Genome-wide association study of water use patterns of common bean (*Phaseolus vulgaris* L.) genotypes in response to drying soil

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Abstract

Common bean (*Phaseolus vulgaris* L.) is the main legume crop for direct human consumption worldwide, especially in developing countries. Among the abiotic factors affecting common bean production, drought is the most limiting condition. Capacity for the accurate identification and selection of drought-tolerant genotypes is a paramount step in the improvement of new cultivars. This study is aimed at characterizing the genetic variability and genetic architecture of transpiration, stomatal regulation and whole plant water use within the Mesoamerican common bean germplasm. Three greenhouse experiments were conducted, and water use was recorded gravimetrically. Transpiration of water-stressed plants was normalized against well-watered plants to obtain a normalized transpiration rate (NTR). A critical fraction of transpirable soil water (FTSWc) was estimated as the inflection point at which NTR starts decreasing linearly. Genome-wide association (GWA) analyses for average NTR and FTSWc were performed. High variation in average NTR and FTSWc was found among genotypes. Genomic signals (QTL) controlling the variation of these traits were identified on *Pv*01 and *Pv*07 some located in intergenic, intronic and exonic regions. A set of novel candidate genes and putative regulatory elements located in these QTL were identified. Most of the genes have been previously reported to be involved in abiotic tolerance, including some of the five transcription factors identified. Candidate genes can be used for marker-assisted selection and further study of drought tolerance mechanisms in common bean. Our results provide tools to accelerate the drought tolerance improvement in the crop.

Keywords

Breeding, abiotic stress, drought, GWAS, transcription factor

Word count: 4880

Introduction

Pulses are a rich source of dietary fiber, micronutrients, vitamins, carbohydrates, and mono- and poly-unsaturated fatty acids (McCrory et al., 2010). Among pulses, common bean (*Phaseolus vulgaris* L.) is the most cultivated pulse crop for direct human consumption (FAOSTAT, 2019). This crop represents a valuable commodity to ensure food security worldwide, mainly in developing countries. In climate change scenarios, increasing temperatures and the reduction of water availability pose serious threats to food production (Fereres and Soriano, 2007; OECD, 2014). Common bean yield is affected by drought (Beebe et al., 2014), therefore the development of drought-tolerant cultivars is an urgent need in breeding programs (Miklas et al., 2006).

One of the main plant responses to water limitations is reducing transpiration to avoid excessive water loss (Osakabe et al., 2014). Transpiration is limited by partial stomatal closure in response to increased atmospheric vapor pressure deficit (VPD) and reduction of the fraction of transpirable soil water (FTSW) (Sanchez et al., 2021). An early plant response to drying soil will conserve water content for late in the season, especially during grain filling, preventing the wilting genotype and improving plant drought-resistance (Jafarikouhini et al., 2020; Chiango et al., 2022). The selection of genotypes with improved capacity to maintain water status is crucial to developing new drought-tolerant cultivars (Ray and Sinclair, 1997; Egan et al., 2021). The limited-transpiration trait is now included in commercial soybean (*Glycine max* Merr. L.) (Carter et al., 2016)and maize (*Zea mays* L.) (Gaffney et al., 2015)cultivars for increased yield under water limiting conditions.

The identification of differences in traits such as transpiration among genotypes can be challenging as they show high plasticity across environments in multiple plant species (Ritchie, 1980). A methodology to identify patterns in water use is to analyze the normalized transpiration rate (NTR) based on soil water content, and the critical fraction of transpirable soil water (FTSWc). Comparisons based on soil water content are more reliable to detect differences between genotypes attributable to actual variation in plant physiology (Ray and Sinclair, 1997). The FTSWc indicates the plant-transpirable water content in soil at which the plant starts closing stomata and reducing transpiration rates. Therefore, FTSWc allows the characterization of genotypes based on their response. FTSW is centered between 0 and 1, where relatively low values of FTSWc indicate that the plant maintains transpiration rates longer and may continue growing under long periods of stress. In contrast, germplasm with relatively high FTSWc thresholds are more sensitive to water deficit and close stomata earlier, making them suitable for intermittent drought stress periods (Egan et al., 2021). High FTSWc may also be evidence for germplasm with faster recovery rates between intermittent drought periods.

The analysis of NTR and FTSWc has been used to characterize stomatal regulation dynamics in maize (Ray and Sinclair, 1997; Devi and Reddy, 2020b); genotypic variation in cotton (Devi and Reddy, 2020a), sorghum (Choudhary and Sinclair, 2014), white clover (Egan et al., 2021); and pearl miller cultivars (*Pennisetum glaucum* (L.) R. Br.) (Kholová et al., 2010a). To date, no GWA have been performed to attempt to identify candidate genes involved in the regulation of these constitutive water-conserving mechanisms.

The identification of candidate genes is a valuable resource to design and implement marker-assisted selection (MAS) strategies that allow a rapid screening and selection of genotypes. The overall objective of this study was to characterize the response of transpiration in Mesoamerican bean accessions to drying soil and identify candidate genes using GWA.

Materials and methods

Plant material and experiment design

A subset of 82 Mesoamerican bean genotypes (hereafter drought diversity panel, DDP) from the larger Mesoamerican diversity panel (MDP, 498 individuals) was used in the present study. The DDP is a selected group of varieties, lines, and landraces that differ in their response to drought (Mukeshimana et al., 2014). Three independent greenhouse experiments were conducted at Michigan State University in 2013 (repetitions one and two) and 2014 (repetition three), with a duration 26, 37, and 32 days after treatment (DAT), respectively.

For each repetition trial, treatments consisted of irrigation (control), and drought with three replicates in a randomized complete design. Prior to the beginning of the treatments, pots were saturated and allowed to drain overnight. The next morning, pots were sealed at the bottom and top to avoid any water loss from runoff and evaporation. At the beginning of the experiment the saturated pot weights were determined, and daily pot weights were recorded. Plants under well-watered conditions were replenished with the exact amount of water that had been transpired in a 24-hr period. Drought treatments underwent a progressive drydown with no water replenishment. The drought treatment finished once all the cultivars had died. Further details on this methodology can be found in Ray and Sinclair (1997), Egan et al. (2021), and Chiango et al. (2022).

Transpiration rate and FTSW

Transpiration was analyzed using the combined data from the three experiments. The transpiration was analyzed following the methodology proposed by Ray and Sinclair (1997) and measured as the difference in pot weights every 24 hours. In days when there was no deficit (e.g. due to cloudy conditions between days), values were eliminated for that replicate. The transpiration rate (TR) was calculated as the ratio between the weight of droughted pots and well-watered pots on each day. A second normalization was applied to TR using the average TR between days two and five (well-watered period) according to the formula:

$$NTR = \frac{TR}{Day\ 2-5\ average\ TR}$$

During days 2 – 5, all the plants were still well-watered, as sufficient soil water was available. With this normalization, plants at full transpiration would have a normalized TR (NTR) near to 1.

To determine the extent of water extracted by plants, the fraction of transpirable soil water (FTSW) was calculated as:

$$FTSW = \frac{(Daily\ pot\ weigth - Final\ pot\ weight)}{(Pot\ weigth\ on\ 1\ DAT - Final\ pot\ weight)}$$

The relationship between NTR and FTSW was obtained by fitting the equation previously described by Muchow and Sinclair, (1991):

$$NTR = \frac{1}{[1 + A\ \times \exp(B \times FTSW)]}$$

Where A and B are empirical coefficients generated for each genotype through curve fitting. A linear-plateau regression was used to determine the critical FTSW (FTSWc) where NTR starts decreasing linearly and indicates the point at which stomata start to close in stressed plants. FTSWc was determined for each genotype in each replicate.

Statistical analysis

The data from the three experiments were combined and analyzed together in a randomized complete block design (RCBD) with average values across replications within repetitions as replicates. One-way analysis of variance (ANOVA) was conducted using the following model:

$$y_{ijk} = \mu + \alpha_i + \beta_j + e_{ij}$$

Where μ is the grand mean, α_i is the effect of the *ith* genotype, β_j is the effect of the *jth* repetition experiment, and e_{ij} is the random error. Best linear unbiased predictors (BLUPs) were estimated with the restricted maximum likelihood (REML) method using the *lme4* package in R v4.1 (Bates et al., 2015) and BLUP-adjusted means were calculated. BLUP-adjusted means were compared by the least-squares method (α=0.05). Broad-sense heritability (H^2) was estimated by:

$$H^2 = \frac{\hat{\sigma}_g^2}{\hat{\sigma}_g^2 + \frac{\hat{\sigma}_e^2}{n}}$$

Where $\hat{\sigma}_g^2$ is the genotypic variance, $\hat{\sigma}_e^2$ is the error variance, and n is the number of replicates (experiments).

Genome-Wide Association Analyses

Genotypic data

The DDP was previously genotyped (Moghaddam et al., 2016). The genotypic data contains around 200K single nucleotide polymorphisms (SNPs) and can be found on the BeanCAP website (http://arsftfbean.uprm.edu/beancap/research/, Accessed Jun. 2022). SNPs with a minor allele frequency (MAF) < 0.02 were filtered. This threshold was chosen to facilitate the

identification of rare genotypes. Linkage disequilibrium (LD) between markers was calculated using all the SNPs within a sliding window of 50 SNPs in TASSEL 5 software (Bradbury et al., 2007).

The LD decay pattern for each chromosome and whole genome was analyzed by nonlinear regression fitting the expectation of the parameter r^2 and the distance between each pair of markers (Hill and Weir, 1988; Remington et al., 2001). Population structure was evaluated using the variational Bayesian inference in fastSTRUCTURE (Raj et al., 2014) with two populations (K = 2) based on previous knowledge of the subpanel (Hoyos-Villegas et al., 2017).

GWAS

A GWAS analysis was performed using 182,243 SNPs with a MAF > 0.02, and the BLUP-adjusted means of the FTSWc and average NTR under water deficit for each genotype. Analyses were carried out using multiple models, including Mixed Linear Model (MLM), compressed MLM (CMLM), Settlement of MLM Under Progressively Exclusive Relationship (SUPER), Fixed and random model Circulating Probability Unification (FarmCPU), and Bayesian-information and LD Iteratively Nested Keyway (BLINK) implemented in GAPIT v.2 (Tang et al., 2016). Individual relatedness was also considered with the kinship matrix that is automatically calculated within GAPIT using the VanRaden method (VanRaden, 2008). Peak SNPs with *p*-values above a Benjamini-Hochberg false discovery rate (FDR) threshold of 0.05 were considered significant and were further examined. The variance explained by significant SNPs was estimated by the coefficient of determination (R^2) of a linear regression model. The model included all the five PCs from PC analysis (PCA), the SNP marker parameterized in accordance with the gene action determined using the general, additive, and simplex dominance models in the R package GWASpoly (Rosyara et al., 2016), and a vector of random residuals (Wallace et al., 2016).

Haplotype analysis and candidate genes

Haplotype blocks were defined using the solid spine of LD method implemented in Haploview v.4.2 software with default parameters (Barrett et al., 2005). The proportion of the phenotypic variance explained by significant SNPs from GWAS (R^2) was recalculated after including the SNPs present in the same haplotype block.

To identify candidate genes, JBrowse on Phytozome v13 (Goodstein et al., 2012) was used to browse the common bean reference genome v.2.1 (Schmutz et al., 2014) within a ± 100-Kb window centered on each associated SNP. Candidate genes were selected based on their annotation and literature review related to drought and other abiotic stresses.

Results

Transpiration rate response to drying soil and heritability

The average NTR per genotype during the evaluation period ranged from 0.33 in Yolano to 0.96 in ABCP-8, with a global mean of 0.52 (Table 1) and an H^2 of 0.53.

There was a consistent relationship between NTR and FTSW. The NTR value decreased with a linear tendency below the FTSWc for each genotype. The FTSW threshold varied from 0.55 in the pink bean genotype Harold to 0.97 in the black bean T-39 with an overall mean of 0.76 and significant differences between the maximum and minimum ($p<0.05$; Table 1). Figure 1 depicts the average response of NTR to a decreasing FTSW for the bottom (average FTSWc = 0.58; Figure 1A) and top five (average FTSWc = 0.94; Figure 1B) genotypes. Using the genotypic and error variances, the estimated H^2 for FTSWc was 0.38.

Population structure and LD decay

Two subpopulations were identified in the DDP (K=2) with varying probabilities of ancestry among genotypes. Admixture between the two subpopulations was also observed. The chromosome-wise analysis of the LD decay pattern showed that in the DDP, LD decayed at a range from 135.5 Kbp in *Pv04* to 848.7 Kbp in *Pv09* with a genome-wise decay distance of 363.3 Kbp.

Genome-Wide Association and haplotype analysis

Based on the adjustment of the models in the QQ plots, all the tested models performed similarly with a slight improvement in Blink for FTSWc (Figure S1) and FarmCPU for average NTR (Figure S2). Blink and FarmCPU were used for the analysis of marker-trait associations for FTSWc and average NTR, respectively. FarmCPU and Blink have also shown improved statistical power with both simulated and real datasets (Huang et al., 2019; Kaler et al., 2020).

In FTSWc, one SNP was identified on *Pv01* at 33,516,386 bp (C/T; *Pv01*FTSWc) and another on *Pv07* at 9,224,979 bp (C/T; *Pv07*FTSWc) (Figure 2A). Each SNP for FTSWc had an effect of +0.26 units and explained the 31% of the phenotypic variation. For average NTR, two significant SNPs were identified in *Pv01* at 28,451,384 bp (C/A; *Pv01*NTR_1) and 35,489,136 bp (A/G; *Pv01*NTR_2) with an effect of -0.22 and +0.19 units, respectively (Figure 2B). *Pv01*NTR_1 explained the 23% of the phenotypic variation (R^2), and *Pv01*NTR_2 the 24%. The four SNPs were detected using the multiple models and had a MAF of 0.02.

The genotype T-39 that had the highest FTSWc was homozygous for the alternative allele (TT) of *Pv01*FTSWc and *Pv07*FTSWc. NW-63 was heterozygous for the significant SNPs of FTSWc and was among the top five values. Harold, lowest FTSWc (0.55) was homozygous for the reference alleles (CC). For *Pv01*NTR_1, ABCP-8 is homozygous (AA) for the alternative allele and had the highest average NTR (0.96), followed by A-55 which is heterozygous (A/G). ABCP-8 and A-55 are homozygous (GG) for the alternative allele of *Pv01*NTR_2. Yolano is homozygous for the reference allele (GG) and had the lowest average NTR.

In the haplotype analysis for Pv01, the SNP *Pv*01FTSWc was grouped with 29 additional SNPs in a haplotype block of 308 Kbp. Out of the 30 SNPs in the haplotype, 15 were in genic regions and the others in intergenic regions. The haplotype containing *Pv*01FTSWc explained a higher variation (42%) compared to the single SNP (31%). In aberage NTR, *Pv01*NTR_1 was grouped with 48 additional SNPs where the marker ss01_28185985 is in a coding region. The block had a size of 462 Kbp and explained a higher total phenotypic variation (36%) compared to the single

SNP (23%). *Pv01*NTR_2 was in a block of 454 Kbp with four SNPs, but no increases in the R^2 were observed for the haplotype compared to the individual significant SNP.

For haplotypes on Pv07, *Pv07*FTSWc was grouped with 6 additional markers in a haplotype of 464 Kbp with the SNP ss07_9279035 located on a genic region. For this haplotype, no increases in the variation explained were detected.

Candidate genes

Using a 100 Kbp window, four genes were associated with the haplotype of *Pv*01FTSWc, 12 with the haplotype for *Pv07*FTSWc, three genes with the haplotype containing *Pv*01NTR_1, and four with the haplotype containing *Pv*01NTR_2. Considering their annotations and potential role in abiotic stress responses, genes were filtered, and seven candidate genes were identified on *Pv01*, and seven on *Pv07* for limited transpiration in common bean (Table 2). Interestingly, four of the genes are annotated as transcription factors (TFs). A TF on *Pv01* was bHLH106-related (*Phvul.001G121200*); and on *Pv07*, TFs were UPBEAT1 (*Phvul.007G089100*), No apical meristem (NAM) protein (*Phvul.007G089600*) on *Pv07*, and C2H2-type Zn-finger protein (*Phvul.007G090500*).

Discussion

The present study investigated the transpiration rate response of common bean and genotypic differences among Mesoamerican accessions. Under drought-like conditions, stomata closure is among the first physiological responses to avoid water loss through transpiration (Osakabe et al., 2014). Stomatal closure under drought is mainly triggered by an increase in the abscisic acid (ABA) concentration in leaves (Bharath et al., 2021). However, it can also be induced by hormones like salicylic acid (SA), methyl jasmonate (MJ) and ethylene; metabolites such as proline and polyamines; and gaseous signals such as hydrogen sulfide (H_2S) (Agurla et al., 2018). Stomatal closure triggered by these components is mediated by hydrogen peroxide ($H2O_2$), calcium (Ca^{2+}), and nitric oxide (NO) (Agurla et al., 2018). Likewise, drought causes the ABA-dependent and independent activation of key transcription factors (TFs) (Nakashima et al., 2014).

Stomatal limitations restrict gas exchange rate, photosynthetic activity, and plant growth and development. Drought tolerant varieties are expected to minimize physiological and yield penalties despite water shortage and can be identified based on a slow leaf wilting phenotype. The soybean cultivar PI 471938 is an example of a slow wilting genotype that exhibits water-conservative traits by maintaining TR (Fletcher et al., 2007). However, a reduced TR is usually observed in drought tolerant genotypes compared to drought sensitive materials (Kholová et al. 2010) for short drought periods. Reductions in TR are associated with early stomatal closure and high FTSW thresholds (Ray and Sinclair, 1997; Egan et al., 2021). For PI 471938 has been ruled out that its resistance is due to differences in FTSWc values compared to non-resistant genotypes (Sadok et al., 2012). Implying additional mechanisms involved in water conservation and may not be fully detected by differences in the critical FTSW.

Among the genotypes with the lowest average NTR (Table 1), Othello has been reported as a drought resistant cultivar, but US-1140 and UI-59 as low yielding cultivars (Muñoz-Perea et al., 2006), which suggests that the stomatal responses of common bean to water deficit have varying impacts on plant performance and is influenced by other traits depending on the cultivar.

A lower TR indicates that the plant favors a conservative water use mechanism and survival for longer periods (Kholová et al. 2010). Devi and Reddy (2020) observed a positive correlation between TR and FTSWc when studying different cotton accessions. In contrast, we observed no relationship between average NTR and FTSWc since the genotypes with the lower average NTR did not have a higher FTSWc (Table 1). This can be explained by genotypic differences in stomatal and hydraulic conductance among the evaluated genotypes. Hydraulic conductance affects stomatal conductivity, transpiration rate, and water potential, and its variation depends on anatomic changes in membrane thickness, structure, and permeability (Hacke and Way, 2014; Simonin et al., 2015). Adjustments in hydraulic conductance may also depend on changes in water transport in roots and shoot via aquaporins (Choudhary and Sinclair, 2014). In French bean leaves, Sôber, (1998) observed that high stomatal conductance rates were accompanied by a high hydraulic conductivity. Additionally, Choudhary and Sinclair (2014) found that differences in TR among sorghum genotypes result from a varying hydraulic conductance where some genotypes with low TR can maintain high rates of both stomatal and hydraulic conductance. The slow wilting soybean PI 471938 has been found to have a limited hydraulic conductance in leaves while maintaining constant TR(Sinclair et al., 2008). It is possible then, that the genetic variation in the evaluated panel allows some cultivars to have an early stomatal closure (high FTSWc) with an improved transpiration and hydraulic conductance. In contrast, low FTSWc may provide a plant with the ability to conserve water under intermittent drought conditions, but this has to be coupled with an equivalent rate of stomatal reopening upon rehydration. In addition, growth and development (as they pertain to seed yield) must not be severely compromised, placing further emphasis on efficiencies between photosynthetic rate and CO_2 exchange under intermittent and terminal drought conditions.

Plants with high TRs may keep stomata open longer in drying soil, which results in lower FTSWc values (Ray and Sinclair, 1997). Genotypes with low FTSWc maximize water use and are desirable for short-term water deficit periods (Egan et al., 2021). Harold had the lowest threshold (0.55) and has been reported to have a moderate to high level of resistance to drought (Singh et al., 2001). Common Red Mexican (FTSWc=0.58) is a landrace that exhibits high level of water stress tolerance (Muñoz-Perea et al., 2007), despite having a moderate average NTR in the present study (0.54). As explained above, a varying dynamic between TR and FTSWc may be explained by genetic differences in stomatal and hydraulic conductance. We did observe that ABCP-8 had the highest average NTR (0.96) and one of the lowest FTSWc (0.58; Table 1). ABCP-8 is a pinto bean line bred for common bacterial blight resistance by crossing the donor XAN 159 and the recurrent parent 'Chase' pinto (Mutlu et al., 2005). It is worth noting that the line XAN 159 was developed using interspecific crosses with tepary bean (*Phaseolus acutifolius* A. Gray) (Thomas and Giles Waines, 1984), which has been referred as a source of resistance for heat and drought stress (Souter et al., 2017; Moghaddam et al., 2021). It is possible that genetic elements involved in the response of the cultivar to drying soil and response to drought were introgressed into ABCP-8 from tepary bean accessions.

Drought tolerance is a complex trait with high variation in multiple structural, physiological, and metabolic components (Bowles et al., 2021). Similar to our results, previous studies on drought responses in common bean have identified QTL on Chr01 and Chr07 (Mukeshimana et al., 2014; Briñez et al., 2017; Dramadri et al., 2019). In a biparental population of Andean genotypes, Sedlar et al. (2020) identified QTL for water potential mainly in linkage groups one and seven. Leitão et al. (2021) found significant associations for stomatal conductance under different water regimes in Portuguese accessions. However, they found no associations on Chr07, and one SNP was located on Chr01 in a different locus compared to our results.

Depending on the breeding purpose, once validated, the identified SNPs can be used for marker-assisted selection (MAS). For short drought periods, selections favoring the alternative alleles (T) for *Pv01*FTSW and *Pv07*FTSW would increase the FTSWc and allow an early stomatal closure. In contrast, if breeding for long drought periods, selection against the alternative allele would be desirable since the plant will keep stomata open, reducing the impact on photosynthesis activity and growth. Nevertheless, this selection must be done considering that a limited NTR would be necessary to avoid excessive loss of water. In this case, a positive selection for the alternative allele (A) of *Pv01*NTR_1 and a selection against the alternative allele (G) in *Pv01*NTR_2 should favor a reduced NRT.

The candidate gene *Phvul.001G108800* encodes for an aquaporin SIP2-1-Related protein (Table 2). In Arabidopsis, the aquaporin SIP2-1 protein is localized in the endoplasmic reticulum (ER) and has been associated with the alleviation of ER stress (Sato and Maeshima, 2019). ER stress results from the accumulation of misfolded or unfolded proteins in the ER during environmental stresses, including drought (Deng et al., 2013).

Thioredoxins (Trx) are thiol:disulfide oxidoreductase proteins involved in the formation or reduction of disulfide bonds (Eklund et al., 1991). This class of proteins can be induced by water deficit in *Solanum tuberosum* (Rey et al., 1998) and have been proposed as candidate genes for salt tolerance in bread wheat (Chaurasia et al., 2020). The candidate gene encoding for a Thioredoxin-Like 1-1 protein (*Phvul.001G109200*) may provide drought tolerance in common bean by regulating the redox state of chloroplast proteins. Recently, Yokochi et al. (2021) demonstrated in Arabidopsis that Trx and Trx-like proteins are involved in the regulation of chloroplast functions, including photosynthesis-related proteins.

*Pv01*NTR_2 had three candidate genes related to abiotic stress (Table 2). Extensins (EXTs) are proline-rich proteins that play a paramount role in cell wall synthesis and modification during root and pollen development (Kishor et al., 2015). Proline is an amino acid that accumulates under stress conditions as a beneficial solute to reduce the osmotic potential and help cope with the effects of drought (Chul et al., 2018). The candidate Phosphatidylinositol N-acetylglucosaminyltransferase subunit Q protein (PIG-Q) (*Phvul.001G127800*) is part of the GPI-GlcNAc-transferase (GPI-GnT) multiprotein complex involved in the glycosylphosphatidylinositol (GPI)-anchor biosynthesis in plants (Beihammer et al., 2020). The GPI-anchor is a post-transcriptional modification of diverse protein families implicated in cell wall composition, cell expansion, biotic and abiotic stress response, stomata development, pollen tube elongation, and hormone signaling (Beihammer et al., 2020). Variations in PIG-Q may

change the modification of key proteins in the water deficit response. However, further investigation would be necessary.

Water stress increases reactive oxygen species (ROS) leading to oxidative stress. Nitric oxide (NO) limits the accumulation of ROS by inhibiting the Nicotinamide adenine dinucleotide phosphate (NADPH) oxidase enzyme complex, reacting with ROS, and inducing the expression of antioxidant enzymes genes (del Río, 2015). Furthermore, NO plays a key role in the abscisic acid (ABA)-induced stomatal closure during stress (Perlikowski et al., 2022). The nitric-oxide synthase (NOS) identified (candidate gene *Phvul.001G128000*) is one of the main enzymes involved in NO production (Neill et al., 2003) that may alleviate the oxidative stress and regulate an early stomatal closure. Cao et al. (2019) showed that an early NOS-mediated nitric oxidative increase mitigates oxidative damage in rice roots under drought.

Alkaline ceramidases have been poorly studied in plants. However, the overexpression of an alkaline ceramidase in Arabidopsis promotes autophagy under abiotic stresses (Zheng et al., 2018). Autophagy is a conserved pathway that plays a critical role in the adaptation of plants to drastically changing environmental stresses (Han et al., 2011). Particularly, the alkaline ceramidase AtACER is involved in disease resistance and salt tolerance (Wu et al., 2015). The Alkaline ceramidase-related candidate gene (*Phvul.007G090000*) is a novel target in common bean to study the role of alkaline ceramidases in crop plants, and also for drought tolerance improvement.

The transport of auxins plays an important role in plant growth and development, and is regulated by influx (AUXIN1/LIKE-AUX1 family) and efflux (mainly PIN-Formed (PIN)) carries (Swarup and Bhosale, 2019). The candidate Auxin efflux carrier component 1 (*Phvul.001G121100,* Table 2) is encoded by the PIN1 gene belonging to the type-I PIN proteins (Armengot et al., 2016). The downexpression of PIN1 and other members of the type-I PIN subfamily has shown to affect root meristem size during salt stress by increasing NO levels (Korver et al., 2018). The potential role of PIN1 in common bean is in accordance with the candidate NOS gene detected also on Chr01. Furthermore, Zhang et al., (2012) showed that in rice PIN3t, another type-I PIN, is involved in drought stress response and tolerance.

On Pv07, the candidate gene *Phvul.007G088800* encodes the ATP-binding Cassette Transporter G family member 25 (ABCG25). ABCG25 is an ABA exporter expressed in vascular tissue that controls cellular ABA levels (Park et al., 2016) and influences stomatal regulation (Kuromori et al., 2010). ABA is the main plant hormone involved in abiotic stress responses, seed processes, and senescence. Particularly, long-distance ABA signaling and its interplay with other processes are involved in the detection of drying soil and plant responses (Davies et al., 2005), which agrees with our experiments. ABCG25 and other transporters have been shown to respond to abiotic stresses including temperature (Baron et al., 2012) and drought (Chen et al., 2011).

Phosphorylation is one of the main signaling mechanisms involved in a myriad of plant responses. The candidate genes *Phvul.007G089200* and *Phvul.007G089301* encoding for a Protein Tyrosine kinase (PTK) and a Calcium-dependent protein kinase (CPK) 11-related protein, respectively, may be involved in the response to drought stress. The role of PTKs has been mostly studied in animals and humans and remains poorly understood in plants. Recently,

(Allimuthu et al., 2020) characterized a set of PTKs in rice, identifying key genes implicated in the osmotic and drought stress response. CPKs also phosphorylate Tyr residues of beta-tubulin and several transcription factors (TF) in Arabidopsis (Nemoto et al., 2015). Interestingly, many of these TFs are related to ethylene and ABA, and have shown to be relevant for plant response to abiotic stresses (reviewed in Miyamoto et al., 2019).

Five candidate genes involved in gene expression regulation were identified. Mitochondrial transcription termination factor (mTERF) proteins (*Phvul.007G089900*) are key components of organellar gene expression (OGE) machinery in chloroplasts and mitochondria (Barkan, 2011). Despite plants having more mTERF genes compared with animals, their role is still poorly understood. Studies in maize and Arabidopsis have shown that mTERFs regulate different developmental processes, including the response to abiotic stresses. For instance, in Arabidopsis, *mTERF* mutants display varying sensitivity to heat and saline stress, as well as response to ABA (Robles and Quesada, 2021). This poses an interesting role for this candidate gene in the drought tolerance of common bean.

The TFs bHLH106-related (*Phvul.001G121200*), UPBEAT1 (*Phvul.007G089100*), C2H2-type Zn-finger protein (*Phvul.007G090500*), and No apical meristem (NAM) protein (*Phvul.007G089600*) are promising candidate genes for drought tolerance improvement in common bean. bHLH TFs are one of the main TF families in angiosperms with paramount roles in abiotic stresses (Khan et al., 2018). In Arabidopsis, Ahmad et al. (2015) showed that bHLH106 is a major regulator that integrates the function of multiple salt tolerance-related genes. The homolog gene in common bean could be a main target for crop improvement. UPBEAT1 is a TF also belonging to the bHLH family. In Arabidopsis, UPBEAT1 regulates peroxidases and is involved in the accumulation of ROS and primary root elongation (Tsukagoshi et al., 2010). C2H2 zinc finger proteins have key regulatory roles in abiotic stress resistance in plants. The CH2H-type proteins have a significant binding diversity characterized by their ability to interact with DNA, RNA, and other proteins (reviewed in (Han et al., 2020). Finally, the NAM proteins are part of the NAC TF family, which has been described in multiple crops (Shao et al., 2015), and associated with stress response in solanaceous (Tweneboah and Oh, 2017) and cereals (Dudhate et al., 2021).

Conclusions

The present study represents the largest FTSW study reported. The high variation in average NTR and FTSWc among Mesoamerican beans shows that variation for the improvement of these traits exists and may enable breeding cultivars with an improved capacity to preserve water status during short or long water deficit periods. The identified genotypes with the extreme values for average NTR and FTSWc such as Othello, Harold, and ABCP-8 can be used as parents for future breeding strategies in either short or long drought periods. The four candidate QTL identified on Pv01 and Pv07 allowed the identification of 15 new candidate genes that can be targets for marker-assisted selection and for further research aimed at identifying causal polymorphisms in gene sequences. Interestingly, five candidate genes corresponded to transcription factors (e.g., *Phvul.001G121200*) which constitute major target genes due to their

role in controlling multiple genes. Some of the candidate genes have been poorly studied in crop plans, which opens new opportunities for further validation in beans and other crop species.

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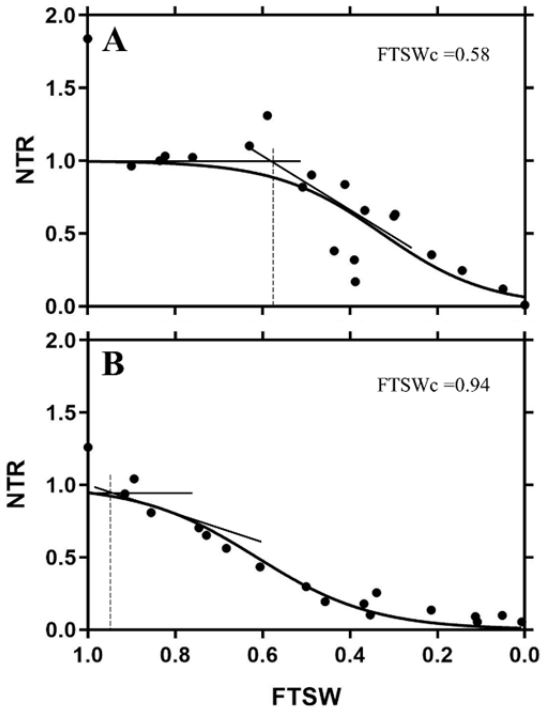


683
684 **Figure 1.** Average normalized transpiration rate (NTR) in response to the fraction of transpirable
685 soil water (FTSW) in the five genotypes with the lowest FTSWc (A) and the five genotypes with
686 the highest FTSWc (B).
687

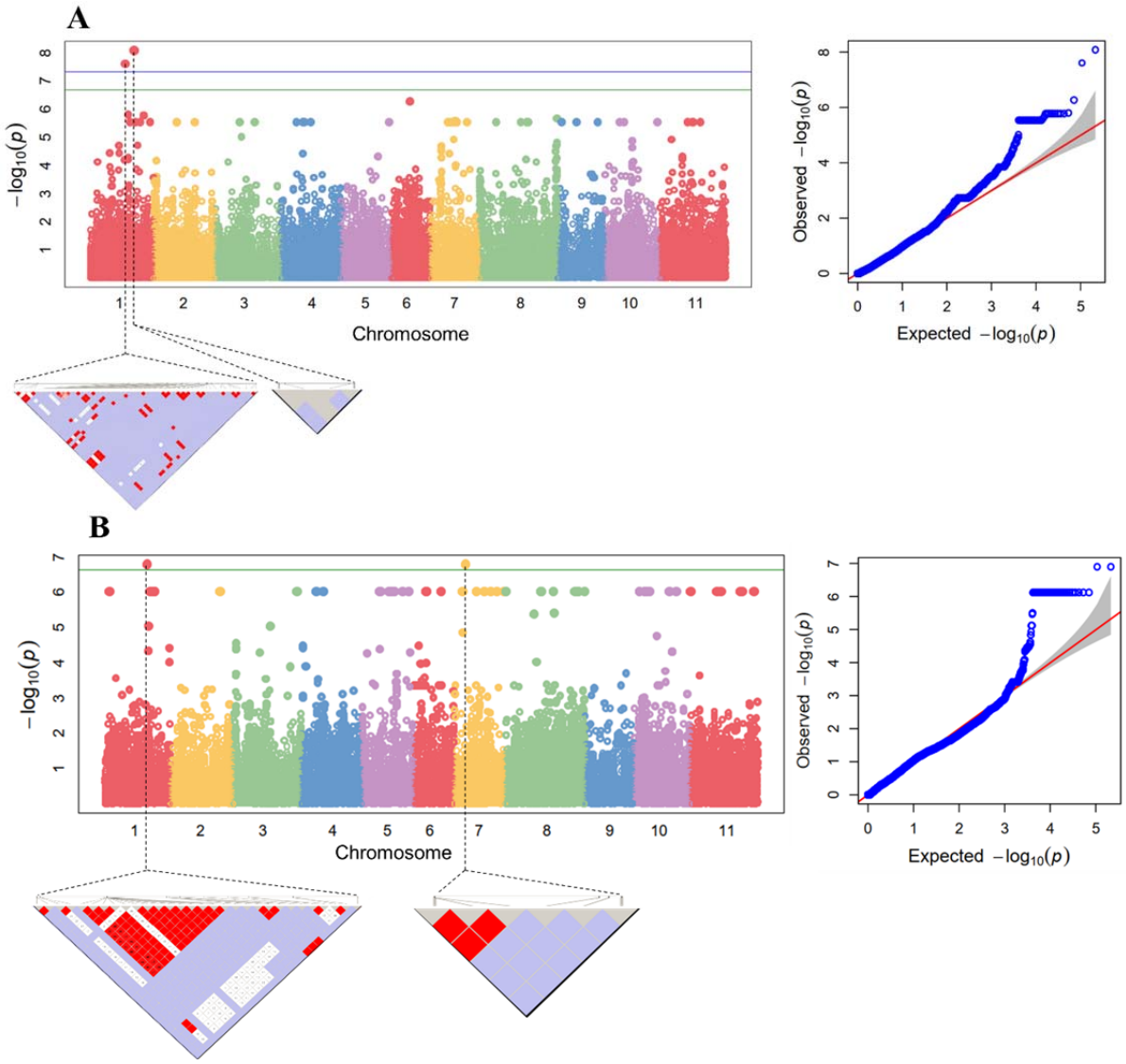
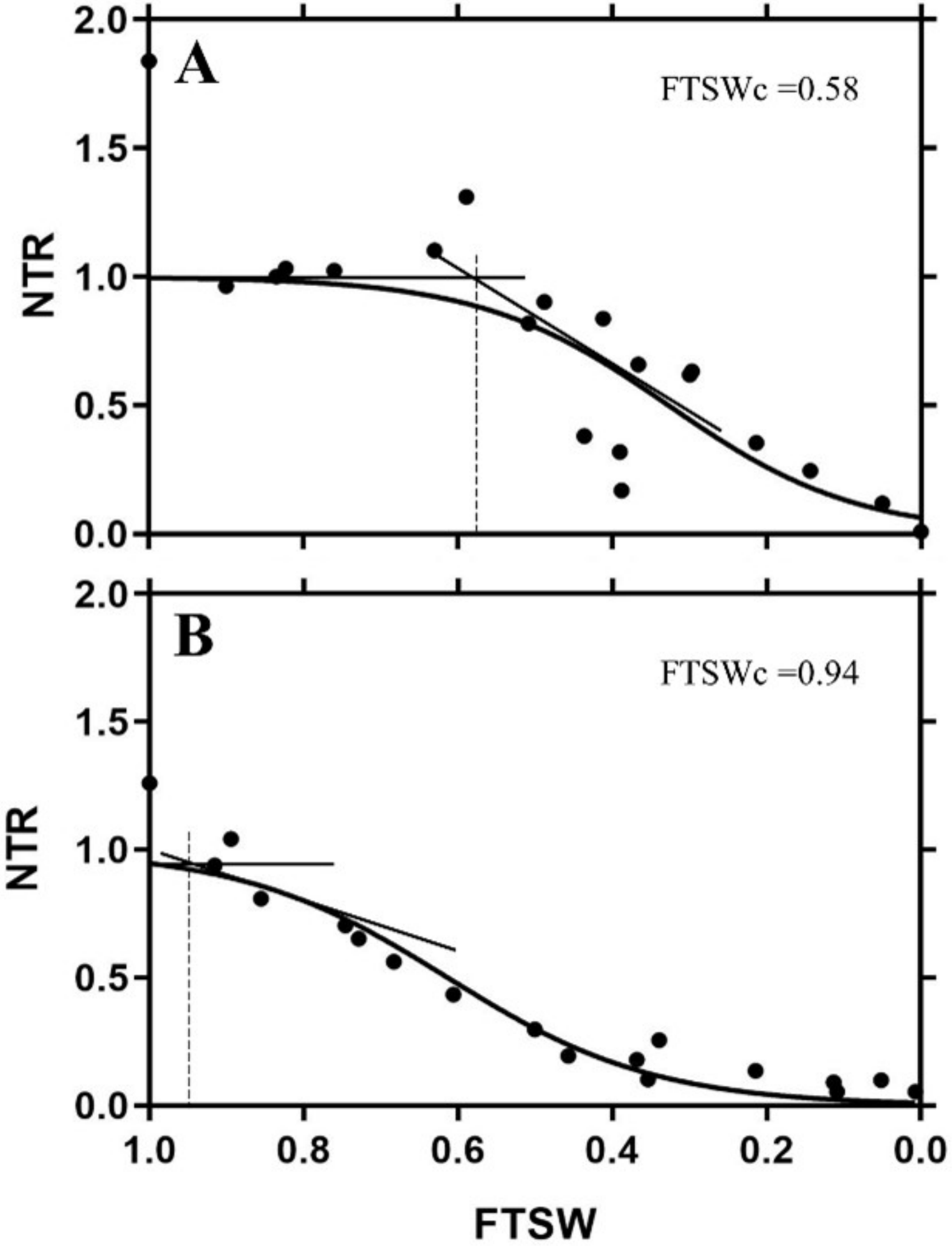
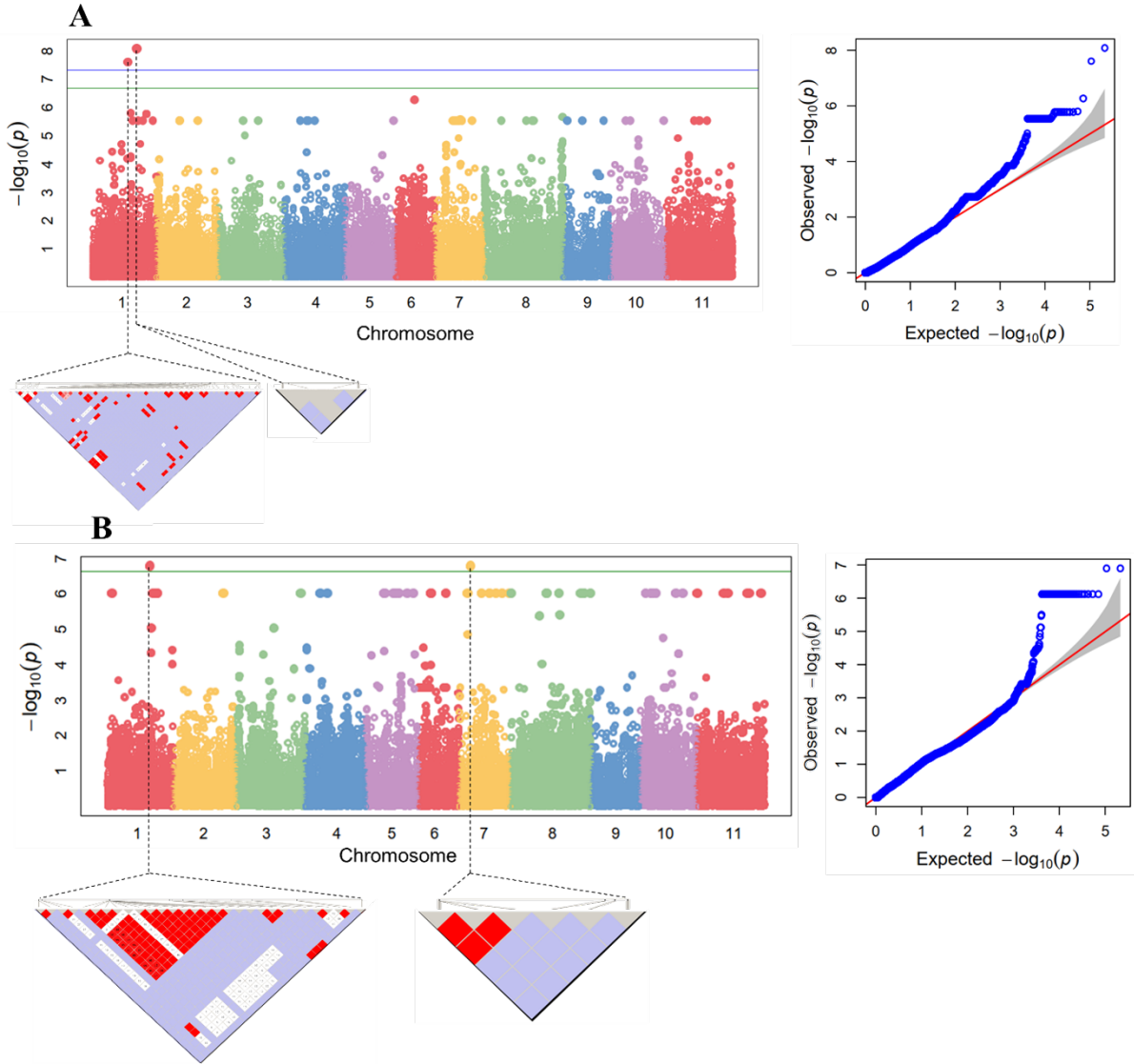


Figure 2. Manhattan plots of QTL identified for NTR (A) using FarmCPU model, and for FTSWc (B) using Blink model in the subpanel of 82 Mesoamerican beans. SNPs above the FDR-corrected threshold were considered as significant. The haplotype block for each significant SNP is depicted in the bottom of each Manhattan plot. The Q-Q plot on the right depicts the adjustment of the model for each trait.


A
FTSWc =0.58
B
FTSWc =0.94
NTR
NTR
2.0
1.5
1.0
0.5
0.0
1.0
0.8
0.6
0.4
0.2
0.0
FTSW


A
−log10(p)
Chromosome
Observed −log10(p)
Expected −log10(p)
B
−log10(p)
Chromosome
Observed −log10(p)
Expected −log10(p)

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