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CROP BREEDING AND
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Pathogenic variability within race 65 of *Colletotrichum lindemuthianum* and its implications for common bean breeding

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ABSTRACT – *The wide pathogenic variability among and within races of* Colletotrichum lindemuthianum *has complicated the process of obtaining cultivars of* Phaseolus vulgaris *that are resistant to anthracnose. Six isolates were inoculated into twelve differential cultivars and seven commercial cultivars of the common bean at concentrations in the range 10^2 to 10^6 spores mL^{-1}. Information concerning the vertical and horizontal resistance of hosts and the virulence of isolates was obtained from diallel analysis. It was clear that the set of differential cultivars recommended for the determination of races of* C. lindemuthianum *is inefficient in detecting differences within race 65, and it is suggested that new sources of resistance should be identified and added to the cultivar set. There were significant differences in the virulence of isolates from race 65, with isolates CL 837 and CL 844 being the most virulence. No horizontal resistance was detected in the* C. lindemuthianum-*common bean system.*

Key words: anthracnose, horizontal resistance, *Phaseolus vulgaris*, vertical resistance.

INTRODUCTION

Anthracnose, caused by *Colletotrichum lindemuthianum* (Sacc. and Magn.) Scribner, is one of the most important diseases in the common bean (*Phaseolus vulgaris*). The effects of infection can be devastating when climatic conditions favour the pathogen, and economic losses can reach 100% (Rava et al. 1993). The main control strategies include the use of clean seed, the application of fungicides and the development of resistant cultivars. In Brazil, however, much of the bean production is in the hands of medium to small, or even subsistence, farmers who do not apply fungicides owing to the high costs involved. As a result, breeding for disease resistance is the most effective,

practical, safe and economically accessible strategy for the control of anthracnose. Obtaining anthracnose resistant cultivars is, however, complicated by the existence of several physiological races of the pathogen (Silva et al. 2007) that have been detected through the set of 12 differential cultivars proposed by Centro Internacional de Agricultura Tropical (CIAT 1990).

In Brazil, more than 50 races of *C. lindemuthianum* have been characterized, although over the last few years races 65, 73 and 81 have been observed most frequently (Silva et al. 2007). Additionally, for more than three decades race 65 has been reported to be stable and widely distributed, and most common bean improvement programs targeting anthracnose resistance have focused on this race. It is known, however, that

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some cultivars are resistant to certain isolates and susceptible to others of the same race (Souza et al. 2005). This situation was observed by Carbonell et al. (1999) following inoculation of cultivars released for planting in the State of São Paulo, Brazil, with two isolates of race 31, two of race 65 and three of race 81. The authors verified differences within these races, thus demonstrating that the proposed set of differential cultivars of *C. lindemuthianum* was not sufficient to differentiate the pathogenic diversity of the isolates, possibly due to the effect of interactions and gene combinations on pathogen virulence. Similar results have also been observed by Silva et al. 2007.

Studies on the variability among and within the physiological races of *C. lindemuthianum* are therefore important for genetic studies as well as for improving the targeting of anthracnose resistance in the common bean. In order to develop cultivars with a more durable resistance, an understanding of the mechanisms of genetic resistance to the pathogen is crucial. In this context, the highest levels of genetic resistance have been found to be controlled by one or a few major genes (Pastor-Corrales et al. 1994). It would thus be very useful to determine the levels of horizontal and vertical resistance (non host resistance and host resistance) presented by each line or cultivar, and to investigate the possible correlation with pathogen virulence, as suggest by Melo and Santos (1999). These authors carried out a simulation of expected disease severity using the additive and interactive models proposed by Parlevliet and Zadoks (1977) with diallel analysis based on the statistical genetic model IV described by Griffing (1956). There was a high correlation between general reaction ability (GRA) and potential host resistance, with the former providing a reliable indicator of horizontal resistance. Moreover, general aggressiveness ability (GAA) was highly correlated with potential pathogenicity of the race and was also shown to be an aggressiveness indicator. Finally, specific interaction ability (SIA) was reported to be an indicator of host vertical resistance and pathogen virulence.

The objective of the present study was to investigate the variation within race 65 of *C. lindemuthianum* by evaluating the virulence of different isolates of the fungus and the genetic resistance (vertical and horizontal) of common bean cultivars to the pathogen. The results obtained were employed to determine whether the set of differential cultivars used at present is able to discriminate small differences in race 65 of the pathogen

MATERIAL AND METHODS

The study was carried out in the Laboratory of Plant Resistance to Disease and in a greenhouse located in the experimental area of the Department of Biology at the Universidade Federal de Lavras, Lavras-MG, Brazil, during the year 2005.

Cultivars of *P. vulgaris*

The set of 12 differential cultivars proposed by CIAT (1990), plus seven commercial cultivars, namely, Ouro Negro, Majestoso, Pérola, Rosinha, Talismã, Valente and VC-3 (Table 1) were employed in the study. The Rosinha cultivar was considered as a positive control.

Origin and maintenance of isolates of *C. lindemuthianum*

Six isolates of *C. lindemuthianum* all of which had been classified as race 65, were chosen for study according to their origin of collection, host cultivar and year of collection (Table 2). Two of the isolates, CL 837 and CL 844, were from Embrapa Feijão e Arroz (Goiânia, Goiás, Brazil), whilst isolates LV 29, LV 57, LV 58 and LV 61 were from the culture collection of the Department of Biology, Universidade Federal de Lavras. Pathogens were isolated and monosporic cultures obtained using the methods described by Mendes-Costa and Mendonça (1996). Isolates were maintained on M3 medium (Junqueira et al. 1984).

Inoculation of the isolates

In order to obtain high levels of sporulation, sterile

Table 1. Agricultural characteristics of commercial bean cultivars

Cultivars	Growth habit	Cycle (days)	Grain type
Ouro Negro	prostrate	80-100	Black
Majestoso	prostrate	87	Carioca
Pérola	semi-erect / prostrate	95	Carioca
Rosinha	prostate	90	Rosinha
Talismã	prostrate	75-85	Carioca
Valente	erect	80-94	Black
VC-3	prostrate	85	Carioca

young green bean pods were inoculated with a suspension of each isolate of *C. lindemuthianum* and incubated at 22 ± 2°C for 10 to 15 days in the dark. A conidial suspension was obtained by filtering the homogenate through two layers of cheesecloth to remove mycelial fragments. Spore concentrations were estimated using a haemocytometer and adjusted to a final value of 10^2, 10^3, 10^4, 10^5 or 10^6 conidia mL^{-1} with sterile distilled water.

Each of the 12 differential cultivars and the 7 commercial cultivars were treated in duplicate with the conidial suspensions of fungal isolates at the 5 concentrations indicated according to a randomised complete block design. Seeds were germinated in

Table 2. Description of isolates of race 65 of *C. lindemuthianum* employed

Isolates	Origin[1]	Cultivar	Year
LV 29	Lavras	-	2001
LV 57	Lambari	Talismã	2004
LV 58	Nepomuceno	-	2004
LV 61	Ijaci	Olath Pinto	2004
Cl 837	Buritis	Pérola	2000
Cl 844	Buritis	Pérola	2000

[1] The cities listed are all located in the State of Minas Gerais, Southeast of Brazil

polystyrene trays with 128 wells each containing Plantmax®. The positive control (Pérola cultivar) was cultivated in all the trays. Ten day-old bean seedlings, with fully expanded primary leaves, were sprayed with 200-250 mL of a conidial suspension using a DeVilbiss air compressor until runoff onto the stem and both surfaces of the unifoliolate leaves. Inoculated plants were incubated for 48 h in a mist chamber (95% relative humidity) under a 12 h day/12 h night period at a temperature of 20 ± 2°C prior to being transferred to greenhouse benches. Disease reactions were scored 7-10 days after inoculation on the basis of a 1 - 9 descriptive scale (Rava et al. 1993) in which resistant phenotype scores of 1-3 were assigned to plants with no or limited symptoms and no fungal sporulation (incompatible reaction), and scores 4 were ascribed to plants considered to be susceptible (compatible reaction).

Statistical analyses

Analysis of variance (ANOVA) was implemented on the square-root transformed mean scores of the disease reaction with the aid of the statistical program MSTAT (1991). The transformation of data was carried out to attend the presuppositions of ANOVA. Individual ANOVAs were performed for the differential and commercial cultivars separately for each isolate and spore concentration. Joint analyses were carried out for each of the five concentrations using the means obtained in the individual ANOVAs. Horizontal and vertical resistances of cultivars, and the aggressiveness and virulence of the pathogens, were evaluated by diallel analysis as described by Melo and Santos (1999) according to the statistical model:

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

where Y_{ij} is the disease severity of the ith cultivar when inoculated with the jth isolate, r_i is the effect of horizontal resistance of the ith cultivar, a_j is the aggressiveness effect of the jth isolate, s_{ij} is the effect of interaction between the ith cultivar and the jth isolate relative to the virulence effects of the jth isolate with vertical resistance of the ith cultivar, and e_{ij} is the random experimental error associated with observation Y_{ij}. Mean scores of the disease reaction, degrees of freedom and mean square error estimates obtained by joint ANOVA were used in the diallel analysis. The estimates of GRA, GAA and SIA were obtained using MAPGEN software. The estimates of GRA and GAA were tested by Student t distribution at the 5% level of probability according to Steel et al. (1997).

RESULTS AND DISCUSSION

Evaluation of the genetic resistance of the differential cultivars of *P. vulgaris* to *C. lindemuthianum*

In the diallel analysis of the differential cultivars (Table 3) all sources of variation were significant at all concentrations (P < 0.05). It was observed that 92.6% of the total sum of squares of the variation was due to GRA at the concentration of 10^6 spores mL^{-1}, and this would indicate a predominance of horizontal resistance. Similar results were also observed with concentrations of 10^5 and 10^4 spores mL^{-1}. However, these results must be interpreted with caution since the vertical resistance alleles in the differential cultivars could have given rise

to overestimated GRA values. These genes are expressed mainly at the highest spore concentrations. This becomes evident when the results obtained at the lowest concentrations (i.e. 10^3 spores mL^{-1}) are considered. In this case, the major part of the variation (58.6%) was due to SIA, which is an indicator of vertical resistance, probably indicating that GRA was not overestimated. Most likely a failure in the expression of the symptoms of the disease within the susceptible cultivars was the reason for the predominance of SIA. Therefore, the use of the term horizontal resistance is not appropriate in this situation and we suggest a modification of the model in order to avoid an overestimation of horizontal resistance.

Estimates of GRA varied between the differential cultivars, with TU, AB 136, G2333 and Cornell 49242 appearing to be the most resistant (Table 4). This result is in agreement with earlier reports in which these cultivars are frequently cited as possible sources of resistance for inclusion in improvement programs targeting anthracnose resistance since few isolates are able to break their resistance (Carbonell et al. 1999; Talamini et al. 2004).

Michelite and Mexico 222 were the most susceptible cultivars since they attained the highest GRA estimates. This demonstrates the sensitivity of the model, since an isolate must cause a susceptible reaction upon inoculation with a high spore concentration (10^6 spores mL^{-1}) in the cultivars Michelite and Mexico 222 in order to be identified as belonging to race 65. The diallel analysis confirmed the results obtained by conventional evaluation (Tabela 5), even at spore concentrations lower than those recommended

(1.2×10^6 spores mL^{-1}). Estimates of GAA revealed that isolates Cl 844, Cl 837 and LV 61 were the most virulent (Table 4).

Evaluation of the genetic resistance of commercial cultivars of *P. vulgaris* to *C. lindemuthianum*

In the diallel analysis of the commercial cultivars (Table 6) all sources of variation were significant (P < 0.05). The contribution of GRA was predominant at a concentration of 10^6 spores mL^{-1}, corresponding to 66.54% of the total sum of squares of the variation. A similar result was obtained for the differential cultivars and the effects of vertical resistance were underestimated by the GRA values.

Estimates of GRA values varied amongst the commercial cultivars, with Ouro Negro, Valente and Majestoso appearing as the most resistant, and Pérola and Rosinha as the most susceptible at the test concentrations. Values of GAA showed that the mean performance of each isolate was statistically different when inoculated into the commercial cultivars. Thus, isolates Cl 844 and Cl 837 were the most aggressive whilst LV 58 and LV 57 were the least aggressive (Table 4). Isolates LV 61 and Cl 837 were not evaluated at concentrations 10^2 and 10^3 spores mL^{-1}, respectively. Isolates Cl 844 and Cl 837 were collected from the cultivar Pérola in 2000 in Buritis, a city situated in the north-western region of the State of Minas Gerais, Brazil, whereas most of the other isolates were collected in the southern region of the State. This may indicate that the difference in virulence is due to the different geographic origin of the isolate.

The reactions of the studied commercial cultivars

Table 3. Summary of the diallel analysis of the severity of anthracnose in differential cultivars of common bean evaluated for four spore concentrations of *Colletotrichum lindemuthianum*

Source of Variation	Degrees of Freedom	Mean Squares			
		10^3 spores mL^{-1}	10^4 spores mL^{-1}	10^5 spores mL^{-1}	10^6 spores mL^{-1}
Crossing	71	0.28**	0.33**	0.37**	0.42**
GRA [1]	11	0.47**	0.89**	1.99**	2.51**
GAA [2]	5	0.37**	0.10**	0.19**	0.10**
SIA [3]	55	0.22**	0.22**	0.06**	0.03*
Error	66	0.04	0.03	0.02	0.02
Means	-	1.33	1.37	1.39	1.48

* Significant at 5% probability (F test); ** significant at 1% probability (F test)
[1] General reaction ability (GRA; indicator of horizontal resistance)
[2] General aggressivity ability (GAA)
[3] Specific interaction ability (SIA; indicator of vertical resistance)

Table 4. Estimates of the general reaction ability (GRA) of the severity of anthracnose in differential and commercial cultivars of common bean and of the general aggressivity ability (GAA) of isolates of *Colletotrichum lindemuthianum* at concentrations of 10^5 and 10^6 spores mL^{-1}

Differential Cultivars	GRA		Isolates	GAA	
	10^5 spores mL^{-1}	10^6 spores mL^{-1}		10^5 spores mL^{-1}	10^6 spores mL^{-1}
Michelite	1.13*	1.30*	LV 29	-0.24*	-0.05
MDRK	0.31*	-0.30*	LV 57	-0.05	-0.01
Perry Marrow	-0.19*	-0.30*	LV 58	0.03	-0.07*
Cornell 49242	-0.34*	-0.37*	LV 61	0.07*	0.16*
Widusa	0.07	0.16*	Cl 837	0.09*	0.06
Kaboon	-0.16*	-0.24*	Cl 844	0.08*	-0.09*
México 222	1.28*	1.40*	-	-	-
PI 207262	-0.24*	-0.29*	-	-	-
TO	-0.30*	-0.28*	-	-	-
TU	-0.25*	-0.40*	-	-	-
AB 136	-0.37*	-0.30*	-	-	-
G2333	-0.32*	-0.37*	-	-	-
Commercial Cultivars	**GRA**		**Isolates**	**GAA**	
	10^5 spores mL^{-1}	10^6 spores mL^{-1}		10^5 spores mL^{-1}	10^6 spores mL^{-1}
Pérola	0.86*	0.78*	LV 29	0.00	-0.23*
Valente	-0.45*	-0.47*	LV 57	-0.16*	-0.26*
Talismã	-0.19*	-0.17*	LV 58	-0.34*	-0.17*
Ouro Negro	-0.64*	-0.56*	LV 61	-0.25*	-0.25*
Rosinha	0.96*	1.00*	Cl 837	0.30*	0.45*
Majestoso	-0.32*	-0.38*	Cl 844	0.45*	0.46*
VC-3	-0.22-	-0.20*	-	-	-

* Significant at 5% probability (F test)

Table 5. Notes average of isolates of *Colletotrichum lindemuthianum* inoculated in all of differential cultivars

	Isolates						
Cultivars	**LV 29**	**LV 57**	**LV 58**	**LV 61**	**Cl 837**	**Cl 844**	**Reaction**
Michelite (2^0)	7.31	8.3	9.00	9.00	6.20	6.74	**S**
MDRK (2^1)	1.5	1.5	1.00	2.07	1.50	1.06	**R**
Perry Marrow (2^2)	1.31	1.13	1.07	1.76	1.63	1.61	**R**
Cornell 49242 (2^3)	1.14	1.65	1.07	1.00	1.67	1.08	**R**
Widusa (2^4)	2.5	2.5	2.19	1.33	2.65	1.63	**R**
Kaboon (2^5)	1.44	1.67	1.00	2.05	1.6	1.69	**R**
Mexico 222 (2^6)	7.14	8.91	9.00	9.00	7.9	8.12	**S**
PI 207262 (2^7)	1.81	1.14	1.00	1.63	2.16	1.08	**R**
TO (2^8)	1.00	1.21	1.69	2.28	1.60	1.12	**R**
TU (2^9)	1.00	1.21	1.00	1.00	1.90	1.00	**R**
AB 136 (2^{10})	1.36	1.13	1.08	1.88	1.87	1.17	**R**
G2333 (2^{11})	1.32	1.17	1.06	1.00	1.48	1.15	**R**

Table 6. Summary of the diallel analysis of the severity of anthracnose in commercial cultivars of common bean evaluated for five spore concentrations of *Colletotrichum lindemuthianum*

Source of Variation	Degrees of Freedom	Mean Squares				
		10^2 spores mL^{-1}	10^3 spores mL^{-1}	10^4 spores mL^{-1}	10^5 spores mL^{-1}	10^6 spores mL^{-1}
Crossing	41	0.11**	0.29**	0.47**	0.52**	0.52**
GRA [1]	6	0.14**	0.25**	1.91**	2.45**	2.35**
GAA [2]	5	0.40**	1.79**	0.71**	0.70**	0.86**
SIA [3]	30	0.05**	0.05*	0.15**	0.10**	0.09*
Error	36	0.01	0.02	0.04	0.01	0.01
Means	-	1.20	1.25	1.63	1.79	1.79

* Significant at 5% probability (F test); ** significant at 1% probability (F test)
[1] General reaction ability (GRA; indicator of horizontal resistance)
[2] General aggressivity ability (GAA)
[3] Specific interaction ability (SIA; indicator of vertical resistance)

to isolates of *C. lindemuthianum* race 65 were tested using the conventional evaluation system (Table 7). Cultivars Pérola and Rosinha were the most susceptible at all concentrations. Thus at 106 spores mL^{-1} these cultivars presented susceptibility to all isolates, indicating their possible use as control cultivars in experiments involving race 65, although at 10^2 spores mL^{-1} only isolate Cl 837 induced a susceptibility reaction.

The resistance of cultivar Valente to different races of *C. lindemuthianum* races has been investigated previously by Sartorato et al. (2004). This cultivar was found to be resistant to 17 (including race 65) of the 19 races evaluated. Cultivar Talismã, considered to be resistant to races 65, 81 and 89 of *C. lindemuthianum* and, the predominant ones in the State of the Minas Gerais, Brazil, has been recommended for cultivation in that State. In the present study, however, this cultivar exhibited susceptibility reactions to isolates Cl 844 and Cl 837 at 10^6 spores mL^{-1}, and to LV 29 and Cl 844 at 10^5 spores mL^{-1}. It should be mentioned, however, that isolates Cl 844 and Cl 837 had been collected in a geographic region different from that in which cultivar Talismã was developed and has been evaluated; furthermore the isolates were relatively old. Conflicting results regarding the susceptibility of cultivar Talismã to isolates of race 65 have been reported previously (Souza et al. 2005).

In the present study, cultivars Majestoso and VC-3 were shown to be resistant to most isolates of race 65 but exhibited susceptible reactions to isolates of Cl 844 and Cl 837 similar to cultivar Talismã. Cintra et

al. (2005) evaluated the cultivars Majestoso and VC-3 for resistance to races 65, 81 and 2047 of *C. lindemuthianum* and found that Majestoso was the most resistant to the three isolates but was susceptible to race 65. On the other hand, line VC-3 was reported to be resistant to race 65 in agreement with the results presented here.

Among the commercial cultivar, only Ouro Negro exhibited resistant reactions to all isolates of race 65 of *C. lindemuthianum*. This Ouro Negro resistance was reported by Faleiro et al (2003; 2004). However, this finding conflicts with others reports in the literature (Lanza et al. 1997; Alzate-Marin et al. 2004). Thus, Souza et al. (2005) observed segregation of reaction to race 65 and considered that cultivars Talismã and G2333 were, on average, the most resistant to all evaluated isolates of this race.

Evidence at the molecular level of genetic variability within race 65 has been provided by the RAPD marker-based cluster analysis of various isolates of different races of *C. lindemuthianum* (Silva et al. 2007), which grouped race 65 isolates into two divergent clusters. Similar results were obtained whether the isolates were derived from all over Brazil or just from the State of Minas Gerais. Alzate-Marin et al. (2001) have also observed variability within race 65 following RAPD marker analyses.

The results obtained in this study confirm the existence of variability within race 65 and substantiate evidence from pathogenicity tests and analyses at the molecular level. Indeed, the observed within-race variability suggests a misclassification of race 65, which

Table 7. Isolates of race 65 of *Colletotrichum lindemuthianum* giving rise to a susceptibility reaction in commercial cultivars

Cultivars	Spore Concentration (spores mL^{-1})				
	10^2	10^3	10^4	10^5	10^6
VC-3	-	-	-	Cl 844	Cl 837, Cl 844
Valente	-	-	-	-	Cl 837
Talismã	-	-	-	LV29, Cl 844	Cl 837, Cl 844
Rosinha	Cl 837	Cl 837, Cl 844	LV57, LV61, Cl 837, Cl 844	LV29, LV57, LV58, LV61, Cl 837, Cl 844	LV29, LV57, LV58, LV61, Cl 837, Cl 844
Pérola	Cl 837	Cl 837, Cl 844	LV57, LV61, Cl 837	LV29, LV57, LV61, Cl 837, Cl 844	LV29, LV57, LV58, LV61, Cl 837, Cl 844
Ouro Negro	-	-	-	-	-
Majestoso	-	-	Cl 837	Cl 837, Cl 844	Cl 837, Cl 844

may constitute two or more separate races. New sources of resistance to this variability need to be identified and incorporated into the set of differential cultivars.

Additionally, the results presented here have direct implications on the strategies employed in breeding programs focusing on the development of common bean cultivars with durable anthracnose resistance. The existence of variability within races can complicate the development of lines with a gene pyramid aiming at durable resistance. In the development of these lines, artificial inoculations are performed that normally use only one isolate per *C. lindemuthianum* race. Given the variation within the race, the resistance spectrum of the incorporated resistance alleles would not cover all of the existing variability. A possible alternative would be the development of multilines derived from cultivars with different resistance alleles, which might allow a more durable resistance to anthracnose in common bean.

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Variabilidade patogênica dentro da raça 65 de *Colletotrichum lindemuthianum* e suas implicações para o melhoramento do feijoeiro

RESUMO - *A ampla variabilidade patogênica entre e dentro de raças do* Colletotrichum lindemuthianum *tem dificultado o processo de obtenção de cultivares de* Phaseolus vulgaris *resistentes à antracnose. Seis isolados foram inoculados em 12 cultivares diferenciadoras e sete cultivares comerciais de feijão nas concentrações de 10^2 a 10^6 esporos mL^{-1}. Informações a respeito da resistência vertical e horizontal dos hospedeiros e da virulência dos isolados foram obtidas a partir de análises dialélicas. Constatou-se que o conjunto de cultivares diferenciadoras recomendado para a determinação das raças de* C. lindemuthianum *é ineficiente em detectar diferenças dentro da raça 65, e isto sugere que novas fontes de resistência devam ser identificadas e adicionadas a esse conjunto de cultivares. Houve diferença significativa na virulência dos isolados da raça 65, sendo os isolados CL 837 e CL 844 os mais virulentos. Não foi detectada resistência horizontal no patossistema* C. lindemuthianum-*feijoeiro.*

Palavras-chave: antracnose, resistência horizontal, *Phaseolus vulgaris*, resistência vertical.

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