CROP BREEDING AND APPLIED BIOTECHNOLOGY

ARTICLE

Association mapping for common bacterial blight in carioca beans

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Abstract: *Common bacterial blight (CBB) is an important disease in Phaseolus vulgaris L. A carioca diversity panel (CDP) composed of 149 cultivars of common bean was genotyped with 1,616 SNPs and evaluated for Xanthomonas phaseoli pv. phaseoli (Xap) resistance aiming to identify QTLs. Phenotypic evaluation was done in controlled conditions. The plants displayed in a randomized block design, with 3 replications were evaluated ten days after inoculation. GWAS analysis using the BLINK model identified one SNP on chromosome Pv07, with a different genomic location in relation to previous studies. Considering a confidence interval of 100 kb, gene annotation identified 13 candidate genes related to defense-associated genes, and their key functional motives were discussed. The marker identified may constitute an important resource for future marker assisted CBB resistance breeding.*

Keywords: *Disease-resistance inheritance, Xap, GWAS*

INTRODUCTION

Common bean accounts for a considerable proportion of daily nutrients (Assefa et al. 2019). Yield losses caused by plant diseases may reach up to 100%, depending on the aggressiveness of the pathogen (Simons et al. 2021). *Xap* is a gram-negative group of γ-proteobacteria. The symptoms of CBB are observable throughout the plant, manifesting effects from leaves to seeds (Rezene et al. 2018, Belete and Bastas 2017). The pathogen has huge survivability, which can be enhanced by the low temperature conditions used in seed storage (Torres et al. 2009). The disease is present throughout Brazil and is found in all producing regions, especially in the rainy season (Torres et al. 2009).

Control of CBB includes crop management practices, use of chemical pesticides, and genetic resistance. Using chemical control as the main treatment is not effective as the pathogen is quite diverse (Rava and Sartorato 1994). CBB genetic architecture involves both minor and major genes (Simons et al. 2021). Until now, up to 25 minor effect resistance *loci* have been identified across the common bean genome (Simons et al. 2021).

Genome-wide association studies (GWAS) are a powerful tool to unveil disease-resistance inheritance (Uffelmann et al. 2021). For CBB resistance, Shi et al. (2011) found twelve SNPs (Single Nucleotide Polymorphisms) with similar map positions to other CBB QTLs (Quantitative Trait *Loci*). Wu et al. (2017) explored the association mapping of NBS-LRR (nucleotide binding site-leucine

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rich repeat) microsatellites and seven of them also mapped by Shi et al. (2011). Ambachew et al. (2021) detected 14 significant SNPs connected to CBB and over Pv02, Pv04, Pv08, Pv10, and Pv11. Simons et al. (2021) identified 8 regions, including 6 previously mapped and two new loci (Pv11 and Pv10).

The goal of this work was to perform the identification of CBB resistance *loci* by GWAS in carioca diversity panel. From the whole genome-wide investigation, one significant SNP with no overlap in relation to previous studies was found on Pv07, probably addressed to a particular resistance CBB-QTL derived from Brazilian carioca germplasm.

MATERIAL AND METHODS

Plant material and SNP analysis

The CDP of 149 carioca accessions selected from the Germplasm Bank of the Instituto Agronômico, Campinas, SP, Brazil (Almeida et al. 2020, Almeida et al. 2021) was used in this study. The CDP consists of some ancient commercial cariocas to recent released cultivars (Almeida et al. 2021).

The carioca accessions were genotyped using a BARCBean6K_3 – Illumina composed of 5,398 SNPs and 1,616 SNPs were filtered and used. Genotypic data was analyzed by TASSEL 5.0 software (Bradbury et al. 2007), and SNPs with MAF (minor allele frequency) < 3%, heterozygosity > 5%, and missing data > 10% were removed. The promising modern BLINK model (Huang et al. 2019) was used for GWAS analysis. Clusters were absent from principal component analysis (PCA) (Figure 1S), and based on that, no correction for population structure was needed. The thresholds of 5% and 1% were applied on the Manhattan plot. ANOVA (analysis of variance) was carried out for comparing means between different groups (Ferreira et al. 2014), and the RBio software (Bhering 2017) was used for estimating the selective accuracy. The REML/BLUE (Restricted Maximum Likelihood/Best Linear Unbiased Estimator) model was used to measure the genotypic values by the Be-Breeder package (Matias et al. 2018). Each marker´s flanking sequence was blasted against the *Phaseolus vulgaris* v2.1 (Schmutz et al. 2014, G19833 genome). For the Blast search, 100 kb (confidence window) was considered, lower than the CDP´s LD decay (r_{mean}^2 = 0.046, Almeida et al. 2020). Unknown positioned markers were not considered, and the imputation performance was achieved by the Beagle 5.0 (Browning et al. 2018).

Pathogenicity test

The pathogenicity of three isolates (Xap 19, from Ponta Grossa, PR, Brazil; Xap 96, from Guarapuava, PR, Brazil; and XFF 205, from an unknown source – all provided by EMBRAPA) was confirmed by artificially inoculating the isolates on the leaves of 18 common bean genotypes (Table 1). The plates with yeast dextrose carbonate (YDC) medium were stored at 30 °C for 48 h in a Biological Oxygen Demand incubator (BOD). The inoculum of each isolate was around 10^7 colony-forming units, CFU / ml. The plants were grown in pots under greenhouse conditions, and at ten days of age, their primary leaves were inoculated using the leaf incision method, which consists of making two cuts perpendicular to the midrib, without reaching it, at a spacing of only two centimeters, with the aid of a scissors previously dipped in the bacterial suspension (Rava 1984). Severity was evaluated using the 1-6 scoring scale proposed by Rava (1984).

CBB´s severity assessment in the CDP

The experiment was executed with an experimental design of a randomized block design with three replications at the Instituto Agronômico (IAC, Campinas, SP) in a greenhouse. The Xap 19 inoculum was prepared as reported above. Plants with ten days of age were inoculated using the same approach as described in the pathogenicity test item above, making 4 cuts per leaf (Figure 1). The rest of the inoculum was sprayed on the plants. The pots, with 2 plants each, were distributed in trays. A control genotype was used within each block ('IAC Formoso'). An automatic sprinkler irrigation system was set up in the greenhouse, as high humidity promotes the disease. Ten days after inoculation, the severity of CBB was evaluated (Rava 1984). Scores were assigned to each plant in the plot, and the mean values of the block were subsequently calculated. The Scott-Knott test was used in the application of ANOVA. Data was transformed using the Box-Cox technique, with a lambda (λ) = 0.16.

Table 1. Pathogenicity test with 18 genotypes and three isolates of common bacterial blight: XAP 19, XAP 96, XAFF 205. Reactions were divided in resistant plants (R) scored as 1; moderately resistant (MR) plants with scores between 1.1 and 3; and susceptible (S) plants, with scores between 3.1 and 6

Genotypes	XAP 19	Reaction	XAP 96	Reaction	XFF 205	Reaction
1- IAC Polaco	6	S	4	S	1	R
2-Xan 112	3	MR	3	MR	2	MR
3-IPR Tangara	3	MR	3	MR	2	MR
4-IPR Camp Gerais	3	MR	-	-	1	R
5-IAC Sintonia	4	MR	1	R	1	R
6-ANFC9	4	MR	2	MR	1	R
7-Dama	2	MR	-	-	2	MR
8-IAC Netuno	4	MR	4	MR	2	MR
9- IAC Veloz	5	S	1	R	2	MR
10-IAC 1850	3	MR	1	R	2	MR
11-IAC-97.2	4	S	1	R	1	R
12-IPR Tuiuiu	6	S	4	S	4	S
13-BRS Estilo	4	MR	3	MR	2	MR
14-IAC Imperador	6	S	5	S	1	R
15-IAC Nuance	6	S	4	S	4	S
16-IAC Tigre	6	S	5	S	4	S
17-IAC Harmonia	6	S	5	S	5	S
18-IAC Formoso	6	S	5	S	5	S

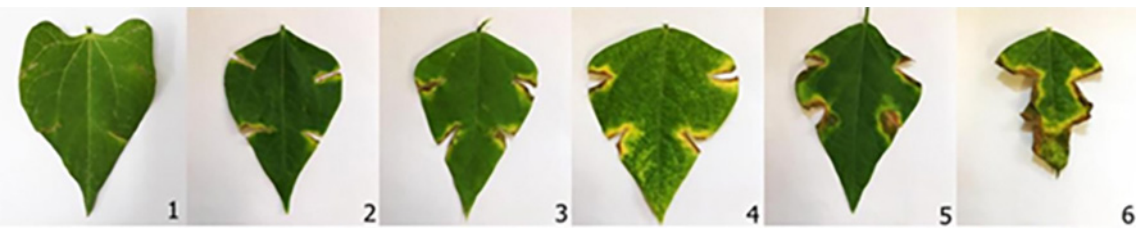

Figure 1. Diagrammatic severity scale (percentage of diseased leaf area, Rava 1984) for CBB: Score 1: Green leaves and no symptoms; score 2: Slight yellowing in the cuts of the leaf; score 3: Yellowing extending slightly even between the cuts of the leaf; score 4: Necrosis in the cuts and strong yellowing between the cuts; score 5: Same aspect as 4, but with yellowing above and below the cuts; score 6: Totally damaged leaf.

RESULTS AND DISCUSSION

All isolates were pathogenic when inoculated onto susceptible bean cultivars (Table 1), and the cultivars exhibited visual symptoms. However, there was no carioca plant resistant (score 1) to Xap 19 among the 18 carioca bean genotypes. Xap 19 was the most aggressive isolate, and it was chosen to evaluate the severity of the CDP. Concerning phenotypical evaluation of the CPD, original and normalized results were presented (Figure 2).

The mean scores of the genotypes of the CPD (Table 1S) show that no carioca genotype was fully resistant (score 1), only 22 (15%) were moderately resistant (score 1.1-3), and the remaining 127 (85%) were susceptible (score >3) to CBB disease. Statistical analysis (Table 2) showed a low CV (coefficient of variation, 2.4%) and, consequently, high

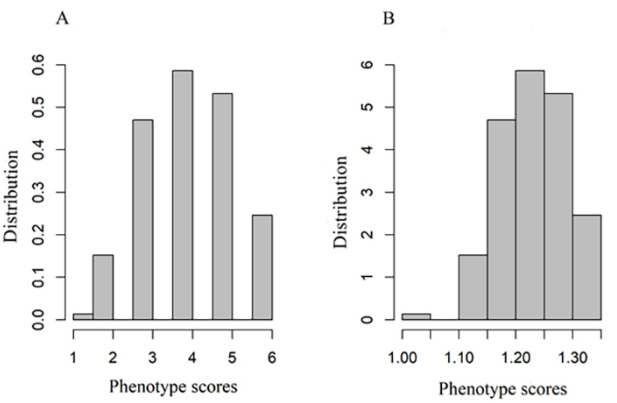

Figure 2. Histogram with (A) original CDP severity average scores and (B) normalized distribution of phenotypical CDP severity scores. Due to the non-normality of the data, the transformation was performed using the BoxCox test, with a lambda (λ) = 0.16.

accuracy for the experiment. In addition, ANOVA showed significant difference between treatments (Table 2). The BoxPlot offered a comparison of the mean scores between blocks 1, 2, and 3 (Figure 3). Block 2 contained a larger number of susceptible genotypes.

This study used the same carioca diversity panel (CDP) as Almeida et al. (2020). Considering the Phaseolus genome (~587 Mb) size and the LD decay reported by Almeida et al. (2020), the minimum number of SNPs required for a study like this would be 995. In this study, through the BLINK association model, a SNP (ss715650404) was identified on chromosome Pv07 at position 46.7 Mb (Figure 4). A total of 1,616 SNPs were used to perform GWAS for CBB resistance (Table 2S), the same number of markers of other studies (Almeida et al. 2020, Almeida et al. 2021).

Wu et al. (2017), surveying NBS-LRR-encoding genes associated with CBB, found that NSSR245 (Pv7, 49260558–49310456 bp in G19833) was associated with CBB architecture and may be in the similar genomic regions (Yu et al. 2004, Shi et al. 2011). Zhu et al. (2016) revealed two markers, BMp10s174 and BMp10s244, on Pv10 (39,730,677 and 40,002,585 bp in G19833). Ambachew et al. (2021) found SNPs with minor effects associated with common bacterial blight resistance on Pv02 (8,541,089 bp), Pv04 (29,756,136 bp), Pv08 (24,383,486; 55,730,740; 55,730,740; 8,738,278 bp), Pv10 (1,437,174 bp), and Pv11 (25,981,923 bp). Among them, Pv08 and Pv10 concentrated most of the CBB resistance genes. Simons et al. (2021) reported a SNP on Pv07 associated with CBB susceptibility at a different location (28.50–28.84 Mb) from the one detected in this study (46.7 Mb).

Table 2. Two-way ANOVA for the CBB phenotypical severity data referred to the 149 beans from the carioca diversity panel (CDP)

Source	df	SS	MS	Fc	Pr>Fc
Treatment	148	1.46	0.01	11.05	0.00
Block	2	0.00	0.00	3.42	0.03
Residuals	296	0.26	0.00		
Total	446	1.73			
Accuracy	0.95				
CV (%)	2.4				

SS: sum of squares; MS: Mean square.

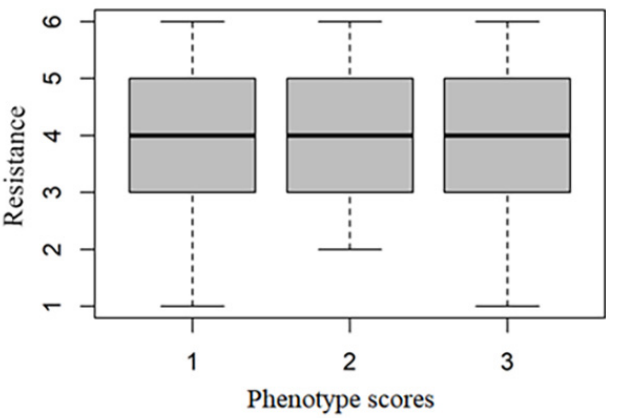

Figure 3. BoxPlot for the scores obtained for each block (1, 2 and 3) for the phenotypical severity evaluation of CBB resistance on the 149 carioca genotypes from the CDP panel.

Considering a confidence interval of 100 kb (Table 3) used to search the candidate genes on both side of the SNP detected as significant, gene annotation identified 13 putative candidate genes related to disease response. Allene oxide synthase (AOS, Phvul. 007.G055700.1) contributes to the biosynthesis of the jasmonic acid (JA). The *Castanea crenata* allene oxide synthase transformed in Arabidopsis improves defense against soilborne pathogen *Phytophthora*

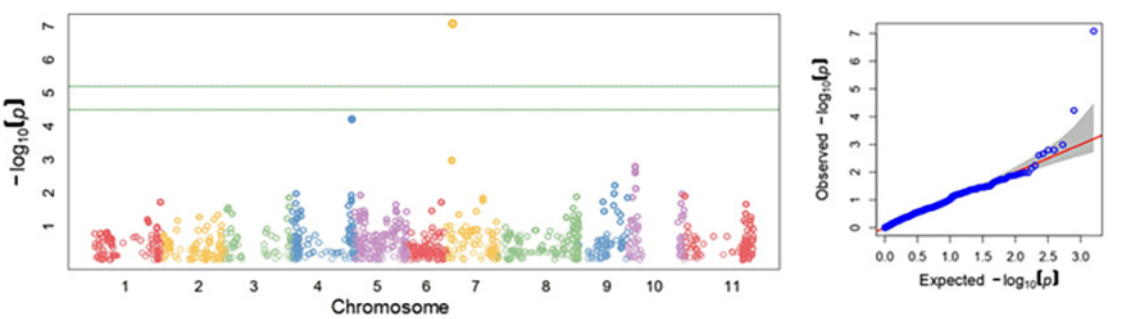

Figure 4. A) Manhattan plot for 1,616 SNPs using the carioca diversity panel (CDP) for *Xanthomonas axonopodis* pv. *phaseoli* resistance and B) Q-Q Plot generated by the Blink model. The green lines correspond to the cut-off lines obtained by bootstrapping and by the Bonferroni method (α =0.05 and 0.01).

Table 3. Gene annotation in a 100 kb window for the significative SNP (ss715650404) mapped for *Xanthomonas axonopodis* pv. *phaseoli* (Xap19) evaluation on the CDP of 149 genotypes of common beans

Chromosome	Position	Gene	Annotation
Pv07	4575766	Phvul.007G055200.1	Major facilitator superfamily protein
Pv07	4591318	Phvul.007G055300.1	
Pv07	4592079	Phvul.007G055400.1	
Pv07	4604591	Phvul.007G055450.1	
Pv07	4622621	Phvul.007G055500.1	Major facilitator superfamily protein
Pv07	4632884	Phvul.007G055600.1	PLAT/LH2 domain-containing lipoxygenase family protein
Pv07	4645045	Phvul.007G055700.1	allene oxide synthase
Pv07	4657073	Phvul.007G055800.1	PLAT/LH2 domain-containing lipoxygenase family protein
Pv07	4666083	Phvul.007G055900.1	photosystem I subunit D-2
Pv07	4670048	Phvul.007G056000.1	Haloacid dehalogenase-like hydrolase (HAD) superfamily protein
Pv07	4712605	Phvul.007G056100.1	S-adenosyl-L-methionine-dependent methyltransferases superfamily protein
Pv07	4726726	Phvul.007G056200.1	Copper amine oxidase family protein
Pv07	4738182	Phvul.007G056300.1	
Pv07	4742025	Phvul.007G056400.2	Copper amine oxidase family protein
Pv07	4752337	Phvul.007G056500.1	Copper amine oxidase family protein
Pv07	4757237	Phvul.007G056600.1	amine oxidase 1
Pv07	4765815	Phvul.007G056700.1	Sec14p-like phosphatidylinositol transfer family protein

cinnamomi (Serrazina et. al. 2021). HAD hydrolases, subfamily I (Phvul.007G056300.1) is modulated by Pi starvation and cyclopentenone oxylipins induction (Caparrós-Martín et al. 2013).

The establishment of *Pseudomonas syringae* in Arabidopsis (Jones et al. 2006) and indicated that components of PSII had been modified during the R-gene-mediated hypersensitive reaction (HR). In this study, we identified photosystem I, subunit D-2 (Phvul.007G055900.1) as a candidate gene mediating the CBB defense response. Medina-Puche et al. (2020) affirm the role of chloroplasts due to biotic threat initiating a signaling pathway that bursts of the pathogenesis-related proteins. Another candidate gene annotation was S-Adenosyl-L-methionine (SAM) (Phvul.007G056100.1), a universal biological cofactor that is involved with salicylic acid, a key enzyme in many important biological processes (Ross et al. 1999).

We identified a Sec14p-like phosphatidylinositol transfer family protein (Phvul.007G056700.1) among the annotated genes. The expression of NbSEC14 (Sec14 phospholipid transfer protein) from *Nicotiana benthamiana* was induced by PAMPs (pathogen-associated molecular pattern), such as those including flg22 and chitin (Kiba et al. 2018). Major facilitator superfamily (MFS, Phvul.007G055200.1; Phvul.007G055500.1) transporters plays a central role in pathogenesis-related processes (Paulsen 2003). Amine oxidases are multifunctional enzymes that catalyze the oxidative deamination of polyamines (Cona et al. 2006; Phvul.007G056600.1). Polyamine oxidases (PAOs) can be oxidatively deaminated by amine oxidases, leading to ROS-dependent stress signaling (Moschou 2018). One class of amine oxidases is the copper-containing amine oxidase (CuAO, Liu et al. 2020, Phvul.007G056200.1; Phvul.007G056400.2; Phvul.007G056500.1), and it has a confirmed role in defense response (Angelini et al. 1993). The PLAT/LH2 (Phvul.007G055600.1; Phvul.007G055800.1) domain conciliates enzyme-membrane interaction (Newcomer and Brash 2015). Pingault et al. (2021) reported that plant LOXs (Lipoxygenases) production may be modulated by plant diseases. A LOX-1 ortholog on Pv10 was related to common bacterial blight resistance (Simons et al. 2021).

Using a carioca diversity panel, GWAS identified a new genomic region connected with common bacterial blight in *Phaseolus vulgaris*. The SNP ss715650404 identified offers potential in selecting candidate genes that may be useful markers for screening of carioca lines with superior common bacterial blight resistance in the plant breeding process.

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