CROP BREEDING AND APPLIED BIOTECHNOLOGY

ARTICLE

Genome-wide association study revealed genetic loci for resistance to fusarium wilt in tomato germplasm

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Abstract: *Tomato Fusarium wilt caused by Fusarium oxysporum f.sp. lycopersici (Fol) constrains tomato production worldwide. Three hundred forty tomato accessions were evaluated for Fusarium wilt resistance and single nucleotide polymorphisms (SNPs) associated with resistance. The disease resistance evaluation revealed that 15, 13, and 15 accessions were identified as Fusarium wilt resistant in Test 1, 2, and Mean data, respectively, with the disease severity index (DSI) ranging from 0-16.7%. A genome-wide association study (GWAS) identified SNPs associated with resistance. Eighteen common SNPs were detected in at least two tests and located on chromosomes 4, 6, 7, 9, and 12. Six unique significant SNPs were found in either Test 1 or 2, located on chromosomes 2, 4, and 7. Candidate genes associated with Fusarium wilt resistance were identified. Notably, two genes encoding leucine-rich repeat-like protein and disease-resistance protein were predicted from the two unique SNPs, solDsnp10606 and solDsnp6266, respectively.*

Keywords: DArTseq, disease resistance, fusarium wilt, GWAS, tomato

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INTRODUCTION

Tomato (*Solanum lycopersicum* L.) is one of the most important vegetable crops grown worldwide. Tomato yield losses are caused by many factors, such as pests and diseases, including viruses, bacteria, fungi, and nematodes. (Bai and Lindhout 2007). The most significant pathogen causing tomato losses is *Fusarium oxysporum* f. sp. *lycopersici* (Fol). Fol can survive in soil as thick-walled chlamydospores for up to ten years and is difficult to eliminate (Jones et al. 2014). Fol can be controlled via various methods, such as cultural practices and biological, chemical, and host resistance. The degree of success varies with each technique. However, resistant plants are the most effective and environmentally friendly strategy to control Fol.

The genetic control of resistance to Fol has previously been reported in tomatoes. To date, three resistant (*R*) genes have been identified, including *I*, *I2*, and *I3*, corresponding to the avirulence genes *AVR1*, *AVR2*, and *AVR3* in Fol (Inami et al. 2012). One resistance gene, *I* (Immunity), was identified in *Solanum pimpinellifolium*, which contained a single and dominant resistance locus. The new resistant cultivar containing the *I* gene was released as the first cultivar

with Fol resistance (Paddock 1950). The *I* (*Solyc11g011180*) gene was identified on chromosome 11, which encodes an atypical membrane-anchored leucine-rich repeat (LRR) receptor-like protein (RLP) (Catanzariti et al. 2017). Similarly, Simons et al. (1998) identified the *I2* gene *Solyc11g071430*, which is also on chromosome 11. This gene encodes a coiled-coil (CC) nucleotide-binding (NB) LRR protein. There was a report that identified a resistance locus from the *S. pennellii* accession LA716, designated *I3*, and the *I3* (*Solyc07g055640*) gene was mapped to chromosome 7 and encodes an S-receptor like-kinase (SRLK) (Catanzariti et al. 2015). Presently, molecular breeding programs generally use molecular markers to assist in selecting desirable traits. The application of genetic markers has changed plant breeding, especially for disease resistance. The programs help breeders reduce the cost of disease screening and utilize specific markers to track the existence of resistance genes in their breeding populations.

With the advancement of sequencing technologies and the availability of tomato genome sequences, DNA sequence variations such as single nucleotide polymorphisms (SNPs) have been used to develop markers for tomato breeding and genetic improvement, including discovering resistance genes (Gonzalez-Cendales et al. 2014). The SNP markers in *I*, *I2*, and *I3* were discovered to facilitate breeding selection and involved Fusarium wilt-resistant mechanisms (Chitwood-Brown et al. 2021). Recently, DArTseq (Diversity Array Technology) is a technique developed to reduce the complexity of the genome based on specific restriction enzymes that separate low-copy sequences in genomes, which are highly related to active genes (Baloch et al. 2017). The technique deployed next-generation sequencing (NGS) to facilitate SNP discovery, marker genotyping, genome-wide characterization, and population structure of germplasms (Allan et al. 2020).

Genome-wide association (GWA), part of association mapping or linkage disequilibrium (LD) mapping, relies on detecting the association between genotype and phenotype of unrelated natural populations with LD patterns and no requirement for segregated populations (Rafalski 2010, Sauvage et al. 2014). This powerful approach allows the detection of genes/quantitative trait loci (QTLs) controlling complex traits, and tightly linked markers can be developed for marker-assisted selection (MAS). However, successful GWA for Fusarium wilt resistance has been reported in many crop plants, such as cowpea (Dong et al. 2022), castor bean (Shaw et al. 2022), sweet basil (Gonda et al. 2022), strawberry (Pincot et al. 2018), cape gooseberry (Osorio-Guarín et al. 2016), cotton (Mei et al. 2014), pigeon pea (Patil et al. 2017), and bottle gourd (Li et al. 2021), but not in tomatoes. Therefore, this study aims to identify SNP markers linked to Fusarium wilt resistance in the natural germplasm of tomatoes using the genome-wide association approach.

MATERIAL AND METHODS

Plant materials and growth conditions

Tomato germplasm (340 accessions) was derived from the Tropical Vegetable Research Center, Department of Horticulture, Kasetsart University, Kamphaeng Saen Campus, Thailand. Seeds of the tomato population and Seedathip 3 (SDT3) variety (Fusarium wilt susceptible check) were sown directly into 50-cell plug trays filled with a ready-to-use mixture of the substrate (Kekkilä Professional, Vantaa, Finland). The germinated seedlings were grown in the greenhouse with natural sunlight and a temperature of 30-33 °C/25-28 °C (day/night). Seedlings were watered once a day until 20 days.

Fusarium wilt resistance evaluation

Fol isolate TFPK401 (race 1) was cultured on potato dextrose agar (PDA) medium for 14 days, and then spores were collected. The collected spores were counted using a hemocytometer under a 400x light microscope. The spore suspension was adjusted to $1x10^6$ spores mL^{-1}. Fol inoculation was performed by the root-dip method (Marlatt et al. 1996). The roots of 20-day-old tomato plants were washed with clean water, and the root tips were then cut off 1 cm long. Seedlings with cut roots were immersed in a prepared Fol spore suspension or autoclaved distilled water (control plants) for 20 min. All inoculated plants were transplanted into a 3-inch x 6-inch plastic bag filled with sterilized soil and watered before transplanting. Seedathip 3 (SDT3) was used as a susceptible control. The experiment was set up in a completely randomized design (CRD) with two independent tests (Tests 1 and 2). Each test had three replicates comprising one plant for each genotype/plastic bag. Screening for Fusarium wilt resistance was carried out in a greenhouse with natural sunlight. The disease symptoms were observed when STD3 showed wilting on a scale of 5.

The observation based on a rating scale, including the disease severity score (DSS) and disease severity index (DSI), was adopted from Marlatt et al. (1996) with some modifications. The DSS was scored using a five-grade severity scale,

with (1) denoting symptomless, (2) chlorotic plants, (3) chlorotic plants and wilting, (4) wilting plants, and (5) plant death. DSI was calculated using the formula: $DSI = [(\sum S_i \times N_i) / (S \times N_t)] \times 100$, where S_i is the disease severity score, N_i is the number of tested tomatoes with S_i severity score, S is the highest disease severity score, and N_t is the total number of tested tomatoes. Tested tomatoes were assigned for their Fusarium wilt resistance type based on the percentage of DSI described by Akram et al. (2014) with slight modifications as follows: 0-20% DSI = resistant (R), 21-40% DSI = moderately resistant (MR), 41-60% DSI = moderately susceptible (MS), and 61-100% DSI = susceptible (S). Two independent tests with three replications were performed for each tomato accession, both mock and Fol inoculation.

Genomic DNA extraction, DArTseq analysis, and SNP calling

The DNA of 340 tomato accessions was extracted according to the procedure reported by Mace et al. (2003). The quantification and purity of extracted DNA samples were evaluated using a NanoDrop™ (Thermo Scientific, Waltham, MA, USA) spectrophotometer. For quality control (QC) of isolated DNA before sending it to DArTseq analysis, the DNA samples were digested with *Eco*RI and compared to the nondigested samples. The high-quality DNA was diluted to an equal concentration of 100 ng μL^{-1} with distilled water. The tomato DNA was digested with two restriction enzymes, *Pst*I and *Mse*I. The fragments of digested DNA were sequenced using an Illumina Genome Analyzer IIx (Illumina Inc., San Diego, CA, USA). The DNA sequence quality was assessed by filtering with a FASTQ confidence threshold of 90%. The filtered DNA sequences were aligned against the tomato genome sequence reference. DArTseq analysis was performed at Diversity Arrays Technology Pty. Ltd. (Australia) (www.diversityarrays.com). The SNP markers derived from DArTSeq were filtered with a maximum reproducibility threshold of 95%, an 80% call rate for markers, and a 20% missing value over samples. SNPs with minor allele frequencies (MAFs) less than 0.05 and heterozygosity greater than 0.10 were removed.

Tomato germplasm diversity analysis

Genetic diversity was analyzed by a simple matching coefficient method (Kethom et al. 2019) using filtered SNPs with a call rate greater than 90% and polymorphic informative content (PIC) higher than 0.1. A dendrogram was generated by DARwin software version 6.0.13 based on the dissimilarity index (DI) using unweighted neighbor-joining with 1000-repeat bootstrap analysis.

Association analysis for resistance to Fusarium wilt and candidate gene identification

The association between phenotyping (DSI values derived from Tests 1 and 2 and the mean across two tests) and SNP genotyping was performed using the mixed linear model. The analyses were run in Genomic Association and Prediction Integration Tool (GAPIT) on RStudio (Lipka et al. 2012). To adjust the population structure, the filtered SNPs were used to calculate kinship among tomato accessions and principal component analysis (PCA). The significance level of the genome-wide threshold was calculated based on 1/total number of SNPs (Ma et al. 2016). The significantly associated SNP marker-trait was searched for gene function using BlastN analyses against the tomato genome chromosome (built SL2.5) (https://solgenomics.net/tools/blast/).

RESULTS AND DISCUSSION

Fusarium wilt resistance evaluation

Fusarium wilt resistance was evaluated in 340 tomato accessions. The tomato germplasm showed an average disease severity score (DSS) and disease severity index (DSI) ranging from 1.00-5.00 and 0-100%, respectively. Disease-resistance types were identified into four groups according to DSI values, including resistant (R), moderately resistant (MR), moderately susceptible (MS), and susceptible (S). The tomato accessions were categorized into four disease-resistance types. The susceptibility (DSI ranged from 62.5 to 100%) comprised 254 (74.7%), 254 (74.7%), and 257 (75.6%) accessions, whereas the tomato MS accessions within 41.7 to 58.3% DSI were 43 (12.6%), 44 (12.9%), and 41 (12.1%) in Test 1, 2, and mean, respectively. There were 28 (8.2%), 29 (8.5%), and 27 (7.9%) accessions showing MR (DSI ranged from 25.0 to 33.3%) in Tests 1 and 2 and the mean, respectively. The resistant tomatoes (DSI ranged from 0 to 16.7%), comprising 15 (4.4%), 13 (3.8%), and 15 (4.4%) accessions, were found in Test 1, 2, and mean, respectively (Figure 1). For the R group, nine common resistant tomato accessions were found in all tests, including LE002, LE184, LE217, LE258, LE297, LE306, LE472, LE482, and LE501. Those accessions showed no symptoms and the lowest DSS (1) and DSI (0%).

Disease severity symptoms of some accessions are shown in Figure 2. These results suggest that the resistant tomatoes may involve their resistant (*R*) gene, which is responsible for detecting and recognizing avirulence (*AVR*) protein from Fol, resulting in a defense mechanism against the pathogen. The interaction between the response of the *R* gene and the avirulence gene is based on the gene-for-gene theory (Inami et al. 2012).

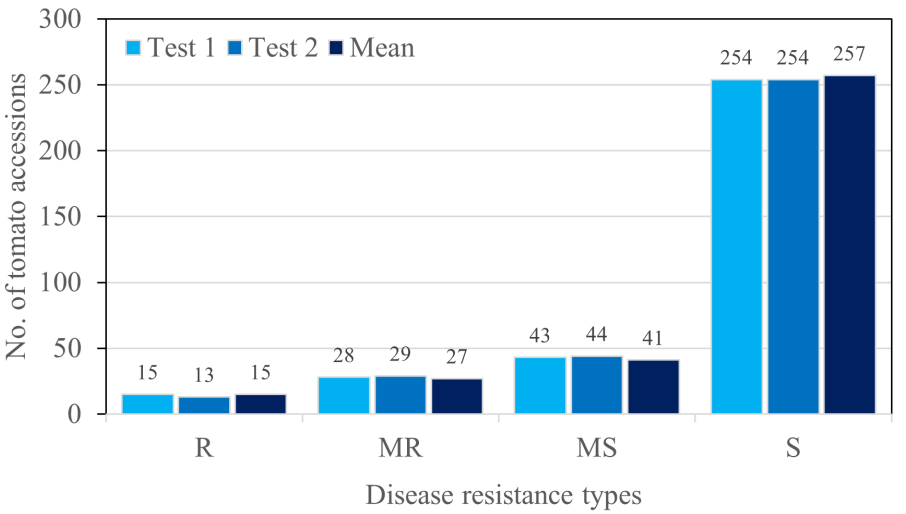

Figure 1. The disease resistance types of 340 tomato accessions identified by the disease severity index (DSI) values in Tests 1 and 2 and the mean of the two tests. R: resistant (0-20% DSI), MR: moderately resistant (21-40% DSI), MS: moderately susceptible (41-60% DSI), and S: susceptible (61-100% DSI).

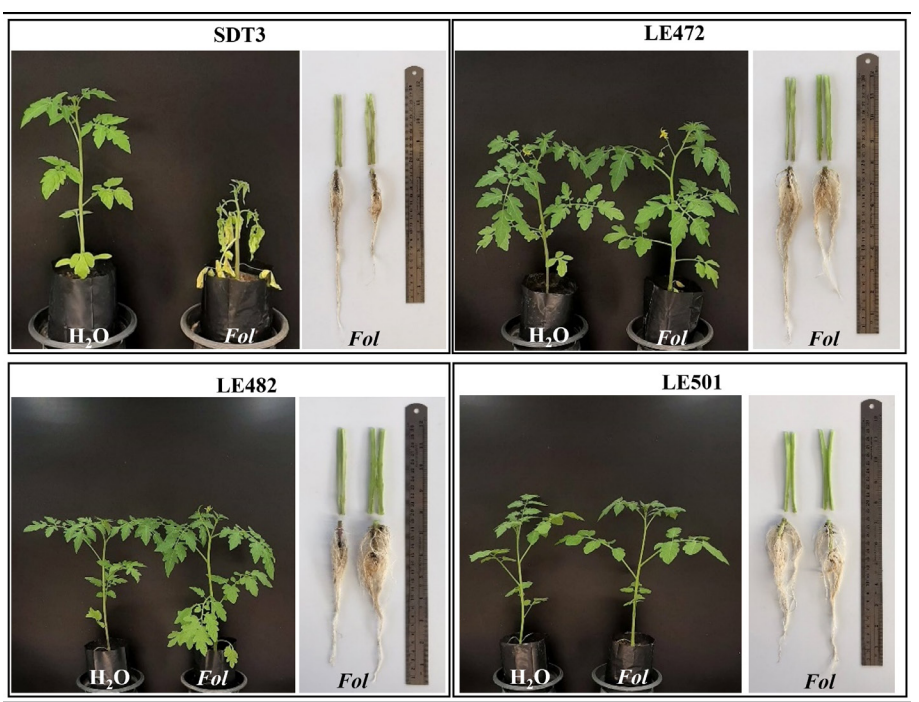

Figure 2. External and internal symptoms of Fusarium wilt susceptible (SDT3) and resistant (LE472, LE482, and LE501). H_2O: mock inoculation with water, Fol: tomato inoculated with Fol.

SNP genotyping and genetic diversity of tomato germplasm

A total of 19,843 SNPs were initially obtained from the DArTseq analysis. After filtering with the criteria of PIC ≥ 0.1 and call rate ≥80%, 4,478 SNPs were selected for further genetic diversity and GWAS of Fusarium wilt response. Cluster analysis generated a dendrogram based on the dissimilarity index (DI). Three hundred forty tomato accessions were divided into two groups, comprising 52 and 288 accessions for Groups I and II, respectively, with DI values ranging from 0.00115-0.39 (Figure 3). Almost all Fusarium wilt-resistant accessions were in group II: LE184, LE217, LE238, LE258, LE297, LE306, LE314, LE373, LE472, LE482, LE489, LE497, LE501, and LE513, except LE002, were in Group I. Genetic diversity based on SNPs showed only two groups, suggesting a narrow genetic background and sharing some alleles within each tomato accession. A previous report indicated that tomato landraces might have lower allelic richness, a higher number of rare alleles, and a lower number of private alleles than bred cultivars (Corrado et al. 2013). However, the close phylogenetic relatedness of germplasm makes it useful in tomato breeding rather than other more phylogenetically distant species (Mata-Nicolás et al. 2020). SNP genotyping is a powerful tool used to study the population structure of plant germplasm. Most studies have been conducted on the genetic diversity and population structure of two different species of tomatoes using SNP markers (Pailles et al. 2017). Wang et al. (2016) used SNPs to study genetic diversity and population structure in a tomato germplasm collection. SNP genotyping demonstrated the pattern of selection and linkage to the trait of interest in contemporary (processing and fresh-market) varieties, vintage varieties, and landraces (Sim et al. 2011).

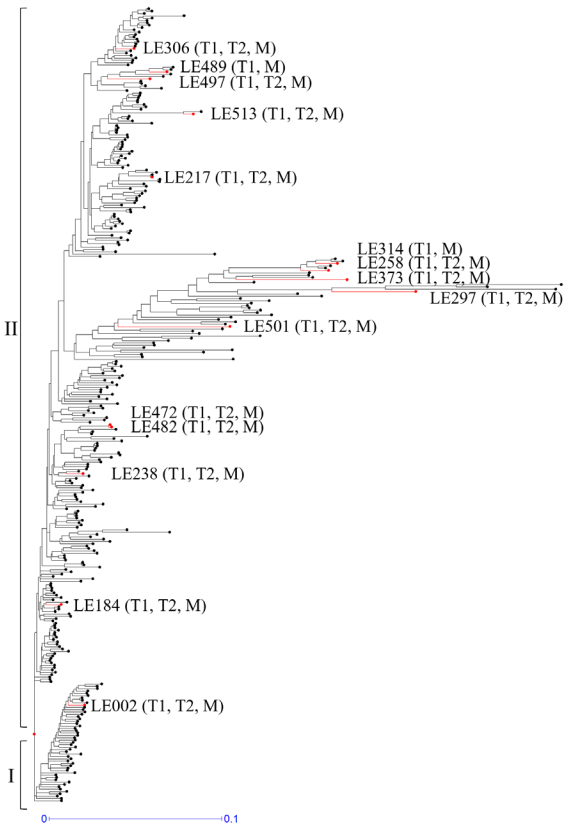

Figure 3. Dendrogram of cluster analysis with UPGMA (unweighted pair group method with arithmetic mean) drawn by DARwin 6 program. The Roman letters indicate each group (I and II). Branches highlighted in red indicate tomato accessions in the Fusarium wilt resistance group (R).

Association analysis for Fusarium wilt resistance

Association analysis was performed between DSI and SNP genotyping using the mixed linear model (MLM) to identify the SNP markers linked to the traits. The Manhattan plots and Q-Q plots are shown in Figure 4. According to the Manhattan plots, 24 SNPs (with a Logarithm of Significant Level [$-\log_{10}(P)$] ≥ 3.0) were significantly associated with DSI in at least one independent test, including 8, 9, and 7 SNPs detected from Test 1, 2, and the mean, respectively. Of the 24 significant SNPs, 18 common SNPs were detected in at least two tests and located on chromosomes 4, 6, 7, 9, and 12 with [$-\log_{10}(P)$] = 3.00-4.06. Six unique significant SNPs, which were located on chromosomes 2, 4, and 7 ([$-\log_{10}(P)$] = 3.04-3.54) (Figure 4, Table 1), were found in either Test 1 or 2. The results indicate that multiple genes control fusarium wilt resistance in tomatoes. All 24 SNPs were searched for gene function using BlastN analyses against the tomato genome chromosome (built SL2.5) (https://solgenomics.net/tools/blast/).

The candidate genes associated with disease response to Fol infection were identified, including solute carrier family 35 member C2 (*Solyc12g010990*), zinc finger family protein (*Solyc06g016770*), pistil extensin-like protein (*Solyc02g078050*), CUE domain-containing protein expressed (Solyc09g064860), peptidyl-prolyl cis-trans isomerase-like protein (*Solyc07g066420*), leucine-rich repeat-like protein (*Solyc07g007400*), WW domain-binding protein 2 (*Solyc04g009190*), nuclear pore complex protein Nup93-like protein (*Solyc04g016240*), BZIP transcription factor family

protein (*Solyc04g071160*), disease resistance protein (*Solyc04g009120*), and pentatricopeptide repeat-containing protein At4g21190 (*Solyc04g056370*) (Table 1).

A genome-wide association study is a powerful approach that allows the detection of genes/quantitative trait loci (QTLs) controlling complex traits, and tightly linked markers can be developed for marker-assisted selection (MAS). We successfully identified SNPs associated with Fusarium wilt resistance (DSI). GWA for Fusarium wilt resistance has been reported in many crop plants. Dong et al. (2022) also identified 3 and 7 SNPs significantly associated with LFD and VD in response to Fusarium wilt in cowpea, respectively, on chromosomes 3, 4, 5, 6, and 9. Thirty candidate genes were identified, including leucine-rich repeat protein kinase family proteins, protein kinase superfamily proteins, and zinc finger family proteins. Gonda et al. (2022) found a cluster of putative disease-resistance genes that encodes a transmembrane leucine-rich repeat-receptor-like kinase-ubiquitin-like protease (LRR-RLK-ULP) associated with resistance to *Fusarium oxysporum* f. sp. *basilici*. In this study, the zinc finger family protein (*Solyc06g016770*) was associated with Fol infection.

A previous report showed that zinc finger proteins were involved in a diverse range of plant growth and development processes, as well as regulating resistance mechanisms to biotic and abiotic stresses. These proteins have a DNA binding domain in the nucleotide binding site-leucine rich repeat (NBS-LRR) class of resistance (R) proteins, which determines the regulatory function of this protein under stress conditions (Feurtado et al. 2011). Interestingly, disease resistance protein (*Solyc04g009120*) and leucine-rich repeat-like protein (*Solyc07g007400*) were associated with DSI. This *Solyc04g009120* gene was classified as an *R*-gene family NB-ARC domain-containing disease resistance protein. Most R proteins contain a central NB-ARC (nucleotide-binding adaptor shared by APAF-1, R proteins, and CED-4) domain, consisting of three subdomains, including NB, ARC1, and ARC2. A previous study showed that the role of the NB-ARC domain in the tomato

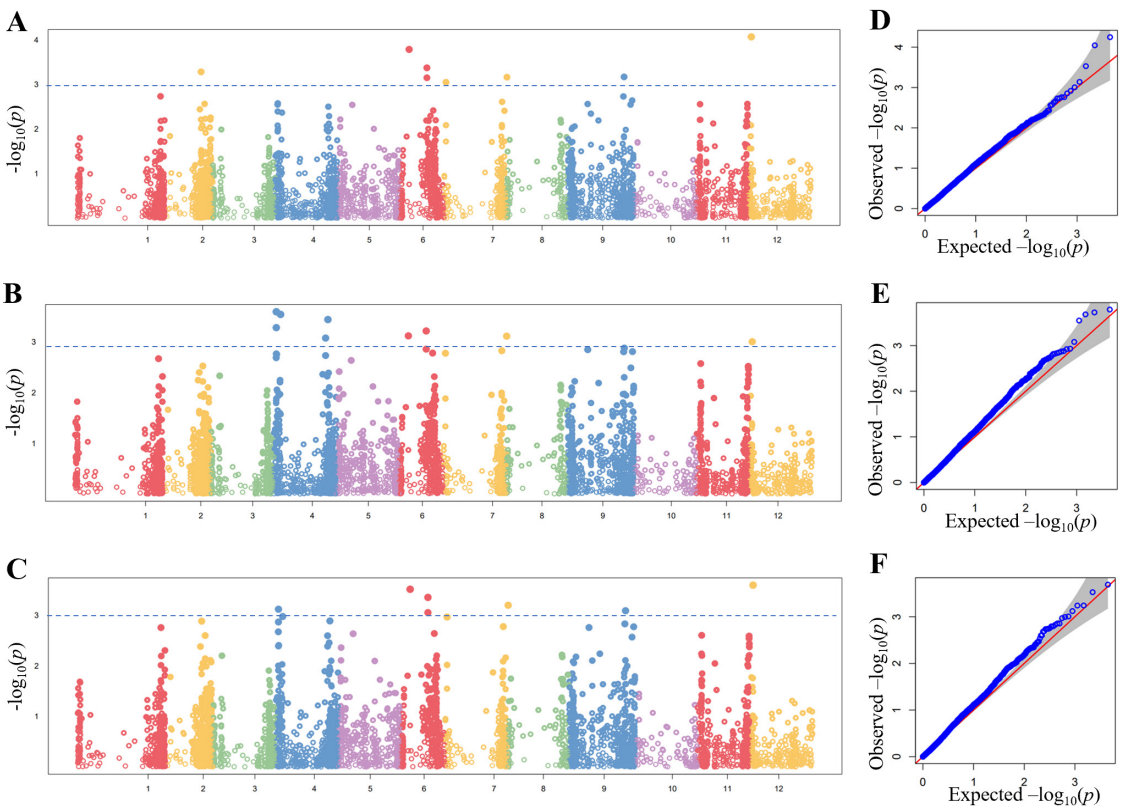

Figure 4. Manhattan plots (A-C) and Q-Q plots (D-F) show the location of SNP markers that were significantly associated ($-\log_{10}$(P) ≥3) with the disease severity index (DSI) in Tests 1 and 2 and the mean across the tests. The blue horizontal dashed line indicates the genome-wide significance threshold ($-\log_{10}$P ≥ 3).

Table 1. Significant SNPs ($-\log_{10}(P) \geq 3$) and candidate genes associated with Fusarium wilt resistance in tomato genotypes with two different tests and the mean across the tests

Test	SNP	Chr.	Position	Allele change	LOD	MAF	R^2 (%)	BlastN search against tomato genome (SL2.50)
1	solDsnp17559	12	3851464	C>G	4.06	0.05	0.11	Solyc12g010990: Solute carrier family 35 member C2
	solDsnp9082	6	9849869	T>C	3.78	0.08	1.57E-09	Solyc06g016770: Zinc finger family protein
	solDsnp9473	6	28178233	C>G	3.36	0.12	0.00	N/A
	solDsnp3197	2	37439422	C>T	3.27	0.13	0.00	Solyc02g078050: pistil extensin-like protein
	solDsnp14242	9	57947829	T>C	3.16	0.38	3.33E-09	Solyc09g064860: CUE domain-containing protein expressed
	solDsnp11863	7	65079504	G>C	3.15	0.43	0.14	Solyc07g066420: Peptidyl-prolyl cis-trans isomerase-like protein
	solDsnp9471	6	28178237	C>A	3.14	0.09	0.00	N/A
	solDsnp10606	7	2131314	C>T	3.04	0.14	0.00	Solyc07g007400: Leucine-rich repeat-like protein
2	solDsnp6271	4	2694174	T>A	3.60	0.07	0.20	Solyc04g009190: WW domain-binding protein 2
	solDsnp6493	4	7041224	G>A	3.54	0.07	4.90E-07	Solyc04g016240: Nuclear pore complex protein Nup93-like protein
	solDsnp7106	4	55672896	T>C	3.44	0.06	0.15	Solyc04g071160: BZIP transcription factor family protein
	solDsnp6266	4	2644352	A>G	3.28	0.06	0.00	Solyc04g009120: Disease resistance protein
	solDsnp9473	6	28178233	C>G	3.21	0.13	4.98E-08	N/A
	solDsnp9082	6	9849869	T>C	3.12	0.09	0.01	Solyc06g016770: Zinc finger family protein
	solDsnp11863	7	65079504	G>C	3.11	0.43	0.24	Solyc07g066420: Peptidyl-prolyl cis-trans isomerase-like protein
	solDsnp6997	4	53301687	G>A	3.07	0.09	0.05	Solyc04g056370: Pentatricopeptide repeat-containing protein At4g21190
	solDsnp17559	12	3851464	C>G	3.00	0.05	0.14	Solyc12g010990: Solute carrier family 35 member C2
Mean	solDsnp17559	12	3851464	C>G	3.58	0.05	0.20	Solyc12g010990: Solute carrier family 35 member C2
	solDsnp9082	6	9849869	T>C	3.50	0.09	7.93E-09	Solyc06g016770: Zinc finger family protein
	solDsnp9473	6	28178233	C>G	3.34	0.13	4.82E-09	N/A
	solDsnp11863	7	65079504	G>C	3.19	0.43	0.21	Solyc07g066420: Peptidyl-prolyl cis-trans isomerase-like protein
	solDsnp6271	4	2694174	T>A	3.11	0.07	0.18	Solyc04g009190: WW domain-binding protein 2
	solDsnp14242	9	57947829	T>C	3.08	0.38	0.01	Solyc09g064860: CUE domain-containing protein expressed
	solDsnp9471	6	28178237	C>A	3.04	0.09	0.00	N/A

Chr.: Tomato chromosome, LOD: logarithm of odds, MAF: minor allele frequency

I2 gene could trigger defense signaling (Tameling et al. 2006). In addition, a candidate gene, peptidyl-prolyl cis-trans isomerase-like protein (*Solyc07g066420*), was identified and located close to the *I3* gene (*Solyc07g*055640), a resistance gene for Fol (tomato genomic resources database; http://223.31.159.9/tomato2/index.html). Peptidyl-prolyl cis-trans isomerase (PPIase) is involved in the folding of target proteins. The essential functions involved cellular processes and pathogen interactions (Romano et al. 2004). PPIase, *ROC1* cyclophilin, *AtCyP19,* and *AtCyP57* from *Arabidopsis thaliana* are involved in the response to *Pseudomonas syringae* infection (Olejnik et al. 2021).

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