AGRONOMY SCIENCE AND BIOTECHNOLOGY

REVIEW ARTICLE

Occurrence of anthracnose pathogen races and resistance genes in common bean across 30 years in Brazil

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ABSTRACT

Anthracnose caused by *Colletotrichum lindemuthianum* is one of the most critical diseases in the common bean (*Phaseolus vulgaris* L.). The characterization and localization of pathogenic fungal races are essential for understanding pathogen population dynamics and recommending strategies to develop resistant cultivars. As resistant genotypes are the most economical and ecologically safe means of controlling plant diseases, there have been efforts to characterize resistance genes in common bean. Several studies using a system of 12 differential bean cultivars have been carried out to monitor anthracnose since 1991, reporting the constant appearance of new fungal races. *C. lindemuthianum* shows high virulence diversity. The objective of the present study was to review the relationship between *C. lindemuthianum* races and the common bean pathogenic processes involved in the risk of developing anthracnose disease. As a result, 89 races occurred in Brazil, wherein 73, 65, and 81 of *C. lindemuthianum* are the most frequent. Furthermore, we built a map with the anthracnose resistance loci, molecular markers, and their respective physical position. The accessibility to the genomes and sequencing technologies permits molecular markers for marker-assisted selection applied to anthracnose-resistant cultivars. This study could be used as a reference for future resistance mapping studies and as a guide for selecting resistance loci in breeding programs aiming to develop common bean cultivars with durable anthracnose resistance.

Keywords: Resistance and virulence index, resistant cultivars, cultivar durability, durable resistance, pyramiding resistance genes, genomic regions.

INTRODUCTION

Common bean (*Phaseolus vulgaris* L.) is one of the primary sources of carbohydrates, proteins, vitamins, and minerals worldwide (Carvalho et al., 2012; Perilla, Cirino, Ruas, Pavan, & Gonçalves, 2015). Anthracnose (ANT) is caused by the fungus *Colletotrichum lindemuthianum* (Sacc. & Magn.) Bri. & Cav. It is considered one of the most severe diseases that affect bean productivity. In fact, under favorable conditions, anthracnose can reduce bean production by up to 100% (Singh & Schwartz, 2010; Campa, Rodríguez-Suárez, Giraldez, & Ferreira, 2014). The most effective approach to protect bean plants from anthracnose pathogens is the use of resistant cultivars (Pacheco, Berrouet, Yepes, Sánchez, & Montoya, 2014). However, resistant cultivars are harmed by the recurrent appearance of new virulence phenotypes, usually referred to as races, of *C. lindemuthianum*. The best strategy for breeding programs to increase the durability of cultivar resistance is to characterize predominant races in the main growing regions and pyramiding anthracnose resistance genes from both Andean and Mesoamerican origins in new cultivars (Kelly, Gepts, Miklas, & Coyne, 2003).

Brazil is the third biggest common bean producer worldwide, mainly of Carioca and Preto's types that belong to the Mesoamerican group (Companhia nacional de abastecimento, 2019; Food and Agriculture Organization, 2019). The most significant variability of *C. lindemuthianum* races is found in Brazil. The diversity found in common bean and *C. lindemuthianum* suggest coevolution, and both species are divided into two distinct groups (Andean and Mesoamerican) (Pastor-Corrales, 2004). Andean races of the anthracnose pathogen are usually isolated from large-seeded beans that belong to the Andean gene pool. Mesoamerican races are often isolated from small- or medium-seeded beans belonging to the Mesoamerican gene pool. However, Mesoamerican races are compatible with Mesoamerican and Andean beans and they exhibit greater virulence and genetic diversity than the Andean races (Pastor-Corrales, 2004).

Studies at the molecular level have been conducted based on sequence data that indicate that the common bean is of Mesoamerican ancestry and originated in Mexico (Schmutz et al., 2014). Later expansion to South America resulted in developing two significant and distinct common bean gene pools: Mesoamerican and Andean (Bitocchi et al., 2017). Moreover, Andean cultivars tend to be more resistant to Mesoamerican races of the pathogen, which have high variability and aggressiveness (Pastor-Corrales, 2004). Hence, one strategy to reduce the susceptibility of common bean plants and develop cultivars with durable resistance is pyramiding resistance genes from Andean and Mesoamerican pools (Melotto & Kelly, 2000). Previous studies revealed intra-race variability based on sequencing of the ITS1, 5.8S and ITS2 regions on pathogen population structure of C. *lindemuthianum* (Coêlho, Gonçalves-Vidigal, Vidigal Filho, Franzon, & Martins, 2020). The authors suggested independent evolution of specific virulence types such as, races 0, 2, 31, 72, 73, 75, 83, and 89 in different geographic regions and they noticed that races 0, 2, 31, 72, 73, 75, 83, and 89 exhibited intra-race molecular variability.

The present study aimed to investigate *C. lindemuthianum* occurrences in Brazil in the last thirty years as described in the literature. In addition, we built a common bean in silico map with genomic regions containing anthracnose resistance genes and the respective molecular markers linked to these regions.

GENETIC STUDIES WITH ANTHRACNOSE IN COMMON BEAN

This study reviews *C. lindemuthianum* races in Brazil from 1991 to 2021 using the methodology proposed by Pastor-Corrales (1991). Furthermore, we sought the anthracnose resistance genes already described in the literature to facilitate common bean breeding for resistance to anthracnose races identified in Brazil. Once molecular markers are essential for marker-assisted selection in breeding programs, we also searched for molecular markers linked to the anthracnose resistance loci.

Phenotyping data using differential cultivars

The group of differential cultivars contains accessions from Mesoamerican and Andean origin. In this system, each cultivar receives a value of 2^{n-1}, where 2 represents the number of reaction classes considered (resistant or susceptible) and "n" is a function of the order of the differentiators (n = 1 to 12). Table 1 presents the differential cultivars, including their anthracnose resistance genes and the binary system used for naming races of *C. lindemuthianum*.

Table 1. Performance of the common bean differential cultivars to *Colletotrichum lindemuthianum* proposed by Pastor-Corrales (1991) using the binary system.

Differential Cultivars	Gene Pool[1]	Resistant Genes	Binary Value	Numeric Value (2^{n-1})
Michelite	MA	*Co-11*	2^0	1
Michigan Dark Red Kidney	A	*Co-1*	2^1	2
Perry Marrow	A	*Co-1*^{3}	2^2	4
Cornell 49242	MA	*Co-2*	2^3	8
Widusa	A	*Co-1*^{5}	2^4	16
Kaboon	A	*Co-1*^{2}	2^5	32
Mexico 222	MA	*Co-3*	2^6	64
PI 207262	MA	*Co-3*^{3}*; Co-4*^{3}	2^7	128
TO	MA	*Co-4*	2^8	256
TU	MA	*Co-5*	2^9	512
AB 136	MA	*Co-6; co-8*	2^{10}	1024
G 2333	MA	*Co-3*^{5}*; Co-4*^{2}*; Co-5*^{2}	2^{11}	2048

[1]MA: Mesoamerican gene pool; A: Andean gene pool.

The terminology of the race consists of the sum of the numerical values of susceptible differential cultivars. For example, anthracnose race 73 overcomes the resistance of Michelite [1], Cornell 49-242 [8], and Mexico 222 [64]; the numerical values of the susceptible cultivars are added [1 + 8 + 64 = 73], and the isolate is

characterized as race 73. The standardization of the system allowed the comparison of data from different research groups and understanding of the population dynamics of the pathogen (Pastor-Corrales, 1991). Figure 1 illustrates the anthracnose symptoms include necrotic or depressed lesions, of various colors and shapes, in leaf, hypocotyl and pods.

Figure 1. Anthracnose symptoms. A - Leaf; B - Hypocotyl; C – Pods.
Source: Nupagri, UEM.

Resistance index (RI) and virulence index (VI) values for 12 differential cultivars were expressed as percentages (Vidigal Filho, Gonçalves-Vidigal, Kelly, & Kirk, 2007). A virulence index (VI) was calculated for each race identified in Brazil by:

$$VI = \frac{S\ x\ 100}{C}$$

Where:
VI = virulence index;
S= total number of differential cultivars that was susceptible to that race;
C= total number of differential cultivars (12).

For instance, race 2 overcomes only the resistance of Michigan Dark Red Kidney; therefore, the VI of race 2 is $VI = \frac{1\ x\ 100}{12} = 8.3\%$. A resistance index (RI) for each of the 12 differential cultivars was calculated for the races reported in Brazil from 1991 to 2021. The RI values were computed by:

$$RI = \frac{R\ x\ 100}{T}$$

Where:
RI = resistance index;
R= total number of races that each differential cultivar was resistant;
T= total number of races of *C. lindemuthianum* evaluated (89 races).

In silico data

An integrated map was built using the anthracnose resistance loci and molecular markers linked to these loci using the last version of the G 19833 common bean reference genome sequence (version 2.1 available at www.phytozome.org). To identify the physical position of ANT resistance loci in the reference genome, we performed a nucleotide essential local alignment search tool

(BLASTn) search using the sequence of the molecular marker (linked to the ANT resistance gene) described in the literature. Then, we built a map with the anthracnose resistance loci and molecular marker and *C. lindemuthianum* races using the MapChart software (Voorrips, 2002).

Characterization of *Colletotrichum lindemuthianum* races in Brazil

Several studies aiming to understand differences in the virulence and population structure of the fungus *C. lindemuthianum* have been conducted. A total of 89 races were characterized using the differential cultivars in Brazil from 1991 to 2021. The presence of many different races reveals the significant variability of this pathogen. This variability could be attributed to the fact that Brazil is one of the largest common bean growers in the world (Food and Agriculture Organization [FAO], 2019). Races of *Colletotrichum lindemuthianum* characterized in each State of Brazil from 1991 to 2021 are illustrated in Table 2.

The States of Paraná, Santa Catarina, and Goiás showed more races identified in the country. Paraná has the highest virulence diversity concerning *C. lindemuthianum*; 65 races are present (73.03% of all races found in Brazil). This state was also Brazil's largest producer of common bean in 2018/2019, with a mean yield of 1,551 kg ha-1 (Companhia Nacional de Abastecimento [CONAB], 2019). The wide distribution of *C. lindemuthianum* in this region facilitates the pathogen's adaptation to various climatic conditions.

Table 2. Races of *Colletotrichum lindemuthianum* characterized in Brazil from 1991 to 2021.

States	Nº of races	Races	References
Bahia	7	23, 65, 71, 81, 87, 101 and 119.	Rava, Purchio and Sartorato (1994); Mesquita, Paula Júnior, Moreira, and Barros (1998); Alzate-Marin and Sartorato (2004).
Distrito Federal	7	65, 69, 73, 81, 87, 101 and 119.	Rava et al. (1994); Alzate-Marin and Sartorato (2004).
Espirito Santo	9	64, 65, 67, 72, 73, 75, 79, 87 and 585.	Rava et al. (1994); Mesquita et al. (1998); Alzate-Marin and Sartorato (2004).
Goiás	18	8, 23, 65, 69, 71, 73, 77, 81, 83, 87, 89, 97, 109, 117, 119, 125, 127 and 593.	Rava et al. (1994); Mesquita et al. (1998); Alzate-Marin & Sartorato (2004); Talamini et al. (2004).
Mato Grosso	11	1, 8, 9, 10, 24, 64, 65, 72, 73, 81 and 114.	Gonçalves-Vidigal, Nunes, Cruz, Sousa and Vidigal Filho (2009); Felipin-Azevedo et al. (2014).
Mato Grosso do Sul	3	89, 339 and 343.	Rava et al. (1994).
Minas Gerais	15	0, 8, 64, 65, 66, 69, 73, 81, 83, 85, 87, 89, 119, 337 and 585.	Rava et al. (1994); Talamini et al. (2004); Alzate-Marin and Sartorato (2004); Silva, Souza, Sartorato, & Ishikawa (2007);

			Pinto, Pereira, Mota, Ishikawa and Souza (2012).
Paraíba	2	65 and 73.	Rava et al. (1994); Mesquita *et al.* (1998); Alzate-Marin and Sartorato (2004).
Paraná	65	0, 1, 2, 3, 7, 8, 9, 10, 11, 17, 24, 25, 26, 27, 31, 52, 55, 64, 65, 67, 69, 72, 73, 75, 77, 79, 81, 82, 83, 85, 87, 89, 90, 91, 93, 95, 96, 97, 101, 102, 105, 109, 123, 127, 137, 193, 249, 259, 283, 287, 320, 321, 337, 339, 343, 345, 346, 351, 453, 457, 465, 475, 585, 1,601 and 1,609.	Rava et al. (1994); Mesquita et al. (1998); Carneiro (1999); Thomazella, Gonçalves-Vidigal, Vidigal Filho, Nunes and Vida, (2002); Alzate-Marin and Sartorato (2004); Sansigolo, Gonçalves-Vidigal, Vidigal Filho, Gonela and Kvitschal (2008); Barcelos, Souza and Silva, (2011); Uchôa et al. (2015); Xavier et al. (2018).
Pernambuco	20	2, 3, 7, 8, 9, 10, 23, 64, 65, 72, 73, 75, 81, 85, 87, 89, 117, 119, 139 and 331.	Rava et al. (1994); Alzate-Marin and Sartorato (2004); Martiniano-Souza et al. (2021).
Rio de Janeiro	1	73	Rava et al. (1994); Alzate-Marin and Sartorato (2004).
Rio Grande do Sul	17	5, 17, 23, 31, 55, 64, 65, 67, 69, 72, 73, 77, 81, 83, 87, 97 and 453.	Rava et al. (1994); Mesquita et al. (1998); Somavilla & Prestes (1999); Alzate-Marin and Sartorato (2004).
Santa Catarina	22	7, 55, 65, 67, 73, 75, 77, 81, 83, 86, 87, 89, 95, 101, 103, 105, 109, 111, 121, 217, 249 and 581.	Balardin, Jarosz and Kelly (1990); Rava et al. (1994); Alzate-Marin and Sartorato (2004); Gonçalves-Vidigal, Thomazella, Vidigal Filho, Kvitschal and Elias (2008).
São Paulo	15	4, 23, 31, 38, 55, 65, 73, 81, 83, 85, 87, 89, 95, 127 and 351.	Talamini et al. (2004); Silva et al., (2007); Ribeiro et al. 2016.
Sergipe	1	89	Rava et al. (1994); Alzate-Marin and Sartorato (2004).
Brazil[1]	26	0, 8, 9, 55, 64, 65, 67, 69, 71, 72, 73, 81, 91, 83, 85, 87, 89, 91, 93, 97, 321, 329, 337, 479, 513, 529, 535 and 593.	Silva et al. (2005); Ishikawa, Souza, Silva and Freire (2008); Wendland, Abud, Melo, Pereira and Díaz (2011).

[1]Races reported in the literature as occurring in Brazil; however, their geographical origin in Brazil was not given.

Santa Catarina ranks second in virulence diversity, with 22 races (24.72% in the country). Pinto et al. (2012) analyzed 74 *C. lindemuthianum* isolates and reported the occurrence of six races, with races 65 and 81 being predominant. The state of Pernambuco ranked third in virulence with 20 races of *C. lindemuthianum* characterized. In Goias state 18 races were characterized, while in the Rio Grande

do Sul were identified 15 races. Studies have reported the importance of races 65, 73, 81, and 87 in Brazil, and these races have been detected in almost all states for more than 20 years (Alzate-Marin & Sartorato, 2004; Talamini et al., 2004; Silva et al., 2007; Ribeiro et al., 2016). Race 73 is the most frequently found over the years, present in 13 of the 14 states examined. Race 65 is currently in 12 states and race 81 is present in 11 states.

Previous studies by Balardin, Jarosz, and Kelly (1997) showed only races 7, 65, and 73 to be widely distributed. Somavilla & Prestes (1999) characterized 100 isolates from different Brazilian regions. Only races 81, 65, 73, and 321 were present in all investigated areas. In 1990, races 7 and 73 were first identified in Michigan, USA, and 73 persevered for over 29 years (Kelly, Awale, & Wiersma, 2020). The appearance of race 109 suggests that the resistance allele *Co-1*^{2} from the Kaboon cultivar had been overcome (Awale, Bornowski, Wright, Varner, & Kelly, 2018). Therefore, monitoring the appearance of new races is essential for breeding programs and the adoption of different resistance genes for pyramiding as a breeding strategy for durable resistance.

Balardin and Kelly (1998) reported that the simultaneous production of Andean and Mesoamerican beans in the same region might allow for the selection of broader virulence in *C. lindemuthianum*, with some races being highly virulent toward genotypes from both gene pools. This fact would explain the capacity of some races to adapt to more than one region; for example, races 65, and 73, which are widely spread across crop regions. In addition, to coevolution between a pathogen and a host, seed handling is a determining factor in the geographical distribution of the pathogen. Ferreira, Campa and Pérez-Veja (2008) noticed that an extensive geographic distribution of some races might be explained by the presence of the pathogen in seeds.

Virulence index

The virulence index of *C. lindemuthianum* races ranges from 0% (no virulence observed in race 0) to 66.7%, corresponding to race 479, which is virulent on eight from the 12 differential cultivars (Figure 2). The 89 races of *C. lindemuthianum* characterized in Brazil were distributed in nine groups based on its virulence index (VI). Besides, two groups are formed by only one race. The first group involves race 0, which does not cause symptoms on the 12 differential cultivars. Therefore, resistance genes of the differential cultivars (Table 1) can control anthracnose in regions where this race was identified (Paraná and Minas Gerais). The other group formed by only one race contains the race 479, the most virulent race found in Brazil because it breaks the resistance of Michelite (*Co-11*), MDRK (*Co-1*), Perry Marrow (*Co-1*^{3}), Cornell 49-242 (*Co-2*), Widusa (*Co-1*^{5}), Mexico 222 (*Co-3*), PI 207262 (*Co-3*^{3} and *Co-4*^{3}) and TO (*Co-4*). The races 127, 351, and 475 formed a group which has in common overcome the resistance of the following differential cultivars: Michelite (*Co-11*), MDRK (*Co-1*), Cornell 49-242 (*Co-2*), Widusa (*Co-1*^{5}), Mexico 222 (*Co-3*).

A total of 12 races had a VI of 16.7%, which can overcome the resistance of two of the 12 differential cultivars. Seventeen races, with a VI of 25%, form one group and can overcome the resistance of three differential cultivars. The 33.3% VI group contains 21 races, overcoming the resistance of four differential cultivars. The next group contains 21 races; however, it had a VI of 41.7%, and the members overcame the resistance of five differential cultivars. These data suggest that among the 89 races, 71 overcome the anthracnose resistance genes present in two

to six differential cultivars.

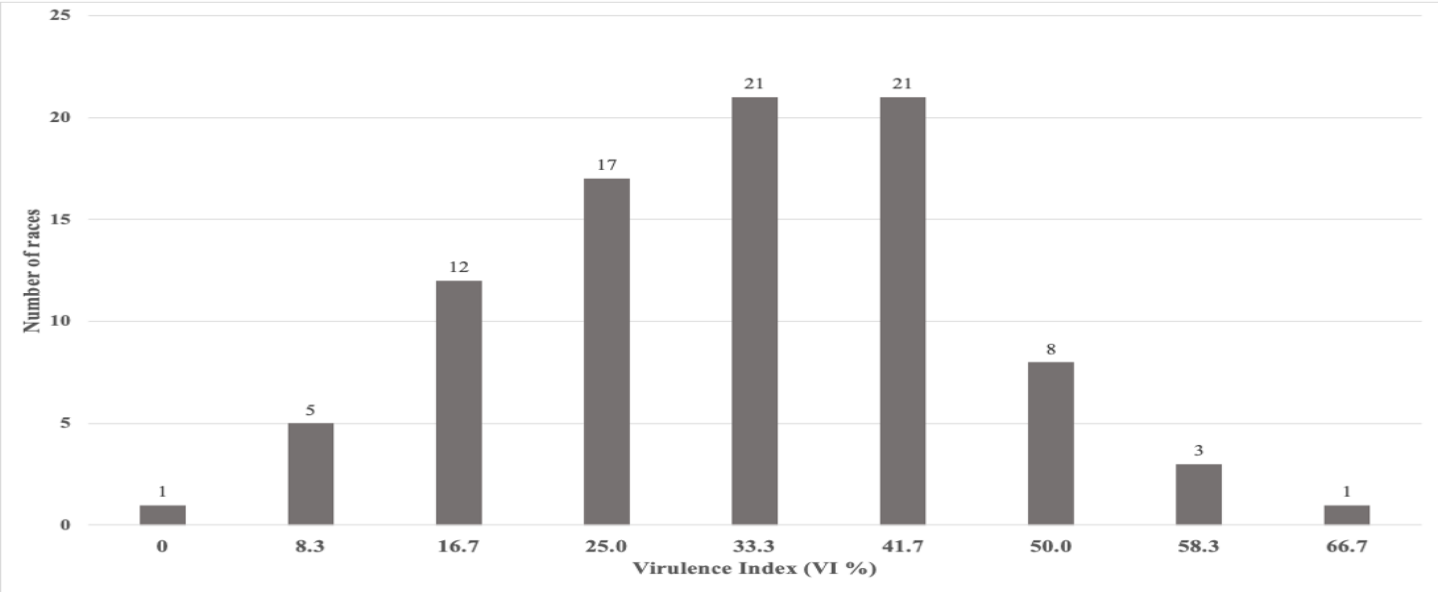

Figure 2. Resistance index of 12 common bean differential cultivars to 89 races of *Colletotrichum lindemuthianum* characterized in Brazil from 1991 to 2021.

Resistance index and resistance sources

Figure 3 shows the resistance index (RI) for each of the 12 differential cultivars calculated for the 89 races reported in Brazil from 1991 to 2021. Many races exhibit strong adaptability in regions of high-yield beans. Concerning resistance reactions to the races in Brazil, we observed that the differential cultivars with the most significant resistance index are the Mesoamerican cultivar G 2333 with 100% resistance to 89 races of the pathogen, followed by AB 136 with 98%, TU with 91%, and PI 207262 with 89%. Furthermore, six differential cultivars, wherein four are Mesoamerican and two Andean, exhibited high resistance to the 89 races in Brazil of *C. lindemuthianum* noticed across 30 years.

These four Mesoamerican differential cultivars harbor different anthracnose resistance alleles. G 2333, a highly resistant genotype originating from Mexico (Chiapas), contains the resistance alleles *Co-3*^{5}, *Co-4*^{2}, and *Co-5*^{2}. TU with resistance gene *Co-5*, AB 136 with *Co-6,* and PI 207262 with *Co-3*^{3} and *Co-4* are also essential sources of anthracnose resistance worldwide. It is important to emphasize that two Andean differential cultivars, Kaboon and Perry Marrow, display high resistance levels, at 79% and 63%, respectively. The cultivars Kaboon and Perry Marrow have broad and effective resistance to highly virulent Mesoamerican races. The Andean cultivars Kaboon has the *Co-1*^{2} allele, and Perry Marrow carries the *Co-1*^{3} allele. By studying the resistance reaction of differential cultivars exposed to two essential races of *C. lindemuthianum* (31 and 89), Gonçalves-Vidigal et al. (2001) verified the efficiency of the differential cultivars G 2333, AB 136, and PI 207262, which possess resistance genes that are not compatible with the prevalent races. These authors suggested the use of these cultivars in breeding programs. These cultivars are excellent sources of resistance to anthracnose in other regions (Thomazella et al., 2002; Gonçalves-Vidigal, Thomazella, Vidigal Filho, Kvitschal, & Elias, 2008).

The Andean genes *Co-1*^{2} (Kaboon), *Co-1*^{4} (AND 277), *Co-13* (Jalo Listras Pretas), *Co-12* (Jalo Vermelho), *Co-14* (Pitanga), *Co-15* (Corinthiano), *Co-Pa* (Paloma), *Co-AC*, (Amendoim Cavalo), Co-*Bf* (Beija Flor), *CoPv01*^{CDRK} (California Dark Red Kidney); and the Mesoamerican genes *Co-3*^{4} (Ouro Negro), *Co-16* (Crioulo 159), *Co-5* (TU) *Co-3*^{3} and *Co-4* (PI 207262), *Co-6* (AB 136), *Co-3/Co-4*^{2}*/Co-5*^{2} (G 2333), and *Co-4*^{2} and *Co-17* (SEL 1308) are known to confer resistance to most races reported in Brazil and around the world. Thus, pyramiding the genes described above through molecular markers can help reduce the time and cost of introducing commercial common bean cultivars. These single resistance genes are easy to transfer to new commercial cultivars, but there is a risk of overcoming the resistance to new virulence races of *C. lindemuthianum*.

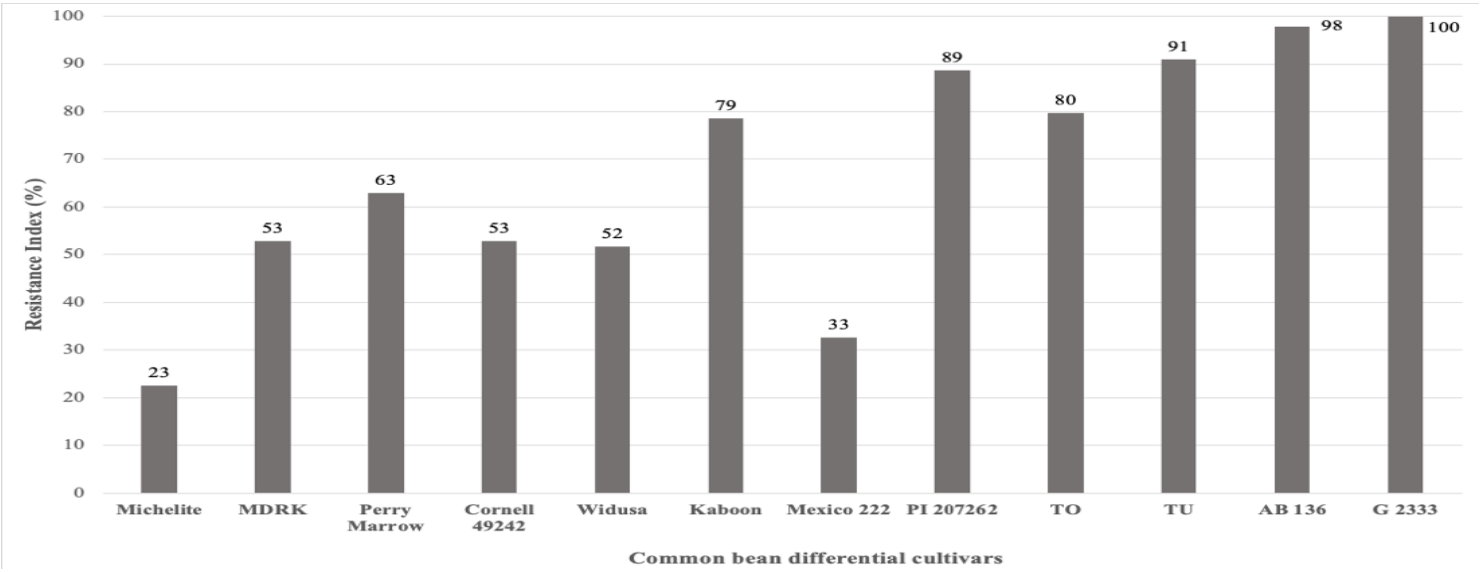

Figure 3. Virulence index of 89 races of *Colletotrichum lindemuthianum* characterized in Brazil from 1991 to 2021 on 12 common bean differential cultivars.

Outline of sources and resistance genes to *Colletotrichum lindemuthianum*

Single and independent genes confer anthracnose resistance in the common bean. Most of these genes have been assigned *Co* symbols, as follows: *Co-1*, *Co-2*, *Co-3*, *Co-4*, *Co-5, Co-6*, *Co-11*, *Co-12*, *Co-13*, *Co-14*, *Co-15*, *Co-16*, and *Co-17* (Campa, Giraldez, & Ferreira, 2009; Vallejo & Kelly, 2009; Gonçalves-Vidigal et al., 2013; Sousa et al., 2014; Sousa et al., 2015; Campa et al., 2014; Lacanallo & Gonçalves-Vidigal, 2015; Trabanco, Campa, & Ferreira, 2015; Zuiderveen, Padder, Kamfwa, Song, & Kelly, 2016; Coimbra-Gonçalves et al., 2016, Murube, Campa, & Ferreira, 2019). Additionally, others genes such as *Co-u, CoPv02* (Geffroy, Sévignac, Billant, Dron, & Langin, 2008; Campa et al., 2014), Co-*y*, *Co-z*, and *Co-RVI* were identified. Some of these genes have been mapped using the reference genome developed by Schmutz et al. (2014) and identified candidate genes. Figure 4 shows the positions of molecular markers linked to anthracnose resistance loci with the physical location on chromosomes Pv01, Pv02, Pv03, Pv04, Pv07, Pv08, and Pv11 of the *Phaseolus vulgaris* reference genome v2.1 (available at https://phytozome.jgi.doe.gov/pz/portal.html). This data is essential to bean breeding programs that seek to broaden the genetic base of the bean crop and to pyramid Andean and Mesoamerican genes conferring resistance to distinct races of

C. lindemuthianum.

Molecular markers linked to anthracnose resistance genes have been identified in the last decades. Remarkably, random amplification of polymorphic DNA (RAPD), amplified fragment length polymorphism (AFLP), and restriction fragment length polymorphism (RFLP) markers were followed by sequence characterized amplified region (SCAR), simple sequence repeat (SSR), and single-nucleotide polymorphism (SNP) marker systems (Young, Melotto, Nodari, & Kelly, 1998; Oblessuc, Francisco, & Melotto, 2015; Gonçalves-Vidigal et al*.,* 2020). Furthermore, the common bean reference genome (Schmutz et al*.,* 2014) has allowed the mapping and comparing the positions of most SCAR, SSR, and SNP markers (Vaz Bisneta & Gonçalves-Vidigal, 2020). This section discussed the progress of anthracnose resistance, focusing mainly on genetic mapping studies and molecular markers linked to ANT resistance alleles in the reference genome of the common bean chromosomes Pv01, Pv02 Pv03, Pv04, Pv07, Pv08, Pv11 (Table 3).

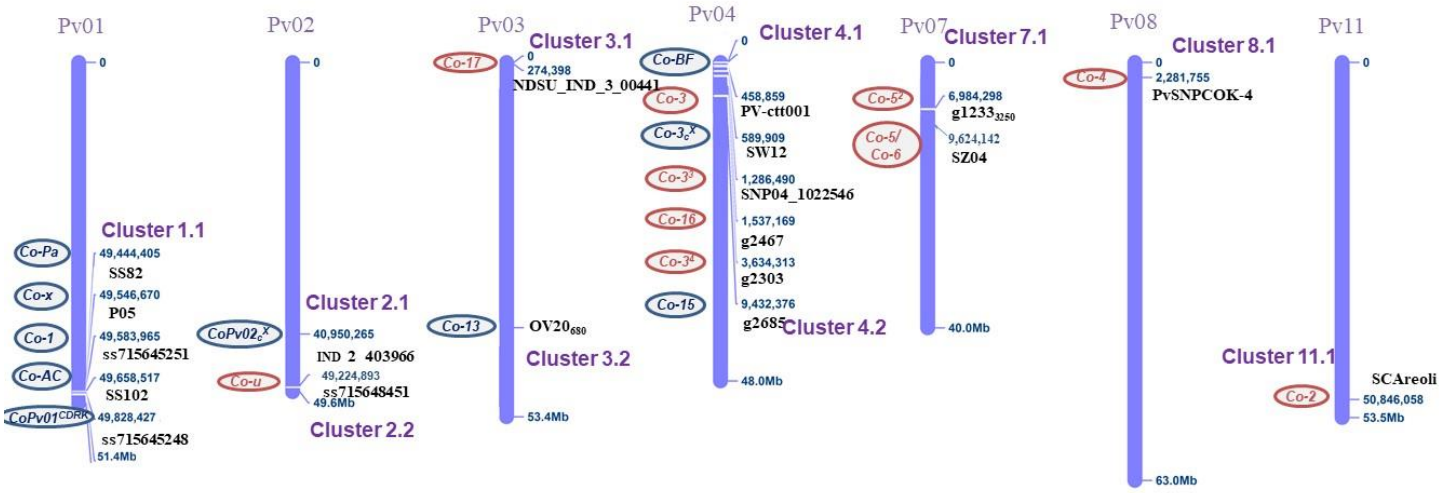

Figure 4. Chromosomal localization of common bean Pv01, Pv02, Pv03, Pv04, Pv07, Pv08, and Pv11 showing the molecular markers tagging ANT resistance loci with their location mapped on the *Phaseolus vulgaris* on reference genome v2.1 (available at https://phytozome.jgi.doe.gov/pz/portal.html).

Chromosome Pv01

The *Co-1* primary resistance locus and its alleles, such as *Co-1*^{2}, *Co-1*^{3}, *Co-1*^{4}, *Co-1*^{5}, *Co-1*^{HY}, and *Co-1*^{X} were mapped in the genomic region of 49,583,965 bp (Gonçalves-Vidigal et al., 2011; Campa et al., 2014; Zuiderveen et al., 2016; Chen et al., 2017; Murube et al., 2019; Melotto & Kelly, 2000).

As shown in Figure 4, the Andean genes *Co-x*, *Co-Pa*, *Co-AC*, and *CoPv01*^{CDRK} are located at the end of Pv01 (Gonçalves-Vidigal et al*.,* 2020; Richard et al., 2014; Castro et al., 2017; Gilio et al., 2020). These genes are mapped in the genomic region from 49,444,405 to 49,828,427 bp, indicating that a gene cluster is involved in resistance to many fungal races. Moreover, the *Co-AC* gene of Amendoim Cavalo was fine-mapped to a 9-kb genomic region at positions between SNP markers SS102 (49,658,517 bp) and SS165 (49,667,961 bp) (Nanami et al., 2017; Gilio et al., 2020). The Andean cultivar California Dark Red Kidney possesses the *CoPv01*^{CDRK} gene flanked by the STS CV542014, and SNP ss715645248 positions 49,795,296 bp

and 49,828,427 bp of chromosome Pv01, spanning 33 kb (Gonçalves-Vidigal et al., 2020).

Table 3. Common bean anthracnose resistance sources, resistance gene or allele, molecular marker, *Phaseolus vulgaris* (Pv) chromosome (chr) and position allele was mapped.

Resistance source	Gene	Molecular Marker	Pv chr	Position v2.1
Michelite	*Co-11*		UM[a]	
MDRK	*Co-1*	ss715645251	Pv01	49,583,965
Perry Marrow	*Co-1*^{3}	ss715645251	Pv01	49,583,965
Cornell 49242	*Co-2*	SCAreoli	Pv11	50,846,058
Widusa	*Co-1*^{5}	ss715645251	Pv01	49,583,965
Kaboon	*Co-1*^{2}	ss715645251	Pv01	49,583,965
Mexico 222	*Co-3*	PV-ctt001	Pv04	458,859
PI 207262	*Co-3*^{3}	SNP04_1022546	Pv04	1,286,490
	Co-4^3	PvSNPCOK-4	Pv08	2,281,755
TO	*Co-4*	PvSNPCOK-4	Pv08	2,281,755
TU	*Co-5*	g12333$_{250}$	Pv07	6,984,298
AB 136	*Co-6*	SZ04	Pv07	9,624,142
G 2333	*Co-3*^{5}	SNP04_1022546	Pv04	1,286,490
	Co-5^2	g12333$_{250}$	Pv07	6,984,298
	Co-4^2	PvSNPCOK-4	Pv08	2,281,755
Jalo EEP558	*Co-x*	P05	Pv01	49,546,670
Hongyundou	*Co-1*^{HY}	TF1	Pv01	49,570,786
Amendoim Cavalo	*Co-AC*	SS102	Pv01	49,658,517
CDRK	*CoPv01*^{CDRK}	ss715645248	Pv01	49,828,427
AND 277	*Co-1*^{4}	ss715645251	Pv01	49,583,965
Paloma	*Co-Pa*	SS82	Pv01	49,444,405
Xana	*Co-1*^{x}	SNP01_483	Pv01	49,512,545
	CoPv02c^X	IND_2_403966	Pv02	40,950,265
	Co-3c^X	SW12	Pv04	589,909
BAT 93	*Co-u*	close to *I* gene	Pv02	
	Co-3^3	SNP04_1022546	Pv04	1,286,490
Jalo Vermelho	*Co-12*		UM	
Jalo Listras Pretas	*Co-13*	OV20$_{680}$	Pv03	NA[b]
Pitanga	*Co-14*		UM	
Corinthiano	*Co-15*	g2685	Pv04	9,432,376
Beija Flor	*Co-Bf*		Pv04	3,592
Crioulo 159	*Co-16*	g2467	Pv04	1,537,169
SEL1308	*Co-17*	NDSU_IND_3_00441	Pv03	551,937
	Co-4^2	PvSNPCOK-4	Pv08	2,281,755
Mexico 227	*Co-3*^{2}	PV-ctt001	Pv04	458,859
Ouro Negro	*Co-3*^{4}	g2303	Pv04	3634313
SEL 1360	*Co-5*^{2}	g12333$_{250}$	Pv07	6,984,298
MSU7-1	*Co-5*^{2}	g12333$_{250}$	Pv07	6,984,298

[a]UM, Unmapped resistance gene; [b]NA, not alligned in the reference genome v2.1.

Chromosome Pv02

The gene *Co-u* in the cultivar BAT 93 was mapped at the end of Pv02 close to the *I* locus, conferring resistance to viruses (Geffroy et al., 2008). The Xana cultivar carries the gene *CoPv02c*^{X} that was mapped to chromosome Pv02, using the markers IND_2_403966 at the position 40,950,265 bp and IND_2_404411 at 40,981,170 bp (Campa et al., 2014).

Chromosome Pv03

On chromosome Pv03 have been mapped the resistance genes *Co-13* and *Co-17* (Lacanallo & Gonçalves-Vidigal, 2015; Trabanco et al., 2015). *Co-13* gene in cultivar Jalo Listras Pretas was mapped at a distance of 1.8 cM of the marker OPV20680, as shown in Figure 4. The *Co-17* gene of SEL1308 was mapped to Pv03 at a distance of 9.7 cM from the InDel marker NDSU_IND_3_0.0441 (551,937 bp); this gene also maps to 554,412 bp, linked to the marker B6 (Trabanco et al., 2015).

Chromosome Pv04

Figure 4 shows the chromosome Pv04 containing the resistance gene *Co-3* and its allelic series (*Co-3*^{2}, *Co-3*^{3}, *Co-3*^{4}, and *Co-3*^{5}) as well as *Co-15* and *Co-16* (Young et al., 1998; Geffroy et al., 1999; Gonçalves-Vidigal et al., 2013; Sousa et al., 2015; Coimbra-Gonçalves et al., 2016). *Co-3* present in Mexico 222 is linked to molecular marker PV-ctt001 in the genomic region from 458,859 bp to 459,022 bp (Rodríguez-Suárez, Ferreira, Campa, Pañeda, & Giraldez, 2008). Additionally, *Co-3*^{3} in BAT 93 was fine-mapped to two regions at the beginning of chromosome 4, from 1,286,490 bp to 1,419,089 bp between markers SNP04_1022546 and SNP04_1308175 and a second region between IND04_10936 (1,908,814 bp) and SNP04_1231633 (2,047,754 bp) markers (Murube et al., 2019). The cultivar Ouro Negro harboring the *Co-3*^{4} allele was first mapped to the Pv04, linked to the STS g2303 marker at position 3,634,313 bp (Gonçalves-Vidigal et al., 2013). *Co-16* in Crioulo 159 is linked to the marker g2467$^{900/800}$ mapped to the position of 1,537,169 bp on Pv04 (Coimbra-Gonçalves et al., 2016). Moreover, the Andean cultivar Corinthiano carries the independent gene *Co-15* linked to the sequence-tagged site (STS) marker g2685 on Pv04, at 9,432,376 bp (Sousa et al., 2015).

Chromosome Pv07

The Mesoamerican cultivars TU, SEL 1360, G 2333, MSU-7, AB 136 carry resistance genes conferring resistance to different races of *C. lindemuthianum* mapped on chromosome Pv07 in Figure 4. The TU cultivar exhibits resistance to races 3, 6, 7, 31, 38, 39, 102, and 449 in a cluster that appears to correspond to *Co-5* (Campa et al., 2009). A second allele, *Co-5*^{2}, is present in cultivars G 2333 and MSU-7. The different resistance spectra between TU and G 2333 present another allele in G 2333, renaming it *Co-5*^{2} (Vallejo & Kelly, 2009).

As shown Figure 4, the *Co-5*^{2} resistance allele, which confers resistance to Race 64 of *C. lindemuthianum*, is also present in MSU 7-1 and linked to the marker g1233$_{3250}$ region from 6,984,298 bp to 7,020,710 bp (Sousa et al., 2014). The gene *Co-6* present in AB 136 confers resistance to races 23, 31, 64, 65, 69, 453, and 449 linked to the marker SZ04 at position 9,624,142 Pv07 (Campa et al., 2017).

Chromosome Pv08

G 2333 carries three resistance genes. The major one is *Co-4²* (Young et al*.,* 1998; Silvério et al*.,* 2002). Mesoamerican resistance gene *Co-4* and its alleles (*Co-4²* and *Co-4³*) have been mapped from 2,281,755 to 2,301,726 on Pv08. Although the RAPD $OAS13_{950}$ and SAS13 markers have been linked to resistance genes in TO (*Co-4*) and G 2333 (*Co-4²*), they are absent in control (susceptible) cultivars (Young et al*.,* 1998). The allele *Co-4²* is present in SEL 1308, a cultivar derived from G 2333. Studies of the fine mapping of *Co-4* have been conducted by cloning the gene sequence associated with the SAS13 marker, linked to *Co-4* at 0.39 cM (Melotto & Kelly, 2001). Oblessuc et al. (2015) mapped the *Co-4* locus in a 325-kb region adjacent to the telomere of Pv08 containing the markers SAS13, PvTA25, and PvSPICK-4. Mesoamerican *Co-4²* anthracnose resistance allele confers resistance to all races of the anthracnose pathogen in Brazil.

Chromosome Pv11

The cultivar Cornell 49-242 possesses the *Co-2* gene, one of the essential ANT resistance genes linked to SCAreoli from 50,846,058 bp to 50,925,118 bp of Pv11 (Kelly & Young, 1996; Geffroy et al., 1998). Cornell 49-242, from Venezuela, was widely used in breeding programs in the 1970s. Nevertheless, the continuous use of cultivars carrying the *Co-2* gene led to host-pathogen coevolution and the appearance of new races able to overcome the resistance due to *Co-2* (Kelly & Vallejo, 2004).

C. lindemuthianum and *Phaseolus vulgaris* L. coevolution

Andean races of the anthracnose pathogen are usually isolated from large-seeded beans that belong to the Andean gene pool. In contrast, Mesoamerican races are often, but not always, isolated from small or medium-seeded beans belonging to the Mesoamerican gene pool—the Mesoamerican races of the fungus exhibit considerably greater virulence genetic diversity than the Andean races (Pastor-Corrales, 2004; Kelly & Vallejo, 2004). More importantly, the Andean races are compatible only or mainly with Andean beans. In contrast, Mesoamerican races are compatible with both Mesoamerican and Andean beans. Also, anthracnose resistance loci from Mesoamerican beans are significant for controlling Andean races (Kelly & Vallejo, 2004).

It has been posited that the Andean and Mesoamerican races of *C. lindemuthianum* have evolved separately. The wide virulence reported in this review suggests that knowing the diversity of the *C. lindemuthianum* pathogen of the common bean is an actual effort to assist breeders in developing cultivars with effective and hopefully durable anthracnose resistance. Anthracnose Andean resistance genes might be used to manage anthracnose disease in areas where Mesoamerican races are more common than the Andean races. Furthermore, sources of resistance to anthracnose of Mesoamerican origin might manage Andean races. Combining several genes in a single cultivar should be helpful to achieve durable resistance to the highly variable pathogen that causes anthracnose in the common bean.

FINAL COMMENTS

In this report, we noticed that C. *lindemuthianum* is widely distributed and adapted to different bean-growing regions in Brazil. Herein we reported 30 years of *C. lindemuthianum* diversity in Brazil. The data shown in this study can help breeding programs to develop common bean cultivars resistant to anthracnose in Brazil. Excellent opportunities for rapid and efficient development of molecular markers tightly linked to resistance genes can be obtained due to the accessibility to complete common bean genome sequence. Herein, information on identified anthracnose resistance genes can be found with the genome position, facilitating marker-assisted selection. In the future, resources should propitiate better marker systems such as KASP, SSRs, and SNPs for the fungus population structure studies. The wide virulence reported in this review suggests that knowing the diversity of the *C. lindemuthianum* pathogen of the common bean is a real effort to assist breeders in developing cultivars with effective and hopefully durable anthracnose resistance.

The availability of genomic information is significant while breeding for resistance is gaining considerable attention, and gene pyramiding represents an ambitious challenge for breeding programs to achieve durable resistance. The ease of using a complete genome sequence of common bean offers many opportunities for the rapid and efficient development of molecular markers tightly linked to resistance genes. The knowledge of specific races of *C. lindemuthianum* in each state of Brazil and the understanding of disease resistance alleles with molecular markers and position in the bean genome will assist the bean breeder and facilitate marker-assisted use selection. The aspects discussed in this review contribute to knowledge that may be helpful for common bean breeding programs focused on developing cultivars resistant to anthracnose.

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