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Genetic characterization of anthracnose resistance genes *Co-4*^{3} and *Co-9* in common bean cultivar tlalnepantla 64 (PI 207262)

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Abstract Tlalnepantla 64 (PI 207262) is an important source of genes for resistance to common bean anthracnose, caused by *Colletotrichum lindemuthianum*. However, these genes have not been fully characterized. Inheritance studies using crosses involving PI 207262 show that two independent genes confer resistance to anthracnose. Allelism tests showed that the genes are located at distinct loci from the previously identified resistance genes *Co-1*, *Co-2*, *Co-3*, *Co-5*, *Co-6*, and *Co-10*. Also, no segregation was observed in relation to *Co-4*, *Co-4*^{2}, *Co-9*, and to the gene present in cultivar Widusa, indicating that PI 207262 harbors alleles of these genes. We conclude that PI 207262 harbors two anthracnose resistance genes, *Co-4* and *Co-9*. The *Co-4* allele of PI 207262 would be different from *Co-4* and *Co-4*^{2} and it is proposed *Co-4*^{3} as the genetic symbol for this resistance allele. As PI 207262 is the parent of BAT 93, the *Co-9* symbol represents the gene of both cultivars. Also, one allele of *Co-9* gene was detected in cultivar Widusa.

Keywords Anthracnose · *Colletotrichum lindemuthianum* · Differential cultivars · *Phaseolus vulgaris* · Resistance genes

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Introduction

Anthracnose, caused by the ascomycete *Colletotrichum lindemuthianum* (Sacc. and Magn.) Lams-Scrib. is one of the most important diseases of the common bean (*Phaseolus vulgaris* L.) in Brazil and in other bean growing regions of the world (Pastor-Corrales 1985). It has been observed that the high diversity of *C. lindemuthianum* virulence can be correlated with the diversity of the host (Pastor-Corrales et al. 1994; Balardin and Kelly 1998). Different anthracnose resistance genes present in the differential cultivars (Pastor-Corrales 1992) have been identified and new gene

symbols were adopted (Bassett 1996; Young and Kelly 1996). The independent resistance genes *Co-1*, *Co-2*, *Co-3*, *Co-4*, *Co-5*, *Co-6*, *Co-7*, *co-8*, *Co-9*, and *Co-10* are present in the cultivars Michigan Dark Red Kidney (MDRK), Cornell 49–242, Mexico 222, TO, TU, AB 136, G2333, AB 136, BAT 93, and Ouro Negro, respectively (Mastenbroek 1960; Fouilloux 1976; Schwartz et al. 1982; Pastor-Corrales et al. 1994; Alzate-Marin et al. 1997, 2003a; Young et al. 1998; Geffroy et al. 1999). Alleles *Co-1*^{2}, *Co-1*^{3}, *Co-1*^{4}, *Co-1*^{5}, *Co-3*^{2}, and *Co-4*^{2} were identified in the cultivars Kaboon, Perry Marrow, and 277, Widusa, Mexico 227, and SEL 1308 (derived from cultivar G 2333), respectively (Young et al. 1998; Melotto and Kelly 2000; Alzate-Marin et al. 2003c; Vidigal et al. 2003; Kelly and Vallejo 2004). According to the pedigree of cultivar BAT 93, its source of *Co-9* is PI 207262 (Voysest 1983, 2000). However, the anthracnose resistance genes present in the differential cultivar PI 207262 have not been fully characterized.

The present work aimed to: (1) determine the number of anthracnose resistance genes in PI 207262 using populations derived from crosses with susceptible cultivars Rudá and Ouro Negro; (2) determine the allelic relationships between the genes present in PI 207262 and *Co-1* (MDRK), *Co-2* (Cornell 49-242), *Co-3* (Mexico 222), *Co-4* (TO), *Co-4*^{2} (SEL 1308), *Co-5* (TU), *Co-6* (AB 136), *Co-9* (BAT 93), *Co-10* (Ouro Negro), and those present in cultivars Kaboon (*Co-1*^{2}) and Widusa, and (3) determine the allelic relationships between resistance genes present in BAT 93 and TO.

Materials and methods

Parents, crosses and seed production

Seeds from cultivars PI 207262, MDRK, Cornell 49-242, Mexico 222, TO, TU, AB 136, BAT 93, Kaboon, and Widusa were provided by EMBRAPA (Goiânia, GO, Brazil) and CIAT (Tropical Agriculture International Center, Cali, Colombia). Kelly from Michigan State University provided seeds of SEL 1308. Seeds of cultivar Ouro Negro, were provided by Vieira, from the Federal University of Viçosa (Minas Gerais, Brazil). All crosses were performed in the greenhouse. In inheritance studies PI 207262 was used as the male parent and cultivars Rudá and Ouro Negro were used as the female parents. In allelism tests PI 207262 was used as the female parent, except in crosses with cultivars Ouro Negro and BAT 93.

Source of *Colletotrichum lindemuthianum* isolates

The pathotypes 23, 65, 73, and 79 used in this work (Table 1) are part of a group of 25 pathotypes collected in different regions of Brazil and identified by Rava et al. (1994). The original inoculum of these pathotypes was provided by Rava and Sartorato (Rice and Bean Research Center—EMBRAPA). Isolates of pathotype 89 were colleted in the Viçosa region (State of Minas Gerais, Brazil) and identified in our bean-breeding program (Table 1). Pathotypes 65, 73, and 79 were used for the inheritance studies, in crosses between the resistant cultivar PI 207262 and susceptible cultivars Rudá (pathotypes 65, 73, and 79) and Ouro Negro (pathotype 65) (Table 2). For allelism studies pathotype 65 was chosen because most of the parents used in this work are resistant to it, except cultivars Mexico 222 and Ouro Negro (Table 1). In these two last cases, pathotypes 23 and 89 were used, respectively. Inoculum was prepared by culturing the fungus for ~10 days in sterile medium containing young green common bean pods (Pio-Ribeiro and Chaves 1975). Identification of the pathotypes was confirmed by inoculation onto the 12 bean anthracnose differential cultivars (Pastor-Corrales 1992).

Inheritance studies: genetic analyses and evaluation of disease symptoms

F_1 seeds from crosses between resistant cultivar PI 207262 and susceptible cultivars Rudá (Mesomerican, indeterminate, with small ''carioca-type'' seeds) and Ouro Negro were sown in the greenhouse and the plants were selfed to produce F_2 seeds. The F_2 seeds and 20 seeds of each parent were planted in the greenhouse. Fourteen days after sowing, the first leaf from each plant was inoculated with spores of *C. lind-*

Table 1 Reactions of common bean cultivars to different pathotypes of *Colletotrichum lindemuthianum*

Cultivar	Pathotypes and phenotypic reaction[a]				
	23[c]	65[b,c]	73[b]	79[b]	89[c]
PI 207262	R	R	R	R	R
MDRK	S	R	R	S	R
Cornell 49–242	R	R	S	S	S
Widusa	S	R	R	R	S
Kaboon	R	R	R	R	R
Mexico 222	R	S	S	S	S
TO	R	R	R	R	R
TU	R	R	R	R	R
AB 136	R	R	R	R	R
G 2333	R	R	R	R	R
SEL 1308	R	R	R	–[d]	R
BAT 93	R	R	R	–	R
Ouro Negro	R	S	R	R	R
Rudá	R	S	S	S	S
Michelite	S	S	S	S	S

[a] *R* resistant, *S* susceptible

[b] Pathotypes used in inheritance studies

[c] Pathotypes used in allelism test

[d] No data available

emuthianum pathotypes 65, 73, and 79 according to Table 2. Spores (1.2×10^6 conidia/ml) were sprayed onto the plants with the aid of a De Vilbiss apparatus. The plants were incubated and maintained in a mist chamber (20–22°C, 100% relative humidity) for 7 days. After this period, the disease symptoms were scored visually using a 1–9 scale (Rava et al. 1993) in which 1 = plants with no visible symptoms; 2 = up to 1% of small lesions in mid-veins on the lower leaf surface; 3 = up to 3% of small lesions in mid-veins on the lower leaf surface; 4 = up to 1% of lesions present in the mid-vein on the lower and upper leaf surfaces and occasionally in secondary leaf veins; 5 = up to 3% of small lesions scattered in mid- and secondary veins on both leaf surfaces; 6 = more than 3% of small lesions as described in grade 5 on both leaf surfaces and in the stems and petioles; 7 = many large lesions scattered on both leaf surfaces and many lesions in the stems and petioles; 8 = many large coalesced lesions accompanied by tissue breakdown and chlorotic or abscised leaflets, reduced plant growth, and many lesions in stems and petioles; and 9 = severely diseased or dead plants. Resistant (*R*) phenotype was assigned to plants with no or limited symptoms (grades 1–3) whereas plants scored as 4 or higher were considered to be susceptible (*S*). To avoid cross-contamination, each experiment was conducted in a separate chamber.

Twelve plants from each of 100 $F_{2:3}$ families from the cross Rudá × PI 207262 that were inoculated with *C. lindemuthianum* pathotype 65, were evaluated for resistance/susceptibility. Inoculation conditions and symptom evaluation were performed as previously described (Pio-Ribeiro and Chaves 1975, Rava et al. 1993).

Allelism studies: genetic analyses and evaluation of disease symptoms

PI 207262 was initially crossed with MDRK, Cornell 49-242, Widusa, Kaboon, Mexico 222, TO,

Table 2 Segregation for resistance to *Colletotrichum lindemuthianum* in the cross Rudá × PI 207262 (pathotypes 65, 73, and 79) and Ouro Negro × PI 207262 (pathotype 65)

Population	Pathotype	Reaction	Generation	Observed ratio[a]		Expected ratio	Chi-square (χ^2)	Probability
				R	S			
Rudá × PI 207262	*65*	*SXR*	F_2	97	13	57:7	0.08	0.77
Rudá × PI 207262	*65*	*SXR*	$F_{2:3}$	87	13	57:7	0.43	0.51
Ouro Negro[b] × PI 207262	65	SXR	F_2	81	13	57:7	0.81	0.37
Rudá × PI 207262	*73*	*SXR*	F_2	92	09	15:1	1.22	0.27
Rudá × PI 207262	79	SXR	F_2	74	12	57:7	0.80	0.37

[a] Anthracnose disease evaluations using a 1–9 rating scale, where 1 = no visible symptoms of the disease and 9 = very severe symptoms (Rava et al. 1993). Anthracnose reaction type: 1–3 = resistant (*R*), 4–9 = susceptible (*S*)

[b] Ouro Negro is only susceptible to *Colletotrichum lindemuthianum* pathotype 65 among 19 pathotypes tested (Alzate-Marin et al. 2003a)

SEL 1808, TU, AB 136, BAT 93, and Ouro Negro. The F_2 seeds and those of the respective parents and of one susceptible control (cultivar Rudá or Michelite) were sown in the greenhouse. Fourteen days after sowing, the first expanded leaf of each plant was inoculated with *C. lindemuthianum* spores using the pathotypes selected according to Tables 1 and 4 for each cross. The conditions of inoculation and evaluation were similar to those described above. To determine the allelic relationships between resistance genes present in BAT 93 and TO these two cultivars were crossed and the F_2 seeds were planted in the greenhouse and inoculated with *C. lindemuthianum* pathotype 65.

Chi-square analyses

The frequency ratios of the phenotypic classes were tested for goodness-of-fit to theoretical ratios with chi-square tests, using the program GENES (Cruz 2001).

Results

Inheritance studies

Resistance of cultivar PI 207262 to *C. lindemuthianum* pathotype 73 appears to be controlled by two independent genes in the crosses with Rudá (segregation ratio of 15:1 in the F_2 population, Table 2). However, inoculation of F_2 populations derived from the crosses PI 207262 × Rudá and PI 207262 × Ouro Negro with *C. lindemuthianum* pathotypes 65 and 79 segregated according to the ratio 57:7 (Table 2). Inoculation of $F_{2:3}$ resistant families derived from crosses between Rudá and PI 207262 with *C. lindemuthianum* pathotype 65 confirmed the segregation ratio of 57:7 obtained in the F_2 (Table 2). These results indicate that PI 207262 carries two independent dominant genes, and that one of them can interact in a complementary way with a third gene depending on the cross and pathotype tested. A tentative model of this interaction is presented in Table 4. In this model resistance conferred by the two complementary genes can only be observed when at least one dominant allele of each gene is present (frequency of 9/64). Our data give support to results obtained in previous inheritance studies that show that PI 207262 carries two complementary dominant genes for resistance to *C. lindemuthianum* pathotype delta and dominant and complementary genes for resistance to *C. lindemuthianum* pathotype kappa (Vidigal 1994; Vidigal et al. 1997).

Allelism tests

In our allelism studies, the chi-square tests support a good fit to the 63:1 expected ratio of

Table 3 Crosses used for the genetic characterization of anthracnose resistance in PI 207262 and BAT 93

Population[a]	Pathotype	Gene	Observed ratio[b]		Expected ratio	Chi-square (χ^2)	Probability
			R	S			
PI 207262 × MDRK	*65*	*Co-1*	165	3	63:1	0.05	0.82
PI 207262 × Cornell 49242	65	*Co-2*	192	6	63:1	7.86	0.10
PI 207262 × Widusa	65	*Co-?*	228	0	–	–	–
PI 207262 × Kaboon	65	*Co-1*^{2}	128	10	57:7	1.93	0.16
PI 207262 × Mexico 222	23	*Co-3*	194	5	63:1	1.16	0.28
PI 207262 × TO	65	*Co-4*	203	0	–	–	–
PI 207262 × SEL 1308	65	*Co-4*^{2}	200	0	–	–	–
PI 207262 × TU	65	*Co-5*	173	5	63:1	1.79	0.18
PI 207262 × AB 136	65	*Co-6*	173	4	63:1	0.55	0.45
Ouro Negro × PI 207262	89	*Co-10*	183	3	63:1	0.03	0.96
BAT 93 × PI 207262	65	*Co-9*	208	0	–	–	–
BAT 93 × TO	65	*Co-4*	195	11	15:1	0.29	0.59

[a]The parents in each cross are resistant to the pathotype tested

[b]Anthracnose disease evaluations using a 1–9 rating scale, where 1 = no visible symptoms of the disease and 9 = very severe symptoms (Rava et al. 1993). Anthracnose reaction type: 1–3 = resistant (*R*), 4–9 = susceptible (*S*)

Table 4 Three loci model for complementary gene action for resistance to *Colletotrichum lindemuthianum* in segregating populations derived from PI 207262

	Genotype[a]	Genotypic frequency	Reaction
PI 207262	AABBcc	–	*R*
Other cultivar	AabbCC[b]	–	*S* or *R*
F_1	AaBbCc	All resistant	*R*
F_2	A_ B_ C_	27	*R*
	A_ B_ cc	9	*R*
	A_ bbC_	9	*R*
	A_bbcc	3	*R*
	aaB_C_[c]	9	*R*
	aaB_cc[d]	3	*S*
	Aabb[d]C_	3	*S*
	aabbcc	1	S
Phenotypic ratio		57R:7S	

[a]The letters used differ from the symbols conventionally used for the anthracnose resistance genes in common bean because of impossibility to define the genes acting in complementary in PI 207262

[b]Gene of complementary mode of action

[c]In segregating populations resistance is only conferred when the two complementary genes are dominant

[d]The recessive allele of one complementary gene is epistatic in relation to the dominant allele of the other complementary gene

resistant to susceptible plants, for F_2 populations derived from crosses between PI 207262 and MDRK, Mexico 222, AB 136, and Ouro Negro indicating the participation of three independent dominant genes governing resistance in these segregating populations (Table 3). In the two F_2 populations derived from the crosses PI 207262 × Cornell 49-242 and PI 207262 × TU, an excess of susceptible plants was observed considering the expected 63:1 ratio. However, our results indicate that resistance genes *Co-2* and *Co-5* carried by Cornell 49-242 and TU, respectively, are independent of the two genes present in PI 207262. These results corroborate those of Vidigal (1994) who also observed segregation of 63:1 in allelism studies in populations derived from the crosses PI 207262 × MDRK and PI 207262 × Cornell 49-242. For crosses with Andean cultivar Kaboon, a segregation ratio of 57:7 ($P = 0.16$) was chosen to explain the segregation of three genes, two of them with complementary mode of action (Table 3). The model presented in Table 4 can also be used to understand these interactions. The recessive allele of one of these genes is epistatic in relation to the dominant allele of the other gene leading to susceptibility. In the crosses PI 207262 × TO and PI 207262 × SEL 1308 no segregation was observed suggesting that PI 207262 harbors an allele of the *Co-4* anthracnose resistance gene. In the same way, no segregation was observed in the crosses PI 207262 × BAT 93 and PI 207262 × Widusa indicating that these cultivars carry at least one of the resistance genes present in PI 207262.

The resistance gene present in BAT 93 could be an allele of *Co-4* also present in PI 207262. This cultivar is the only known source of anthracnose resistance for BAT 93. To answer this question, allelism tests were conducted between TO that harbors the *Co-4* gene and BAT 93 that harbors *Co-9*. These tests showed that BAT 93 carries a dominant gene located at a different locus from *Co-4* (Table 3). According to these results, the second gene that confers anthracnose resistance in PI 207262 and the gene that confers resistance in BAT 93 are the same gene and it is different from other anthracnose resistance genes previously characterized (Table 3).

Previous allelism studies have shown a segregation ratio of 15:1 for segregating populations from crosses involving Widusa and cultivars TO and SEL 1308, indicating independence between the gene present in Widusa and the *Co-4* gene present in TO and SEL 1308 (Alzate-Marin et al. 2002a). According to these results, the gene shared by Widusa and PI 207262 detected in this study is *Co-9*.

Discussion

PI 207262 (Tlalnepantla 64, Mexico 56 or G 1320) is an important common bean anthracnose resistance source and one of the differential cultivars used to characterize the phenotypic (virulence) diversity of *C. lindemuthianum*. In Brazil it has been shown that PI 207262 is resistant to 45 pathotypes of *C. lindemuthianum* and susceptible to pathotypes 137, 193, 217, 249, and 453 (Rava et al. 1994; Balardin 1997; Balardin et al. 1997; Andrade et al. 1999; Thomazella et al. 2000;

Sartorato 2002). PI 207262 has been frequently used as a parent for the development of many elite Brazilian cultivars (Alzate-Marin et al. 2003b). In addition, an important number of entries of CIAT (Tropical Agriculture International Center) derived from PI 207262 are also used as resistance sources to *Xanthomonas* (Voysest 1983). In this study, we characterized the two-anthracnose resistance genes present in cultivar PI 207262 (*Co-4* and *Co-9*) and confirmed the presence of *Co-9*, the anthracnose resistance gene in BAT 93 (Geffroy et al. 1999) and Widusa. The *Co-4* and *Co-9* loci have been mapped to linkage groups B8 and B4, respectively (Kelly and Vallejo 2004; Méndez-Vigo et al. 2005). Extensive discussion on the breeding value of both genes is available (Kelly and Vallejo 2004).

Previous works have shown that PI 207262 possesses a narrower anthracnose resistance spectrum than TO (*Co-4*) and SEL 1308 ($Co\text{-}4^2$) (Araya et al. 1991; Balardin et al. 1999; Sharma et al. 1999). This weaker resistance pattern in PI 207262 which carries two resistance genes, compared with other sources of the *Co-4* gene (TO and SEL 1308), suggests that PI 207262 carries a different allele at the *Co-4* locus which conditions resistance to fewer *C. lindemuthianum* races. We propose the genetic symbol $Co\text{-}4^3$ for the *Co-4* allele present in PI 207262. In previous work of our group it was demonstrated that the RAPD molecular marker $OPAS13_{950C}$, previously identified as linked to the allele $Co\text{-}4^2$, co-segregate at 3.5 cM of the *Co-4* allele of PI 207262 (Alzate-Marin et al. 2002b). This molecular marker will be useful for selecting the resistance allele $Co\text{-}4^3$ but will not allow the distinction between $Co\text{-}4^2$ and $Co\text{-}4^3$ in populations where these two alleles are segregating.

The second gene in PI 207262 is *Co-9*. As BAT 93 derived from PI 207262, the *Co-9* allele present in PI 207262 is the same present in BAT 93. However, different resistance indexes (RI) between PI 207262 (79) and BAT 93 (85) (Balardin and Kelly 1998) may suggest that BAT 93 possesses other resistance genes or complementary factors.

Mendez-Vigo et al. (2005) observed that the *Co-9* locus of PI 207262 and BAT 93 is allelic of locus *Co-3* of cultivar Mexico 222 when inoculated with *C. lindemuthianum* pathotype 38. The present work shows that the *Co-9* and *Co-3* loci are independent when inoculated with *C. lindemuthainum* pathotype 23. Phenetic analyses carried through by Balardin and Kelly (1998) has suggested the presence of both Middle American and Andean virulence factors within pathotype 23. On the other side, pathotype 38 only showed Andean factors of virulence. These facts can suggest that the cultivars used in these studies can possess specific resistance genes for the factors of virulence of the pathotypes used in the allelism tests. Thus, PI 207262 and Mexico 222 could share alleles that confer resistance to Andean factors of virulence (race 38) and, at the same time, to possess independent genes conferring resistance to factors of virulence of bigger complexity (as the Middle American/Andeans) of race 23. As Mendez-Vigo et al. (2005) discussed in their work, it is possible that these genes and its alleles would be part of a complex gene cluster, which can be detected when different races of the pathogen are used. These grouped resistance genes can occupy a segment of the genome and confer resistance to different pathotypes from the same pathogenic agent. On the other hand, Kelly and Vallejo (2004) showed that Mexico 222 possesses two genes that confer resistance to *C. lindemuthianum* race 7. In agreement to these findings, which of the two genes of cultivar Mexico 222 is detected when inoculated with race 23 or 38 and which is allelic to *Co-9*? Only works aiming separation of genes in lines, identification of molecular markers and final characterization with the studied pathotypes will help to decide these questions.

In this study, it was not detected independence between PI 207262 and Widusa. Previous allelism studies with *C. lindemuthianum* pathotype 65 have demonstrated that the gene present in Widusa is not the *Co-4* gene (Alzate-Marin et al. 2002a). Consequently, the gene found in Widusa could be an allele of the *Co-9* gene present in PI 207262 as no relationships are known between these two cultivars. However, other allelism studies using *C. lindemuthianum* pathotypes 7 (Vidigal et al. 2003), 38 and 73 (Ferreira et al. 2003; Vidigal et al. 2003) have showed independence between Widusa and

BAT 93 and Widusa and PI 207262, respectively. In these same studies, allelism between Widusa and MDRK (Vidigal et al. 2003), Michelite, TO and AB 136 (Ferreira et al. 2003) had been observed. Since that Widusa is a Mesoamerican cultivar with Andean characteristics (Balardin and Kelly 1998), it is probable that it possesses Mesoamerican and Andeans *C. lindemuthianum* resistant genes. In this way, the presence of complex gene cluster of disease resistance genes in cultivar Widusa is in accordance with these observations. The divergence in the published data and the present work prevents the authors from proposing new symbols for the allele found in Widusa until more complete information about this locus would be available.

The facts cited above suggest the complexity of the locus *Co-9*. In broad sense, the original *Co-9* allele is present in both BAT 93 and PI 207262, another is allelic to the *Co-3* allele, and another appears to be one of the genes in 'Widusa'.

The novel information presented in this work is extremely important for the understanding of the performance of cultivar PI 207262 and the implications of the broad use of this cultivar as a resistance source in breeding programs.

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