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Citation:

Wang, Weijia, Jacobs, Janette L., Chilvers, Martin I., Mukankusi, Clare, Kelly, James D., Cichy, Karen A. (2018). QTL Analysis of Fusarium Root Rot Resistance in an Andean × Middle American Common Bean RIL Population. Crop Science, 58, 1166–1180.

Publisher's DOI:
https://doi.org/10.2135/cropsci2017.10.0608

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Crop Breeding & Genetics

QTL Analysis of Fusarium Root Rot Resistance in an Andean × Middle American Common Bean RIL Population

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Received 11 Oct. 2017. Accepted 5 Feb. 2018. *Corresponding author (karen.cichy@ars.usda.gov). Assigned to Associate Editor Jeffrey Endelman.

Abbreviations: DS, disease severity; FRR, Fusarium root rot; FSSC, *Fusarium solani* species complex; LOD, logarithm of odds; LRR, leucine-rich repeat; ~~FOSC, *Fusarium oxysporum* species complex;~~ MAS, marker-assisted selection; MRF, Montcalm Research Farm; MSU, Michigan State University; RIL, recombinant inbred line; QTL, quantitative trait locus; RAPD, random amplified polymorphic DNA; SNP, single nucleotide polymorphism; SSR, simple sequence repeat.

ABSTRACT

Fusarium root rot (FRR) is a soil-borne disease that constrains common bean (*Phaseolus vulgaris* L.) production. Its causal pathogens include clade 2 members of the *Fusarium solani* (Mart.) Sacc. species complex. Here, we characterize common bean reaction to different *Fusarium* species and identify genomic regions associated with resistance. Four *Fusarium* species—*F. brasiliense* T. Aoki & O'Donnell, *F. cuneirostrum* ~~,~~ O'Donnell & T. Aoki, *F. solani* sensu stricto, and *F. oxysporum* Schltdl. sensu lato—were tested for virulence on two bean genotypes, 'CAL96' (Andean) and 'MLB-49-89A' (Middle American), and virulence varied from mild to strong. The ~~RIL~~ recombinant inbred line population of CAL96 × MLB-49-89A was phenotyped in a greenhouse for FRR resistance with the *F. brasiliense* isolate and screened in the field under natural FRR disease pressure. Quantitative trait locus (QTL) mapping was conducted on a map developed with 822 polymorphic ~~SNP~~ single nucleotide polymorphism markers. Two QTLs associated with disease severity score ~~(DS)~~ in the greenhouse and field colocalized on chromosome Pv02 (R^2 = 0.09 and 0.1, respectively). Other QTLs associated with root–shoot biomass, taproot diameter, lodging, and seed weight were also identified across nine chromosomes. Root and shoot weight QTLs from field and greenhouse screens also colocalized on Pv07 and Pv11. The FRR-related QTLs identified in this study, especially on Pv02, are good candidates for marker-assisted selection.

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Common bean (*Phaseolus vulgaris* L.) is an important grain legume for human consumption, valued as a rich source of plant protein, micronutrients, and folate (Siddiq and Uebersax, 2012). In Latin America and eastern and southern Africa, beans are a dietary staple (Beebe et al., 2012). However, bean productivity has been severely constrained by diseases such as Fusarium root rot (FRR), a soil-borne disease. Small-scale farms in Africa have experienced up to 100% crop losses caused by FRR (Ongom et al., 2012), and it is also the most serious root rot disease in the United States that reduces yield of dry bean production (Román-Avilés et al., 2011).

The symptoms of FRR begin with red to brown streaks on taproots, followed by lesions and necrosis, which form gradually. Disease severity (DS) increases as the plant develops, and eventually complete rotting of root systems can occur (Hall, 1991). Historically, *Fusarium phaseoli* (Burkh.) T. Aoki & O'Donnell (Hall, 1991) was recognized as the causal agent of FRR; however, it is becoming apparent that other species within clade 2 of the *Fusarium solani* (Mart.)

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Sacc. species complex (FSSC), which includes *F. brasiliense* T. Aoki & O'Donnell, *F. virguliforme* O'Donnell & T. Aoki, and *F. cuneirostrum* O'Donnell & T. Aoki, are also involved (O'Donnell et al., 2008; Aoki et al., 2014). There are also other species that do not belong to the FSSC that may be capable of causing FRR, such as *F. oxysporum* Schltdl., which is now known as the *Fusarium oxysporum* species complex ~~(FOSC)~~ and is commonly associated with wilt or yellowing symptoms but also has been found to cause root rot in some cases (Abawi, 1989; Aoki et al., 2014).

The development of cultivars with root rot resistance has been generally considered the best long-term management option among the many root rot control strategies (Tu, 1992; Park and Rupert, 2000; Abawi et al., 2006; Conner et al., 2014). Typically, Middle American genotypes show higher levels of FRR resistance, and large-seeded Andean genotypes are more susceptible to FRR (Beebe et al., 1981; Schneider et al., 2001; Román-Avilés and Kelly, 2005; Mukankusi et al., 2010). Bean genotypes that are susceptible to FRR tend to have weak root systems with limited branching and reduced dry weight when infected by *Fusarium* spp. (Román-Avilés et al., 2004). There is a need to develop determinate Andean bean genotypes with FRR resistance and improved root systems. Breeding for FRR resistance is challenging because resistance is quantitative (Mukankusi et al., 2011; Román-Avilés et al., 2011) and routine screening must occur in the presence of the pathogen under suitable environmental conditions. To discover resistant sources and to study FRR-resistance-related quantitative trait loci (QTLs), screening bean genotypes or populations with suitable virulent *Fusarium* isolates is also critical. The selection of the *Fusarium* isolate influences the effectiveness and reliability of the phenotyping process. Ideally, a *Fusarium* isolate that could distinguish between two parent genotypes for resistance to FRR can be used to detect resistance in the recombinant inbred line (RIL) population derived from the cross.

Marker-assisted selection (MAS) for root rot resistance would be beneficial, as selections could be made in the early stages of the breeding process and with less reliance on phenotyping in the presence of the pathogen. The identification of ~~quantitative trait loci~~ QTLs associated with FRR resistance will help identify the genetic basis of resistance and facilitate the MAS process. Early studies on identifying QTLs related to FRR resistance using random amplified polymorphic DNA (RAPD) markers in different bean populations (Schneider et al., 2001; Chowdhury et al., 2002; Román-Avilés and Kelly, 2005) had limited genomic coverage, and the QTLs were not always assigned to specific chromosomes or chromosomal regions. As a result, none of those QTLs were used for MAS. The QTLs associated with FRR varied between studies and populations, and the researchers were not able to compare the physical positions of those QTLs due to the limited genomic coverage of the RAPD markers.

Single nucleotide polymorphism (SNP) markers have replaced other marker systems in QTL analysis in recent years, as they have higher density and better marker coverage (Song et al., 2015), and permitted the identification of QTLs with the known physical positions that can be compared in different studies and populations. Hagerty et al. (2015) used SNP markers to identify QTLs associated with FRR resistance in a RIL population of RR6950 (a resistant dry bean) × OSU5446 (a susceptible snap bean). Two QTLs for FRR resistance were found on Pv03 and Pv07, one QTL on Pv02 was found for taproot diameter ~~(TD)~~, and one QTL was found for shallow basal root angle ~~(SBRA)~~ on Pv05 (Hagerty et al., 2015). Nakedde et al. (2016) identified

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four QTLs associated with root architecture traits on Pv01, Pv05, and Pv09 using SNP markers, and one QTL associated with FRR resistance on Pv05 was found in the black bean RIL population of 'Puebla 152' (resistant) × 'Zorro' (susceptible).

Kamfwa et al. (2013) investigated QTLs for FRR resistance with 62 $F_{4:5}$ RILs of MLB-49-89A (resistant) × K132 (also known as CAL96, susceptible) using 12 simple sequence repeat (SSR) markers. A significant QTL associated with FRR resistance was detected on Pv03 (Kamfwa et al., 2013). This population is especially valuable because it is derived from an intergene pool cross, and there has been limited success in transferring FRR resistance from the Middle American to the Andean genepool. Therefore, we considered it worthwhile to further evaluate this population for FRR resistance as described here. The following changes were made from the previous study: the number of RILs was increased from 62 to 121, resistance screening was conducted with an FRR isolate from a major US Andean bean growing region (Montcalm County, Michigan), whereas previously it had only been screened with an African *F. cuneirostrum* isolate, and a dense linkage map was developed with ~~single nucleotide polymorphism (~~SNP~~)~~ markers.

The objectives of this study were (i) to characterize FRR resistance to *Fusarium* species collected from Michigan, where FRR has been a major soil-borne disease that affects bean production, and (ii) to detect QTLs related to FRR resistance in the RIL population derived from a cross of 'CAL96' × 'MLB-49-89A', which is rich in variability for root traits related to *Fusarium* resistance.

MATERIALS AND METHODS

Plant Materials

A cross between CAL96 and MLB-49-89A was made at the International Center for Tropical Agriculture (CIAT), Kampala, Uganda. The large-seeded, red-mottled, Andean cultivar CAL96 with Type-I upright determinate bush growth habit is commonly consumed in East Africa and is also highly susceptible to root rot. The medium-seeded black Middle American bean variety MLB-49-89A with Type-III indeterminate growth habit is a germplasm from the Democratic Republic of Congo and was found by CIAT Uganda to have moderate resistance to *F. oxysporum* wilt, *Pythium ultimum* Trow, and *F. solani* f. sp. *phaseoli* (Burkholder) W. C. Snyder & H. N. Hansen (FSP-3 isolate) (Buruchara and Camacho, 2000; Mukankusi et al., 2010, 2011). The FSP-3 strain was recently confirmed as *F. cuneirostrum* by M. Chilvers (personnel communication) at Michigan State University (MSU).

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The RIL population of CAL96 × MLB-49-89A (F_3–generation seeds) was sent to the USDA-ARS bean breeding and genetics laboratory at ~~Michigan State University (~~MSU~~)~~ and advanced to F_4 generation through single-seed descent. A single plant of each F_4 line was harvested, and seeds from each plant were bulked to get $F_{4:5}$ RILs. Seed was increased on a total of 121 $F_{4:5}$ RILs, and phenotypic evaluation was conducted on this population. DNA of the RIL population was extracted from the F_4 generation for SNP genotyping.

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Field Data Collection

In 2015, the RIL population ($F_{4:5}$) was planted at the MSU Montcalm Research Farm (MRF) (Entrican, MI), which was previously identified as having FRR disease pressure (Román-Avilés et al., 2004). The lines were planted in four-row plots 6.4 m in length with 0.5-m row spacing in a randomized complete block design. Standard agronomic practices were followed. The center two rows contained individual RILs (25 seeds per row), and the outer two rows were planted to a uniform border with the FRR-susceptible bean cultivar Red Hawk. Forty-five days after planting, three plants of each line of the RIL population were uprooted with a shovel to extract the whole root system. The roots were washed with tap water to remove soil and evaluated for root rot symptoms using the CIAT 1-to-9 scale (Schoonhoven and Pastor-Corrales, 1987), where 1 indicates no disease and 9 indicates that the root is completely rotted. Data were collected on morphological traits including root length, root diameter, root dry weight, and shoot dry weight of the samples. Root length (cm) was measured as the length from tap root tip to the middle point of the hypocotyl. Root diameter (mm) was measured at the middle point of the hypocotyl with a digital caliper. Root and shoot dry weights (g) were measured after drying plants in an oven at 60°C for 3 d. Agronomic traits including days to flower, days to maturity ~~(DM)~~, lodging ~~(LDG)~~, and seed weight were recorded. D~~F~~ays to flower was recorded as the number of days from planting to when ~ 50% of plants in a plot have at least one opened flower. Days to maturity~~M~~ was recorded as the number of days from planting to when ~50% of plants in a plot have at least one dry pod. ~~LDG~~ Lodging was recorded at harvest with scores of 1 to 5, where 1 = 100% plants standing erect and 5 = 100% plants flat on the ground. Seed weight was measured as the weight (g) of 100 seeds for each line at harvest.

Screening Different *Fusarium* Species for Virulence

Four *Fusarium* isolates collected from infected dry bean roots in different research fields in Michigan were provided by Plant Pathology Laboratory of Dr. Martin Chilvers at MSU. The four isolates were identified as different *Fusarium* species and coded as F_14-7 (*F. solani* sensu stricto), F_14-38 (*F. oxysporum* sensu lato), F_14-40 (*F. cuneirostrum*), and F_14-42 (*F. brasiliense*) (Table 1). The isolates were collected from MRF except for the F. *solani* isolate, which was collected from MSU Plant Pathology Farm (East Lansing, MI). Sorghum [*Sorghum bicolor* (L.) Moench] inoculum was made for these isolates, which consisted of sorghum kernels colonized with *Fusarium* mycelium and air dried in a drying oven. The inoculum was ground into powder (1-mm particles) before use. The two parental lines, CAL96 and MLB-49-89A, were used for testing the isolates for virulence. The containers used to plant bean seeds were 354-mL coffee cups with three holes on the bottom for drainage. Different quantities of inoculum were tested for each *Fusarium* isolate (Table 1), according to the results of a preliminary experiment conducted by Chilvers's laboratory to determine the amount of inoculum to use. Ground *Fusarium* spp. sorghum inoculum was mixed thoroughly with 200 mL of vermiculite (medium) in each cup with another 70 mL of vermiculite layered on top. Bean seeds were placed on the top and covered with another 70 mL of vermiculite. Experiment controls were set up in the same method but without inoculum. Five replicates and five seeds per replicate were established with each parental line for each *Fusarium* isolate and control. The experiment was set up as a completely randomized design ~~(CRD)~~ with two experimental factors (genotype and treatment).

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Greenhouse temperature was set at 26°C during the day and 22°C at night. Plants were watered once daily in the morning.

Fourteen days after experimental setup, the whole root systems were removed and cleaned by washing the hypocotyls and roots in tap water. The roots were evaluated for FRR ~~disease severity~~DS using a five-score scale (1 = healthy, no lesion on the roots or hypocotyls; 3 = discrete, light or dark brown, superficial necrotic lesion; 5 = necrosis and decay of the adventitious roots or taproot but with good root biomass; 7 = extensive root rot with obvious root loose; 9 = plant is dead). The scale was adapted by Dr. Martin Chilvers's Plant Pathology Laboratory from a Rhizoctonia root rot ~~disease severity~~DS rating scale (Sharma-Poudyal et al., 2015). This scale was found to be more suitable than the standard CIAT 1-to-9 scale for evaluating greenhouse inoculated plants. The ~~disease severity~~DS was lower than what is seen in the field, and this scale was more useful to distinguish between the resistant and susceptible lines. After visual evaluation, plants were oven dried at 60°C for 24 h and shoots and roots were weighed separately. The percentage loss of root and shoot dry weight of inoculated plants compared with noninoculated controls was calculated.

The experiment was repeated with only the *F. brasiliense* isolate at levels of 0.25, 0.5, and 1 g using CAL96, MLB-49-89A, and six RILs as plant materials.

Greenhouse Phenotyping of the RIL Population

The *F. brasiliense* isolate was used at the rate of 1 g per cup to phenotype 121 RILs for root rot resistance. The experiment was set up similar to screening the *Fusarium* isolates for virulence. Five replicates and five seeds per replicate were established for each individual RIL for both inoculated screening and noninoculated control. Plants were evaluated for disease symptoms using the same method as for the plants in screening the *Fusarium* isolates for virulence. The experiment was conducted twice with the same conditions. To account for the variability in seed size in the population, which will influence early root and shoot growth, the percentage of biomass reduction was also calculated as a measure of FRR resistance of each RIL.

SNP Genotyping and Genetic Map Construction

Fresh first-trifoliate young leaves of the F_4 RIL population were collected from the field and used for DNA extraction. The DNA samples were genotyped through the Illumina 6000-SNP BARCbean6K_3 SNP chip (USDA-ARS Soybean Genomic and Improvement Laboratory, Beltsville, MD) (Song et al., 2015). The SNP alleles were called using the GenomeStudio Genotyping Module 1.8.4 (Illumina, 2008~~Inc.~~), and 2359 polymorphic SNPs between CAL96 and MLB-49-89A were selected. Redundant markers were filtered out, and markers exhibiting segregation distortion were included unless they caused map distortion. The genetic linkage map of the RIL population was constructed in JoinMap 4.0 (~~Kyasma, NL~~van Ooijen, 2006) with Kosambi's mapping function. The map positions of markers were then compared with their physical positions in the in *P. vulgaris* reference genome 2.1 (http://www.phytozome.net) to confirm the ordering of the markers.

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QTL Analysis and Disease-Related Gene Identification

Windows QTL Cartographer 2.5 (Wang et al., 2010) was used to detect QTLs related to each phenotypic trait. The composite interval mapping ~~(CIM)~~ procedure was performed with the parameters set to 10-cM window size, 1-cM walk speed, five significant background markers, and the forward and backward multiple linear regression method. The logarithm of odds (LOD) threshold for each QTL was determined by 1000 permutations, and QTLs with LOD values lower than the threshold from permutations were considered as not significant and discarded. The confidence interval ~~(CI)~~ of each QTL was determined by using one-LOD and two-LOD support intervals as 95 and 99% confidence intervals, respectively~~CI~~. The Phaseolus genes website (http://phaseolusgenes.bioinformatics.ucdavis.edu/) was used to search for the related QTL in previous studies, and QTLs with the same traits in this study were named after existing QTLs according to the guidelines for common bean QTL nomenclature (Miklas and Porch, 2010). Linkage map and detected QTLs were displayed using MapChart 2.3 (Voorrips, 2002). Disease-resistance-related genes were located within the interval of the two flanking SNP markers of each QTL according to the *P. vulgaris* reference genome 2.1 (http://www.phytozome.net) and were considered candidate genes associated with FRR resistance.

Statistical Analysis

The statistical analyses for all experiments were conducted in SAS 9.4 (SAS Institute, ~~Cary NC~~2013). The normality of data distribution was checked via quantile plots and residual plots. For the *Fusarium* isolates screening experiment, the statistical model was established with genotypes and levels of treatment as fixed effects, and replications as a random effect. For the greenhouse FRR phenotyping of the RIL population, five plants per replicate were evaluated. The statistical model was established with genotypes as fixed effect, and experimental replicates and repeats of experiment as random effects. The ~~analysis of variance~~ANOVA of the fixed effects in the statistical models were conducted in PROC MIXED procedure. The differences of least squares means~~(LSM)~~ were checked for comparison of differences among response variables with the LSD at $\alpha = 0.05$. The PROC CORR command was used to analyze Pearson correlations among response variables.

RESULTS

Virulence of *Fusarium* Isolates

Four *Fusarium* isolates were evaluated for virulence on the determinate Andean red-mottled bean cultivar CAL96 and the indeterminate, Middle American, black bean line, MLB-49-89A. On the ~~disease severity~~DS score scale of 1 to 9, any rating >5 indicated moderate to severe root rot. Each of the four species caused root rot symptoms, and virulence varied from mild to severe depending on genotype and inoculation level (Table 1). Plants inoculated with the *F. solani* isolate exhibited mild DS from 2.6 to 3.8 on both CAL96 and MLB-49-89A. The percentage root reduction in the inoculated plants was 29 to 55% and was similar between the two genotypes. Inoculation of CAL96 with the *F. solani* isolate resulted in reduced shoot biomass as compared with the noninoculated control, whereas MLB-49-89A showed an increase in shoot biomass

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when inoculated with this isolate. The *F. oxysporum* isolate also caused mild DS on CAL96 and MLB-49-89A, but MLB-49-89A lost more root and shoot biomass than CAL96. The *F. cuneirostrum* isolate caused moderate DS and root loss on MLB-49-89A but caused greater shoot loss on CAL96. The *F. brasiliense* isolate was the most virulent of the four isolates where plants exhibited DS from 4.6 to 6.4, whereas the MLB-49-89A always had lower root or shoot loss than CAL96 except at the 2-g inoculum level (Table 1).

The *F. brasiliense* isolate was selected for further screening for disease reaction on MLB-49-89A, CAL96, and six RIL lines, since this isolate was the most virulent of the four isolates and clearly distinguished reaction to FRR between CAL96 and MLB-49-89A parents. Traits related to root rot disease resistance were analyzed for variance within the eight bean genotypes and three levels of inoculum quantity. Significant genotypic effects were found on DS and root and shoot reduction, but the level of inoculum quantity had a significant effect only on DS (Table 2). The parental line MLB-49-89A had the lowest DS among all lines at the 0.5-g level, unlike the previous run (Table 1), where CAL96 had lower DS. Although no significant difference was detected for DS between the parental lines at the 1-g inoculum level, the greatest variation among the progeny was observed at this level. Although both MLB-49-89A and CAL96 had root and shoot reduction at all three inoculum quantity levels, CAL96 showed greater reductions than MLB-49-89A at the 0.5- and 1-g levels, which agreed with the previous run. In addition, the six RILs exhibited large variation in root and shoot reduction at each inoculation level, which indicated the potentially large genetic variability for FRR resistance and susceptibility within this RIL population.

RIL Population Greenhouse Root Rot Evaluation

The 121 RILs were evaluated for response to the *F. brasiliense* isolate in a greenhouse screen. The RILs exhibited continuous distribution for all traits including DS, inoculated root dry weight, inoculated shoot dry weight, control root dry weight, control shoot dry weight, root loss, and shoot loss (Fig. 1). The RIL population varied from resistant to susceptible to the *F. brasiliense* isolate, with ~~disease severity~~DS scores ranging from 2.4 to 7.6 (Table 3). The inoculated root dry weight and shoot dry weight of the population ranged from 0.02 to 0.09 g and 0.04 to 0.2 g, respectively. The control root dry weight and shoot dry weight of the population ranged from 0.04 to 0.14 g and 0.06 to 0.22 g, respectively. The root loss in the RILs ranged from −13.6 to 70.7%, and shoot loss ranged from −4.3 to 58.4%, where the negative values indicate that the inoculated plants had greater root or shoot biomass than the noninoculated plants. Both MLB-49-89A and CAL96 inoculated with the *F. brasiliense* isolate had reduction in root and shoot biomass, but CAL96 had more reduction than MLB-49-89A, even though CAL96 had greater root and shoot biomass than MLB-49-89A under both inoculated and noninoculated treatments. The ~~coefficient of variation (~~CV~~)~~ of all traits varied from 17 to 60%, which indicated the difficulty in obtaining repeatable results in phenotyping bean plants for FRR infection.

The DS was negatively correlated with root and shoot biomass ($r = -0.5$), and positively correlated with root and shoot reduction ($r = 0.3$ and 0.4, respectively) (Table 4). The DS was negatively correlated with lodging score ($r = -0.2$). This may reflect the growth habit of the resistant parent MLB-49-89A, which was indeterminate with a lodging score of 4.0. The 100-seed weight was positively correlated with root and shoot biomass, which indicated that RILs with larger seed size tended to have more root and shoot biomass either infected by FRR or not.

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This finding is likely related to the short time (14 d) of growth of beans in the greenhouse experiment and indicated that the larger seeded beans have a growth advantage in these conditions. However, the root and shoot reduction values were not related to seed size; therefore, we were able to draw valid conclusions on resistance for FRR in spite of seed size differences.

RIL Population Field Root Rot Evaluation

The RIL population was evaluated for FRR symptoms under natural inoculum at MRF. This field was chosen for evaluation of the population because Andean beans have been grown here for >30 yr and there is a history of severe root rot (J. Kelly, personal communication). Pathogen isolations also indicated that *F. brasiliense*, *F. cuneirostrum*, *F. solani*, *F. phaseoli*, and *F. oxysporum* are all highly abundant *Fusarium* species present at MRF (Jacobs and Chilvers, personal communication). The RIL population showed continuous normal distribution in all measured traits except DS (Fig. 2). Most of the RILs had DS of 7 to 9, and the lowest score in the population was 5. The two parents also had high DS and were not significantly different in root rot symptoms (Fig. 2). This is an indication of the high disease pressure ~~conditions~~ during the 2015 field season.

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Root length ranged from 4.9 to 23.1 cm and taproot diameter ranged from 2.0 to 7.5 mm in the population. Root dry weight and shoot dry weight ranged from 0.06 to 1.9 g and 0.8 to 14.5 g, respectively. Root and shoot dry weights of the two parents were not significantly different, and the shoot dry weight of MLB-49-89A was slightly higher than that of CAL96. This is in contrast with the root and shoot weight differences observed between MLB-49-89A and CAL96 in the greenhouse evaluations. Since this was an inter-gene-pool cross between a determinate Andean bean and an indeterminate Middle American small–seeded bean, large phenotypic variability was expected within the population.

The ~~DF~~days to flower of the population ranged from 40 to 60 d, with most of the RILs flowering in 45 to 55 d, and ~~DM~~days to maturity ranged from 88 to 124 d (Supplemental Fig. S1). There was also wide variability for lodging scores. The 100-seed weight varied among the population with a range of 24 to 58 g (Fig. 2). From the perspective of cultivar improvement, there is a need for a root-rot-resistant cultivar with large seed size and determinate, upright plant architecture with a maturity of ∼95 d or less. The variation in agricultural traits indicated the possibility of developing a root-rot-resistant cultivar with desired seed size and plant architecture from this RIL population.

Linkage Map and QTL Analysis

A genetic map of 11 chromosomes was constructed with 822 SNP markers, and the total length was 862.5 cM (Table 5). Chromosome Pv01 had the largest number of markers, whereas Pv04 had the smallest number and Pv03 was the longest, with 90.6 cM in map distance (Table 5). The average distance between markers was ∼1 cM.

A total of 17 QTLs related to FRR resistance and root–shoot biomass were identified across seven chromosomes in the CAL96 × MLB-49-89A RIL population (Table 6). The QTLs associated with DS in both the greenhouse ($FRR2.2^{CM}$) and field ($FRR2.3^{CM}$) were found on Pv02 with 9 and 10% of phenotypic variation explained, respectively, and the parent MLB-49-89A contributed the beneficial allele for lower DS for these two QTLs. These two QTLs also

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colocalized with a QTL associated with control root dry weight (RTWC2.1^{CM}) on Pv02 (Fig. 3). We identified QTLs for inoculated root dry weight (RTWI1.1^{CM}) and inoculated shoot dry weight (STWI1.1^{CM}) on Pv01, and both explained 8% of phenotypic variation. These QTLs also colocalized with the QTL for lodging on Pv01 (LDG1.1^{CM}), and parent CAL96 contributed the allele for a lower lodging score. The closest SNP of LDG1.1^{CM} matched with the most significant SNP (ss715639272) associated with determinacy in the association mapping of the Andean bean diversity panel (Cichy et al., 2015), which is also the location of the single *fin* gene that controls the determinacy in growth habit of common bean (Kwak et al., 2008). A QTL associated with inoculated root dry weight (RTWI11.1^{CM}) was found on Pv11, which colocalized with QTLs related to control root and shoot dry weight (RTWC11.1^{CM} and STWC11.1^{CM}) as well as root dry weight in field (RTW11.1^{CM}), and the phenotypic variation explained by these QTLs ranged from 9 to 16%. We also found QTLs associated with control root and shoot dry weight on Pv02 (RTWC2.1^{CM} and STWC2.1^{CM}) and Pv09 (RTWC9.1^{CM}). We found QTLs for root and shoot loss on Pv03 (RTL3.1^{CM}) and Pv07 (RTL7.1^{CM} and STL7.1^{CM}), and the QTL on Pv07 colocalized with a QTL associated with field root dry weight (RTW7.1^{CM}); the explained phenotypic variation ranged from 8 to 12%. Both MLB-49-89A and CAL96 contributed beneficial alleles for the QTLs of the above traits. We found QTLs associated with seed weight on Pv04, Pv05, and Pv06.

Disease-resistance-related genes (R genes) were found in some of the QTL regions according to the *P. vulgaris* 2.1 reference genome (Schmutz et al., 2014) (Table 7). For instance, a gene (Phvul.002G152100) encoded with a leucine-rich repeat (LRR) was found 11.4 kb away from FRR2.3^{CM}. Two genes (Phvul.007G029900 and Phvul.007G032100) encoding LRR proteins were found to be close to QTLs RTL7.1^{CM} and STL7.1^{CM} with distances of 31.7 and 133.6 kb from the closest SNP, respectively. Three genes (Phvul.011G212100, Phvul.011G181366, and Phvul.011G166100) encoding an LRR or NB-ARC domain (a nucleotide-binding adaptor in R genes) were found in the overlapped QTL region of RTWI11.1^{CM}, STWC11.1^{CM}, and RTW11.1 on Pv11 (Table 7).

The five most resistant and five most susceptible RILs to FRR according to the DS and root–shoot reduction in the greenhouse experiment were further studied for the importance of QTLs in FRR (Table 8). Although the five susceptible lines were also susceptible in the field, some of the resistant lines did not show strong resistance when grown in the field, which is possibly due to greater disease pressure and diverse species of pathogen presented in the field, as well as a different soil environment. These 10 RILs were characterized for SNP variation at the location of QTLs that were most important indicators of FRR, including the FRR2.2^{CM} and FRR2.3^{CM} on Pv02; RTL7.1^{CM}, STL7.1^{CM}, and RTW7.1^{CM} on Pv07; and RTWI11.1^{CM} on Pv11. Four of the most resistant lines (CxM_425, CxM_433, CxM_517, and CxM_521) were found to have all five QTLs, and CxM_274 had four of these QTLs. However, the most susceptible lines were found to have none of those QTLs. In total, 10 RILs had all five QTLs, 18 RILs had any three of the QTLs, and 13 RILs none of these QTLs. The more QTLs the RILs possessed, the lower their average DS and root–shoot loss were compared with the RILs with five, three, or zero QTLs (Fig. 4).

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DISCUSSION

Screening *Fusarium* Isolates on Parents and RILs

The four *Fusarium* isolates tested included three species that belong to the FSSC and one *F. oxysporum* that is not commonly known as a causal pathogen of FRR. Results from the screening showed that the virulence among the tested *Fusarium* species varied. This behavior of the isolates is similar to results of some previous research in screening *Fusarium* species for virulence. In a study of soybean [*Glycine max* (L.) Merr.] sudden death syndrome ~~(SDS)~~, *F. brasiliense, F. cuneirostrum*, *F. phaseoli*, and *F. virguliforme* were found to have intraspecific variation in pathogenicity on soybean (Aoki et al., 2005). Ondrej et al. (2008) observed that different isolates of *F. oxysporum* and *F. solani* had variations in virulence on pea (*Pisum sativum* L.). We observed that when an isolate had mild virulence, such as the *F. solani* isolate tested in this study, the increase of inoculum amount did not have an effect on the severity of disease symptoms, but when the isolate had severe virulence, the amount of inoculum did affect the disease symptom expression, most notably on susceptible genotypes. The parental line MLB-49-89A, which was previously identified as resistant to *F. solani* (Mukankusi et al., 2011), showed variation in disease symptoms to different *Fusarium* species tested in this study. Therefore, species and isolate information should be included when defining the resistance of a bean cultivar to FRR.

The results of the second run of screening of the *F. brasiliense* isolate indicated similar variation to the first run of DS and root–shoot reduction between the two parents, with MLB-49-89A exhibiting less root and shoot reduction than CAL96. The RILs also exhibited a range in DS and root–shoot reduction. However, DS and root–shoot reduction were not always related, since some progenies had an increase in root–shoot biomass while superficial disease symptoms were observed. The variation of reaction of the eight genotypes to the tested *F. brasiliense* isolate in DS and root and shoot reduction indicated that this isolate was suitable to be used in phenotyping the whole RIL population for FRR resistance.

Phenotyping of Parents and RILs

Transgressive segregation was observed in the RIL population at both the low and high extremes for DS. In the greenhouse experiment, MLB-49-89A showed moderate resistance to the tested isolates, and the root and shoot losses were smaller than those of CAL96, which supported the results from screening *F. brasiliense* for virulence on six RILs and the parents. Although all the inoculated plants showed mild to severe FRR disease symptoms, the resistant lines had slightly higher biomass in roots and shoots than the noninoculated controls. The increase of root–shoot biomass suggests that resistant lines produced more biomass at the early growth stage in response to disease infection (Román-Avilés et al., 2004).

Previous studies have suggested that cultivars that produce more adventitious roots and larger basal roots tend to be more tolerant to root rot (Snapp et al., 2003; Cichy et al., 2007), as the weaker roots of the infected plants are unable to absorb and transport water and nutrient effectively (Román-Avilés et al., 2004). In this study, the RILs with higher root–shoot biomass at early stages tended to have less FRR disease symptoms, as well as less root–shoot loss under inoculated condition. Since plant biomass is a more objective measurement than DS, it could be

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used as a complementary indicator for FRR resistance. The ability of a plant to produce biomass under FRR pressure also suggests tolerance to the disease. Tolerance is an important strategy for plants to deal with root rot in a field setting where many pathogenic isolates may be present.

Although RILs with moderate to high resistance to the *F. brasiliense* isolate were identified, most RILs showed moderate to severe susceptibility to FRR in the field evaluation. The possible reason is that the MRF has been known to have high FRR pressure and the soil pathogens in the field composed a complex of different species, whereas plants were inoculated with a single *Fusarium* isolate in the greenhouse. Additionally, the plant samples were harvested from the field 45 d after planting, whereas plants were kept for only 14 d in the greenhouse, so the plants in the field were exposed to the FRR disease for one-third of their life cycle. Schneider et al. (2001) suggested that genetic resistance to FRR might be overcome under severe disease pressure, as the resistant parent FR266 in that study showed root rot rating >4.0 (which means moderate susceptibility) in a field test at MRF. In this study, the parental line MLB-49-89A had high DS in the field, but relatively low DS and biomass reduction in the greenhouse experiment. Kamfwa et al. (2013) concluded in their study that the gains from selection for resistant genotypes to FRR may increase when the selection is made in the greenhouse, which provides an environment with less variation. In this study, a strong environmental effect on FRR resistance was also observed by comparing the different phenotyping results from the greenhouse and field. This could be due to the more controlled environment in the greenhouse, and the inoculum load could have been higher and the disease organisms' composition more complex in the field.

QTL Analysis

The QTL for root dry weight under noninoculated greenhouse conditions (RTWC2.1^{CM}) and the QTL for DS in field (FRR2.3^{CM}) and greenhouse colocalized on Pv02. Interestingly, CAL96 is the source for the increased control root dry weight, whereas MLB-49-89A is the source of both DS QTLs. This finding suggests that this QTL region is important for further study and that the role of root biomass may be more complex than simply "larger is better." This region has strong potential for marker development associated with FRR resistance.

The overlapping of QTLs related to root–shoot loss (RTL7.1^{CM} and STL7.1^{CM}) in the greenhouse and root dry weight in the field (RTW7.1^{CM}) on Pv07 and the R genes identified in that region also suggest the importance of this region for further study on FRR resistance. The region on Pv11 with those colocalized QTLs related to root dry weight (RTWI11.1^{CM}, STWC11.1^{CM}, and RTW11.1) was found to have a cluster of R genes as identified in the common bean reference genome by Schmutz et al. (2014), and disease resistance genes for rust (*Ur-3* and *Ur-11*) were also identified near that region on Pv11 (Meziadi et al., 2016).

The beneficial alleles for DS in the greenhouse and field were both derived from the MLB-49-89A parent. The QTLs from resistant parent MLB-49-89A are likely indicators of regions of resistance genes to FRR that functioned in MLB-49-89A and the RILs inherited from it. The large-seeded parent CAL96 has a larger root system than MLB-49-89A early in development; therefore, it is possible that the QTL with CAL96 as the beneficial allele contributor is more likely an indicator of higher root biomass, as opposed to an indicator of resistance to FRR.

In previous studies for QTLs of FRR resistance, significant QTLs were identified on chromosomes Pv02, Pv03, and Pv05 with RAPD or SSR markers (Schneider et al., 2001;

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Román-Avilés and Kelly, 2005; Kamfwa et al., 2013) and on chromosomes Pv03, Pv05, and Pv07 with SNP markers (Hagerty et al., 2013; Nakedde et al., 2016). Román-Avilés and Kelly (2005) identified a QTL related to FRR on Pv02 (FRR2.1), but it was not possible to directly compare the physical position of the QTLs detected in this study with the QTLs identified with RAPD markers, which were not aligned to a physical map of the genome. The major QTL identified by Kamfwa et al. (2013) with SSR markers (PVBR87 and PVBR109) was located at 46.8 Mb on Pv03, which is different from the QTL for root loss (RTL3.1 ^{CM}) on Pv03 (at 28.6 Mb) in this study. Hagerty et al. (2013) identified two QTLs related to FRR (FRR3.1 and FRR7.1) with SNP markers. The QTL RTL3.1^{CM} in this study is ~7 Mb away from FRR3.1 on Pv03 (at 35.8 Mb), and the QTLs of root–shoot loss (RTL7.1 and STL7.1 at 2.4 Mb) in this study are ~5 Mb away from FRR7.1(at 7.9 Mb). The QTLs of DS in the greenhouse (FRR2.2^{CM} at 35.4 Mb) and control root dry weight (RTWC2.1^{CM} at 32.6 Mb) in this study are very close to the QTL for taproot diameter (TD2.1) on Pv02 (at 34.6 Mb) identified in the Hagerty et al. (2013) study.

Zuiderveen et al. (2016) identified QTLs related to anthracnose [*Colletotrichum lindemuthianum* (Sacc. & Magn.) Briosi & Cavara] resistance in Andean bean cultivars on Pv02 with SNP position at 48.6 Mb, which is close to the QTL for control shoot dry weight (STWC2.1^{CM} at 46.3 Mb) in this study. Vasconcellos et al. (2017) identified meta-QTLs related to white mold [*Sclerotinia sclerotiorum* (Lib.) de Bary] on Pv01 (WM1.1 at 49.9 Mb) and Pv07 (WM7.5 at 3.3 Mb), which are close to the QTLs for inoculated root–shoot dry weight (RTWI1.1 and STWI1.1) on Pv01 and root–shoot loss (RTL7.1 and STL7.1) on Pv07 in this study. In general, the QTLs on Pv02, Pv03, and Pv07 in this study are located in regions similar to QTLs discovered in previous studies, whereas the QTL on Pv11 in this study could be a novel QTL. The colocalized QTLs in different genetic backgrounds from different studies can be used for marker development in ~~marker-assisted selection~~MAS and are potentially useful for FRR resistance detection in other genetic backgrounds.

The R genes identified in QTL regions provide clues as to the underlying disease response mechanisms involved. R genes are usually monogenic or major genes that control resistance to specific pathogen races (Michelmore et al., 2013), but they can also be polygenic, with many genes providing small additive effects, such as primary metabolism genes that play a role in providing energy for the resistance response (Bolton, 2009). In this study, the phenotypic variations explained by the QTLs of ~~those~~ plants with R genes identified in their regions were relatively low (R^2 = 8–16%); thus, those R genes could be polygenic and function together in response to plant infection. However, there is a potential of overestimating some QTL effects due to the relatively small population size (121 individuals).

Lodging and seed size traits varied among the five most resistant and susceptible RILs. This is encouraging from a breeding perspective and indicates that even though the lodging scores were correlated with DS, root–shoot biomass, and shoot biomass reduction in greenhouse study across the entire population, recombinants were identified. The most resistant lines can be used for future breeding practices to transfer FRR resistance to susceptible genotypes, but selection will be needed to obtain genotypes with both FRR resistance and an ideal growth habit.

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CONCLUSIONS

Fusarium root rot~~RR~~ has been a major constraint to common bean yield in many production areas around the world. Characterization of the causal pathogen and identification of genetic resistance are needed for disease management and bean cultivar improvement. Our findings indicate that *Fusarium* virulence is species specific, and FRR resistance reactions vary in bean genotypes and can also be specific to certain species. Through QTL analysis in an intergene pool population, we found evidence that FRR resistance is related to genotypic variability for root biomass; however, the role of root biomass may be more complex than simply bigger is better. A QTL for noninoculated control root weight in the greenhouse experiment colocalized with QTLs for DS in both greenhouse and field experiments on Pv02, which is a region with strong potential for development of molecular markers to use in breeding for FRR resistance. The most resistant RILs that contained several FRR-resistance-related QTLs in this study can be used as useful genetic sources in future breeding programs for introgressing FRR resistance from Middle American bean genotypes to Andean genotypes.

Conflict of Interest

The authors declare that there is no conflict of interest.

Supplemental Material Available

Supplemental Fig. 1. Frequency and distribution of root length, days to flower, and days to maturity of the RIL population of CAL96 × MLB-49-89A in the field. Black and white arrows indicated the phenotypic values of MLB-49-89A and CAL96, respectively.

Supplemental Data File. CAL96 × MLB-49-89A recombinant inbred line population SNP marker and phenotypic data used for QTL analysis.

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ACKNOWLEDGMENTS

We would like to acknowledge the USDA National Institute of Food and Agriculture Initiative Competitive Grant no. 2012-39571-20296 that funded this research. We thank Dr. Qijian Song at the USDA-ARS Soybean Genomic and Improvement Laboratory (Beltsville, MD) for the SNP genotyping service.

REFERENCES

Abawi, G.S. 1989. Root rots. In: H.F. Schwartz and M.A. Pastor-Corrales, editors, Bean production problems in the tropics. 2nd ed. CIAT, Cali, Colombia. p. 105–107

Aoki, T., K. O'Donnell, and D.M. Geiser. 2014. Systematics of key phytopathogenic *Fusarium* species: Current status and future challenges. J. Gen. Plant Pathol. 80:189–201. doi:10.1007/s10327-014-0509-3

Aoki, T., K. O'Donnell, and M.M. Scandiani. 2005. Sudden death syndrome of soybean in South America is caused by four species of *Fusarium*: *Fusarium brasiliense* sp. nov., *F. cuneirostrum* sp. nov., *F. tucumaniae*, and *F. virguliforme*. Mycoscience 46:162–183. doi:10.1007/S10267-005-0235-Y

Beebe, S.E., I.M. Rao, C. Mukankusi, and R.A. Buruchara. 2012. Improving resource use efficiency and reducing risk of common bean production in Africa, Latin America, and the Caribbean. CIAT, Cali, Columbia.

Bolton, M.D. 2009. Primary metabolism and plant defense-fuel for the fire. Mol. Plant Microbe Interact. 22:487–497. doi:10.1094/MPMI-22-5-0487

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TOC Head: ; Section Head: ; Article Type: ARTICLE

Buruchara, R.A., and L. Camacho. 2000. Common bean reaction to *Fusarium oxysporum f. sp. phaseoli*, the cause of severe vascular wilt in Central Africa. J. Phytopathol. 148:39–45. doi:10.1111/j.1439-0434.2000.tb04622.x

Chowdhury, M.A., K. Yu, and S.J. Park. 2002. Molecular mapping of root rot resistance in common beans. Annu. Rep. Bean Improv. Coop. 45:96–97.

Cichy, K.A., T.G. Porch, J.S. Beaver, P. Cregan, D. Fourie, R.P. Glahn, et al. 2015. A diversity panel for Andean bean improvement. Crop Sci. 55:2149–2160. doi:10.2135/cropsci2014.09.0653

Cichy, K.A., S.S. Snapp, and W.W. Kirk. 2007. Fusarium root rot incidence and root system architecture in grafted common bean lines. Plant Soil 300:233–244. doi:10.1007/s11104-007-9408-0

Conner, R.L., A. Hou, P. Balasubramanian, D.L. McLaren, M.A. Henriquez, K.F. Chang, and K.B. McRae. 2014. Reaction of dry bean cultivars grown in western Canada to root rot inoculation. Can. J. Plant Sci. 94:1219–1230. doi:10.4141/cjps2013-416

Hagerty, C.H., A. Cuesta-Marcos, P.B. Cregan, Q. Song, P. McClean, S. Noffsinger, and J.R. Myers. 2015. Mapping and root rot resistance and root architecture quantitative trait loci in common bean. Crop Sci. 55:1969–1977. doi:10.2135/cropsci2014.11.0805

Hall, R. 1991. Fusarium root rot. In: R. Hall, editor, Compendium of bean diseases. Am. Phytopathol. Soc. Press, St. Paul, MN. p. 9–10.

Illumina. 2008. GenomeStudio Genotyping Module. Release 1.8.4. Illumina, San Diego, CA.

Kamfwa, K., M. Mwala, P. Okori, P. Gibson, and C. Mukankusi. 2013. Identification of QTL for Fusarium root rot resistance in common bean. J. Crop Improv. 27:406–418. doi:10.1080/15427528.2013.786775

Kwak, M., D. Velasco, and P. Gepts. 2008. Mapping homologous sequences for determinacy and photoperiod sensitivity in common bean (*Phaseolus vulgaris*). J. Hered. 99:283–291. doi:10.1093/jhered/esn005

Meziadi, C., M.M. Richard, A. Derquennes, V. Thareau, S. Blanchet, A. Gratias, et al. 2016. Development of molecular markers linked to disease resistance genes in common bean based on whole genome sequence. Plant Sci. 242:351–357. doi:10.1016/j.plantsci.2015.09.006

Michelmore, R.W., M. Christopoulou, and K.S. Caldwell. 2013. Impacts of resistance gene genetics, function, and evolution on a durable future. Annu. Rev. Phytopathol. 51:291–319. doi:10.1146/annurev-phyto-082712-102334

Miklas, P.N., and T. Porch. 2010. Guidelines for common bean QTL nomenclature. Annu. Rep. Bean Improv. Coop. 53:202–204.

Mukankusi, C. 2008. Improving resistance to Fusarium root rot [*Fusarium solani* (Mart) Sacc. f. sp. phaseoli (Burkholder) W.C Snyder and H.E Hans] in common beans (*Phaseolus vulgaris* L.). PhD. diss., Univ. of KwaZulu-Natal, Durban, South Africa

Mukankusi, C.M., J. Derera, R. Melis, P.T. Gibson, and R. Buruchara. 2011. Genetic analysis of resistance to Fusarium root rot in common bean. Euphytica 182:11–23. doi:10.1007/s10681-011-0413-2

Mukankusi, C.M., R. Melis, J. Derera, M. Laing, and R.A. Buruchara. 2010. Identification of sources of resistance to Fusarium root rot in common bean in Uganda. J. Anim. Plant Sci. 7:876–891.

Nakedde, T., F.J. Ibarra-Perez, C.M. Mukankusi, J.G. Waines, and J.D. Kelly. 2016. Mapping of QTL associated with Fusarium root rot resistance and root architecture traits in black beans. Euphytica 212:51–63. doi:10.1007/s10681-016-1755-6

O'Donnell, K., D.A. Sutton, A. Fothergill, D. McCarthy, M.G. Rinaldi, M.E. Brandt, et al. 2008. Molecular phylogenetic diversity, multilocus haplotype nomenclature, and in vitro antifungal resistance within the *Fusarium solani* species complex. J. Clin. Microbiol. 46:2477–2490. doi:10.1128/JCM.02371-07

Ondrej, M., R. Dostalova, and R. Trojan. 2008. Evaluation of virulence of *Fusarium solani* isolates on pea. Plant Prot. Sci. 44:9–18. doi:10.17221/519-PPS

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Ongom, P.O., P. Rubaihayo, S.T. Nkalubo, and P. Gibson. 2012. Inheritance of resistance to Fusarium root rot in three common bean genotypes. Electron. J. Plant Breeding 3:892–897.

Román-Avilés, B., and J.D. Kelly. 2005. Identification of quantitative trait loci conditioning resistance to Fusarium root rot in common bean. Crop Sci. 45:1881–1890. doi:10.2135/cropsci2005.0028

Román-Avilés, B., J.M. Lewis, and J.D. Kelly. 2011. *Fusarium* genetic control: A long term strategy. In: F.M. Alves-Santos and J.J. Diez, editors, Control of *Fusarium* disease. Res. Signpoint, Kerala, India. p. 65–108.

Román-Avilés, B., S.S. Snapp, and J.D. Kelly. 2004. Assessing root traits associated with root rot resistance in common bean. Field Crops Res. 86:147–156. doi:10.1016/j.fcr.2003.08.001

SAS Institute. 2013. The SAS system for Windows. Release 9.4. SAS Inst., Cary, NC.

Schmutz, J., P.E. McClean, S. Mamidi, G.A. Wu, S.B. Cannon, J. Grimwood, et al. 2014. A reference genome for common bean and genome-wide analysis of dual domestications. Nat. Genet. 46:707–713. doi:10.1038/ng.3008

Schneider, K.A., K.F. Grafton, and J.D. Kelly. 2001. QTL analysis of resistance to Fusarium root rot in bean. Crop Sci. 41:535–542. doi:10.2135/cropsci2001.412535x

Schoonhoven, A.V., and M.A. Pastor-Corrales, editors. 1987. Standard system for the evaluation of bean germplasm. CIAT, Cali, Colombia.

Sharma-Poudyal, D., T.C. Paulitz, L.D. Porter, and L.J. du Toit. 2015. Characterization and pathogenicity of *Rhizoctonia* and *Rhizoctonia*-like spp. from pea crops in the Columbia basin of Oregon and Washington. Plant Dis. 99:604–613. doi:10.1094/PDIS-08-14-0803-RE

Siddiq, M., and M.A. Uebersax. 2012. Dry beans and pulses production and consumption: An overview. In: M. Siddiq and M.A. Uebersax, editors, Dry beans and pulses: Production, processing and nutrition. John Wiley & Sons, New York. p. 1–22. doi:10.1002/9781118448298.ch1

Song Q., G. Jia, D.L. Hyten, J. Jenkins, E.Y. Hwang, S.G. Schroeder, et al. 2015. SNP assay development for linkage map construction, anchoring whole-genome sequence, and other genetic and genomic applications in common bean. G3: Genes, Genomes, Genet. 5:2285–2290. doi:10.1534/g3.115.020594

van Ooijen, J.W. 2006. JoinMap 4: Software for the calculation of genetic linkage maps in experimental populations. Wageningen, the Netherlands.

Vasconcellos, R.C., O.B. Oraguzie, A. Soler, H. Arkwazee, J.R. Myers, J.J. Ferreira, et al. 2017. Meta-QTL for resistance to white mold in common bean. PLoS One 12:e0171685. doi:10.1371/journal.pone.0171685

Voorrips, R.E. 2002. MapChart: Software for the graphical presentation of linkage maps and QTLs. J. Hered. 93:77–78. doi:10.1093/jhered/93.1.77

Wang, S., C.J. Basten, and Z.B. Zeng. 2010. Windows QTL Cartographer 2.5. North Carolina State Univ, Raleigh.

Zuiderveen, G.H., B.A. Padder, K. Kamfwa, Q. Song, and J.D. Kelly. 2016. Genome-wide association study of anthracnose resistance in Andean beans (*Phaseolus vulgaris*). PLoS One 11:e0156391. doi:10.1371/journal.pone.0156391

Fig. 1. Frequency and distribution of disease severity scores, inoculated root dry weight, inoculated shoot dry weight, control root dry weight, control shoot dry weight, root loss, and shoot loss of the ~~RIL~~ recombinant inbred line population of CAL96 × MLB-49-89A in greenhouse phenotyping. Black and white arrows indicate the phenotypic values of MLB-49-89A and CAL96, respectively.

Fig. 2. Frequency and distribution of disease severity scores, root diameter, root dry weight, shoot dry weight, lodging, and 100-seed weight of the ~~RIL~~ recombinant inbred line population of

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CAL96 × MLB-49-89A in the field. Black and white arrows indicated the phenotypic values of MLB-49-89A and CAL96, respectively.

Fig. 3. Genetic linkage map of the recombinant inbred lines~~RILs~~ of CAL96 × MLB49-89A with four chromosomes that have quantitative trait loci (QTLs) related to *F. brasiliense* root rot resistance colocalized. The solid bars indicate the QTL regions with a 95% confidence interval, and the lines attached to the bars indicate the QTL regions with a 99% confidence interval. RTWI, inoculated root dry weight; STWI, inoculated shoot dry weight; LDG, lodging score in the field; FRR, Fusarium root rot resistance indicated by disease severity score of inoculated plants in greenhouse or field; RTWC, control root dry weight; STWC, control shoot dry weight; RTL, root dry weight loss; STL, shoot dry weight loss; RTW, root dry weight in the field.

Fig. 4. Disease severity scores of recombinant inbred lines~~RILs~~ (RILs) in the greenhouse and field, and the percentage biomass loss of root~~/~~s and shoots of RILs in the greenhouse with varied numbers of quantitative trait loci (QTLs). Five QTLs include individuals with the QTLs FRR2.2^{CM}, FRR2.3^{CM}, RTL7.1^{CM}, RTW7.1^{CM}, RTWI11.1^{CM}; three QTLs include individuals with any three of those five QTLs.

Table 1. Average disease severity score (DS), root loss, and shoot loss of two parent genotypes, CAL96 (CAL) and MLB-49-89A (MLB), inoculated with three inoculum quantities of different *Fusarium* species: *F. solani*, *F. oxysporum*, *F. cuneirostrum*, and *F. brasiliense*.

Species	Inoculum quantities	DS		Root loss		Shoot loss	
		CAL	MLB	CAL	MLB	CAL	MLB
	g	—— 1–9 scale† ——		———— % ————			
F. solani (F_14-7)	1.0	3.4a‡	2.7a	29.1a	23.7a	10.2a	−6.8b§
	2.0	3.3a	2.6a	49.7a	55.3b	28.7a	−2.0b
	3.0	3.8a	3.4a	36.6a	33.7a	**26.8a**§	**−36.0a**
F. oxysporum (F_14-38)	1.5	3.2a	3.2a	**−6.3a**	**36.4a**	**15.7a**	**−41a**
	3.0	3.8ab	–#	30.8b	–	19a	–
	5.0	4.5b	4.7b	38.9b	45.8a	5.7a	−19.1a
F. cuneirostrum (F_14-40)	0.5	5.1b	5.0ab	**3a**	**34.6a**	7.1a	−18.5a
	1.0	4.6b	4.7a	11.9a	22.3a	**6.8a**	**−18.7a**
	2.0	**3.8a**	**5.6b**	**25.2a**	**52.3a**	19.7a	4.8a
F. brasiliense (F_14-42)	0.5	**4.6a**	**5.7a**	32.7a	29.6a	**35a**	**5.1a**
	1.0	5.7b	5.6a	30.7a	13.6a	19.5a	9.9a
	2.0	6.0b	6.4a	13.8a	24.4a	29.3a	12a

† Disease severity was rated on a 1-to-9 scale where any rating >5 indicated moderate to severe root rot.

‡ Values followed by different letters within columns are significantly different from each other (LSD, $\alpha = 0.05$).

§ Negative root loss and/or shoot loss values indicate that the inoculated plants had greater root and/or shoot dry weight than the noninoculated control plants.

¶ Bold numbers indicate significant differences between two bean genotypes (LSD, $\alpha = 0.05$).

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Missing data: seeds did not germinate.

Table 2. ANOVA and summary of average disease severity score (DS), root loss, and shoot loss for two parent genotypes CAL96 (CAL) and MLB-49-89A (MLB), and range and mean of six progenies inoculated with *F. brasiliense* isolate F_14-42 at three different quantities (0.25, 0.5, and 1 g cup^{-1}) of inoculum.

	DS			Root loss			Shoot loss		
Parameter	0.25 g	0.5 g	1 g	0.25 g	0.5 g	1 g	0.25 g	0.5 g	1 g
	—— 1–9 scale† ——			———— % ————					
Parents									
MLB	3.8a‡	4.7a	6.7a	30a	29.6a	21.5a	17.9a	17.5a	8.8a
CAL	4.5a	6.5b	6.6a	28.3a	35.5a	46.7b	12.7a	23.1a	26.8b
Progenies									
Lowest	3.4	5.1	5.6	5.9	16.3	11.1	–5.8	11.9	–2.1
Highest	4.9	5.9	7.2	35	39.7	31.4	27.3	18.6	18.4
Mean	4.2	5.2	6.5	18.9	18.2	17.7	8.4	9.8	7.2
CV (%)	10.5	48.0	41.3	10.3	56.8	58.4	9.6	17.7	53.8
	***P*-value**								
Geno§	<0.0001			<0.0001			<0.0001		
Trt	<0.0001			0.28			0.20		
Geno × Trt	0.02			0.33			0.36		

† Disease severity was rated on a 1-to-9 scale where any rating >5 indicated moderate to severe root rot.

‡ Values followed by different letters within columns are significantly different from each other (LSD, $\alpha = 0.05$).

§ Geno, bean genotypes; Trt, different quantities of inoculum treatment; Geno × Trt, interaction between genotype and treatment.

Table 3. ANOVA and summary of average disease severity scores (DS), inoculated root (Root_Inoc) and shoot (Shoot_Inoc) dry weight, control root (Root_Ctrl) and shoot (Shoot_Ctrl) dry weight, root loss and shoot loss for the two parent genotypes CAL96 (CAL) and MLB-49-89A (MLB), and range in their ~~RIL~~ recombinant inbred line population for each trait in greenhouse evaluation. †

Parameter	DS	Root_Inoc	Shoot_Inoc	Root_Ctrl	Shoot_Ctrl	Root loss	Shoot loss
	1–9 scale‡	———— g ————				———— % ————	
Parents							
MLB	3.5a§	0.06a	0.10a	0.08a	0.12a	30a	14.5a
CAL	4.8b	0.07b	0.11b	0.11a	0.22a	37.3a	48.7b
Progenies							
Lowest	2.4	0.02	0.04	0.04	0.06	−13.6	−4.3
Highest	7.6	0.09	0.20	0.14	0.22	70.7	58.4
Mean	5	0.05	0.09	0.08	0.13	34.9	33.7
CV (%)	17.0	35.3	37.9	30.4	28.3	60.2	47.5
	***P*-value**						
Genotype‡	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001

† Plants were inoculated with the *F. brasiliense* isolate (F_14-42) at the rate of 1 g cup^{-1}.

‡ Disease severity was rated on a 1-to-9 scale where any rating >5 indicated moderate to severe root rot.

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§ Values that followed with different letters within columns are significantly different from each other (LSD, α = 0.05).

~~§Geno: Bean genotypes~~

Table 4. Pearson correlation coefficients (*r*) of disease severity score (DS), inoculated root (Root_Inoc) and shoot (Shoot_Inoc) dry weight, control root (Root_Ctrl) and shoot (Shoot_Ctrl) dry weight, root loss, shoot loss from greenhouse phenotyping results, and lodging (LDG) and 100-seed weight (seed wt.) from field results of the ~~RIL~~ recombinant inbred line ~~RIL~~ population.

Trait	Root_Inoc	Shoot_Inoc	Root_Ctrl	Shoot_Ctrl	Root loss	Shoot loss	LDG	Seed wt.
DS	−0.5***†	−0.5***	−0.4***	−0.4***	0.3***	0.4***	−0.2*	NS‡
Root_Inoc		0.8***	0.7***	0.66***	−0.5***	−0.5***	0.2*	0.4***
Shoot_Inoc			0.62***	0.8***	−0.5***	−0.5***	0.4***	0.4***
Root_Ctrl				0.7***	NS	NS	0.3**	0.4***
Shoot_Ctrl					NS	NS	0.3**	0.4***
Root Loss						0.8***	NS	NS
Shoot Loss							−0.2*	NS
LDG								NS

*,**,*** Significant at the 0.05, 0.01, and 0.001 probability levels, respectively.

† Negative *r* values indicate negative correlation and positive *r* values indicate positive correlation.

‡ NS, not significant.

Table 5. Number of markers and map distance by chromosome of the genetic linkage map developed from the ~~RIL~~ recombinant inbred line population of CAL96 × MLB-49-89A with single nucleotide polymorphism ~~(SNP)~~ markers.

Chromosome	No. of markers	Distance
		cM
Pv01	101	76.0
Pv02	70	90.1
Pv03	83	90.6
Pv04	55	74.4
Pv05	86	65.1
Pv06	57	75.9
Pv07	62	89.8
Pv08	87	83.4
Pv09	79	88.1
Pv10	69	60.4
Pv11	73	68.6
Total	822	862.5

Table 6. Quantitative trait loci (QTLs) associated with root rot resistance, root–shoot biomass, lodging, and seed weight detected in the recombinant inbred line (RIL) population of CAL96 × MLB-49-89A.

QTL name	Trait	ENV†	Chr.	LOD‡	R^2§	Map position	Physical position	Add¶	Flanking markers	CI# (95%)	CI (99%)
						cM	Mb				

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FRR2.2CM	Disease severity score	GH	Pv02	3.85	0.09	50.71	35.4	0.35	ss715648472, ss715648481	49.2, 54.5	46.6, 58.4
FRR2.3CM	Disease severity Score	MRF	Pv02	2.56	0.10	39.61	30.57	0.38	ss715639514, ss715649049	36.5, 43.6	34.2, 49.6
RTWC2.1	Control root dry wt.	GH	Pv02	2.73	0.08	46.21	32.62	0.01	ss715645964, ss715646140	44.8, 48.2	38.2, 49.2
RTWC9.1		GH	Pv09	3.94	0.12	5.51	7.87	−0.01	ss715645748, ss715645741	5.0, 12.6	4.6, 15.5
RTWC11.1		GH	Pv11	4.45	0.12	68.11	53.25	0.01	ss715649519, ss715640756	62.5, 68.4	60.2, 68.4
RTWI1.1	Inoculated root dry wt.	GH	Pv01	3.17	0.08	46.91	45.12	−0.01	ss715650911, ss715647371	46.8, 47.7	44.5, 50.9
RTWI11.1		GH	Pv11	5.84	0.16	68.11	53.25	0.01	ss715649519, ss715640756	67.9, 68.4	66.3, 68.4
STWC2.1	Control shoot dry wt.	GH	Pv02	3.09	0.09	78.01	46.31	−0.01	ss715647527, ss715639664	74.8, 83.0	72.4, 84.8
STWC11.1		GH	Pv11	3.39	0.09	57.91	49.11	0.01	ss715649352, ss715650717	56.7, 60.0	55.1, 60.0
STWI1.1	Inoculated shoot dry wt.	GH	Pv01	3.10	0.08	46.91	45.12	−0.01	ss715650911, ss715647371	43.7, 50.2	39.5, 53.9
RTL3.1	Root loss	GH	Pv03	3.82	0.12	31.71	28.59	0.06	ss715641329, ss715640990	29.3, 32.1	29.2, 32.1
RTL7.1		GH	Pv07	3.41	0.10	15.41	2.42	−0.06	ss715648280, ss715648692	12.6, 17.6	8.1, 23.6
STL7.1	Shoot loss	GH	Pv07	2.72	0.08	15.61	2.42	−0.04	ss715648636, ss715648280	13.9, 18.8	12.1, 24.5
RTW7.1	Root dry wt.	MRF	Pv07	3.67	0.12	14.41	2.17	0.12	ss715648692, ss715646498	9.7, 19.4	7.1, 18.4
RTW11.1		MRF	Pv11	3.60	0.12	52.51	46.93	−0.12	ss715640807, ss715648956	48.2, 55.8	46.1, 55.8
STW4.1	Shoot dry wt.	MRF	Pv04	3.30	0.12	49.71	44.42	−1.05	ss715649259, ss715646131	47.3, 52.5	45.4, 52.5
TD11.1	Taproot diameter	MRF	Pv11	2.95	0.11	13.51	1.68	0.42	ss715645475, ss715645476	11.6, 14.4	2.4, 17.4
LDG1.1	Lodging	MRF	Pv01	12.9	0.42	45.81	44.54	−0.77	ss715646076, ss715650911	43.9, 46.3	43.9, 46.7
SW4.3	Seed wt.	MRF	Pv04	2.98	0.08	36.71	28.14	2.14	ss715650213, ss715641823	32.6, 40.9	32.4, 40.9
SW5.1		MRF	Pv05	9.32	0.28	12.81	1.54	−3.49	ss715649583, ss715646173	10.5, 13.6	6.5, 14.2
SW6.1		MRF	Pv06	2.79	0.07	45.01	26.5	1.79	ss715647111, ss715645671	43.1, 52.7	40.3, 54.3

† EVN, environment; GH: greenhouse, MRF, Montcalm Research Farm.

‡ LOD, logarithm of odds.

§ R^2, coefficients of determination represent the phenotypic variance explained by the QTL.

¶Add, additive values. Negative additive values indicate that RILs with an allele from MLB-49-89A had a greater sample mean in that phenotypic measurement, whereas positive additive values indicate that RILs with an allele from CAL96 had a greater sample mean in that phenotypic measurement.

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CI, confidence interval.

Table 7. Physical position and annotation of disease resistance (R) genes identified in some quantitative trait locus (QTL) regions.

QTL	Chromosome	QTL physical position	R genes in this region	Gene physical position	Annotation†
		Mb		Mb	
FRR2.3[CM]	Pv02	30.57	Phvul.002G152100	30.58	Leucine-rich repeatLRR N-terminal domain
RTWC2.1 [CM]		32.62	Phvul.002G171400	32.71	TIR-NBS-LRR domain
STWC2.1 [CM]		46.31	Phvul.002G291100	45.97	Disease resistance protein (TIR-NBS class)
STW4.1 [CM]	Pv04	44.42	Phvul.004G145300	44.66	Leucine-rich repeatRR transmembrane protein kinase
RTL7.1 [CM]	Pv07	2.42	Phvul.007G029900	2.39	Leucine-rich repeat-RR transmembrane protein kinase
STL7.1 [CM]		2.42	Phvul.007G032100	2.56	Leucine-rich repeatRR- protein kinase
RTWC11.1 [CM], RTWI11.1 [CM]	Pv11	53.25	Phvul.011G212100	53.23	Leucine-rich repeatRR family protein
STWC11.1 [CM]		49.11	Phvul.011G181366	49.36	Leucine-rich repeatRR-containing protein
RTW11.1 [CM]		46.93	Phvul.011G166100	47.00	NB-ARC domain-containing disease resistance protein

† LRR, leucine-rich repeat; TIR, Toll/interleukin-1 receptor; NBS, nucleotide binding site; NB-ARC, a nucleotide-binding adaptor in R genes.

Table 8. The five most resistant and five most susceptible lines to Fusarium root rotRR in the RIL recombinant inbred line population of CAL96 × MLB-49-89A selected on the basis of disease severity score (DS) in the greenhouse (GH) and field, and root and shoot loss under greenhouse conditions, and their seed color, 100-seed weight (seed wt.), and lodging score (LDG).

Line	DS (GH)	DS (field)	Root loss (GH)	Shoot loss (GH)	Seed color	Seed wt. (field)	LDG (field)
	—— 1–9 scale† ——			———— % ————		g	1–5 scale‡
Resistant							
CxM_274	4.9	5.7	9.0	15.0	Black mottled	33.5	4
CxM_425	4.0	4.3	12.5	15.1	Pink	33.8	4
CxM_433	4.8	5.3	−4.2	16.6	Red mottled	39.5	1
CxM_517	2.4	7.0	8.6	5.7	Purple mottled	41.1	2
CxM_521	2.4	7.7	10.7	8.6	Black mottled	54.3	3
Susceptible							
CxM_121	7.0	6.7	70.7	58.4	Purple mottled	32.1	2
CxM_138	6.6	7.3	64.0	48.9	Red mottled	38.8	1
CxM_208	7.0	7.5	39.8	49.6	Black	38.2	1
CxM_222	7.0	8.0	40.2	40.8	Black mottled	29.5	3
CxM_246	7.2	7.7	55.5	47.6	Light brown	35.0	3
MLB49	3.3	7.3	23.5	15.2	Black	41.2	4
CAL96	5.4	8.0	35.4	46.3	Red mottled	60.9	2

† Disease severity was rated on a 1-to-9 scale where any rating >5 indicated moderate to severe root rot.

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‡ Lodging was rated on a 1-to-5 scale where 1 is completely upright and 5 is completely prostrate.