Characterization of genetic resistance in Andean common bean cultivar Amendoim Cavalo to *Colletotrichum lindemuthianum*

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ABSTRACT

The Anthracnose, caused by *Colletotrichum lindemuthianum* (Sacc. and Magnus) Briosi and Cavara, is one of the most important fungal disease of common bean. Several strategies have been used for its control, such as the use of pathogen-free seeds, chemical control and crop rotation. However, the most efficient method to control this disease is the use of resistant cultivars. Previous studies conducted by the Laboratory of Common Bean Breeding and Molecular Biology of the Nucleus of Research Applied to Agriculture (Laboratório de Melhoramento de Feijão Comum e de Biologia Molecular do Núcleo de Pesquisa Aplicada à Agricultura-NUPAGRI) revealed that the Andean cultivar Amendoim Cavalo is resistant to races 2, 7, 9, 19, 23, 39, 55, 65, 73, 89, 1545, 2047 and 3481 of *C. lindemuthianum*. The objective of this work was to characterize the genetic resistance to anthracnose in Amendoim Cavalo using inheritance and allelism tests. The results of inheritance tests in F_2 generation of Amendoim Cavalo × PI 207262 cross, inoculated with 2047 race, fitted in a ratio of 3R:1S, proving the action of a single dominant gene in Amendoim Cavalo cultivar. Allelism tests demonstrated that the dominant gene present in Amendoim Cavalo is independent from the genes previously characterized. The authors propose the *Co-AC* symbol to designate the new resistant gene to *C. lindemuthianum*. The results show high contribution to breeding programs, once Amendoim Cavalo cultivar can be considered an important Andean source of resistance to *C. lindemuthianum*.

Key words: *Co-AC* gene, resistance sources, anthracnose, resistant gene, *Phaseolus vulgaris* L.

INTRODUCTION

Common bean (*Phaseolus vulgaris* L.) is the most widely cultivated species of genus *Phaseolus* and is one of the most important constituents of the Americas and Africa population diet. It is recognized as an excellent source of protein, rich in lysine, fiber, and has a significant content of complex carbohydrates, lipids, calcium and iron (Broughton et al., 2003).

The genus *Phaseolus* represents approximately 95% of the world's *Phaseolus* bean production (Gonçalves-Vidigal et al., 2013). However, its yield is much below crop potential and it has been affected by the incidence of several fungal, bacterial and viral diseases. Among fungal diseases, anthracnose, which is caused by the fungus *Colletotrichum lindemuthianum* (Sacc. and Magnus) Briosi and Cavara, stands out as one of the most important diseases of common bean (Pastor-Corrales et al., 1994; Gonçalves-Vidigal et al., 2012).

Anthracnose occurs in different planting dates and can be transmitted through seeds. As a consequence, it devaluates the quality of grain and pods. Losses and decreases in production depend on environmental factors that favor the development of the pathogen and its high genetic variability (Pastor-Corrales, 1995; Genchev et al., 2010).

In Brazil, 73 different races of *C. lindemuthianum* have been detected, and it is known that in the state of Paraná, races with higher incidence are 64, 65, 73, 81, 87 and 89 (Rava et al., 1994; Thomazella et al., 2002; Alzate-Marin and Sartorato 2004; Gonçalves-Vidigal et al., 2008a; Sansigolo et al., 2008; Padder et al., 2010; Nunes et al., 2013).

Given the wide variability and the high number of races of this pathogen, breeders and geneticists have been conducting extensive research to identify new sources of resistance to anthracnose. Twenty-one resistance genes and four allelic series were identified (Sousa et al., 2015; Trabanco et al., 2015). The search for new resistance sources to *C. lindemuthianum* is of utmost importance to the common bean genetic improvement. Priority should be given to the identification of Andean sources, since 11 of the 21 genes identified belongs to the Andean origin.

Preliminary studies carried out by the Nucleus of Research Applied to Agriculture- Nupagri (Núcleo de Pesquisa Aplicado a Agricultura), belonging to the State University of Maringá-(Universidade Estadual de Maringá -UEM), with several traditional cultivars of common bean, showed that Andean cultivar Amendoim Cavalo, collected in the State of Santa Catarina is resistant to races 2, 7, 65, 73, 89 and 2047 of *C. lindemuthianum*, suggesting that this cultivar has different gene or allele from those previously characterized. Therefore, this study aimed to characterize the common bean Andean cultivar Amendoim Cavalo genetic resistance to *Colletotrichum lindemuthianum*.

MATERIAL AND METHODS

Plant material

Experiments were conducted in the greenhouse of the Laboratory of Common Bean Breeding and Molecular Biology of the Nucleus of Research Applied to Agriculture- (Laboratório de Melhoramento de Feijão Comum e de Biologia Molecular of Núcleo de Pesquisa Aplicada à Agricultura -Nupagri), that belongs to the State University of Maringá, (Universidade Estadual de Maringá -UEM) from March 2012 to November 2013.

In order to characterize the resistance genes to *C. lindemuthianum* present in 'Amendoim Cavalo' (Figure 1), F_2 segregating populations and F2:3 families obtained from crossings of 'Amendoim Cavalo' and differential cultivars proposed by Pastor-Corrales et al. (1991): Michelite, Michigan Dark Red Kidney (MDRK), Cornell 49-242, Mexico 222, PI 207262, TO, TU, AB 136 and G 2333. Another crosses were also carried out with cultivars that have resistance genes to *C lindemuthianum* already identified: Ouro Negro, Jalo Vermelho, Jalo Listras Pretas, Pitanga, Corinthiano, Crioulo 159, Paloma, Jalo Pintado 2 (Frias et al., 2016) and Perla.

Figure 1. Common bean cultivar Amendoim Cavalo seeds.

Obtaining segregating populations

For the crosses, seeds of cultivars and differentials were sown in plastic pots with a capacity of 5 dm^3 containing sterilized peat-based substrate and fertilized with NPK. In order to keep the soil close to its field capacity, plants were irrigated daily. Nitrogen fertilization was performed at the time of emergency, and potassium fertilizer before flowering, to promote plant development. Ammonium sulfate (50g of ammonium sulfate in 2L of water) was used by applying 250mg of N in 50 mL of water per pot and potassium chloride (14g K_2O in 2L of water).

Crosses were carried out during the flowering period, especially in the morning (7am to 8:30 am) and in the afternoon (16 to 18:30h), with the use of sterile tweezers and identifying which were the parents of the crossings. The cultivar Amendoim Cavalo was used both as male or female parent.

F_1 populations were obtained from the crossings. The hybrid seeds were sown and through self-pollination, generated F_2 populations, which were later inoculated with races 2, 65, 73 and 2047 of *C. lindemuthianum.*

Physiological races of *Colletotrichum lindemuthianum*

In this work physiological races 2, 65, 73 and 2047 of *C. lindemuthianum* were used. The inoculum was obtained from mycology collection belonging to Nupagri (Nucleus of Research Applied to Agriculture). Race 2 was used in the inoculation of F_2 cross population between the resistant cultivars Amendoim Cavalo × Michelite. Race 65 was used in the crosses Amendoim Cavalo × Cornell 49-242, Amendoim Cavalo × PI 207262, Amendoim Cavalo × TO, Amendoim Cavalo × TU, Amendoim Cavalo × AB 136 and Amendoim Cavalo × Jalo Vermelho.

Race 73 was inoculated in F_2 populations of the crosses between resistant cultivars Amendoim Cavalo × Michigan Dark Red Kidney, Amendoim Cavalo × Jalo Listras Pretas and Amendoim Cavalo × Ouro Negro. Race 2047 was used to generate F_2 populations derived from the crosses between Amendoim Cavalo × G 2333, Amendoim Cavalo × Corinthiano, Amendoim Cavalo × Crioulo 159, Amendoim Cavalo × Pitanga, Amendoim Cavalo × Perla,

Amendoim Cavalo × Paloma and Amendoim Cavalo × Jalo Pintado 2.

Resistance inheritance test

Resistance inheritance test was performed using race 2047, inoculated in the F_2 population derived from the Amendoim Cavalo × PI 207262 cross. It is where the cultivar Amendoim Cavalo shows resistance reactions to the pathotype, while PI 207262 cultivar is susceptible to race 2047. This test aimed to identify the number of the genes conferring resistance in the cultivar Amendoim Cavalo to the race 2047 of *C. lindemuthianum*.

Allelism test

Allelism test was conducted in the F_2 population of crosses (R × R), in which both cultivars showed resistance reaction to races 2, 65, 73 and 2047 (Table 1). Through this test, independence of the gene in cultivar Amendoim Cavalo from other genes previously characterized.

Table 1. Crossings between cultivars for use in allelic test and their reactions to *C. lindemuthianum* races.

Crosses	Reaction	Race
Amendoim Cavalo × Michelite	R × R	2
Amendoim Cavalo × Cornell 49-242	R × R	65
Amendoim Cavalo × PI 207262	R × R	65
Amendoim Cavalo × TO	R × R	65
Amendoim Cavalo × TU	R × R	65
Amendoim Cavalo × AB 136	R × R	65
Amendoim Cavalo × Jalo Vermelho	R × R	65
Amendoim Cavalo × MDRK	R × R	73
Amendoim Cavalo × Jalo Listras Pretas	R × R	73
Amendoim Cavalo × Ouro Negro	R × R	73
Amendoim Cavalo × G 2333	R × R	2047
Amendoim Cavalo × Corinthiano	R × R	2047
Amendoim Cavalo × Crioulo 159	R × R	2047
Amendoim Cavalo × Pitanga	R × R	2047
Amendoim Cavalo × Perla	R × R	2047
Amendoim Cavalo × Jalo Pintado 2	R × R	2047
Amendoim Cavalo × Paloma	R × R	2047

Evaluation of Susceptibility and resistance

Obtaining segregant populations

The crossings derived from Amendoim Cavalo with Mesoamerican cultivars yielded sufficient amount of F1 and F2 seeds (Figure 2) for the resistance inheritance and allelism tests. F2 seeds derived from self-pollination of the F1 generation were sown in plastic trays containing peat-based substrate. According to the seed availability, about 100 of each cross were sown for the tests, except from the cross of 'Amendoim Cavalo' × G 2333, where 254 F2 seeds were used in order to obtain greater certainty of results.

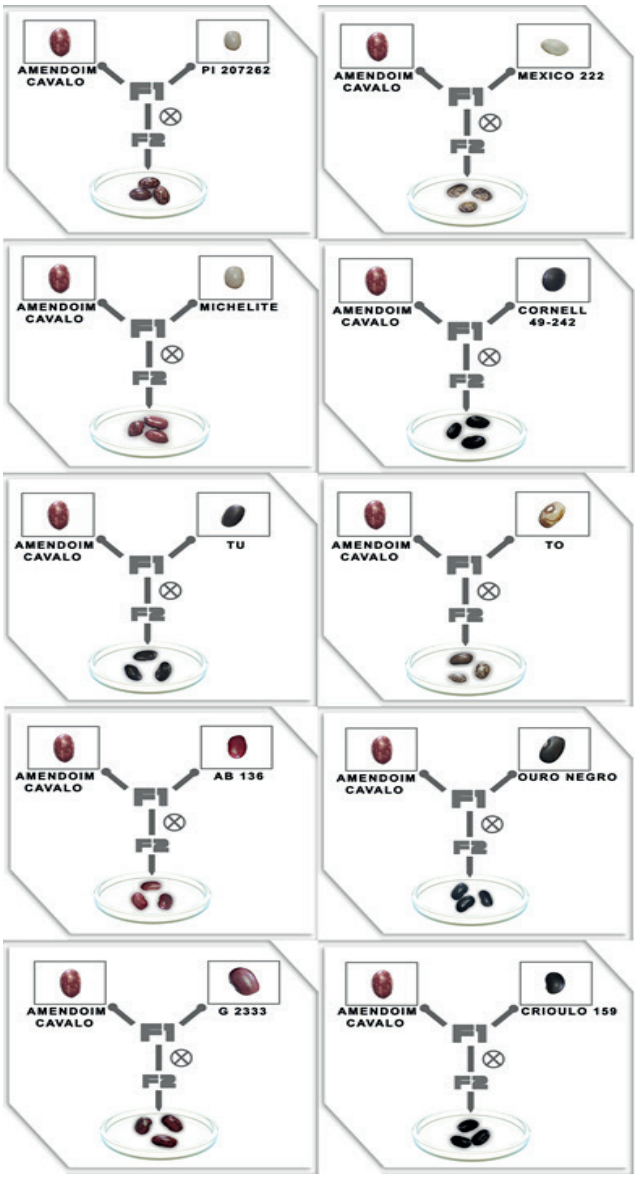

Figure 2. F2 seeds obtained from the crossings from 'Amendoim Cavalo' with Mesoamerican resistant cultivars of common bean.

Trays were kept in the greenhouse environment until full expansion of the first trifoliate. Subsequently, plants were acclimated for 1 hour in an environment with controlled temperature and lighting, and then inoculation was performed.

Inoculum preparation and Inoculation

According to the methodology proposed by Cárdenas et al. (1964), which involves multiplying the spore pathotype of *C. lindemuthianum* in tubes containing sterile young green common bean pod medium. The tubes were kept in a BOD (Biochemical Oxygen Demand) incubator at 22 °C for 14 days.

After incubation, the fungus was fully developed and beans were transferred to a container with sterile distilled water. This mixture was filtered through a double layer of gauze to give a spore suspension. For each *C. lindemuthianum* race, five counts were made using a Chamber of Neubauer-Preciss or hemacytometer. After counting, the spore suspension was adjusted to a concentration of 1.2 x 10^6 spore ml^{-1} of sterile distilled water. For each 100 mL of the solution obtained, one drop of Tween 20 was added to assist in the attachment of the solution to the leaves during inoculation process.

Inoculation of each race was performed separately, so that there was no contamination. This process was performed by using an electric air compressor DeVilbiss type, number 15, from the adaptation of the method proposed by Cárdenas et al. (1964). The inoculated plants were kept in a mist chamber for 72 hours at a temperature of 20 ± 2 °C by controlling the light (12-hour light of 680 lux/12 hour dark) and approximately 100% relative humidity. After the incubation period, plants were transferred to tables in an ambient temperature of 22 ± 2 °C, under artificial light, where they remained until assessments were undertaken.

Evaluation method of the symptoms induced by *Colletotrichum lindemuthianum*

Visual symptom assessments were carried out in the seventh and tenth day after inoculation, using the scale proposed by Pastor-Corrales et al. (1995). The notes were assigned according to disease severity in the first trifoliate leaves, whose values can vary 1-9 in individual plants. Plants with scores 1-3 were considered resistant, and those that presented notes 4-9 were classified as susceptible.

Statistical analysis

From data obtained by Mendelian segregation using the resistant and susceptible phenotypes, genetic-statistical analysis was performed using the chi-square test with Genes program (Cruz 2013).

RESULTS AND DISCUSSION

Resistance inheritance test

Inoculation with the race 2047 in the F_2 generation of the cross between Amendoim Cavalo × PI 207262 (X^2 = 0.102; p = 0.749) provided a segregation of 87 resistant and 31 susceptible plants. It fits the ratio 3R:1S, indicating the presence of a single dominant gene controlling resistance to race 2047 in this population (Table 2). The cultivar PI 207262 has the *Co-4*^{3} gene (Arruda et al., 2000) and *Co-9* (Geffroy et al., 1999) renamed *Co-3*^{3}, but they do not work in the resistance to race 2047, considering that this cultivar is susceptible to that race. Therefore, the dominant gene is present in cultivar Amendoim Cavalo.

Table 2. Inheritance of anthracnose resistance in the common bean cultivar Amendoim Cavalo.

Cross	Race	Observed ratio		Expected ratio	X^2	*P* Value
		R[a]	S[b]	R:S		
AC* × PI 207262	2047	87	31	3:1	0.102	0.749

*AC: Amendoim Cavalo. [a]Resistant plants and [b]Suscetible plants.

Inheritance studies using Cornell 49-242 as a parental cultivar, Coimbra-Gonçalves et al. (2016) obtained similar results in the characterization of cultivar Crioulo 159, when the F_2 population was inoculated with race 2047 of *C. lindemuthianum*. In this resistance inheritance study, segregation also fitted a ratio of 3R:1S, demonstrating the action of a dominant gene present in Crioulo 159. The same ratio 3R:1S was found when the F_2 population of the cross between Pitanga × AB 136 was inoculated with the race in 2047, indicating the presence of a dominant gene present in cultivar Pitanga (Gonçalves-Vidigal et al., 2012). The results of chi-square tests raised the hypothesis of a single dominant gene present in cultivar Amendoim Cavalo.

Allelism test

Table 3 shows results of the segregation pattern of F_2 populations obtained from crosses (R × R) in allelism tests. It can be observed that allelic tests in F_2 generations of crosses between Amendoim Cavalo and cultivars Michigan Dark Red Kidney, Cornell 49-242, PI 207262, TO, TU, AB 136, G 2333, Ouro Negro, Michelite, Jalo Vermelho, Jalo Listras Pretas, Pitanga, Corinthiano, Crioulo 159, Paloma, Perla and Jalo Pintado 2, fitted in a ratio of 15R:1S,

indicating the action of two dominant genes for resistance to anthracnose, one in each of the aforementioned cultivars and another in the cultivar Amendoim Cavalo.

Table 3. Allelism tests for the anthracnose resistance gene in the common bean cultivar Amendoim Cavalo.

Cross	Race	Resistance Gene	Observed ratio		Expected ratio	X^2	*P* Value
			R[a]	S[b]	R:S		
AC* × Michelite	2	*Co-11*	102	7	15:1	0.005	0.941
AC × Cornell 49-242	65	*Co-2*	81	5	15:1	0.028	0.867
AC × TO	65	*Co-4*	65	6	15:1	0.587	0.444
AC × PI 207262	65	*Co-4*^{3}	105	7	15:1	0.000	1.000
AC × TU	65	*Co-5*	73	5	15:1	0.003	0.953
AC × AB 136	65	*Co-6*	106	5	15:1	0.557	0.447
AC × Jalo Vermelho	65	*Co-12*	92	6	15:1	0.003	0.958
AC × MDRK**	73	*Co-1*	53	3	15:1	0.761	0.783
AC × Ouro Negro	73	*Co-3*^{4}	81	5	15:1	0.028	0.867
AC × JLP***	73	*Co-13*	81	5	15:1	0.028	0.867
AC × G 2333	2047	*Co-4*^{2}	237	17	15:1	0.085	0.771
AC × Pitanga	2047	*Co-14*	103	4	15:1	1.152	0.283
AC × Corinthiano	2047	*Co-15*	77	5	15:1	0.003	0.955
AC × Crioulo 159	2047	*Co-16*	89	7	15:1	0.178	0.673
AC × Paloma	2047	*Co-Pa*	109	7	15:1	0.009	0.924
AC × Perla	2047	*Co-Pe*	73	6	15:1	0.244	0.621
AC × Jalo Pintado 2	2047	*Co-18*	94	6	15:1	0.011	0.918

*Amendoim Cavalo, **Michigan Dark Red Kidney and ***Jalo Listras Pretas. [a]Resistant plants and [b]Suscetible plants.

In the allelism tests using F2 population from the cross between Amendoim Cavalo × Michelite (X^2 = 0.005; p = 0.941) inoculated with race 2, a segregation 15R:1S was obtained, indicating the presence of two independent dominant genes, one gene is *Co-11* (Gonçalves-Vidigal et al., 2007), present in cultivar Michelite and another in Amendoim Cavalo. The differential cultivar Michelite was characterized by Gonçalves-Vidigal et al. (2007), using races 8 and 64 of *C. lindemuthianum*.

The same ratio of 15R:1S was obtained using race 65 in the crosses between Amendoim Cavalo × Cornell 49-242 (X^2 = 0.028; p = 0.867), indicating the action of two dominant genes. In this case, the gene present in Amendoim

Cavalo is independent of gene *Co-2* (Mastenbroek 1960) present in Cornell 49-242.

Still using race 65, ratio 15R:1S was obtained at the crosses between Amendoim Cavalo × PI 207262 (X^2 = 0; p = 1), and despite the cultivar PI 207262 present two resistance alleles to anthracnose, *Co-4*^{3} and *Co-3*^{3}, only the allele *Co-4*^{3} (Alzate-Marin et al., 2007) acts in the process of resistance to race 65. Hence, it justified the reason why 15R:1S was found in this assay.

The results obtained from the allelism test conducted in the F2 population of Amendoim Cavalo × TO (X^2 = 0.587; p = 0.444), inoculated with the race 65, are similar to those obtained by Gonçalves-Vidigal et al. (2008b), when the F2 population of Jalo Vermelho × TO was inoculated, using the race 65, and obtained the same segregation, which corresponds to a ratio 15R:1S. Therefore, this result confirms the assumption of resistance gene independence in Amendoim Cavalo of the *Co-4* gene present in TO.

As shown in Table 3, race 65 was inoculated in the populations derived from Amendoim Cavalo × TU (X^2 = 0.003; p = 0.953), Amendoim Cavalo × AB 136 (X^2 = 0.557; p = 0.447) and Amendoim Cavalo × Jalo vermelho (X^2 = 0.003; p = 0.958). Allelism tests fitted to a ratio 15R:1S, indicating that the gene of Amendoim Cavalo is independent *Co-5* (Young et al., 1998; Alzate-Marin et al., 2007), *Co-6* (Schwartz et al., 1982; Kelly and Young 1996) and *Co-12* (Gonçalves-Vidigal et al., 2008b), respectively.

Through these results, it is revealed that the dominant gene present in the cultivar Amendoim Cavalo is independent of the genes *Co-2, Co-4, Co-4*^{3}*, Co-5, Co-6* and *Co-12*. Similar results were obtained by Gonçalves-Vidigal et al. (2012), which observed a 15R:1S ratio in allelism tests, using the F2 populations derived from crosses between Pitanga and cultivars Cornell 49-242, TU, AB 136 and Jalo. A ratio 63R:1S was obtained due to the presence of three resistance genes to the pathogen, wherein *Co-3*^{3} and *Co-4*^{3} genes were present in the cultivar PI 207262 and the other in Pitanga. Despite cultivar PI 207262 has two resistance alleles, only the *Co-4*^{3} confers resistance to race 65 of *C. lindemuthianum*, which explains the ratio 15R:1S found in the F2 population derived from the Amendoim Cavalo × PI 207262 cross.

In the F2 population inoculated with race 73, the cross between Amendoim Cavalo × Michigan Dark Red Kidney (X^2 = 0.761; p = 0.783) showed the segregation ratio of 15R:1S, therefore, it is claimed that this gene in Amendoim Cavalo is independent of the *Co-1* gene (McRostie 1919). It is remarkable that the *Co-1* gene present in Michigan Dark Red Kidney was the first gene with Andean origin to be identified. The ratio 15R:1S was also found by Lima-Castro et al. (2017) using the F2 population originated from the Ouro Negro × Paloma, inoculated with race 73. Still using the same race for inoculation, Gonçalves-Vidigal et al. (2009) found the same segregation ratio in allelism test performed in F2 population of Jalo Listras Pretas × Michigan Dark Red Kidney.

The 15R:1S ratio was also found in F2 generations of crosses between Amendoim Cavalo × Ouro Negro (X^2 = 0.028; p = 0.867) and Amendoim Cavalo × Jalo Listras Pretas (X^2 = 0.028; p = 0.867), using the race 73. Results revealed independence of this gene in Amendoim Cavalo from *Co-3*^{4} (Gonçalves-Vidigal, 2013) and *Co-13* (Gonçalves-Vidigal et al., 2009) present in Ouro Negro and Jalo Listras Pretas, respectively.

Allelism tests involving race in 2047 inoculated in F2 populations of crosses between Amendoim Cavalo × G 2333 (X^2 = 0.085; p = 0.771), Amendoim Cavalo × Pitanga (X^2 = 1.152; p = 0.283), Amendoim Cavalo × Corinthiano (X^2 = 0.003; p = 0.955) and Amendoim Cavalo × Crioulo 159 (X^2 = 0.178; p = 0.673), the same ratio was obtained. This demonstrates the presence of two dominant genes resistant to race 2047. Therefore, it can be said that this gene in Amendoim Cavalo is independent of allele *Co-4* (Young et al., 1998; Awale and Kelly 2001) and of genes *Co-14* (Gonçalves-Vidigal et al., 2012), *Co-15* (Sousa et al., 2015), and *Co-16* (Coimbra-Gonçalves et al., 2016).

Likewise, the same result was observed in the F2 generations of crosses between Amendoim Cavalo × Paloma (X^2 = 0.009; p = 0.924), Amendoim Cavalo × Perla (X^2 = 0.244; p = 0.621) and Amendoim Cavalo × Jalo Pintado 2 (X^2 = 0.011; p = 0.918). Therefore, by allelism tests, it was confirmed that the gene in 'Amendoim Cavalo' is independent from *Co-Pa* (Lima-Castro et al., 2017), *Co-Pe* and *Co-18* (Frias et al., 2016), respectively.

The cultivar Amendoim Cavalo is considered an important source of Andean resistance to *C. lindemuthianum*, since it has a wide spectrum of resistance to the various races of the pathogen, highlighting races 2047 and 3481 presenting high virulence. When comparing to cultivar in a study with the other Andean sources, only cultivars AND 277, Pitanga, Corinthiano, Jalo Pintado 2 and Paloma present resistance genes to race 2047 of *C. lindemuthianum* (*Co-1*^{4}, *Co-14, Co-15, Co-18* and *Co-Pa*, respectively). However, resistance spectrum of 'Amendoim Cavalo' is distinct from such cultivars, since it confers resistance to races 2, 7, 65, 73 and 89 of *C. lindemuthianum* frequently found in Brazil.

CONCLUSION

The importance of cultivar Amendoim Cavalo should be emphasized as a new Andean source of resistance to anthracnose, once the dominant gene present in this cultivar confers resistance to races 2, 65, 73, 2047 and 3481 of *C. lindemuthianum*. Additionally, this gene is independent of those Mesoamerican and Andean genes previously characterized: *Co-1, Co-2, Co-3*^{4}*, Co-4, Co-4*^{2}*, Co-4*^{3}*, Co-5, Co-6, Co-11, Co-12, Co-13, Co-14, Co-15, Co-16, Co-Pa*

and *Co-Pe*. The authors propose *Co-AC* symbol to name the resistance gene to *C. lindemuthianum* present in the cultivar Amendoim Cavalo. It can be used in future common bean breeding programs aiming at the development of cultivars with durable resistance as pyramiding of genes conferring resistance to different races of *C. lindemuthianum*.

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