

Evaluation of resistance in sorghum genotypes to the causal agent of anthracnose

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ABSTRACT – *The high degree of variability of the fungus Colletotrichum sublineolum, causal agent of sorghum anthracnose, has hindered the development of resistant hybrids. The objective of this research was to compare the aggressiveness of different fungal isolates and evaluate the genetic resistance (vertical and horizontal resistance) of various sorghum lines and hybrids. Twelve isolates, collected from different regions, were inoculated on 87 lines and 63 hybrids in the field and disease severity was evaluated. The diallel crossing method provided information about the vertical and horizontal resistance of the host, as well as the aggressiveness/virulence of the pathogen. This genetical method was very promising for the identification of horizontal resistance in the sorghum-Colletotrichum sublineolum pathosystem, and for the prediction of anthracnose resistance in hybrids in the absence of vertical resistance. Dilatory resistance was detected in 14.94% of the inbred lines, and in 19.04% of the hybrids. Significant differences in aggressiveness and virulence of the isolates were also observed.*

Key words: *Breeding, horizontal resistance, vertical resistance, Sorghum bicolor, Colletotrichum sublineolum.*

INTRODUCTION

Sorghum (*Sorghum bicolor* (L.) Moench) is one of the most important cereals planted in the world, and Brazil is among the ten top producers worldwide (Rodrigues 2008, CONAB 2009). One of the major factors limiting sorghum production in Brazil is diseases. The most important disease affecting sorghum in all areas in Brazil is anthracnose, caused by the fungal pathogen *Colletotrichum sublineolum* P. Henn., Kabat; Bulbak. The most efficient way to control anthracnose is to use genetically resistant cultivars (Rezende et al. 2004). There are several sources of resistance that are intensely used in sorghum breeding programs to obtain anthracnose-resistant cultivars.

A limiting factor to this strategy is the high degree of variability in the pathogen population (Casela and Frederiksen 1994). The existence of physiological races of *C. sublineolum* was first demonstrated in Brazil by Casela and Ferreira (1987) using a differential series of nine cultivars. Several subsequent studies have confirmed this result (Ferreira and Casela 1986, Ali and Warren 1987, Cardwell et al. 1989, Casela and Frederiksen 1994). The variability and adaptability of the pathogen has significantly reduced the durability of vertical resistance sources worldwide. Some alternatives have been studied to obtain a more stable resistance to this pathogen, for example the selection of genotypes with dilatory resistance,

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characterized as a higher capacity of some genotypes for limiting disease progress (Casela et al. 1993). However, this resistance has also proven to be somewhat unstable, due to pathogen population variability (Guimarães et al. 1998, Casela et al. 2001).

A better ability to predict the relationship between pathogen population variability in aggressiveness and virulence and genetic resistance (vertical and horizontal) of available hybrids is essential to increase the stability and durability of anthracnose resistance in the field. Melo and Santos (1999) performed a simulated study to predict disease severity using the additive model proposed by Parlevliet and Zadoks (1977), and analyzed the data with the model IV of Griffing, using a partial diallel scheme. They reported a high correlation between the general reaction ability and host horizontal resistance, and between the general aggressivity ability and the virulence of isolates. The specific interaction ability turned out to be a good predictor of the host vertical resistance and the pathogen virulence. The objective of this work was to evaluate the performance of the model developed by Melo and Santos (1999) for predicting the resistance (vertical and horizontal) of sorghum hybrids to anthracnose in Brazil.

MATERIAL AND METHODS

The experiments were conducted at the experimental field of Agrocerees Seeds S.A., in Cachoeira Dourada, MG, and in the Disease Plant Resistance Lab in the Biology Department of University of Lavras, in Lavras, MG.

C. sublineolum isolates and culture

Twelve single-spore isolates of *C. sublineolum* (Table 1) were obtained from the Embrapa Milho e Sorgo and from Sementes Agrocerees S.A. The isolates were maintained on oatmeal agar (OMA) with ampicillin (50 mg mL⁻¹) and the colonies were transferred every three weeks for maintenance.

S. bicolor lines and hybrids

Twelve experiments were conducted between October and December of 2006 in Cachoeira Dourada, MG, in an area where no sorghum had been planted for 5 years. The experiments consisted of evaluations of 150 sorghum genotypes, including 87 inbred lines and 63 hybrids (Table 2). Hybrids with one of the genitors represented by a question mark indicate that the genitor was not evaluated

in the experiment. Each experiment consisted of inoculations of all 150 sorghum genotypes with a different isolate of *C. sublineolum* (Table 1). Each plot was constituted of a 1.5 m row with 8 plants meter⁻¹. Rows were spaced 0.5 m apart. Cultural practices were performed as needed. To prevent interexperiment contamination, each plot was separated by 1,5 meters of corn rows, as described in the literature (Costa et al. 2005). The line BR009 (treatment 71) was the susceptible control and the line Tx283 (treatment 66) was the resistant control.

Table 1. Description of isolates of *Colletotrichum sublineolum*

Identification	Isolates	Origin	State	Year
1	E03	Indianópolis	MG	2005
2	E11	Indianópolis	MG	2005
3	E33	Indianópolis	MG	2005
4	E84	Ipiáçu	MG	2005
5	E104	Ipiáçu	MG	2005
6	E125	Guaira	SP	2005
7	E165	Guaira	SP	2005
8	E222	Sete Lagoas	MG	2005
9	RIII42	Sete Lagoas	MG	2005
10	RIII44	Sete Lagoas	MG	2005
11	Jataí	Jataí	GO	2006
12	Montividiu	Montividiu	GO	2006

Inoculation and evaluation

The single spore isolates were maintained in oatmeal agar Petri dishes under continuous light for 10 to 11 days at 25 ± 2 °C. To induce abundant sporulation, mycelia were scraped on the fifth day of growth, and 5 to 6 days later, sterile water was added to cover each plate and the culture was rubbed with a pestle to liberate the conidia. Spores in each suspension were counted using a Neubauer chamber and the concentration was adjusted to 1x10⁶ conidia mL⁻¹. Tween 20 was added at 0.1% to all spore suspensions. The inoculations were done 30 days after plant emergence with a sprayer attached to a CO₂ pump under pressure. The first three plants of each row were inoculated in the evening, with approximately 4 x 10⁶ conidia applied to each plant.

Plants in each row were evaluated as a group, and each plot was classified with an infection type score. The evaluation was done 12 days after inoculation, using a 1-to-5 scale, according to Cardwel et al. (1989), where:

- 1 – presence of chlorotic flecks;
- 2 – small red spots in the leaf lamina;
- 3 – necrotic lesions, sometimes elongated, but no acervuli formed;

Table 2. Description of the *Sorghum bicolor* genotypes evaluated

Code	Genitors	Type	Code	Genitors	Type
88	6 ¹ x 83 ²	Forage Hybrid	119	1 x 70	Experimental Hybrid
89	5 x ?	Forage Hybrid	120	1 x ?	Experimental Hybrid
90	8 x 84	Forage Hybrid	121	1 x 72	Experimental Hybrid
91	8 x 85	Forage Hybrid	122	1 x 73	Experimental Hybrid
92	12 x 82	Forage Hybrid	123	1 x ?	Experimental Hybrid
93	2 x 5 x 86	Forage Hybrid	124	1 x 76	Experimental Hybrid
94	10 x 83	Forage Hybrid	125	? x 35	Experimental Hybrid
95	1 x 28	Comercial Hybrid	126	? x 39	Experimental Hybrid
96	3 x 27	Comercial Hybrid	127	? x 35	Experimental Hybrid
97	1 x 27	Comercial Hybrid	128	? x 35	Experimental Hybrid
98	1 x 29	Comercial Hybrid	129	? x 45	Experimental Hybrid
99	1 x 31	Comercial Hybrid	130	? x 35	Experimental Hybrid
100	10 x 30	Experimental Hybrid	131	11 x 40	Experimental Hybrid
101	10 x 32	Experimental Hybrid	132	14 x 36	Experimental Hybrid
102	12 x 32	Experimental Hybrid	133	1 x 50	Experimental Hybrid
103	1 x 39	Experimental Hybrid	134	1 x 51	Experimental Hybrid
104	1 x 40	Experimental Hybrid	135	1 x 81	Experimental Hybrid
105	1 x 42	Experimental Hybrid	136	1 x ?	Experimental Hybrid
106	13 x 34	Experimental Hybrid	137	11 x ?	Experimental Hybrid
107	1 x 38	Experimental Hybrid	138	1 x 35	Experimental Hybrid
108	1 x 48	Experimental Hybrid	139	? x 45	Experimental Hybrid
109	14 x 52	Experimental Hybrid	140	? x 39	Experimental Hybrid
110	1 x 49	Experimental Hybrid	141	? x 35	Experimental Hybrid
111	1 x ?	Experimental Hybrid	142	? x 35	Experimental Hybrid
112	1 x 54	Experimental Hybrid	143	? x 35	Experimental Hybrid
113	1 x 60	Experimental Hybrid	144	? x 35	Experimental Hybrid
114	12 x 81	Experimental Hybrid	145	? x 36	Experimental Hybrid
115	12 x 69	Experimental Hybrid	146	? x 44	Experimental Hybrid
116	1 x 69	Experimental Hybrid	147	? x 44	Experimental Hybrid
117	12 x 68	Experimental Hybrid	148	? x 35	Experimental Hybrid
118	1 x 68	Experimental Hybrid	149	? x 45	Experimental Hybrid
			150	12 x 35	Experimental Hybrid

¹ Male sterile line (1-26); ² Maintainer line (27-87).

4 – necrotic lesions formed with acervuli present in the center;

5 – necrotic lesions, sometimes coalescing with abundant sporulation.

Two classes of reaction were considered: R = resistant reaction, including infection types 1, 2 and 3; and S = susceptible reaction, including infection types 4 and 5.

Statistical analyses

The infection types of each repetition of each isolate inoculated on each of the lines and hybrids were transformed by natural logarithm plus 2 to better fit the assumptions of analysis of variance (ANOVA).

Individual ANOVAs of the mean infection type of all genotypes were performed with the aid of the software SAS (SAS Institute 2005) for each isolate, each line, and each hybrid. Joint analyses were carried out by using the mean infection type scores obtained from the individual ANOVAs. To evaluate the genetic resistance of sorghum to *C. sublineolum* we used a modification of the model proposed by Melo and Santos (1999). This model allows obtain information about the vertical and horizontal resistances as well as the aggressiveness and virulence of the isolates.

The original model of Melo and Santos (1999) does not provide a reliable estimate of the horizontal resistance

in the presence of vertical resistance. The proposed modification by the authors (personal information) was to include the ANOVA only for genotypes that did not display vertical resistance, using an unbalanced model. To estimate the horizontal resistance in the sorghum anthracnose pathosystem, we used this modified model, including data with a mean infection type score above 2.50. This value was chosen because of the scale used.

We used the means, degrees of freedom and mean squares of the errors from the results from the joint ANOVAs to obtain the partial diallel, and to estimate the general reaction ability (GRA), the general aggressiveness ability (GAA) and the specific interaction ability (SIA), using Griffing (1956) model IV with the aid of the software SAS. Each treatment is a combination of the different isolates and genotypes, as shown in the model in Table 3.

The diallel analysis was performed according to the statistical model:

$$Y_{ij} = m + r_i + a_j + s_{ij} + e_{ij}$$

where Y_{ij} is the disease severity of i^{th} host when inoculated with the j^{th} isolate; r_i is the effect of general reaction ability of the host i (HR); a_j is the effect of the general aggressiveness ability of the isolate j (AH); s_{ij} is the effect of the specific interaction ability of the host i inoculated with the isolate j (VR); and e_{ij} is the random experimental error associated with Y_{ij} .

The estimates of the general reaction ability, general aggressiveness ability and specific interaction ability where tested by Student t distribution at the 1% and 5% level of probability, according to Ramalho et al. (1993).

RESULTS AND DISCUSSION

The results of diallel analysis of the sorghum genotypes inoculated with the 12 *C. sublineolum* isolates are summarized in Table 3. All sources of variation were significant ($P < 0.02$), except SIA. We observed that 69% of the total sum of squares of the variation among crosses was due to the general reaction ability (GRA), indicating a predominance of horizontal resistance.

The hybrids and the lines differed in the estimates of the general reaction ability (g_i) (Table 4). The g_i 's estimates varied from -0.4388 (genotypes 49 and 143) to 0.2443 (genotype 2), being 40% significant. The most resistant lines, those with lower g_i 's estimates, included 3, 7, 16, 19, 22, 30, 35, 47, 49, 57, 76, 81 and 87, while 95, 99, 112, 114, 117, 125, 126, 136, 137, 138, 140, 141 and 143 were the most

Table 3. Summary of the diallel analysis of the severity of anthracnose in the genotypes, inoculated with 12 isolates of *C. sublineolum*

Source of variation	df*	Mean Squares	Pr > F
Crosses	247	0.08678	0.0000
GRA (HR)	84	0.06043	0.0000
GAA (AH)	11	0.05604	0.0283
SIA (VR)	152	0.02748	0.5768
Error	399	0.00916	
Means	3.29		

* As the data used in this analysis are unbalanced (See Material and Methods) there is a disconnection between the degrees of freedom (df) values. The number of degrees of freedom of SIA is due to the different combinations between genotypes and isolates that participate in the analysis, therefore the number of df of the source of variation crosses is the sum of the dfs of the sources of variation GRA, GAA and SIA.

Table 4. Estimates of the general reaction ability (g_i) of anthracnose severity in sorghum genotypes inoculated with different isolates of *C. sublineolum*

Genotypes	g_i	Genotypes	g_i
1	0.1690 **	89	0.1071
2	0.2443 *	93	0.0669
3	-0.2770 **	95	-0.1031 **
4	0.1351 **	96	-0.0170
5	0.2255 **	97	0.0478
6	0.1490 **	98	0.1756 **
7	-0.1676 *	99	-0.1059 **
8	0.0956	102	-0.0078
9	0.0204	103	0.0676
13	-0.0543	104	0.0695
16	-0.2314 *	105	0.1136 *
19	-0.2294 *	106	0.0204
20	-0.0635	107	-0.0790
22	-0.3740 **	108	-0.0365
23	-0.0461	110	0.0058
26	-0.0003	111	-0.0824
27	-0.0436	112	-0.1679 **
29	-0.1654	113	0.0047
30	-0.2294 *	114	-0.2034 **
33	-0.1268	115	-0.1616
35	-0.3614 **	116	0.0201
37	-0.0721	117	-0.0264 *
41	0.0666	118	0.0695
42	-0.0959	119	-0.1070
44	0.0580	121	0.1388 **
46	-0.0917	122	-0.0332
47	-0.1359 *	123	-0.0572
49	-0.4389 **	125	-0.2790 **
56	0.0741	126	-0.2790 **
57	-0.3286 **	131	0.0695
58	-0.1303	132	-0.0277
59	-0.1645	133	-0.0003
60	0.0141	134	0.0237
63	0.0141	135	-0.1645
65	-0.0451	136	-0.3740 **
71	0.2062 **	137	-0.2938 **
74	-0.1392	138	-0.1294
76	-0.1485 *	139	-0.1654
78	-0.1570	140	-0.1648 *
80	0.1484	141	-0.2575 **
81	-0.1485 *	143	-0.4389 **
85	-0.1570	150	-0.0241
87	-0.2997 **		

** and * significant at 1 and 5% probability, respectively, by the F test.

resistant hybrids. The most susceptible lines included 1, 2, 4, 5, 6 and 71, and the most susceptible hybrids were 98, 105 and 121.

The interaction of genotypes x isolates indicate that there are different resistant alleles between the genotypes. The comparison between hybrids and lines was done by the infection type scores given to the hybrids for which we had information about the genitors (Table 2). Based on this analysis, we can infer the presence of alleles with complete and incomplete dominance, as well as recessive alleles that control the vertical resistance observed.

There is evidence for the presence of both vertical and horizontal resistance alleles in the sorghum genotypes (Table 3). Vertical resistance alleles are most effective in diminishing the losses caused by the sorghum anthracnose pathogen. The high pathogenic variability observed in *C. sublineolum* (Ferreira and Casela 1986, Casela and Ferreira 1987, Ali and Warren 1987, Cardwell et al. 1989, Casela and Frederiksen 1994, Casela et al. 2004) has increased the use of vertical resistance alleles in the commercial hybrids but this type of resistance is less durable. This has resulted in a search for more stable disease resistance sources, including dilatory resistance. Levels of dilatory resistance are highest in the lines with the biggest negative estimated values of g_j 's (Table 4). For example, the hybrid 91, obtained by crossing lines 8 and 85, showed complete vertical resistance to all tested isolates. Its genitors, on the other hand, showed severity scores higher than 2.50 for isolate 1. Analyzing the scores obtained for each genitor, we observed a high complementarity between the lines, allowing us to hypothesize that the lines 8 and 85 have dominant alleles that confer resistance to all isolates except isolate 1. Resistance of the hybrid to isolate 1 is due to dilatory rather than vertical resistance. Dilatory resistance was detected in 14.94% of the lines and in 19.04% of the hybrids evaluated.

For the 39 hybrids evaluated in this study whose genitors were also tested, there was a high degree of complementarity between the parent lines. In most of the cases, dominant alleles conferred resistance in the hybrids. Hybrids 90, 91, 94, 101 and 109 were particularly interesting as they didn't show any infection score above 2.50. The resistance to isolate 7 (E165) was conferred mainly by dominant alleles. The same behavior is not observed for other isolates. Resistance to isolate 1 was mainly due to dominant alleles that conferred vertical resistance but also by incomplete dominance alleles (hybrids 121, 122, 133, 134 and 138) and recessive alleles (hybrids 98 and 112), by

comparing the genitors and hybrids infection scores to those that present both information. In many cases, alleles that conferred resistance to isolate 11 (Jataí) were recessive (hybrids 95, 98, 99, 103, 104, 106, 108, 110, 113, 118, 119, 121, 122, 134 and 150), which is in accordance with studies done by Boora et al. (1998), Mehta et al. (2005) and Singh et al. (2006). Hybrid 93 was the only three-way hybrid tested. Among its genitors (2, 5 e 86), the only one that showed complete vertical resistance was line 86. The male-sterile line 5 was susceptible to all isolates tested, with a high g_i value (0.2255), and line 2 was susceptible only to isolate 1. The hybrid, however, was susceptible only to isolate 9. Some studies suggest that three-way hybrids are valuable for control of diseases (Tapsoba and Wilson 1999, Wilson and Gates 2002, Costa et al. 2005), but those materials are often not very uniform, an important characteristic for producers.

The estimates for the general aggressivity ability (g_j 's) for each isolate are in Table 5. These varied from -0.1444 (E222 - Isolate 8) to 0.1248 (E104 - Isolate 5): 58.33% of the g_j 's estimates were significant. The estimates of general aggressivity ability (Table 5) show the difference in the isolates aggressiveness, inside and between regions. These results are similar to others in the literature that have identified a high degree of variability in aggressiveness among sorghum isolates, as cited above. Isolate E104, from Sete Lagoas city, was the most aggressive of the twelve tested in this study. This may be because there is a continuous planting of sorghum genotypes at Embrapa. The frequency of susceptibility among lines observed in this study (more than 50% had severity scores higher than 2.50 with at least 1 isolate), reinforces the importance of using multiple diverse isolates to screen for highly resistant hybrids.

To our knowledge, this is the first study to evaluate sorghum resistance using the model proposed by Melo and Santos (1999). Previously used by Maranha et al. (2002) and Davide and Souza (2009), this model appeared promising for identification of both horizontal and vertical resistance sources. However, in the study by Davide and Souza (2009), it was found that horizontal resistance could not be adequately assessed because vertical resistance resulted in overestimation of GRA values. The authors of the original model suggested that the analysis could be done without including the vertical resistance data, in order to produce more accurate horizontal resistance estimates (Melo and Santos, personal information). This modified model was applied in the current study. Results showed

Table 5. Estimates of the general aggressivity ability (g_i) of anthracnose severity in sorghum genotypes inoculated with different isolates of *C. sublineolum*

Isolate	Identification	g_i
E03	1	-0.0017
E11	2	0.0058
E33	3	-0.0195
E84	4	0.0707 **
E104	5	0.1248 **
E125	6	-0.1227 **
E165	7	-0.1143 **
E222	8	-0.1444 **
RIII42	9	-0.0688 *
RIII44	10	0.0282
Jataí	11	0.0244
Montividiu	12	-0.1401 **

** and * significant at 1 and 5% probability, respectively, by the F test.

that the male-sterile 3 and 22 and the maintainer lines 35, 49, 57 and 87 had the highest negative values of g_i , and thus the greatest horizontal resistance. These should be considered for use as genitors in breeding programs for anthracnose resistance.

The methodology of Melo and Santos (1999) was compared by Maranhã et al. (2002) in the pathosystems *Xanthomonas campestris* pv. *Malvacearum*-cotton and

Ramularia areola-cotton to the methodology proposed by Eberhart and Russel (1966) to evaluate stability parameters, which was reportedly used to evaluate sorghum genotypes resistance to anthracnose (Guimarães et al. 1999). According to Maranhã et al. (2002), both methodologies had similar results, indicating the cultivars with higher horizontal resistance.

The results of this study demonstrate that the modified model of Melo and Santos (1999) was effective for evaluating sorghum genotypes for anthracnose resistance as well as for assessing the aggressiveness/virulence of isolates of *C. sublineolum* in a simple way, thus being a great tool in the genetic study of host-pathogen interaction.

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Avaliação da resistência de genótipos de sorgo ao agente causal da antracnose

RESUMO - O fungo *Colletotrichum sublineolum*, agente causal da antracnose do sorgo, apresenta ampla variabilidade patogênica, o que tem dificultado o desenvolvimento de híbridos resistentes. Foram utilizados 12 isolados do patógeno que foram inoculados em 87 linhagens e 63 híbridos de sorgo no campo e avaliados quanto à severidade da doença. Informações a respeito da resistência vertical e horizontal dos genótipos de sorgo, e sobre agressividade e/ou virulência do patógeno foram obtidas por meio de cruzamentos dialélicos. Essa metodologia mostrou-se promissora na identificação de resistência horizontal no patossistema sorgo-*Colletotrichum sublineolum*. Foi detectada a presença de resistência dilatória em 14,94% das linhagens e 19,04% dos híbridos de sorgo avaliados. Constatou-se diferença na agressividade e virulência dos isolados de *C. sublineolum* avaliados.

Palavras-chave: Melhoramento, resistência horizontal, resistência vertical, *Sorghum bicolor*, *Colletotrichum sublineolum*.

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