) but has not been investigated in the *S. sclerotiorum*-*Glycine max* pathosystem.

Therefore, the objectives of the present study were to determine the genetic resistance (vertical and horizontal) of soybean cultivars from the Active Germplasm Bank of the Department of Agriculture of the Federal University of Lavras inoculated with various different isolates of *S. sclerotiorum*.

MATERIAL AND METHODS

The experiments were conducted at the Laboratory of Plant Resistance to Diseases in a greenhouse of the Department of Biology, Federal University of Lavras (Universidade Federal de Lavras - UFLA). Twenty cultivars from the UFLA Soybean Germplasm Bank were used; these cultivars were previously classified as resistant or susceptible according to Garcia et al. (2012). Ten cultivars with a relatively high level of resistance and 10 relatively susceptible cultivars were used (Table 1). Four isolates of *S. sclerotiorum* were applied: three collected in the South and Campo das Vertentes Mesoregions of the state of Minas Gerais (IG, NAZ and UFLA 24) and one from the Paraná state (MS), Brazil. All the isolates were collected for this study, except UFLA 24, which is an isolate normally used by the Laboratory of Plant Resistance to Diseases team.

Table 1. Soybean cultivars with a relatively high resistance level or susceptibility to *Sclerotinia sclerotiorum.*

Cultivars[1]	Origen	Cultivars[2]	Origen
1 Emgopa 316	Emater-GO	11 7166RSF IPRO	GDM
2 Emgopa 315	Agencia Rural	12 BRS 213	Embrapa
3 BRS Milena	Embrapa	13 NS 7338 IPRO	Nidera
4 BRSMG 790A	Embrapa	14 BRSMG Garantia	Embrapa
5 BRSMG 850GRR	Embrapa	15 MG/BR 46 Conquista	Embrapa
6 BRS Baliza RR	Embrapa	16 BRS Silvânia RR	Embrapa
7 BRS Favorita RR	Embrapa	17 M-SOY 8001	D&PL(Br)
8 BRSGO Luziânia	Embrapa	18 M-SOY 6101	D&PL(Br)
9 M-SOY 8000RR	D&PL(Br)	19 M-SOY 8329	D&PL(Br)
10 BRSMG 68 Vencedora	Embrapa	20 TMG123RR	TMG

[1] Resistant cultivars (1 to 10); [2] Susceptible cultivars (11 to 20).

The cultivars were evaluated for resistance to *S. sclerotiorum* using the detached-leaf method. For this purpose, the plants were grown in the greenhouse in 500-ml pots

containing substrate mixed with soil in a 2:1 ratio (two parts substrate to one part soil containing clay and sand). The trefoil of plants at stage V2 (first fully expanded trefoil) was collected and taken to the laboratory to set up the experiment. The trefoil was placed in an acrylic germination box containing a sheet of paper towel moistened with sterile distilled water. Before inoculation, the trefoil was sprayed with water and then received a 6-mm, 5-day-old mycelial disc of each isolate. The germination boxes containing the trefoils were incubated at 20 ± 2ºC under a 12-hour photoperiod for 72 hours.

To disinfect the isolates especially collected for this study (IG, NAZ, and MS) the sclerotia were disinfected with 50% ethanol and 0.5% sodium hypochlorite diluted in sterile distilled water for 30 and 60 seconds, respectively. Subsequently, to obtaining the mycelium, the sclerotia were rinsed in sterile distilled water and transferred to Petri dishes containing potato dextrose agar (PDA) medium. The Petri dishes were incubated at 22 ± 3ºC under a 12-hour photoperiod for myceliogenic germination until the formation of sclerotia, which took about two weeks. The UFLA 24 isolate is stored by the paper method (Oliveira, 2014). Thus, to obtain mycelium, we proceeded in the same way as for the other isolates, with the difference that instead of sclerotia, we use a piece of paper.

The evaluations were performed 72 hours after inoculation, based on a diagrammatic scale (Garcia et al., 2008 apud Garcia et al., 2012). The cultivars were classified as one - immune (absence of disease), two - resistant (> 0 to 11%), three - moderately resistant (12 to 24%), four - less resistant (25 to 50%) and five - susceptible (S > 50%).

The experiment was conducted in a completely randomized design with a factorial arrangement (20 plants and four isolates), and each leaflet of the trefoil constituted a replicate. The data were analyzed using analysis of variance and diallel analysis to determine the general and specific virulence capacity, following Melo et al. (1999).

For the diallel analysis, a modified version of the method IV of Griffing (1956) was used, in a partial diallel arrangement proposed by Geraldi et al. (1988). One group was formed by the isolates (group I) and another by the cultivars (group II). In the isolate x cultivar interaction, the general combining ability of group I corresponds to the general reaction capacity (GRC), representing the horizontal resistance of the pathogen, which is dependent on the average performance of the cultivar with the different isolates. The general combining ability of group II corresponds to the general aggressiveness capacity (GAC) of the pathogen, which represents the average pathogenicity of each isolate in inoculations with all the cultivars. The specific interaction capacity (SIC) indicates the interaction between the components of the two groups, i.e., the pathogenicity of the pathogen and the vertical resistance of the cultivar.

RESULTS AND DISCUSSION

The analysis of variance showed significant differences for the isolate, cultivar, and isolate x cultivar sources of variation. The significant interaction indicates that the response of the cultivars to the different isolates was dissimilar. Thus, isolates vary in their ability to cause symptoms and based on the response to these isolates, cultivars have different resistance alleles. These results not only reinforce the need to conduct several experiments to obtain suitably accurate estimates even when inoculations are conducted under controlled conditions but also show that the experiment was conducted with good experimental

accuracy, indicated by the magnitude of the coefficient of variation (CV), which was 17.14%.

The diallel analysis revealed significant differences for all the sources of variation, corroborating the results from the analysis of variance. The significance of GAC and GRC indicates a difference in aggressiveness among the pathogen isolates and the presence of variability in horizontal resistance among the cultivars. However, a significant SIC value also indicates the existence of vertical resistance (Table 2). Vertical resistance alleles are the most efficient in reducing the losses caused by stem rot in soybean. The high pathogenic variability observed in *S. sclerotiorum* (Viteri et al., 2015; Willbur et al., 2017; Miorini et al., 2018) makes this type of resistance less durable. Thus, a need exists to develop cultivars with more stable resistance to this pathogen.

Table 2. Summary of the diallel analysis for the detached-leaf method data for analyzing fungal resistance of soybean cultivars. Sources of variation (SV), degree of freedom (DF), medium square (MS).

SV	DF	MS	F	Probability (%)
Inoculations	79	4.7063	15.6876	. **[1]
G.R.C. G-I[2]	3	19.4819	64.3998	. **
G.A.C. G-II[3]	19	4.0989	13.6630	. **
S.I.C. I x II[4]	57	4.1310	13.7702	. **
Error	160			

[1] Significant at 1% probability; [2] General reaction capacity of group I (isolates); [3] General aggressiveness capacity of group II (cultivars); [4] Specific interaction capacity between isolates and cultivars.

The occurrence of both types of resistance has been reported for *S. sclerotiorum* on *Phaseolus vulgaris* (Silva et al., 2014; Leite et al., 2017). In those studies, SIC was significant, indicating the possible participation of vertical resistance in controlling the character. However, the SIC estimates were 15 to 30 times lower than the GRC estimate. This small SIC estimate was due to a weak cultivar x isolate interaction. Therefore, these results cannot be compared to those of our study, where such a small SIC compared to GRC magnitude was not observed (Table 2).

The lower scores in the severity disease assessment indicated a higher level of resistance; therefore, via the GRC estimates, negative values specify the cultivars that obtained the highest level of horizontal resistance (Table 3). The Emgopa 316, BRS Baliza RR, M-SOY 8001, and M-SOY 8329 cultivars presented higher horizontal resistance levels than those of the other cultivars.

A different result was observed, in part, in other studies (Garcia et al., 2012; Garcia et al., 2015) in which the M-SOY cultivars were considered susceptible to *S. sclerotiorum.* This difference in the resistance pattern may be due to the method that was used to inoculate the cultivars. The above-cited authors inoculated the plants *in vivo* in a greenhouse, instead of the detached trefoil, as in our study. In addition, the isolate used was also different. In our study, the estimated GRC is derived from the interaction of one cultivar inoculated with four different isolates. This type of analysis was not performed in the other studies, which explains the divergence in the results obtained. A nonsignificant GRC indicates noninfluence in the cultivar of horizontal resistance against the inoculated isolates. By contrast, the cultivars that showed a significant and positive GRC were susceptible to the tested isolates.

Table 3. Estimated general reaction capacity (GRC) of the soybean cultivars with the different fungal isolates, general aggressiveness capacity (GAC) of the isolates in inoculations with all the cultivars and specific interaction capacity (SIC) between the cultivars and isolates. The isolates were Mauá da Serra (MS), Ingaí (IG), Nazareno (NAZ) and UFLA 24. The data refer to the detached-leaf method.

CULTIVARS / ISOLATES	MS	IG	NAZ	UFLA 24	GRC
	SIC				
Emgopa 316	.7625*	-.7042*	.6792*	-.7375*	-.6125**
Emgopa 315	-.8208*	2.0458**	.7625*	-1.9875**	-.0292NS
BRS Milena	.5958*	.4625*	.5125*	-1.5708**	-.4458**
BRSMG 790A	.4292NS	.2958NS	.0125NS	-.7375*	-.2792*
BRSMG 850GRR	1.0958**	-.0375NS	-.3208NS	-.7375*	.0542NS
BRS Baliza RR	.84583*	-.2875NS	-.2375NS	-.3208NS	-.6958**
BRS Favorita RR	-2.4041**	.4625*	1.5125**	.4292NS	1.5542**
BRSGO Luziânia	-.57084*	1.6292**	-.6542*	-.4042NS	.3875**
M-SOY 8000RR	-.90417*	-1.0375*	.0125NS	1.9292**	.0542NS
BRSMG 68 Vencedora	.5958*	-.5375*	.1792NS	-.2375NS	-.4458**
7166RSF IPRO	-1.7375**	1.1292**	.5125*	.0958NS	.8875**
BRS 213	.4292NS	-.7042*	-.9875*	1.2625**	.7208**
NS 7338 IPRO	-.3208NS	.5458*	-.4042NS	.1792NS	.4708**
BRSMG Garantia	1.4292**	-.0375NS	-.3208NS	-1.0708**	.0542NS
MG/BR 46 Conquista	.5125*	.3792NS	1.0958**	-1.9875**	-.3625**
BRS Silvânia RR	.0125NS	-.1208NS	-1.7375**	1.8458**	.1375NS
M-SOY 8001	-.1542NS	-1.6208**	-.9042*	2.6792**	-.6958**
M-SOY 6101	.3458NS	-.7875*	.2625NS	.1792NS	-.1958*
M-SOY 8329	.7625*	-.3708NS	.3458NS	-.7375*	-.6125**
TMG123RR	-.9042*	-.7042*	-.3208NS	1.9292**	.0542NS
GAC	-.6792**	.4542a	-.2625**	.4875a	

** and * significantly different from zero to 1 and 5% of probability, respectively, by Student's t-test; a: values do not differ by the Student t test

In all, 80 combinations between cultivars and isolates were obtained for SIC, and these combinations indicate the virulence of the pathogen and the vertical resistance of the cultivar. Of these, 51 combinations were significant and represent specific interactions between the isolate and the soybean cultivar. These estimates included negative and positive values, which indicate the presence or absence of resistance to an isolate, respectively. Among the significant estimates, 26 were negative. Negative values indicate the presence of a specific resistance of a given genotype. The combinations that presented the lowest SIC values were BRS Favorita RR x MS, Emgopa 315 x UFLA 24, MG/BR 46 (Conquista) x UFLA 24, 7166RSF IPRO x MS, BRS Silvânia RR x NAZ, M-SOY 8001 x IG and BRS Milena x UFLA 24. These cultivars exhibited the highest specific resistance to these isolates (Table 3).

The GAC estimate indicates the aggressiveness of the isolates, so isolates with a higher positive estimated GAC are characterized by a greater ability to cause symptoms in the different soybean cultivars. Thus, the isolate from Ingaí and the UFLA 24 isolate, which did not differ significantly from each other by the t test, were the most aggressive. This result indicates that these isolates should be preferred for evaluating the level of resistance carried by soybean genotypes. The UFLA 24 isolate was identified as one of the most aggressive isolates in a study conducted by Abreu et al. (2015) on bean. The isolate from Ingaí was collected in soybean production fields that have been cultivated for several years.

The isolate from Nazareno, despite being the least aggressive, was highly pathogenic to the BRS Favorita RR and MG/BR 46 (Conquista) cultivars (Table 3).

The four cultivars with the highest horizontal resistance were analyzed for their specific resistance to the four isolates. The BRS Baliza RR and M-SOY 8329 cultivars exhibited greater stability with regard to the reactions, while Emgopa SOY 316 and M-8001 were less stable and exhibited greater variation regarding the aggressiveness of the isolates (Figure 1).

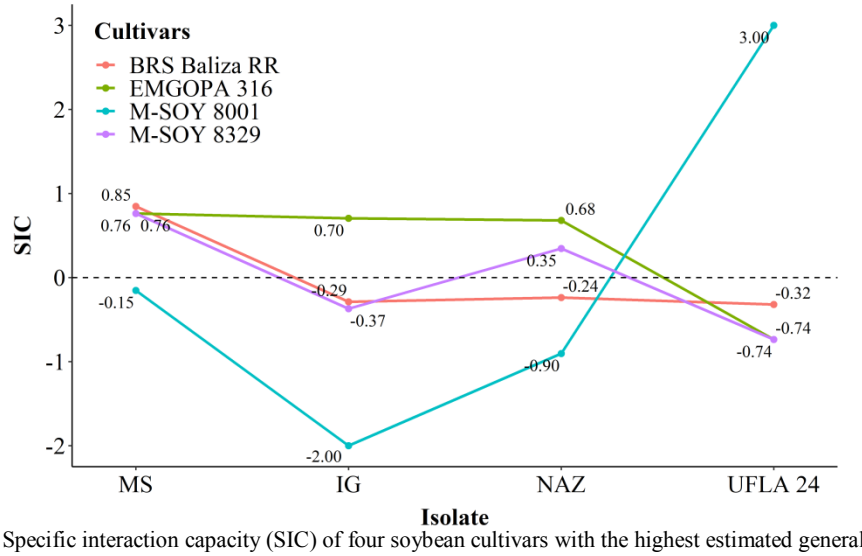

Figure 1. Specific interaction capacity (SIC) of four soybean cultivars with the highest estimated general reaction capacity (GRC), inoculated with four different *Sclerotinia sclerotiorum* isolates.

CONCLUSIONS

We found differential interaction among soybean cultivars and *S. sclerotiorum* isolates. For the first time, the partial diallel model was described for this pathosystem. The BRS Baliza RR, M-SOY 8001, Emgopa 316 and M-SOY 8329 cultivars showed horizontal resistance; and Emgopa 315, 7166RSF IPRO and BRS Silvânia RR presented specific resistance to disease caused by two isolates. The UFLA 24 and Ingaí isolates were the most aggressive, indicating that these isolates should be preferred for evaluating the level of resistance of soybean genotypes.

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CONFLICTS OF INTEREST

The authors declare no conflict of interest.

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