Received: 9 June 2022 | Accepted: 9 December 2022

DOI: 10.1002/csc2.20905

Crop Science

ORIGINAL ARTICLE

Genomics, Molecular Genetics & Biotechnology

Genetic fine-mapping of anthracnose disease-resistance allele *Co-1*^{4} present in the Andean common bean cultivar AND 277

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Assigned to Associate Editor Francisco Gomez

Funding information
Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, Grant/Award Numbers: BEX 88881.170662//2018-01, BEX 88887.470337/2019-00; Conselho Nacional de Desenvolvimento Científico e Tecnológico, Grant/Award Numbers: 301861/2017-0, 311599/2017-6, 408472/2018-9

Abstract

Anthracnose (ANT) is among the common bean fungal diseases responsible for significant yield and grain quality losses. Durable genetic resistance is the primary ANT control method due to the pathogen's high variability. Genetic studies showed that the common bean chromosome Pv01 contains multiple disease resistance genes, including the ANT resistance loci *Co-1* (*Co-1*^{2}, *Co-1*^{3}, *Co-1*^{4}, *Co-1*^{5}, *Co-1*^{HY}, and *Co-1*^{x}), *Co-AC*, *Co-1*^{4}, *Co-Pa*, *Co-Perla*, *Co-w*, *Co-x*, and *CoPv01*^{CDRK}. This work aimed to: (i) perform the genetic fine-mapping of the *Co-1*^{4} allele present in the cultivar AND 277, using recombinant inbred lines derived from the cross between Rudá × AND 277; and (ii) identify candidate resistance genes in the *Co-1*^{4} allele based on the common bean reference genome. Initially, the *Co-1*^{4} allele was mapped between the single-nucleotide polymorphism markers ss715645251 and ss715645250 at a distance of 2.0 and 19.6 cM, respectively. Fine-mapping localized *Co-1*^{4} between the markers ss715645251 and BARCPVSSR01356, spanning a 40.51 kb region at the end of Pv01. Two genes are described within the *Co-1*^{4} region in the reference genome, Phvul.001G243800 and Phvul.001G243900. The linkage between the *Co-1*^{4} allele and the markers ss715645251 and BARCPVSSR01356 will be essential for plant breeding programs during the resistance gene transfer to elite cultivars via marker-assisted selection (MAS). Identifying and functionally analyzing candidate resistance genes in this region will allow more efficient MAS by developing accurate markers for ANT resistance.

Abbreviations: ALS, angular leaf spot; NT, anthracnose; bp, base pair; CIAT, International Center for Tropical Agriculture; *Co*, *Colletotrichum lindemuthianum* resistance locus; LOD, minimum likelihood of odds; LRR-RLK, leucine-rich repeat-receptor-like kinase; MAS, marker-assisted selection; NBS-LRR, nucleotide-binding site-leucine-rich repeat; NCBI, National Center for Biotechnology Information; *Phg*, *Pseudocercospora griseola* resistance locus; Pv, *Phaseolus vulgaris* chromosome; RA, Rudá x AND 277 cross; RIL, recombinant inbred line; SNP, single-nucleotide polymorphism; SSD, single-seed descent; SSR, simple sequence repeats; STS, sequence-tagged site; *Ur*, *Uromyces appendiculatus* resistance locus.

1 | INTRODUCTION

The common bean is an essential legume for direct human consumption globally. It constitutes one of the most traditional foods in the diet of Brazilians and thousands of people in several countries, being a cheap alternative protein source (Broughton et al., 2003; Gepts et al., 2008; Vaz Patto et al., 2015). Rich in essential nutrients such as protein, iron, calcium, magnesium, zinc, vitamins (mainly B-complex), carbohydrates, and fiber, common bean grains have great nutritional value, especially when complemented with a carbohydrate source such as rice (Mesquita et al., 2007).

Domesticated differently in the Mesoamerican and Andean regions, the common bean genetic variability in the Mesoamerican and Andean large gene pools allows its exploitation for breeding programs (Gepts, 1988). Mesoamerican and Andean cultivars are commercially important worldwide and are commonly grown in the American, European, and African continents (Bitocchi et al., 2012; Bitocchi et al., 2013; Cichy et al., 2015; Gepts, 1988; Kelly & Vallejo, 2004). Nonetheless, despite this wide variability, the common bean genetic improvement still presents significant limitations due to the great influence of edaphoclimatic factors, which can lead to abiotic or biotic stresses.

Anthracnose (ANT) stands out among the main issues faced by the bean crop. Triggered by the fungus *Colletotrichum lindemuthianum* (Sacc. and Magnus) Briosi and Cavara, ANT development is favorable in environmental conditions of moderate temperature and high humidity, causing considerable yield losses and grain quality depreciation. ANT is mainly a seed born disease (Ferreira et al., 2013; Singh & Schwartz, 2010; Wortmann et al., 1998), and the large pathogenic (Balardin & Kelly, 1998) and molecular (Ansari et al., 2004; Coêlho et al., 2016; Davide, 2006) variability of the pathogen are observed in bean-producing areas worldwide, highlighting the use of resistant cultivars as the primary ANT control strategy (Caldas et al., 2016; Nunes et al., 2021). On the other hand, small and medium producers have widely adopted integrated management when resistant cultivars are not readily available.

Unlike other plant species, the common bean presents a highly organizational clustering of disease resistance genes, usually located at the ends of its chromosomes (Meziadi et al., 2016). Common bean chromosome Pv01 is known to have the ANT resistance locus *Co-1*, the alleles *Co-1*^{2}, *Co-1*^{3}, *Co-1*^{4}, *Co-1*^{5}, *Co-1*^{HY}, *Co-1*^{X}, as well as the other loci *Co-AC*, *Co-Pa*, *Co-Perla*, *Co-14*, *Co-w*, *Co-x*, and *CoPv01*^{CDRK}, as well as *Ur-9* and *Phg-1* against rust and angular leaf spot (ALS), respectively (Alzate-Marin et al., 2003; Campa et al., 2014; Chen et al., 2017; Geffroy et al., 2008; Gilio et al., 2020; Gonçalves-Vidigal & Kelly, 2006; Gonçalves-Vidigal et al., 2011; Gonçalves-Vidigal et al., 2012; Gonçalves-Vidigal et al., 2016; Gonçalves-Vidigal et al., 2020; Jung et al., 1998; Lima Castro et al., 2017; McRostie, 1919; Melotto & Kelly, 2000; Paulino et al., 2019).

Core Ideas

- Fine mapping *Colletotrichum lindemuthianum* race 3481 resistance in cultivar AND 277.
- The cultivar AND 277 shows a significant resistance spectrum and presents *Co-1*^{4}*/Phg-1* genes mapped in the Pv01.
- Genetic mapping of the *Co-1*^{4} allele using recombinant inbred lines.
- Molecular markers linked to *Co-1*^{4} allele at the end of the Pv01.
- Candidate genes in the region of the *Co-1*^{4} allele for anthracnose resistance.

The Andean cultivar AND 277, developed by the International Center for Tropical Agriculture, Colombia (CIAT; Arruda et al., 2008), is considered an important source of resistance to multiple diseases such as ANT, ALS, and rust and has been widely used in bean breeding programs in Brazil and Southern Africa (Arruda et al., 2008; Carvalho et al., 1998). Notably, AND 277 possesses a resistance gene cluster at Pv01 containing two strongly linked disease resistance loci *Co-1*^{4} and *Phg-1* (Gonçalves-Vidigal et al., 2011), exhibiting a broad-spectrum resistance to races 9, 23, 64, 65, 67, 73, 75, 81, 83, 87, 89, 97, 117, 119, 339, 343, 449, 453, 1033, 2047, and 3481 of *C. lindemuthianum* (Alzate-Marin et al, 2003; Arruda et al., 2008; Lima Castro et al., 2017) and races 7–15, 15–7, 23–23, 31–7, 31–17, 31–31, 31–39, 47–39, 61–31, 61–41, 63–6, 63–7, 63–19, 63–23, 63–31, 63–35, 63–47, and 63–63 of *Pseudocercospora griseola* (Borges et al., 2013; Caixeta et al., 2005). Still, a low genetic variability is observed in the Andean common bean gene pool relative to the Mesoamerican gene pool; therefore, timely information on resistance genes in cultivars belonging to this group provides an additional variability source reservoir. Consequently, additional information generated by studying the Andean gene pool benefits the pyramiding of resistance genes to obtain durable genetic resistance, controlling the rapid evolution of new races of the pathogen (Zuiderveen et al., 2016).

Obtaining molecular markers linked to multiple disease resistance genes has contributed to the common bean breeding worldwide (Valentini et al., 2017). Due to the high-throughput characteristic of single-nucleotide polymorphism (SNP) genotyping technologies, SNP markers have been increasingly used to evaluate the implementation of multiple alleles in elite cultivars (Burt et al., 2015), mainly the ones strongly linked to loci associated with traits of interest (Michelmore et al., 2013). Therefore, it has allowed obtaining

elite cultivars with multiple resistance genes and more precise information about gene clusters' dynamics.

The present research aimed to perform the genetic fine-mapping of the *Co-1*^{4} allele present in the cultivar AND 277, using recombinant inbred lines (RILs) derived from the cross between Rudá × AND 277 and to identify candidate resistance genes in the *Co-1*^{4} allele based on the common bean reference genome. This study offers an opportunity for the rapid development of gene-specific markers that will promote the breeding of resistant elite cultivars.

2 | MATERIALS AND METHODS

2.1 | Plant genetic material

A total of 137 RILs from the cross between the common bean cultivars Rudá and AND 277 (RA) were used in this work (Sanglard et al., 2013; Silva et al., 2018). Parental lines were kindly provided by the Embrapa Arroz e Feijão, Santo Antônio de Goiás, Brazil. The parental line Rudá was developed by the CIAT, Colombia, from the cross between Carioca and Rio Tibagi, thus having carioca-type grains belonging to the Mesoamerican gene pool. Rudá was released as a cultivar in Brazil in 1995 by the Embrapa Arroz e Feijão (Embrapa-Empresa Brasileira de Pesquisa Agropecuaria, 2022). The AND 277 cultivar is a cranberry type grain and is considered an essential source of Andean resistance to ANT and ALS, containing the resistance loci *Co-1*^{4} and *Phg-1* (Gonçalves-Vidigal et al., 2011). AND 277 was developed by the CIAT from the multiple crosses: (Cargabello × [Pompadour Checa x Linea17]) × (Linea 17 x RedCloud) (Aggarwal et al., 2004; Arruda et al., 2008).

The Rudá × AND 277 (RA) RILs were developed by the BIOAGRO common bean genetics and breeding research groups from the Universidade Federal de Viçosa, Brazil and Embrapa Arroz e Feijão, Brazil. As the parental lines have contrasting flower phenotypes, white (recessive phenotype) in the female Rudá and pink (dominant phenotype) in the male AND 277, the F_1 hybrid plants were identified by flower color. The F_2 individuals were grown and self-fertilized to the F_9 generation in a greenhouse using the single seed descent (SSD) method; subsequently, individual plants were harvested, and seeds multiplied in the field until F_{12} (Sanglard et al., 2013; Silva et al., 2018).

2.2 | Genotyping-by-sequencing

DNA from RA RILs was extracted using bulked leaf tissue samples from 10 plants for each RIL and parental lines. The DNA extraction and purification were performed using the Spin Plant Mini Kit (Invisorb®, Berlin, Germany), according to the manufacturer's instructions. SNP genotyping of all 137 RILs and the two parental lines was performed at the Soybean Genomics and Improvement Laboratory, USDA-ARS/BARC-W (Beltsville, MD, USA), using the Illumina BARCBean6K_3 BeadChip (consisting of 5,398 SNP) and the Illumina Infinium® HD Assay Ultra genotyping platform, as described by Song et al. (2015). The results obtained from the BeadChip were visualized using the Illumina BeadArray Reader, and the SNP calling was performed using the Genome Studio v2.0 software (Illumina, San Diego, CA, USA). Automatic allele recall for each locus was performed with the GenomeStudio Genotyping Module v2.0 software (Illumina, San Diego, CA, USA) and later visually checked for manual cluster adjustment in cases of erroneous clusters. Data were filtered by removing SNPs no polymorphic between the parents Rudá and AND 277 (Zhao et al., 2018), resulting in 219 high-quality SNPs, which were included in the mapping analysis in the PV01.

2.3 | Genetic mapping

SNP markers with an expected segregation ratio of 1:1 in the RA RIL mapping population, based on the chi-square test (χ^2) performed by the Genes software (Cruz, 2013), were used to create a linkage map using the default settings of the JoinMap 4.0 software (Van Ooijen, 2006). Distances between markers were calculated from the default settings of the Regression Mapping algorithm based on the Kosambi map function and by converting recombination frequencies into genetic distances in centimorgans (cM). A minimum likelihood of odds of 3.0 or above (LOD $\geq$ 3.0) and a recombination frequency inferior to 4.0 (rf $<$ 0.40) were used to test the linkage among markers. The map that best fitted the order of markers was selected to represent the chromosome for all generated linkage groups. Co-segregating markers were considered a single locus. The linkage map was designed using the MapChart software (Voorrips, 2002).

2.4 | Phenotypic evaluation

A total of 137 RA RILs had the reaction to *C. lindemuthianum* evaluated twice. Before sowing, 10 seeds from each RILs and parental lines were disinfected in 1.5% NaClO solution for 2 min and washed in tap water. Disinfected seeds were sowed in plastic trays (dimensions 0.45 × 0.29 × 0.10 m) containing MecPlant® commercial substrate (Register EP PB 09549-4/Mapa Brazil, MEC PREC—Ind. Com Ltda, Telemaco Borba, PR, Brazil), previously sterilized in a Phoenix AV-225 Plus autoclave at 120°C and 1 atm for 1 h. Plants were kept in the greenhouse until the inoculation date.

Plants were inoculated with *C. lindemuthianum* race 3481, obtained from the mycology collection of the Núcleo de Pesquisa Aplicada à Agricultura (Nupagri), Universidade Estadual de Maringá, Brazil. The *C. lindemuthianum* race 3481 was selected due to its contrasting pathogenic spectrum concerning the parentals Rudá (susceptible) and AND 277 (resistant), as reported in a previous study (Lima Castro et al., 2017). In addition, in each assay, the cultivars Paloma (resistant) and Jalo Vermelho (susceptible) were used as inoculation controls as reported by Lima Castro et al. (2017). The race 3481 was confirmed by evaluating the reaction of the 12 common bean differential cultivars for ANT (Pastor-Corrales, 1991), as well as the RIL parental lines to confirm the contrasting phenotype. The inoculum was prepared at the Nupagri (Núcleo de Pesquisa Aplicada à Agricultura, Universidade Estadual de Maringá, State of Paraná, Brazil.

Initially, the *C. lindemuthianum* race 3481 was grown in test tubes containing water agar medium and sterilized young green bean pods, incubated in a biochemical oxygen demand (BOD) chamber at 22°C for 14 days (Cárdenas et al., 1964). Next, the inoculum was produced by collecting the spores of the pathogen. The spore's concentration was adjusted to 1.2×10^6 conidia mL^{-1} using sterile distilled water and one drop of Tween 20 emulsifier for each 100 mL of the solution, promoting its interfacial tension reduction and allowing a more consistent inoculation. The RA RILs and parents (Rudá and AND 277) inoculation was performed by sprinkling the inoculum on the abaxial and adaxial faces of the first fully expanded trifoliolate leaf (V_3 stage) with the help of a hand sprayer. After inoculation, the plants were kept in a mist chamber with a relative humidity greater than 95% for 72 h, under 20 ± 2°C, with controlled light (680 lux) and 12 h of photoperiod. After this period, the plants' trays were removed from the mist chamber and maintained on benches with the same controlled temperature and luminosity for seven days. The symptoms were evaluated according to the disease scale proposed by Pastor-Corrales et al. (1995), which grades from 1 to 9, wherein plants with disease reaction scores of 1 to 3 were considered resistant, while those with 4 to 9 were considered susceptible.

2.5 | *Co-1*^{4} fine-mapping

After analyzing and identifying the recombinant RA RILs containing the resistant *Co-1*^{4} allele, the first young trifoliate leaf from each selected RIL and parents were collected and stored in −80°C freezer for further DNA extraction. Genomic DNA extraction was performed according to the method described by Afanador et al. (1993), modified by using 400 µL of CTAB extraction buffer.

Fine-mapping was performed from the amplification of 12 single sequence repeat (SSR) markers (Table 1) and two sequence-tagged site (STS) markers, namely CV542014 (forward—CACTTTCCACTGACGGATTTGAACC and reverse—CAGAGGATGCTTCTCACGGT) and TGA 1.1 (forward—CAGAGGATGCTTCTCACGGT and reverse—AAGCCATGG ATCCCATTTG), using the genomic DNA extracted from Rudá (susceptible), AND 277 (resistant), and 29 RA RILs. The SSR and STS markers used were selected based on the SNP mapping results.

The PCR mixes were prepared following the procedures validated at Nupagri laboratory: "30 ng of genomic DNA, 0.25 µM of forward and reverse primers, 1 X PCR Buffer (200 mM Tris-HCl [pH 8.0], 500 mM KCl, 2 mM each dNTP, 10% glycerol, 15 mM $MgCl_2$, and 20 ng/µL of single-strand binding protein [SSB]), and 0.1 unit of Taq DNA polymerase (Invitrogen, Carlsbad, CA, USA). The amplification cycles consisted of 3 min at 92°C; followed by 38 cycles of 50 s at 90°C, 45 s at 58°C, and 45 s at 72°C; a 5 min extension at 72°C; and a hold at 10°C. A 2 µL aliquot of loading buffer (30% glycerol and 0.25% bromophenol blue) was added to the PCR products, which were then fractionated on 6% polyacrylamide gels at $3WA^{-1}$ cm^{-1}. The amplified fragments were stained using SYBR Safe (0.02%), and the DNA bands were visualized under ultraviolet light. Digital images were recorded using an L-PIX Image EX (Loccus Biotecnologia-Loccus do Brasil, Cotia, SP, Brazil)" according to Gonçalves-Vidigal et al. (2020).

The additional markers that mapped within the *Co-1*^{4} region established by the SNPs mapping analysis were used to resolve the *Co-1*^{4} physical position in the common bean reference genome.

2.6 | Identification of candidate genes for ANT resistance and their functional annotation

Aiming at identifying putative candidate genes for the resistance loci, the methodology described by Gonçalves-Vidigal et al. (2020) was used. The *P. vulgaris* reference genome v.1.0 (Schmutz et al., 2014) available in NCBI v.1.0 (https://www.ncbi.nlm.nih.gov) was used to define the physical position of the markers flanking the *Co-1*^{4} resistance loci. The putative genes within this genomic region were attributed as candidate genes for resistance or susceptibility to ANT. The putative functional annotation of each candidate gene was based on the descriptions available in Phytozome v.1.0 (https://phytozome.jgi.doe.gov#).

For each candidate gene, the possible *Arabidopsis thaliana* homologs were identified using the BLASTp tool of the NCBI (https://www.ncbi.nlm.nih.gov). Protein alignments with the lowest E-value (E-value < 0.0) and highest identity (identity > 40%) were considered putative homologs and used to infer molecular function.

TABLE 1 Simple sequence repeats (SSR) markers used for fine-mapping the *Co-1*^{4} allele. SSR motifs, size, physical position in the common bean reference genome v1.0, and forward and reverse primer sequences are listed

SSR BARC	Motif	Motif length (bp)	Physical position (bp)	Forward (F) and reverse (R) primer sequence
BARCPVSSR01356	(TA)12	24	50,342,103	F: CCATTAACCAAGGCATAATCAC
				R: TCGATTTGGTTGGTGAGTTAAA
BARCPVSSR01358	(AAG)10	30	50,350,345	F: TGGCTGGTTGGTGTTTATGA
				R: GGTCCCACCCTCTTCTCTTC
BARCPVSSR01360	(TA)17	34	50,360,637	F: ACTCAATTGAATTTTGGCGA
				R: ATGGGCTTTACCCAAAGGAT
BARCPVSSR01361	(AT)10	20	50,388,017	F: GAATGGTTCATCGTTCATGG
				R: TCGGCTGTTTAACGTGGTCT
BARCPVSSR01364	(TA)10	20	50,533,162	F: TCATAAAGTATTTTTATGCAACACATT
				R: CCATTATTGATTTTGGGCGT
BARCPVSSR01370	(AT)16	32	50,685,692	F: ATGCCGTGACGGACAATAAT
				R: TGCATTGGCTTCCATTGATA
BARCPVSSR01372	(AT)13	26	50,724,094	F: GAAAATATGACAAGTTAGTCCAACAA
				R: GAAGATGAAGATCCACCTCTTTTT
BARCPVSSR01377	(TTA)10	30	50,856,104	F: TTTTTCCTCTGATGTTGGCA
				R: TTTCCCATTTTACCAACCAAA
BARCPVSSR01382	(AAT)16	48	51,029,620	F: TGGTGTTTACCCAATGGTTC
				R: GAACTGCGTTAAAAACATCCG
BARCPVSSR01385	(TA)21	42	51,131,421	F: TGGAGAGAAAACAAATGCGA
				R: TCCGTAACGATTTTGTTCCTAAA
BARCPVSSR01390	(TA)22	44	51,228,222	F: TGGGCTAACATAATTTAAAATCGAA
				R: ACCCTTGCTAAGCCTGTGAA
BARCPVSSR01398	(TA)14	28	51,406,854	F: GAGAGCCCTTGATGTTGCAT
				R: TCCGAATTTCTTAATTTCACTTT

TABLE 2 Segregation for resistance to race 3481 of *Colletotrichum lindemuthianum* observed in the common bean Rudá × AND 277 RIL population

Genotype	Generation	Expected frequency (1R:1S)	Observed frequency (1R:1S)	χ^2	*p*-Value
AND 277	*RP*	20:0	–	–	–
Rudá	*SP*	0:20	–	–	–
RILs (Rudá × AND 277)	F_{12}	68.5:68.5	71:66	0.182	0.669

Abbreviations: R, resistant; S, susceptible; RP, resistant parent; SP, susceptible parent.

3 | RESULTS AND DISCUSSION

3.1 | Inheritance of resistance

Phenotyping analysis of 137 RILs derived from the cross Rudá (susceptible) × AND 277 (resistant) inoculated with the race 3481 of *C. lindemuthianum* showed an expected adjusted segregation ratio of 1AA:1aa ($\chi^2 = 0.182$; $p = 0.669$). Among these, 71 RILs presented resistant phenotype, and 66 were susceptible plants (Table 2). Such results corroborate with the segregation of the *Co-1*^{4} allele observed in previous studies conducted by Alzate-Marin et al. (2003) and Gonçalves-Vidigal et al. (2011), indicating inheritance conditioned by a dominant gene.

The Andean cultivar AND 277 is an essential resistance source for breeding programs because of its broad-spectrum resistance against both Andean and Mesoamerican races of *C. lindemuthianum*. Notably, AND 277 shows resistance to the highly virulent races 2047 and 3481 which, together with the cultivars Paloma and Amendoim Cavalo, is the only Andean cultivar resistant to both races (Gilio et al., 2020; Lima Castro et al., 2017).

C. lindemuthianum race 3481 was first collected and identified in Costa Rica and Argentina (Mahuku & Riascos, 2004). It has significant economic importance because it overcomes the resistance of 7 (Michelite, Cornell 49–242, Widusa, PI 207262, TO, AB136, and G2333) out of the 12 differential cultivars, with emphasis on cultivar G2333, which carries three resistance genes (*Co-3*^{5}, *Co-4*^{2}, and *Co-5*^{2}) against ANT. For this reason, studies to identify resistance sources to different *C. lindemuthianum* races are critical to support common bean breeding programs, such as the present research on the AND 277 that contains the *Co-1*^{4} allele.

3.2 | Mapping the *Co-1*^{4} allele

Mapping studies play an essential role in identifying trait-related genetic markers, allowing the understanding of resistance alleles' behavior and their pyramiding into elite cultivars. The *Co-1*^{4} allele was first identified by Alzate-Marin et al. (2003) and mapped by Gonçalves-Vidigal et al. (2011) between the STS molecular markers CV542014 and TGA 1.1 at the end of the chromosome Pv01.

Genetic linkage analysis was performed with the SNP genotyping data of the BARCBean6K_3 Illumina BeadChip and phenotyping data of the 137 RA RILs infected with *C. lindemuthianum* race 3481. All 29 SNPs polymorphic for the RA parents and with expected segregation ratio (1:1) among RILs were positioned at the chromosome Pv01 end, spanning a region of 38.4 cM (Figure 1a). This region containing the *Co-1*^{4} allele was flanked by the SNP markers ss715645251 (50,301,592 bp) and ss715645250 (51,726,047 bp).

Pv01 is considered one of the major and most studied common bean chromosomes for presenting a resistance gene cluster at its terminal end against three of the principal economically important diseases of common bean (Meziadi et al., 2016; Schmutz et al., 2014). This region features a total of eight ANT resistance loci (*Co-1*, *Co-AC*, *Co-Pa*, *Co-Perla*, *Co-14*, *Co-w*, *Co-x*, and *CoPv01*^{CDRK}) and one allelic series (*Co-1*^{2}, *Co-1*^{3}, *Co-1*^{4}, *Co-1*^{5}, *Co-1*^{HY}, and *Co-1*^{x}) so far identified and mapped (Vaz Bisneta & Gonçalves-Vidigal, 2020).

3.3 | Fine-mapping of the *Co-1*^{4} allele

High-resolution mapping of the 1.4 Mb genome region between the SNP markers ss715645251 (50,301,592 bp) and ss715645250 (51,726,047 bp), which flank the *Co-1*^{4} allele on chromosome Pv01, was performed by genotyping 29 RA RILs showing recombination between these SNPs (Figure 1a). According to the molecular data obtained from 12 SSR and two STS markers (Table 1), nine recombination events were observed at the *Co-1*^{4} allele. RA RILs named 23, 263, 293, 296, 300, 331, 336, 342, and 368 were identified as recombinants (Table 3). The refined *Co-1*^{4} region resulting from the fine-mapping analysis was delimited between the markers ss715645251 and BARCPVSSR01356 (Figure 1b). Based on the G19833 reference genome v1.0, the refined *Co-1*^{4} genome location lies between 50,301,592 and 50,342,103 bp at the end of Pv01, encompassing a region of 40.51 kb (Table 3; Figure 2b).

Similar results were obtained by Zuiderveen et al. (2016) from a genome-wide association analysis (GWAS) using an Andean Diversity Panel and the RIL population derived from the cross Jaguar × Puebla 152. The authors found *Co-1* resistance gene against races 65, 73, and 3481 associated with the SNP marker ss715645251 at the position 50,301,592 bp at Pv01. Additionally, Zuiderveen et al. (2016) identified the InDel marker NDSU_IND_1_50.2219 (50.22 Mb) tightly linked to four alleles at the *Co-1* locus (Michigan Dark Red Kidney), *Co-1*^{2} (Kaboon and Bolt cultivars), *Co-1*^{3} (Perry Marrow), *Co-1*^{4} (AND 277), and *Co-x* (Jalo EEP558).

The *Co-x* was first identified in the cultivar Jalo EEP 558 by Geffroy et al. (2008) and is considered a possible allele of the *Co-1* locus. Later, *Co-x* was mapped on chromosome Pv01, between markers P05 and K06, physically located at 50,264,307 and 50,322,583 bp, respectively (Richard et al., 2014). As the *Co-1*^{4} mapped between ss715645251 and BARCPVSSR01356 markers, it overlaps in 20.99 kb with the genome region defined for the *Co-x* locus (Figure 2b). Moreover, Chen et al. (2017) identified an ANT resistance allele in the cultivar Hongyundou, which was named *Co-1*^{HY} because allelism tests identified it as an allele of the *Co-1* locus. *Co-1*^{HY} high-resolution mapping delimited its position between TF1 and Clp-N1 InDel markers, corresponding to a physical position between 50,286,325 and 50,332,945 bp at Pv01. Thus, a large part of the *Co-1*^{HY} allele overlaps with the *Co-1*^{4} region (Figure 2b).

Other ANT resistance locus present in Pv01 was subjected to high-resolution mapping to identify candidate genes acting during the pathogen infection process. In the Andean cultivar Amendoim Cavalo, the *Co-AC* gene was identified by Gilio et al. (2020) in the region flanked by markers SS102 (50,377,247 bp) and SS165 (50,386,692 bp); therefore, *Co-AC* is located 35.14 kb from *Co-1*^{4} (Figure 2b). More recently, Gonçalves-Vidigal et al. (2020) identified and mapped the *CoPv01*^{CDRK} ANT resistance locus present in the cultivar California Dark Red Kidney (CDRK) between the markers CV542014 (50,513,853 bp) and ss715645248 (50,546,985 bp), at the end of chromosome Pv01. Based on the physical position of the markers found in this study, the *CoPv01*^{CDRK} locus is 171.75 kb from the *Co-1*^{4} (Figure 2b). Additionally, the authors identified

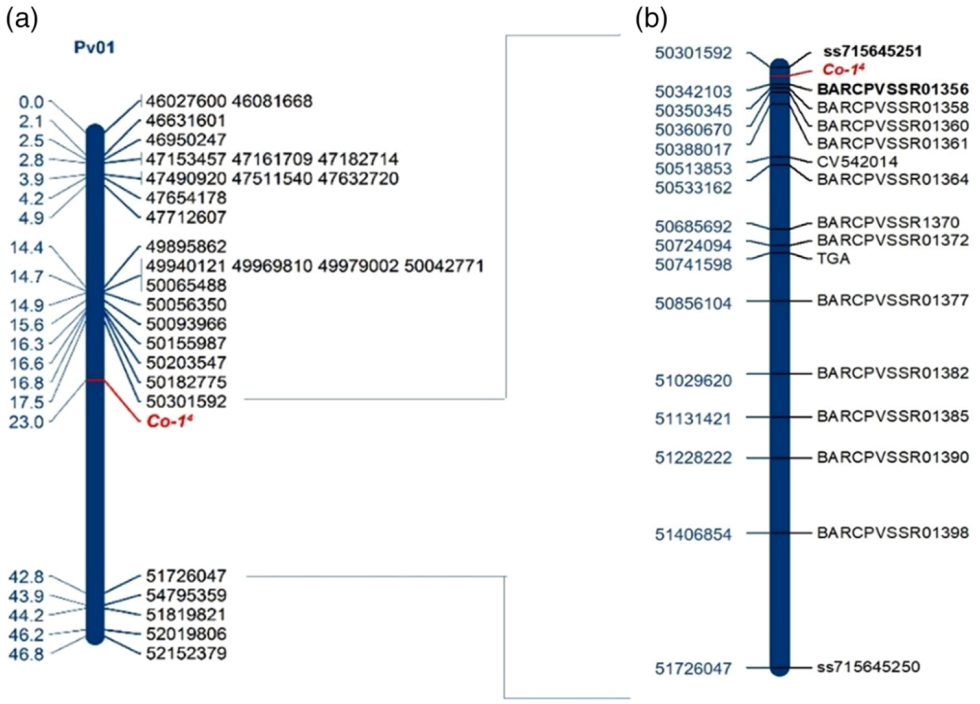

FIGURE 1 (a) Genetic map of common bean linkage group Pv01 containing the anthracnose resistance allele and single-nucleotide polymorphism (SNP) markers segregating in the recombinant inbred line (RIL) population Rudá × AND 277. The genetic distances in centimorgans (cM) are shown on the left side, and the physical positions (bp) on the right side. (b) Fine-mapping of the *Co-1*^{4} allele using simple sequence repeats (SSR) and sequence-tagged site (STS) markers positioned in a region of 40.511 kb

TABLE 3 The genotype of 29 F_{12} recombinant events with two single-nucleotide polymorphisms (SNPs), 12 simple sequence repeats (SSRs), two sequence-tagged site (STS) markers, and phenotype using race 3481 for fine mapping of the Co-1^4 anthracnose resistance allele. The ss715645251 and BARCPVSSR01356 markers enabled the positioning of the Co-1^4 allele in a 40.51 kb region

Marker	Position	Recombinant inbred lines Rudá × AND 277																												
		8	23	27	56	81	110	130	131	140	149	182	214	226	236	242	263	281	293	296	300	304	313	331	336	342	346	361	368	385
ss715645251	50301592	AA	BB	AA	AA	BB	BB	BB	BB	BB	BB	AA	AA	AA	BB	BB	AA	AA	AA	AA	BB	AA	AA	BB	AA	BB	AA	BB	AA	AA
Co-1^4		AA	BB	AA	AA	BB	BB	BB	BB	BB	BB	AA	AA	AA	BB	BB	AA	AA	AA	AA	BB	AA	AA	BB	AA	BB	AA	BB	AA	AA
BARCPVSSR01356	50342103	AA	AA	AA	AA	BB	BB	BB	BB	BB	BB	AA	AA	AA	BB	BB	BB	AA	BB	BB	AA	AA	AA	AA	BB	AA	AA	BB	BB	AA
BARCPVSSR01358	50350345	AA	BB	AA	AA	BB	BB	BB	BB	BB	BB	AA	AA	BB	BB	BB	BB	AA	AA	AA	BB	AA	AA	AA	AA	BB	AA	BB	AA	AA
BARCPVSSR01360	50360670	AA	BB	AA	AA	BB	BB	BB	BB	BB	BB	AA	AA	BB	BB	BB	BB	AA	AA	AA	BB	AA	AA	AA	AA	BB	AA	BB	AA	AA
BARCPVSSR01361	50388017	AA	BB	AA	AA	BB	BB	BB	BB	BB	BB	AA	AA	BB	BB	BB	BB	AA	AA	AA	BB	AA	AA	AA	AA	BB	AA	BB	AA	AA
CV542014	50513853	-	BB	AA	AA	BB	BB	BB	BB	BB	BB	AA	AA	BB	BB	BB	BB	AA	AA	AA	BB	AA	AA	AA	AA	BB	AA	BB	AA	AA
BARCPVSSR01364	50533162	AA	BB	AA	AA	BB	BB	BB	BB	BB	BB	AA	BB	BB	BB	BB	BB	AA	AA	AA	BB	AA	-	AA	AA	BB	AA	BB	AA	AA
5BARCPVSSR1370	50685692	BB	BB	AA	AA	AA	AA	BB	BB	BB	BB	AA	BB	BB	BB	BB	BB	AA	AA	BB	BB	AA	AA	AA	AA	BB	AA	BB	AA	BB
BARCPVSSR01372	50724094	BB	BB	AA	AA	BB	AA	BB	BB	BB	AA	AA	AA	AA	AA	AA	AA	AA	AA	AA	BB	AA	AA	AA	AA	BB	AA	BB	AA	BB
TGA 1.1	50741598	BB	BB	BB	AA	BB	AA	BB	BB	BB	BB	BB	BB	BB	AA	BB	AA	AA	AA	BB	BB	AA	AA	AA	AA	BB	AA	BB	AA	BB
BARCPVSSR01377	50856104	BB	BB	BB	AA	BB	AA	BB	BB	BB	BB	BB	BB	BB	AA	BB	AA	AA	AA	BB	BB	AA	BB	AA	AA	BB	AA	BB	AA	BB
BARCPVSSR01385	51131421	BB	BB	BB	AA	BB	AA	BB	BB	BB	BB	BB	BB	BB	AA	BB	BB	AA	AA	BB	BB	AA	BB	AA	AA	BB	BB	BB	AA	BB
BARCPVSSR01382	51029620	BB	BB	BB	AA	BB	AA	BB	BB	BB	BB	BB	BB	BB	AA	BB	BB	AA	AA	BB	AA	AA	BB	AA	AA	BB	BB	BB	AA	BB
BARCPVSSR01390	51228222	BB	BB	BB	AA	BB	-	BB	BB	BB	BB	BB	-	BB	AA	BB	BB	AA	AA	BB	-	AA	BB	AA	AA	BB	BB	BB	BB	BB
BARCPVSSR01398	51406854	BB	BB	BB	AA	BB	AA	BB	BB	BB	AA	BB	BB	BB	AA	AA	BB	BB	BB	BB	BB	AA	BB	AA	AA	BB	BB	AA	BB	BB
ss715645250	51726047	BB	AA	BB	BB	AA	AA	AA	AA	AA	AA	BB	BB	BB	AA	AA	BB	BB	BB	BB	AA	BB	BB	AA	BB	AA	BB	AA	BB	BB

Abbreviations: AA, resistant; BB, susceptible; AB, heterozygous; –, not evaluated.

co-segregation between *CoPv01*^{CDRK} and *PhgPv01*^{CDRK}, a resistance locus against ALS (Gonçalves-Vidigal et al., 2020).

The results obtained in this study confirmed that the *Co-1*^{4} allele is physically in the same region of the previously mapped *Co-1* locus, and distance 171.75 kb from *CoPv01*^{CDRK}. The high-resolution mapping performed by different research groups indicates the existence of a resistance gene cluster and shows a partial overlap between *Co-1*^{4}, *Co-1*^{HY}, and *Co-x* (Figure 2b; Chen et al., 2017; Richard et al., 2014; Zuiderveen et al., 2016). Further studies are necessary to identify the specific genes and/or alleles,

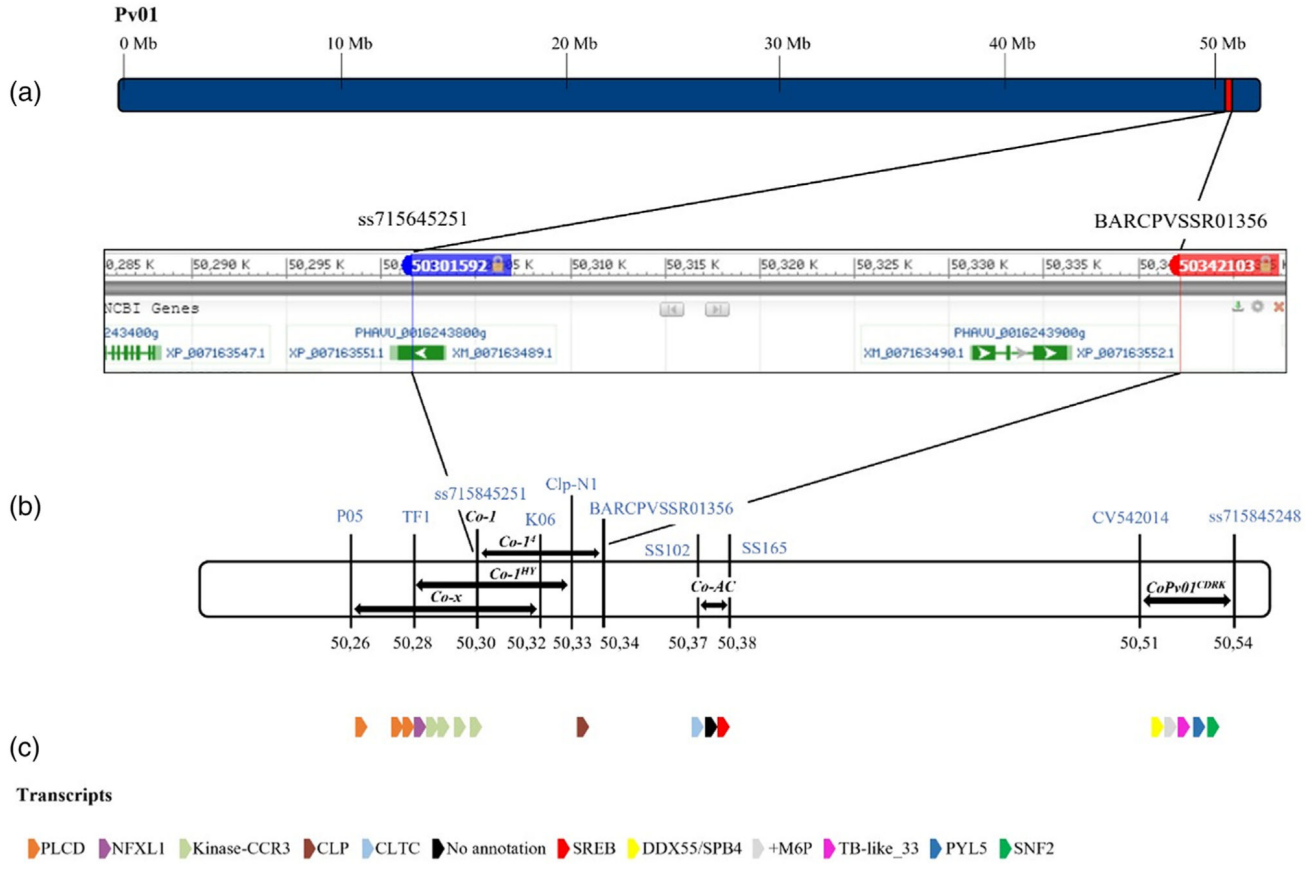

FIGURE 2 Genomic boundaries of the bean anthracnose resistance *Co-1*^{4} allele. (a) Genome browser representation of the common bean chromosome 1 (Pv01), in which the *Co-1*^{4} allele region is highlighted in red and zoomed out, revealing two predicted genes in this region. (b) Comparison between the physical positions (Mb) of the *Co*-loci at the end of Pv01 and their predicted transcripts is shown below (arrows). Genes are color-coded according to their predicted functions. Orange: phosphatidylinositol phospholipase C delta protein (PLCD); purple: NF-X1 type zinc finger protein (NFXL1); green: serine/threonine-protein kinase-like CCR3-related protein (kinase-CCR3); brown: double Clp-n motif-containing P-loop nucleoside triphosphate hydrolases superfamily protein (CLP); blue: clathrin heavy chain protein (CLTC); black: Protein with unknown function; red: sterol regulatory element binding protein (SREB); yellow: ATP-dependent RNA helicase (DDX55/SPB4); gray: cation-dependent mannose-6-phosphate receptor (+M6P); pink: protein trichome birefringence-like 33 (TB-like_33); dark blue: abscisic acid receptor PYL5; dark green: SNF2 domain-containing protein CLASSY 1-related

and the relationship between them, conferring resistance to each pathogen/race.

3.4 | Candidate genes for ANT resistance in the *Co-1*^{4} allele

Candidate genes involved in the common bean resistance against ANT were identified based on the information from the *P. vulgaris* G19833 reference genome v1.0. Two predicted genes (*Phvul.001G243800* and *Phvul.001G243900*) were positioned within the 40.51 kb region of the *Co-1*^{4} allele (Figure 2b). The *Phvul.001G243800* gene encodes a Serine/Threonine-Protein Kinase-Like CCR3-Related whereas *Phvul.001G243900* encodes for a double Clp-N motif-containing P-loop nucleoside triphosphate hydrolases superfamily protein. Additional functional reference was obtained by homology analysis with *A. thaliana* proteins, considering identity values above 40%. The *Phvul.001G243800* is a putative homolog of the *A. thaliana* CRINKLY4-related 3 (CCR3), and *Phvul.001G243900* shows homology to the *A. thaliana* SMAX1-Like (Table 4).

Among the different mechanisms activated during plant defense against pathogens, the specific recognition mediated by nucleotide binding site (NBS)-leucine-rich repeat (LRR) proteins is usually and frequently indicated for the genetic improvement of plants. This recognition is responsible for activating different biochemical pathways and processes within cells, including ion flux, oxidative reactions, defense gene expression, antimicrobial compounds production, and systemic resistance (Oliveira et al., 2016). Moreover, defense responses can be accompanied by a localized programmed cell death at the site of infection, called hypersensitivity response (HR) (Oliveira et al., 2016). The LRR-receptor-like

TABLE 4 Gene models found in the fine-mapped Co-1^4 region, their functional annotation in the reference genome v1.0, and homology (identity > 40%) with *Arabidopsis thaliana* proteins

Phaseolus vulgaris gene identifier	*A. thaliana* homolog	E-value[a]	Identity[a]	Functional annotation on TAIR[b]	Functional annotation on Phytozome[c]
Phvul.001G243800	AT3G55950	0	58.57%	CRINKLY4-related 3 (CCR3)	Serine/threonine-protein kinase-like protein CCR3-related
Phvul.001G243900	AT2G40130	2×10^{-128}	49.90%	Suppressor of MAX1-Like (SMAX1-Like)	Double Clp-N motif-containing P-loop nucleoside triphosphate hydrolases superfamily protein

[a]E-values and Identity for BLASTp analysis performed on NCBI (National Center for Biotechnology Information; https://www.ncbi.nlm.nih.gov);
[b]Functional gene annotation resource: TAIR—The Arabidopsis Information Resource (https://www.arabidopsis.org);
[c]Functional gene annotation resource: Phytozome—Common bean reference genome v1.0 (https://phytozome.jgi.doe.gov).

kinase (RLK) class of proteins stands out as the largest receptor-like group in plants activating HR, among other plant responses. Among the superfamily of protein kinases, serine/threonine kinases (STKs) are responsible for phosphorylating serine and threonine residues and allow interaction with other proteins, thereby affecting a wide range of processes, including disease resistance and developmental regulation (Goring & Walker, 2004).

In the genomic region of the *Co-1*^{4} allele, the candidate gene *Phvul.001G243800* encoding serine-threonine kinase was identified, corroborating those results obtained by Zuiderveen et al. (2016) and Richard et al. (2014) for *Co-1* and *Co-x* locus, respectively. Moreover, as a CCR3-related, *Phvul.001G243800* is probably a CRINKLY4 (CR4) family member like its *A. thaliana* homolog AT3G55950. CR4 are RLK proteins characterized by having a predicted signal sequence, a unique transmembrane region, and a cytoplasmic kinase domain (Shiu & Bleecker, 2001). First identified in maize (*Zea mays*), ZmCR4 was shown to be essential for a complex set of processes in plant and grain endosperm development (Becraft et al., 1996).

In *A. thaliana*, the CR4 family of kinases is represented by five members: the ARABIDOPSIS CR4 (ACR4), AtCRR1, AtCRR2, AtCRR3, and AtCRK1 (Cao et al., 2005; Meyer et al., 2015). The ACR4 role in resistance was observed on the *A. thaliana* mutant *acr4* inoculated with the pathogen *Botrytis cinerea*. The knocking-down *acr4* mutant showed a reduction in leaf necrosis caused by this pathogen. Furthermore, previous studies of the *acr4* floral meristem indicated that the *Lipoxygenase2* (*LOX2*) was responsible for encoding an essential enzyme in the jasmonic acid (JA) biosynthesis pathway, which is a critical phytohormone for plant defense (Zereen & Ingram, 2012). Moreover, different interactions between ACR4 and other molecules have been observed in critical signaling pathways controlling root apical meristem development (Hanemian et al., 2016; Stahl et al., 2013). CLV1 is considered an essential molecule with a general function in the disease response during different plant-pathogen interactions (Hanemian et al., 2016; Stahl et al., 2013).

The second candidate gene found in the *Co-1*^{4} genome interval was the *Phvul.001G243900*, which encodes a homolog protein of the *A. thaliana* SUPPRESSOR OF MAX1-LIKE (SMAX1-like). The SMAX1-like family is known to repress strigolactones (SL) signal transduction and is represented by eight members in *A. thaliana*, AtSMAX1 to AtSMAX8 (Stanga et al., 2013). The SLs are plant hormones responsible for vital roles in regulating many aspects of plant development, including seed germination, seedling development, promotion of leaf senescence, and responses to environmental stresses (Stanga et al., 2013; Ueda & Kusaba, 2015). Physiological investigations showed that *smax6*, *smax7*, and *smax8* mutant plants are more tolerant to drought than the wild type. Moreover, these mutant plants showed stomatal hypersensitivity to abscisic acid (ABA), decreased cuticular permeability, and increased anthocyanin biosynthesis during water deficit conditions. Thus, these proteins negatively regulate drought responses (Yang et al., 2020). Further studies suggested that SMAX6, SMAX7, and SMAX8 negatively regulate the expression of genes in the ABI5 water stress response signaling pathway. Among these, the genes *F3H*, *WSD1*, *LEA*, *WRKY46*, and *SAG29* are involved in anthocyanin biosynthesis (thus, having antioxidant properties), cell membrane integrity, cuticle formation, stomatal closure, and ABA responsiveness, respectively (Li et al., 2020). Phvul.001G243900 may also suppress these genes in common bean, regulating plant defense responses and possibly abiotic stress responses. Further studies are needed to verify this hypothesis.

Vaz Bisneta and Gonçalves-Vidigal (2020) identified specific resistance genes near the ANT resistance loci in the chromosome Pv01, revealing an enrichment for genes encoding kinases (22 genes) and NBS-LRR (7 genes). However, the high-resolution mapping performed with different cultivars containing resistance genes mapped on chromosome Pv01 has

shown that most of the ANT resistance candidate genes in the *Co*-loci do not belong to the NBS-LRR family. Instead, these genes are generally linked to secondary pathogen responsive pathways (Gilio et al., 2020; Gonçalves-Vidigal et al., 2020; Lima Castro et al., 2017; Richard et al., 2014).

Richard et al. (2014) mapped the *Co-x* gene in a 58 kb region of Pv01 containing eight candidate genes (Figure 2b), including candidate genes encoding Kinase-CCR3 known to be implicated in a wide range of biological processes, including biotic stress responses. Recently, Richard et al. (2021) analyzed the genes identified in the fine-mapped *Co-x* locus through gene expression analysis during infection with *C. lindemuthianum* strain 100. These authors identified a CR4-family gene, the *CRINKLY4 Kinase Truncated 2/3* (*KTR2/3*), as the primary candidate gene for ANT resistance in this locus. To confirm this hypothesis, 192 common bean genotypes from different geographic regions (including commercial cultivars and wild genotypes) were genotypic and phenotypic evaluated. The results confirmed that the atypical truncated *KTR2/3* kinase gene resulted from recent unequal recombination in the Andean gene pool and is involved in plant immune responses (Richard et al., 2021).

Interestingly, the same four genes from the CR4 family previously described for *Co-1* locus *Phvul.001G243500*, *Phvul.001G243600*, *Phvul.001G243700*, *Phvul.001G243800* were identified in the $Co\text{-}1^{HY}$ allele spanning a 46 kb region in Pv01, between the InDel markers TF1 and Clp-N1 (Chen et al., 2017; Figure 2b). Expression analysis in parental cultivars to identify the candidate genes involved in resistance demonstrated that the four genes are expressed at significantly higher levels in the resistant genotype than in the susceptible genotype, indicating these Kinase-CCR3 genes participate in the resistance response against ANT (Chen et al., 2017).

Moreover, three candidate genes were found within the *Co-AC* locus, encoding a hypothetical protein with clathrin heavy chain (CLTC; *Phvul.001G244300*), an unnamed protein (*Phvul.001G244400*), and a sterol regulatory element-binding protein (SREB; *Phvul.001G244500*) (Figure 2b), involved in plant defense signaling, unknown function, and possible gene transcription, respectively (Gilio et al., 2020). For the $CoPv01^{CDRK}$/$PhgPv01^{CDRK}$ locus, Gonçalves-Vidigal et al. (2020) observed five genes: *Phvul.001G246000* (ATP-dependent RNA helicase), *Phvul.001G246100* (cation-dependent mannose-6-phosphate receptor), *Phvul.001G246200* (protein trichome birefringence-like 33), *Phvul.001G246300* (abscisic acid receptor PYL5), and *Phvul.001G246400* (SNF2 domain-containing protein class 1-related; Figure 2b), which play regulatory roles in chloroplast biogenesis, cell division in root meristems, antifungal hormone responses, cellulose synthesis and deposition, and flavonoid synthesis, respectively. Additionally, these genes were associated with the cell wall strengthening processes in response to fungal penetration and activation of antifungal hormones (Gonçalves-Vidigal et al., 2020).

The defense response against biotic stresses in plants is predominantly regulated by the plant hormones ABA, JA, salicylic acid (SA), and ethylene (ET) (Verma et al., 2016). Plant hormones are generally involved in specific responses or pathways, although crosstalk between them is also observed. However, this interaction between different plant hormones is not entirely understood, in which the type of crosstalk (positive or negative) and the individual contributions of each hormone may affect the final plant response (Verma et al., 2016). In this sense, physiological and biochemical studies would help clarify the signaling networks implicated in plant responses to biotic and abiotic stresses.

Most of the resistance genes identified so far in most studied plant species encode NBS-LRR proteins (Richard et al., 2021). NBS-LRRs frequently reside in mega-clusters with several members located within a few million base pairs (Young, 2000). However, chromosome Pv01 has fewer NBS-LRR genes than the other typical bean chromosomes; therefore, Pv01 is considered an atypical chromosome (Richard et al., 2014). Therefore, further research combining genetic mapping and gene expression analysis of the resistance present in the AND 277 cultivar and other ANT resistant sources will allow a better understanding of the genes identified so far in the Pv01 *Co*-cluster. Besides that, it will improve the overall knowledge of defense mechanisms that do not involve the traditional NBS-LRR pathway.

4 | CONCLUSION

The $Co\text{-}1^4$ allele was fine-mapping in a 40.51 kb interval at Pv01 containing two candidate genes *Phvul.001G243800* and *Phvul.001G243900*, flanked by the markers ss715645251 (50,301,592 bp) and BARCPVSSR01356 (50,342,103 bp). These markers will contribute to common bean breeding programs during the process of resistance gene transfer to elite cultivars via marker-assisted selection (MAS). Additionally, the further investigation of the candidate genes identified in this work by gene expression analysis will allow a better understanding of the $Co\text{-}1^4$ allele performance during common bean resistance to ANT and will allow the development of more accurate markers and consequent efficient MAS.

ACKNOWLEDGMENTS

This research was financially supported by the National Council for Scientific and Technological Development (CNPq). M. C. Gonçalves-Vidigal and P. S. Vidigal Filho are grateful for Grants from CNPq. L. R. L. Lima, M. Vaz Bisneta, and V. S. R. Martins were supported by a scholarship from Capes. The authors acknowledge Dr. T. L. P. O. Souza of the

Embrapa Arroz e Feijão (Santo Antônio de Goiás, GO, Brazil) for kindly provided the seeds of RA RILS.

AUTHOR CONTRIBUTIONS

Laíze Raphaelle Lemos Lima: data curation; formal analysis; investigation; methodology; software; writing—original draft; writing—review and editing. **Maria Celeste Gonçalves-Vidigal**: conceptualization; data curation; formal analysis; funding acquisition; methodology; project administration; resources; writing—original draft; writing—review and editing. **Mariana Vaz Bisneta**: data curation; formal analysis; methodology; software; validation; writing—original draft; writing—review and editing. **Giseli Valentini**: formal analysis; methodology; software. **Pedro Soares Vidigal Filho**: funding acquisition; investigation; project administration; resources. **Vanusa da Silva Ramos Martins**: formal analysis; methodology; supervision. **Thiago Lívio Pessoa Oliveira de Souza**: conceptualization; data curation; resources; software; writing—review and editing.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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How to cite this article: Lima, L. R. L., Gonçalves-Vidigal, M. C., Vaz Bisneta, M., Valentini, G., Filho, P. S. V., Martins, V. S. R., & de Souza, T. L. P. O. (2023). Genetic fine-mapping of anthracnose disease-resistance allele *Co-1*^{4} present in the Andean common bean cultivar AND 277. *Crop Science*, 1–14. https://doi.org/10.1002/csc2.20905