



Genetic resistance of common bean cultivar Beija Flor to *Colletotrichum lindemuthianum*

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ABSTRACT. Anthracnose, which is caused by the fungus *Colletotrichum lindemuthianum*, is one of the most widespread and important diseases of the common bean (*Phaseolus vulgaris* L.) in the world. The objective of the present study was to characterize the genetic resistance of the Beija Flor cultivar by inheritance and to conduct allelism tests. The inheritance test was conducted in the F₂ population derived from the Beija Flor (resistant) x TU (susceptible) cross inoculated with race 2047 of *C. lindemuthianum*. Furthermore, allelism tests exhibited a fitted segregation ratio of 15R:1S, thereby indicating the independence of the Beija Flor gene from the following previously characterized genes: *Co-1*, *Co-2*, *Co-4*, *Co-42*, *Co-6*, *Co-12*, *Co-14*, *Co-15*, and *Co-Pe*. Based on the aforementioned results, we are proposing the symbol *Co-Bf* to designate the new anthracnose resistance gene in the Brazilian Andean common bean cultivar Beija Flor. This cultivar is an important source of resistance to *C. lindemuthianum* that should provide a valuable contribution to the common bean breeding program for anthracnose resistance.

Keywords: *Phaseolus vulgaris* L.; pathogen; disease resistance; anthracnose.

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Introduction

The common bean (*Phaseolus vulgaris* L.) is an important protein source, especially in developing countries, for instance, in Latin America and Africa (Broughton et al., 2003). The most productive areas are among these main consuming regions; currently, Latin America shows the largest common bean production in the world followed by Africa (CGIAR, 2015).

The common bean is a crop with broad edaphoclimatic adaptation; therefore, it is affected by many diseases, which depreciate the quality of the product and decrease the crop productivity. These diseases can be fungal, bacterial or viral in origin (Pastor-Corrales & Schwartz, 2005). Anthracnose, whose causal agent is *Colletotrichum lindemuthianum*, is among the major fungal diseases that present symptoms in the aerial part of the common bean.

This disease stands out as one of the most important because it causes losses of up to 100% of the production and because it causes stains in the grains, depreciating the product (Rey, Balardin, & Pierobom, 2005). Temperatures above 25°C or below 18°C are limiting for both infection and pathogen development. In addition, sporulation is abundant in the pods at temperatures between 14 and 18°C (Pastor-Corrales & Schwartz, 2005).

Genetic resistance is the most effective, easy-to-use, and environmentally friendly, management strategy for common bean anthracnose (Pastor-Corrales & Tu, 1994; Kelly & Vallejo, 2004). However, the implementation of resistance is challenged by the recurrent appearance of new virulence phenotypes, usually referred to as races, of *C. lindemuthianum*. The repeated appearance of new races has resulted in failures of previously anthracnose-resistant commercial varieties (Tu, 1994; Kelly, Afanador, & Cameron, 1994; del Río, Lamppa, & Gross, 2002; Mahuku, Jara, Cajoao, & Beebe, 2002; del Río, Lamppa, Gross, Brolley, & Prischmann, 2003). The extensive virulence diversity of *C. lindemuthianum* has been the foremost limitation to the development of bean cultivars with effective and durable anthracnose resistance in Europe, Central America and South America (Pastor-Corrales, Otoyá, Molina, & Singh, 1995; González et al., 1998; Rodríguez-Guerra, Ramirez-Rueda, Vega, & Simpson, 2003; González-Chavira et al., 2004; Padder, Sharma,

Awale, & Kelly, 2017). In Brazil, a country where the common bean is an introduced crop, at least 70 different races of *C. lindemuthianum* have been identified (Menezes & Dianese, 1988; Rava, Purchio, & Sartorato, 1994; Balardin, Jarosz, & Kelly, 1997; Thomazella, Gonçalves-Vidigal, Vidigal Filho, Nunes, & Vida, 2002; Alzate-Marin & Sartorato, 2004; Damasceno e Silva, Souza, & Isikawa, 2007; Gonçalves-Vidigal, Lacanallo, & Vidigal Filho, 2008; Nunes, Gonçalves-Vidigal, Lacanallo, & Coimbra, 2013). To overcome the vast virulence diversity of *C. lindemuthianum*, bean scientists are required to continually broaden the genetic base of the bean crop by identifying new sources of resistance and incorporating new anthracnose resistance genes (Schwartz, Pastor-Corrales, & Singh, 1982; Pastor-Corrales et al., 1995; Mahuku et al., 2002). The wide assortment of anthracnose resistance genes makes the development of an effective resistance strategy that protects common bean from *C. lindemuthianum* possible.

Several of these Andean cultivars have been reported as sources of new anthracnose resistance genes (Gonçalves-Vidigal et al., 2008; Gonçalves-Vidigal et al., 2011; Gonçalves-Vidigal et al., 2012; Sousa et al., 2015; Castro et al., 2017). Among these Andean cultivars, the Beija Flor (BF) was collected in the state of Paraná, has a type I growth habit, medium-size seeds (36.02 g per 100 seeds), and morphological characteristics of the Andean gene pool (Singh, Gepts, & Debouck, 1991). The phaseolin seed protein test, as described by Kami, Velásquez, Debouck, and Gepts (1995) and conducted on seeds of Beija Flor, showed the presence of phaseolin 'T', which is characteristic of common beans from the Andean gene pool. Previous studies of anthracnose resistance showed that Beija Flor is resistant to the Andean race 7 and to the Mesoamerican races 9, 64, 65, 73, 89, 453, and 2047 of *C. lindemuthianum*. Due to its good resistance spectrum and resistance to one of the most virulent races, the race 2047, for which only one of the 12 differentiating cultivars is resistant (Pastor-Corrales, Erazo, Estrada, & Singh, 1994), the Beija Flor cultivar is of great value for the common bean breeding programmes. The search for new sources of Andean resistance to *C. lindemuthianum* is extremely important for common bean breeding programmes in tropical and subtropical regions.

Therefore, the objective of this study was to characterize the genetic resistance and to conduct allelism tests in the Beija Flor cultivar to *Colletotrichum lindemuthianum*.

Material and methods

Beija Flor (BF), which is studied herein, belongs to the Andean gene pool and is one of 26 Andean and Mesoamerican common bean landraces collected in the Northern and North-western regions of the state of Paraná in Southern Brazil (Vidigal Filho, Gonçalves-Vidigal, Kelly, & Kirk, 2007). The present work was conducted from March 2015 to October 2016 under greenhouse conditions and at the Common Bean Breeding and Molecular Biology Laboratory of the Núcleo de Pesquisa Aplicada à Agricultura (Nupagri), Universidade Estadual de Maringá, Paraná State, Brazil.

Population development

The inheritance resistance studies were conducted on the F₂ population derived from the Beija Flor (R) × TU (S) cross. The resulting segregating F₂ population was inoculated with race 2047 of *C. lindemuthianum*. TU is susceptible to race 2047, whereas Beija Flor is resistant. To determine the independence of the anthracnose resistance allele present in Beija Flor (BF) from other previously characterized anthracnose resistance alleles, BF was crossed with Andean bean cultivars Michigan Dark Red Kidney (*Co-1*), Jalo Vermelho (*Co-12*), Pitanga (*Co-14*), Corinthiano (*Co-15*), and Perla (*Co-Pe*), and with the Mesoamerican cultivars Cornell 49-242 (*Co-2*), TO (*Co-4*), AB 136 (*Co-6*), and G 2333 (*Co-4²/Co-5²/Co-3⁵*). In all cases, BF was used as the female parent. F₁ seeds were planted and self-pollinated to obtain the corresponding F₂ seeds.

C. lindemuthianum races used in the study

The *C. lindemuthianum* races used in this work were 65 and 2047, which were obtained from the mycology collection of the Nupagri, and the monosporic cultures were prepared at the Common Bean Breeding and Molecular Biology Laboratory. The Mesoamerican race 2047 was chosen in this study due to its high virulence and importance in common bean breeding programs for anthracnose resistance, as well as the resistance response shown by BeijaFlor against this race. In the inheritance test, race 2047 was inoculated into the F₂ generation of the cross (R × S) Beija Flor × TU, and in the allelism tests with the F₂ generation of

the crosses (R x R) between Beija Flor and resistant cultivars. The identification of the races was confirmed by inoculation of the isolates on a set of 12 common bean anthracnose differential cultivars (Pastor-Corrales, 1992).

Inoculation and disease evaluation

Monosporic cultures of each race of *C. lindemuthianum* used in this study were prepared in young green common bean pod medium and incubated at 25°C for 14 days. The inoculation of the parents and the F₁ and F₂ populations from each cross was carried out separately. Seedlings were grown under natural light in greenhouses supplemented by 400-w, high-pressure, sodium lamps, yielding total light intensity of 115 $\mu\text{moles m}^{-2} \text{s}^{-1}$ for 7 to 10 days until the seedlings had reached the first trifoliolate leaf stage. Twelve parental and F₁ seedlings from each cross were inoculated, and the number of F₂ seedlings inoculated varied by cross, as shown in Table 1. Seedlings with fully developed first trifoliolate leaves of common bean cultivars and the F₁ and F₂ populations were inoculated with spores of selected races of *C. lindemuthianum*. Spore suspensions containing 1.2×10^6 spores mL^{-1} were spray-inoculated on seedlings using a De Vilbiss, Model 15 Atomizer powered by an electric air compressor. In each cross, the F₂ seeds and those of the respective parents and one susceptible control (Michelite, Mexico 222) were used. After inoculation, the plants were maintained at >95% relative humidity at 21-23°C, with a 16-h day length (light intensity of 300 micromoles $\text{m}^{-2} \text{s}^{-1}$ at 1 m height) in a mist chamber for 2 days. After this period, the plants were removed from the mist chamber and transferred to benches under suitable environment at 22°C with artificial light (12-h day length at 25°C) for seven days. Anthracnose disease reactions were rated visually using a scale from 1 to 9 (Pastor-Corrales et al., 1995).

Statistical analysis of data

Individual plants with disease reaction scores between 1 and 3 were considered resistant, whereas plants that scored 4-9 were considered susceptible. Segregation analysis of the disease reaction of 100 F₂ plants from the cross Beija Flor \times TU were performed by the Chi-square (χ^2) test, according to the Mendelian segregation hypothesis of a 3:1 (resistant to susceptible) ratio. Similarly, the disease reaction of the 829 F₂ plants derived from the crosses Beija Flor and the cultivars Michigan Dark Red Kidney, Jalo Vermelho, Pitanga, Corinthiano, Perla, Cornell 49-242, TO, AB 136, and G 2333 were tested for a goodness of fit of 15:1 (resistant to susceptible) ratio.

Results and discussion

Inheritance of anthracnose resistance

Beija Flor and Pitanga (Co-14), Corinthiano (Co-15), Perla (Co-Pa), and G 2333 (Co-3⁵, Co-4², Co-5²) were resistant to Mesoamerican races 65 and 2047 of *C. lindemuthianum* used in this study. However, the Jalo Vermelho (Co-12), TU (Co-5), Michigan Dark Red Kidney (Co-1), Cornell 49-242 (Co-2), TO (Co-4), and AB 136 (Co-6) included in this study were susceptible to race 2047 and resistant to race 65 (Table 1). The differential cultivar TU, which was crossed with BF to study the inheritance of resistance, was susceptible to race 2047. This race was chosen because is one of the most virulent and only the G 2333 of the 12 differentiating is resistant to it. The Mesoamerican differential cultivar G 2333, which has three anthracnose resistance genes, has been evaluated as resistant to several hundred races of the anthracnose pathogen worldwide, including race 2047 (Pastor-Corrales et al., 1994; Padder et al., 2017). Eleven different cultivars were susceptible to race 2047. Previous studies had revealed that the Beija Flor is an important source of resistance against races 7, 9, 64, 65, 73, 89, 453, and 2047 of *C. lindemuthianum*. Thus, the results of this study underscored the comprehensive resistance of BF to a broad diversity of Mesoamerican and Andean races of *C. lindemuthianum*.

All F₁ plants from the Beija Flor \times TU cross were resistant to race 2047, suggesting that a single dominant gene conditioned anthracnose resistance in Beija Flor. Segregation for resistance in the F₂ populations was consistent with a 3 resistant:1 susceptible ratio for Beija Flor \times TU ($\chi^2 = 0.00$; $p = 1.0$). These results support the hypothesis that a single dominant gene in the Andean common bean cultivar Beija Flor provides anthracnose resistance to race 2047 of *C. lindemuthianum*; thus, the anthracnose resistance of BF is monogenic and dominant.

In this test, the segregation at the F₂ population occurred at a ratio of 3R:1S ($\chi^2 = 0.00$; $p = 1.0$), showing that the action of only one dominant gene, present in the Beija Flor cultivar, gives resistance to race 2047 (Table 1). When Gonçalves-Vidigal et al. (2012) tested the F₂ population derived from a Pitanga × AB 136 cross, the authors obtained segregation of 3 resistant:1 susceptible with ($\chi^2 = 0.012$; $p = 0.91$), providing evidence that the resistance to race 2047 is conferred by a dominant gene present in the Pitanga cultivar. In 2015, Sousa and collaborators reported such results ($\chi^2 = 0.002$; $p = 0.97$) when they used race 2047 in F₂ population from the cross of Corinthiano × Cornell 49-242. According to the Chi-square test applied to the data obtained in the resistance inheritance test, dominant monogenic inheritance was hypothesized to be present in the Beija Flor cultivar in response to race 2047.

Allelism tests

The allelism tests evaluated the independence of the gene present in the Beija Flor cultivar relative to nine genes previously characterized and described in the literature. The allelism tests were conducted in the F₂ populations, where both cultivars involved showed resistance. Allelism tests were carried out with nine F₂ populations from crosses between the BF and Andean (Michigan Dark Red Kidney, Jalo Vermelho, Pitanga, Corinthiano and Perla) and Mesoamerican (TO, Cornell 49-242, AB 136, and G 2333) cultivars (Table 1). Segregation for resistance in the nine crosses fitted a 15 resistant:1 susceptible ratio.

These nine F₂ populations were from crosses between BF and the Andean cultivars Michigan Dark Red Kidney ($\chi^2 = 0.609$; $p = 0.43$), Jalo Vermelho ($\chi^2 = 0.266$; $p = 0.60$), Pitanga ($\chi^2 = 0.170$; $p = 0.68$), Corinthiano ($\chi^2 = 0.006$; $p = 0.93$), and Perla ($\chi^2 = 0.011$; $p = 0.92$), and Mesoamerican cultivars Cornell 49-242 ($\chi^2 = 0.011$; $p = 0.92$), TO ($\chi^2 = 0.001$; $p = 0.98$), AB 136 ($\chi^2 = 0.011$; $p = 0.92$), and G 2333 ($\chi^2 = 0.606$; $p = 0.80$). These results support the hypothesis that two independent dominant genes confer resistance to *C. lindemuthianum* in these F₂ populations; one anthracnose resistance gene present in the Andean bean BF was used as the female parent and the other gene was from the male parent. The segregation results for anthracnose resistance in the F₂ population from crosses between BF and the other Andean bean cultivars indicated that the anthracnose resistance dominant gene in BF is independent of Andean anthracnose resistance genes *Co-1*, *Co-12*, *Co-14*, *Co-15*, and *Co-Pe*. Similarly, the segregation for anthracnose resistance in the F₂ populations derived from the crosses between BF and the Mesoamerican cultivars Cornell 49-242, TO, AB 136, and G 2333 indicate that the dominant anthracnose resistance gene in BF is also independent of Mesoamerican anthracnose resistance genes *Co-2*, *Co-4*, *Co-6*, and *Co-4²*.

The F₂ population of the cross between Beija Flor × Cornell 49-242, when inoculated with race 65 the segregation ratio, fitted a 15R:1S ratio and showed statistical results of the $\chi^2 = 0.011$ and $p = 0.92$. Similar results were found in 2006 by Gonçalves-Vidigal and Kelly (2006) when they inoculated race 65 in a population from a Widusa cultivar × MDRK cross ($p = 0.79$).

The F₂ population derived from the crosses Beija Flor × TO ($\chi^2 = 0.001$; $p = 0.98$) and Beija Flor × AB 136 ($\chi^2 = 0.011$; $p = 0.92$), inoculated with race 65, showed segregation of 15R:1S, demonstrating the presence of two dominant genes. This indicates that the gene which confers resistance to the race 65 present at Beija Flor is independent of the genes *Co-1*, *Co-2*, *Co-4* and *Co-6*.

The segregation results of the F₂ population of the crosses between Beija Flor × Jalo Vermelho ($\chi^2 = 0.266$; $p = 0.60$), Beija Flor × Pitanga ($\chi^2 = 0.017$; $p = 0.68$) and Beija Flor × Corinthiano ($\chi^2 = 0.006$; $p = 0.93$) showed a ratio of 15 resistant to 1 susceptible. This result indicates the presence of a dominant and independent gene from the genes *Co-12* (Jalo Vermelho), *Co-14* (Pitanga), and *Co-15* (Corinthiano).

The allelism test using the differentiating cultivar G 2333 was made with race 2047 of *C. lindemuthianum* because the cultivar has one anthracnose resistant allele, *Co-4²*, which confers resistance to that race. The result obtained from the F₂ population from the Beija Flor × G 2333 cross (15R:1S) shows the action of two independent and dominant genes, with one of them being the *Co-4²* present in the cultivar G 2333 and the other being a gene present in the Beija Flor cultivar. This segregation could be observed because, although cultivar G 2333 has three resistance genes, only *Co-4²* allele confers resistance to race 2047.

In the literature, we can observe similar results in studies that used the same parental (MDRK, Cornell 49-242, TO, AB 136, Jalo Vermelho, Pitanga, Corinthiano, Perla, and G 2333), as for example, the Paloma × Cornell 49-242 cross, also inoculated with race 65, where Castro et al. (2017) found a segregation ratio of 15R:1S. Furthermore, Frias, Gonçalves-Vidigal, Nanami, Castro, and Vidigal Filho (2016) conducted testes on the F₂ populations from the Jalo Pintado 2 × Cornell 49-242, Jalo Pintado 2 × TO, and Jalo Pintado 2 ×

AB 136 crosses and reported a segregation ratio of 15R:1S. Likewise, Nanami et al. (2017) also performed the inoculation of race 65 on the F₂ populations Amendoim Cavalo × TO and Amendoim Cavalo × AB 136.

Table 1. The F₂ segregation from resistant (R) × susceptible (S) and R × R *Phaseolus vulgaris* cultivar crosses for the genetic characterization of resistance to the *Colletotrichum lindemuthianum* races 65 and 2047 in the Beija Flor (BF) Cultivar.

Cross	Race	Resistant Gene	Observed Plants		Expected Ratio R:S	χ^2	p value
			R ^a	S ^b			
BF × TU (R × S)B	2047		75	25	3:1	0.00	1.00
F × MDRK ^c (R × R)	65	<i>Co-1</i>	71	3	15:1	0.609	0.43
BF × Cornell 49-242 (R × R)	65	<i>Co-2</i>	94	6	15:1	0.011	0.92
BF × TO (R × R)	65	<i>Co-4</i>	89	6	15:1	0.001	0.98
BF × AB 136 (R × R)	65	<i>Co-6</i>	94	6	15:1	0.011	0.92
BF × Jalo Vermelho (R × R)	65	<i>Co-12</i>	95	5	15:1	0.266	0.60
BF × Pitanga (R × R)	65	<i>Co-14</i>	74	4	15:1	0.170	0.68
BF × Corinthiano (R × R)	65	<i>Co-15</i>	87	6	15:1	0.006	0.93
BF × Perla (R × R)	65	<i>Co-PE</i>	94	6	15:1	0.011	0.92
BF × G 2333 (R × R)	2047	<i>Co-4²</i>	84	5	15:1	0.606	0.80

^aResistant; ^bSusceptible; ^cMichigan Dark Red Kidney.

Moreover, Frias et al. (2016) obtained similar results evaluating F₂ populations derived from the Jalo Pintado 2 × Jalo Vermelho, Jalo Pintado 2 × Pitanga Jalo, and Pintado 2 × Corinthiano crosses. Inheritance studies conducted by Castro et al. (2017), using the F₂ populations derived from the Paloma × Jalo Vermelho, Paloma × Pitanga, and Paloma × Corinthiano crosses reported the segregation of 15R:1S, providing evidence of the action of two dominant genes. Similar results were obtained by Sousa et al. (2015) when inoculated with race 2047 in the F₂ population from the Corinthiano × G 2333. In addition, Gonçalves-Vidigal et al. (2012), who reported segregation that fitted a 15R:1S ratio, when inoculating the race 2047 in the F₂ population from the cross Pitanga × G 2333.

In summary, the current study on anthracnose resistance inheritance revealed that the resistance in BF is monogenic and dominant. Similarly, the allelism tests carried out in nine F₂ populations revealed that the anthracnose resistance gene in the Andean common bean landrace Beija Flor is independent from the Andean *Co-1*, *Co-12*, *Co-14*, *Co-15*, and *Co-Pe*, and from the Mesoamerican *Co-2*, *Co-4*, *Co-6*, *Co-4²* genes.

Previous work conducted by our group showed that the Beija Flor cultivar has morphological characteristics similar to bean cultivars from the Nueva Granada race of the Andean gene pool (Singh et al., 1991). The Beija Flor cultivar, which was collected in the state of Paraná, has a type I growth habit, medium-size seeds (36.02 g per 100 seeds), and morphological characteristics of the Andean gene pool (Singh et al., 1991). The phaseolin seed protein test, conducted on seeds of BF, as described by Kami et al. (1995), showed that these seeds had phaseolin 'T', which is characteristic of common beans from the Andean gene pool. The initial anthracnose resistance studies of BF showed that BF was resistant to Andean race 7 and to the Mesoamerican races 9, 64, 65, 73, 89, 453, and 2047 of *C. lindemuthianum*. Due to its good resistance spectrum and resistance to one of the most virulent races, the race 2047, and because it is only one of the 12 different cultivars resistant to that race (Pastor-Corrales et al., 1994), the cultivar Beija Flor is of great value for the common bean breeding programmes.

The combined results of the monogenic inheritance and the allelism tests support the hypothesis that only a single dominant locus confers resistance to races 65 and 2047 of *C. lindemuthianum* in the Andean common bean landrace Beija Flor and that this cultivar is independent from other Andean and Mesoamerican bean anthracnose resistance loci previously reported. The authors propose that this single dominant anthracnose resistance locus in the Beija Flor cultivar provisionally be named as *Co-Bf*.

These results are particularly relevant to bean breeding programmes that wish to broaden the genetic base of the bean crop and the pyramid of Andean and Mesoamerican genes by conferring resistance to distinct races of *C. lindemuthianum*. Gene pyramiding results in bean cultivars with durable anthracnose resistance (Young & Kelly, 1996). The data obtained in the present research provides breeders with an anthracnose resistant gene of Andean origin that can be deployed in commercial cultivars, thereby providing an opportunity to improve the effectiveness of the anthracnose resistance gene pyramiding in common bean breeding programmes while also broadening the germplasm base of the common bean.

Conclusion

The inheritance and allelism tests revealed that Beija Flor has a dominant gene for resistance to *C. lindemuthianum*, being independent of previously characterized genes, which include the following: *Co-1*, *Co-2*, *Co-4*, *Co-6*, *Co-12*, *Co-14*, *Co-15*, *Co-4²*, and *Co-Pe*.

The results indicate that the Beija Flor cultivar is an important source of anthracnose resistance because it presents a new gene that can be used as a potential source of resistance. This gene can contribute to future common bean breeding programmes and commercial cultivars, with the purpose of increasing the spectrum of resistance to anthracnose.

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References

- Alzate-Marin, A. L., & Sartorato, A. (2004). Analysis of the pathogenic variability of *Colletotrichum lindemuthianum* in Brazil. *Annual Report of the Bean Improvement Cooperative*, 47, 241-242.
- Balardin, R. S., Jarosz, A. M., & Kelly, J. D. (1997). Virulence and molecular diversity in *Colletotrichum lindemuthianum* from South, Central and North America. *Phytopathology*, 87(12), 1184-91. DOI: 10.1094/PHYTO.1997.87.12.1184
- Broughton, W. J., Hernandez, G., Blair, M. W., Beebe, S. E., Gepts, P., & Vanderleyden, J. (2003). Beans (*Phaseolus* spp.) - model food legumes. *Plant Soil*, 252(1), 55-128. DOI: 10.1023/A:1024146710611
- Castro, S. A. L., Gonçalves-Vidigal, M. C., Gilio, T. A. S., Lacanallo, G. F., Valentini, G., Martins, V. S. R., & Pastor-Corrales, M. A. (2017). Genetics and mapping of a new anthracnose resistance locus in Andean common bean Paloma. *BMC Genomics*, 18(306), 1-12. DOI: 10.1186/s12864-017-3685-7
- CGIAR. (2015). *Common Bean*. Retrieved on Dec. 10, 2015 from <http://www.cgiar.org/our-research/cropfactsheets/beans/>
- Damasceno e Silva, K. J., Souza, E. A., & Ishikawa, F. H. (2007). Characterization of *Colletotrichum lindemuthianum* isolates from the state of Minas Gerais, Brazil. *Journal of Phytopathology*, 155(4), 241-247. DOI: 10.1111/j.1439-0434.2007.01226.x
- del Río, L. E., Lamppa, R. S., & Gross, P. L. (2002). First report of dry bean anthracnose (*Colletotrichum lindemuthianum*) race 73 in North Dakota. *Plant Disease*, 86(5), 562. DOI: 10.1094/PDIS.2002.86.5.562B
- del Río, L. E., Lamppa, R. S., Gross P. L., Brolley, B., & Prischmann, J. (2003). Identification of *Colletotrichum lindemuthianum* race 73 in Manitoba, Canada. *Canadian Journal of Plant Pathology*, 25(1), 104-107. DOI: 10.1080/07060660309507055
- Frias, A. A., Gonçalves-Vidigal, M. C., Nanami, D. S. Y., Castro, S. A. L., & Vidigal Filho, P. S. (2016). Genetic resistance to *Colletotrichum lindemuthianum* in the Andean cultivar Jalo Pintado 2 of common bean. *Agronomy Science and Biotechnology*, 2(1), 21-28.
- Gonçalves-Vidigal, M. C., Cruz, A. S., Garcia, A., Kami, J., Vidigal Filho, P. S., Sousa, L. L., ... Pastor-Corrales, M. A. (2011). Linkage mapping of the *Phg-1* and *Co-1⁴* genes for resistance to angular leaf spot and anthracnose in the common bean cultivar AND 277. *Theoretical and Applied Genetics*, 122(5), 893-903. DOI: 10.1007/s00122-010-1496-1
- Gonçalves-Vidigal, M. C., Lacanallo, G. F., & Vidigal Filho, P. S. (2008). A new Andean gene conferring resistance to anthracnose in common bean (*Phaseolus vulgaris* L.) cultivar Jalo Vermelho. *Plant Breeding*, 127(6), 592-596. DOI: 10.1111/j.1439-0523.2008.01530.x
- Gonçalves-Vidigal, M. C., & Kelly, J. D. (2006). Inheritance of anthracnose resistance in the common bean cultivar Widusa. *Euphytica*, 151, 411-419. DOI: 10.1007/s10681-006-9164-x
- Gonçalves-Vidigal, M. C., Meirelles, A. C., Poletine, J. P., Sousa, L. L., Cruz, A. S., Nunes, M. P., & Vidigal Filho, P. S. (2012). Genetic analysis of anthracnose resistance in Pitanga dry bean cultivar. *Plant Breeding*, 131(3), 423-429. DOI: 10.1111/j.1439-0523.2011.01939.x

- González, M., Rodríguez, R., Zavala, M. E., Jacobo, J. L., Hernández, F., Acosta, J., & Simpson, J. (1998). Characterization of Mexican isolates of *Colletotrichum lindemuthianum* by using differential cultivars and molecular markers. *Phytopathology*, 88(4), 292-299. DOI: 10.1094/PHYTO.1998.88.4.292
- González-Chavira, M., Rodríguez Guerra, R., Hernández-Godínez, F., Acosta-Gallegos, J. A., Martínez de la Vega, O., & Simpson, J. (2004). Analysis of pathotypes of *Colletotrichum lindemuthianum* found in the central region of Mexico and resistance in elite germ plasm of *Phaseolus vulgaris*. *Plant Disease*, 88(2), 152-156. DOI: 10.1094/PDIS.2004.88.2.152
- Kami, J., Velásquez, V. B., Debouck, D. G., & Gepts, P. (1995). Identification of presumed ancestral DNA sequences of phaseolin in *Phaseolus vulgaris*. *Proceedings of the National Academy of Sciences*, 92(4), 1101-1104. DOI: 10.1073/pnas.92.4.1101
- Kelly, J. D., & Vallejo, V. A. (2004). A comprehensive review of the major genes conditioning resistance to anthracnose in common bean. *HortScience*, 39(6), 1196-1207. DOI:10.21273/HORTSCI.39.6.1196 31
- Kelly, J. D., Afanador, L., & Cameron, L. S. (1994). New races of *Colletotrichum lindemuthianum* in Michigan and implications in dry bean resistance breeding. *Plant Disease*, 78(9), 892-894. DOI: 10.1094/PD-78-0892
- Mahuku, G. S., Jara, C. E., Cajiao V., & Beebe, S. E. (2002). Sources of resistance to *Colletotrichum lindemuthianum* the secondary gene pool of *Phaseolus vulgaris* and in crosses of primary and secondary gene pools. *Plant Disease*, 86(12), 1383-1387. DOI: 10.1094/PDIS.2002.86.12.1383
- Menezes, J. R., & Dianese, J. C. (1988). Race characterization of Brazilian isolates of *Colletotrichum lindemuthianum* and detection of resistance to anthracnose in *Phaseolus vulgaris*. *Phytopathology*, 78, 650-655. DOI: 10.1094/Phyto-78-650
- Nanami, D. S. Y., Gonçalves-Vidigal, M. C., Elias, H. T., Lima Castro, S. A., Frias, A. A. T., & Vidigal Filho, P. S. (2017). Characterization of genetic resistance in Andean common bean cultivar Amendoim Cavalo to *Colletotrichum lindemuthianum*. *Agronomy Science and Biotechnology*, 3(1), 43-52. DOI: 10.33158/ASB.2017v3i1p43
- Nunes, M. P., Gonçalves-Vidigal, M. C., Lacanallo, G. F., & Coimbra, G. K. (2013). *Comprehension of genetic variability and virulence of Colletotrichum lindemuthianum in common bean*. Portland, US: Biennial Meeting of the Bean Improvement Cooperative.
- Padder, B. A., Sharma, P. N., Awale, H. E., & Kelly, J. D. (2017). *Colletotrichum lindemuthianum*, the causal agent of bean anthracnose. *Journal of Plant Pathology*, 99(2), 317-330. DOI: 10.4454/jpp.v99i2.3867
- Pastor-Corrales, M. A. (1992). Recomendaciones y acuerdos del primer taller de antracnosis en América Latina. In M. A. Pastor-Corrales (Ed.), *La antracnosis del frijol común, Phaseolus vulgaris, en América Latina* (p. 240-250). Cali, CO: CIAT.
- Pastor-Corrales, M. A., Erazo, O. A., Estrada, E. I., & Singh, S. P. (1994). Inheritance of anthracnose resistance in common bean accession G 2333. *Plant Disease*, 78, 959-962. DOI: 10.1094/PD-78-0959
- Pastor-Corrales, M. A., & Tu, J. C. (1994). Antracnosis. In M. A. Pastor-Corrales, & H. H. Schwartz (Eds.), *Problemas de producción de frijol en los trópicos* (p. 87-120). Cali, CO: CIAT.
- Pastor-Corrales, M. A., Otoya, M. M., Molina, A., & Singh, S. P. (1995). Resistance to *Colletotrichum lindemuthianum* isolates from Middle America and Andean South America in different common bean races. *Plant Disease*, 79, 63-67. DOI: 10.1094/PD-79-0063
- Pastor-Corrales, M. A., & Schwartz, H. F. (2005). Anthracnose. In H. F. Schwartz, J. R. Steadman, R. Hall, & R. Forster (Eds.), *Compendium of bean diseases* (p. 25-27). St. Paul, US: The American Society of Phytopathology.
- Rava, C., Purchio, A., & Sartorato, A. (1994). Caracterização de patótipos de *Colletotrichum lindemuthianum* que ocorrem em algumas regiões produtoras de feijoeiro comum. *Fitopatologia Brasileira*, 19(2), 167-172.
- Rey, M. S., Balardin, R. S., & Pierobom, C. R. (2005). Reação de cultivares de feijoeiro comum (*Phaseolus vulgaris*) a patótipos de *Colletotrichum lindemuthianum*. *Revista Brasileira de Agrociência*, 11(1), 113-116. DOI: 10.18539/cast.v11i1.1170
- Rodríguez-Guerra, R., Ramirez-Rueda, M. T., Martínez de la Vega, O., & Simpson, J. (2003). Variation in genotype, pathotype and anastomosis groups of *Colletotrichum lindemuthianum* isolates from Mexico. *Plant Pathology*, 52(2), 228-235. DOI: 10.1046/j.1365-3059.2003.00808.x

- Schwartz, H. F., Pastor-Corrales, M. A., & Singh, S. P. (1982). New Sources of resistance to anthracnose and angular leaf spot of beans (*Phaseolus vulgaris*). *Euphytica*, *31*(3), 741-754. DOI: 10.1007/BF00039213
- Singh, S. P., Gepts, P., & Debouck, D. G. (1991). Races of common bean (*Phaseolus vulgaris*, Fabaceae). *Economic Botany*, *45*, 379-396. DOI: 10.1007/BF02887079
- Sousa, L. L., Gonçalves, A. O., Gonçalves-Vidigal, M. C., Lacanallo, G. F., Fernandez, A. C., Awale, H., & Kelly, J. D. (2015). Genetic characterization and mapping of anthracnose resistance of common bean landrace cultivar Corinthiano. *Crop Science*, *55*(5), 1900-1910. DOI: 10.2135/cropsci2014.09.0604
- Thomazella, C., Gonçalves-Vidigal, M. C., Vidigal Filho, P. S., Nunes, W. M. C., & Vida, J. B. (2002). Characterization of *Colletotrichum lindemuthianum* races in Paraná state, Brazil. *Crop Breeding and Applied Biotechnology*, *2*(1), 55-60. DOI: 10.12702/1984-7033.v02n01a08
- Tu, J. C. (1994). Occurrence and characterization of the alpha-Brazil race of bean anthracnose (*Colletotrichum lindemuthianum*) in Ontario. *Canadian Journal of Plant Pathology*, *16*(2), 129-131. DOI: 10.1080/07060669409500770
- Vidigal Filho, P. S., Gonçalves-Vidigal, M. C., Kelly, J. D., & Kirk, W. W. (2007). Sources of resistance to anthracnose in traditional common bean cultivars from Paraná, Brazil. *Journal of Phytopathology*, *155*(2), 108-113. DOI: 10.1111/j.1439-0434.2007.01203.x
- Young, R. A., & Kelly, J. D. (1996). Characterization of the genetic resistance to *Colletotrichum lindemuthianum* in common bean differential cultivars. *Plant Disease*, *80*(6), 650-654. DOI: 10.1094/PD-80-0650