Evaluation of Drought Tolerance in USDA Tomato Germplasm and Genome-wide Association Study and Genomic Prediction of Fusarium wilt Resistance in Common Bean Core Collection

A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Science in Horticulture

by

Kenani Edward Chiwina
Lilongwe University of Agriculture and Natural Resources
Bachelor of Science in Horticulture, 2016

August 2023
University of Arkansas

This dissertation is approved for recommendation to the Graduate Council.

Ainong Shi, Ph. D.
Thesis Director

Ryan William Dickson, Ph. D.
Committee member

Neelendra Joshi, Ph. D.
Committee member

Abstract

Drought stress and Fusarium wilt disease present significant challenges to plant growth and agricultural productivity, particularly affecting crops such as tomato and common beans. To address these issues, researchers have extensively evaluated germplasm collections under field and greenhouse conditions to identify genotypes with drought tolerance and disease resistance. This study aimed to achieve two objectives. Firstly, we conducted a phenotypic evaluation of drought tolerance in USDA tomato germplasm to identify drought-tolerant accessions for future breeding programs targeting enhanced drought tolerance in tomato cultivars. Secondly, we conducted a genome-wide association study (GWAS) and genomic prediction (GP) on USDA common bean germplasm using publicly available disease response and SNP datasets to identify single nucleotide polymorphism (SNP) markers and candidate genes associated with Fusarium wilt resistance.

Chapter 1 describes the evaluation of tomato accessions in a greenhouse at the Arkansas Agricultural Research and Extension Center, Fayetteville, AR. The experiment involved planting tomato seeds in pots and subjecting the plants to drought conditions alongside control sets under optimal irrigation. After 35 days of growth, we withheld water from the drought-treated plants for approximately 10 days until the more susceptible plants began to die off. We collected data on leaf wilting, leaf rolling, plant height, and leaf chlorophyll content from both the drought-treated and control groups to understand how different genotypes respond to drought stress. This study identified four highly drought-tolerant tomato accessions, which can be valuable for breeding programs to develop elite drought-tolerant tomato cultivars.

Chapter 2 focuses on GWAS and GP for Fusarium wilt resistance in 157 USDA common bean accessions. These accessions were previously evaluated by (Brick et al., 2006) for resistance to Fusarium wilt caused by Fusarium oxysporum (Fop) race 1 and race 4 in a greenhouse condition. We utilized a dataset from this evaluation and performed comprehensive GWAS and GP analyses using SNP markers from the BARCBean6K_3 Infinium BeadChips. As a result, we identified significant SNP markers associated with Fusarium wilt resistance and the discovery of candidate genes, shedding light on the genetic factors contributing to resistance in common beans. The study also explores the potential of genomic prediction techniques for predicting resistance to Fusarium wilt, offering valuable insights into marker-assisted and genomic selection strategies for breeding programs.

In conclusion, this thesis contributes important knowledge on drought tolerance in tomatoes and Fusarium wilt resistance in common beans. The findings can serve as a foundation for future breeding efforts focused on improving these traits in crop cultivars, ultimately enhancing agricultural productivity and sustainability.

© 2023 by Kenani Edward Chiwina
All Rights Reserved

Acknowledgement

I am deeply grateful to my advisor, Dr. Ainong Shi, for granting me the opportunity to work alongside him on this research project and for his exceptional mentorship. His unwavering support throughout my program has been invaluable, and I am truly thankful for his guidance and paternal care.

I would also like to extend my appreciation to Dr. Gehendra Bhattarai and Dr Haizheng Xiong for their excellent support and guidance, which have greatly contributed to my professional growth. Additionally, I would like to thank my committee members, Dr. Ryan William Dickson and Dr. Neelendra Joshi for their invaluable feedback and suggestions that have helped shape my knowledge and improve my research.

To the Agricultural Transformation Initiative Fellowship and Scholarship Fund (ATI FSF) for providing financial resources and required facilities supporting my academic studies.

Special thanks to Fayetteville Seventh-Day Adventists Church members, Arkansas, for their encouragement and unwavering support throughout my program

Finally, I am deeply grateful to all those who have supported me on this journey, and I acknowledge their contributions with profound appreciation. Their unwavering support, encouragement, and guidance have been instrumental in my academic and personal growth.

Dedication

To Chiwina Family

Table of Contents

Chapter 1. Evaluation of drought tolerance in USDA tomato germplasm

Introduction and review of literature

Chapter 2. Genome-wide association study and genomic prediction of fusarium wilt resistance in common bean core collection

Introduction and review of literature

List of abbreviations and acronyms

AD: Absolute decrease

FarmCPU: Fixed and Random Model Circulating Probability Unification

FOP: Fusarium oxysporum

GP: Genomic Prediction

GLM: General Linear Model

GWAS: Genome-wide association study

II: Inhibition Index

LOD: Logarithm of odd

LML: Mixed Linear Model

LR: Leaf rolling

LW: Leaf wilting

PA: Prediction accuracy

PCA: Principal component analysis

PLHT: Plant height

RDT: Relative drought tolerance

ROS: Reactive oxygen species

SMR: Single Marker Regression

SNP: Single nucleotide polymorphism

USDA: United States Department of Agriculture

Introduction

Tomatoes (*Solanum lycopersicum* L.*)* and common bean (*Phaseolus vulgaris* L.) are widely grown and consumed crops worldwide, recognized for their nutritional value and positive impact on human health (Blair, 2013; Burton-Freeman & Reimers, 2011; De Ron et al., 2016; Karavidas et al., 2022). However, these crops face significant challenges to their growth and agricultural productivity, mainly attributed to drought stress and Fusarium wilt disease caused by *Fusarium oxysporum f. sp. phaseoli* (*Fop*). These factors pose substantial threats to crop yields and overall plant health, especially in the case of tomato and common bean.

Drought stress is a primary limiting factor in crop production, leading to decreased fruit quality, smaller fruit size, and substantial yield losses ranging up to 50% depending on the severity and duration of water scarcity during critical growth phases (Pervez et al., 2009). Among water-demanding crops, tomato cultivation is significantly affected by inadequate water supply, negatively impacting its production and overall agricultural output (Chandra Rai et al., 2012; Saqlan Naqvi et al., 2014).

To address these challenges, the utilization of drought-tolerant cultivars has been proposed as an effective approach to ensure sustainable crop production under diverse abiotic stresses, including drought, salinity, and temperature variations. Identifying genotypes with drought tolerance through germplasm characterization is a crucial initial step in breeding for stress tolerance. Previous studies have explored characterizing germplasm collections for drought tolerance in various crops, such as tomato and cowpea, successfully identifying drought-tolerant genotypes (Aghaie et al., 2018; Cui et al.,2020; Rahman et al.,1998; Ravelombola et al., 2020a; Wahb-Allah et al., 2011). Thus, this study aimed to evaluate USDA tomato accessions under controlled greenhouse conditions at the seedling stage to identify tomato genotypes capable of thriving in dry conditions. The drought-tolerant tomato accessions identified in this study can serve as promising parental lines for future tomato breeding programs, focusing on developing varieties resilient to water scarcity.

In the case of common bean production, Fusarium wilt poses a significant threat, caused by the fungal pathogen *Fusarium oxysporum f. sp. phaseoli* (*Fop*). This disease is prevalent in major common bean producing regions and can spread through contaminated seeds or farm equipment, leading to severe symptoms such as vascular tissue discoloration, leaf chlorosis, and plant death (Alves-Santos et al., 2002; Batista et al., 2017). To manage this disease effectively, cultivating disease-resistant varieties and employing crop breeding have been suggested as sustainable and reliable strategies (Panth et al., 2020; van Esse et al., 2020).

It is crucial to identify potential parent accessions with resistance to *Fop* to support common bean production even in the presence of the pathogen. This study aimed to utilize advanced genetic approaches to understand the distribution and effects of resistance loci related to Fusarium wilt resistance. Single nucleotide polymorphisms (SNPs) are widely used molecular markers throughout the genome, providing valuable information on genetic variability among individuals (Bartoli & Roux, 2017). The focus of this study was to identify SNP markers associated with Fusarium wilt resistance in common bean by employing a genome-wide association study (GWAS) approach. Additionally, the study aimed to discover potential accessions with resistance to *Fop*, serving as valuable genetic resources for breeding programs aimed at developing disease-resistant common bean varieties using marker-assisted selection (MAS) and genomic selection (GS) techniques.

CHAPTER 1. EVALUATION OF DROUGHT TOLERANCE IN USDA TOMATO GERMPLASM

Abstract

Tomato (Solanum lycopersicum L.) is one of the most consumed horticultural and vegetable crops worldwide. Drought conditions are among the major threats to sustainable tomato production, causing great yield and production losses of the crop. Utilization of drought-tolerant cultivars and breeding for tolerance to drought have been suggested to be the best options to combat the effects of drought in many crops growing regions. This study aimed to evaluate and select tomato accessions for drought-tolerance. Sixty-eight USDA tomato accessions were subjected to water deficiency treatment and normal watering (control set) in greenhouse experiments. The results showed that the four accessions PI 365956, PI 584456, PI 390510, and PI 370091 were highly tolerant to dry conditions. High broad-sense heritability was found for leaf wilting, leaf rolling, and SPAD chlorophyll content. High positive correlations were detected among leaf wilting, leaf rolling and SPAD chlorophyll content-related parameters. This study generated information that is valuable for tomato breeding programs with a focus on improving tolerance to drought in elite cultivars of tomato.

Introduction

Tomatoes (*Solanum lycopersicum* L.) are diploidy (2n = 24) (Sahu & Chandel, 2016) and the most popular and consumed vegetables in many parts of the world. They are known to be great sources of valuable nutrients which aid in reducing the risks of many ailments such as cancer, heart disease, osteoporosis, skin infection, and cognitive impairment (Burton-Freeman & Reimers, 2011). Many reports demonstrate that tomato was first domesticated in South America and became popular as one of the extensively cultivated and used vegetable crops across the continents (Barone et al., 2008; Ranjan et al., 2012). Importantly, tomato consists of a simple genome of 0.95pg or 950Mb per haploid nucleus (Barone et al., 2008) and has been reported to have potential to survive in dry conditions even though most of its commercial cultivars are reported to be moderately to highly vulnerable to water stress early, middle, and late stages of their growth (Ripoll et al., 2014). Additionally, tomato crops have been utilized as a model organism for various molecular and genetic studies (Barone et al., 2008; Ranjan et al., 2012)

Drought is among the most restrictive factors for crop cultivation and horticultural production in most of the world agriculture dependent regions. Extremely low-soil water levels have shown to have a damaging influence on the physiological, morphological, and anatomical features of the plants (Massimi, 2021) triggering a decrease in fruit quality, decreased fruit size and significant crop yield loss of approximately 50% depending on the magnitude and period of soil dryness and plant growth phase (Pervez et al., 2009). Tomato is one of the several horticultural crops that are widely cultivated globally, and whose production is greatly affected by insufficient irrigation(Chandra Rai et al., 2012; Saqlan Naqvi et al., 2014). Tomato production requires sufficient rainfall, and short water supply arising at initial stage of growth is injurious to tomato production though being reported to have capability to withstand drought stress (Massimi, 2021; Solankey et al., 2014).

The seedling stage is highly susceptible to unfavorable factors such as drought in several crops (Cui et al., 2020; Kamanga, 2020; Ravelombola et al., 2020). In the vegetative stage of tomato, proper soil moisture supply is a very crucial process as it speeds up food production through enhanced normal chlorophyll production and maintains optimal shoot growth which is one of the critical yield related traits in tomato. Long periods of low soil moisture reduce the ability of the plants to absorb required amount of water and nutrients, adversely affecting chlorophyll synthesis (Sepehri & Golparvar, 2011) which eventually negatively impacts shoot growth, making the plant unable to complete some phases of its growth. Some studies have suggested that mild stress leads to an increase in concentration of leaf chlorophyll whereas severe stress causes chlorophyll production to stop (Sakya et al., 2018; Sepehri & Golparvar, 2011). Additionally, some literature has found that most drought tolerant cultivars of species exhibit increased leaf chlorophyll content especially in the trifoliate leaves drought sensitive cultivars demonstrate reduced chlorophyll content (Cardoso et al., 2022; Mou et al., 2018) , but this situation varies from cultivar to cultivar (Sepehri & Golparvar, 2011). Also, many reports show a decreased plant height in both drought susceptible and tolerant cultivars under water-deprived environments (Pervez et al., 2009; Sakya et al., 2018; Singh, 2021). Thus, identification and utilization of drought tolerant cultivars has been suggested to supporting sustainable production and yield under a wide range of abiotic stresses such as drought, salinity, and temperature in many crops.

The most important step in breeding for tolerance to stress is the identification of drought tolerant genotypes by characterization of germplasm collection of plants. Previously, screening for drought tolerance at seedling stage has been emphasized in several crops, and some drought-tolerant cultivars have been identified. (Cui et al., 2020) subjected thirty-six Arkansas cowpea breeding lines at seedling stage to a 4-weeks drought treatment and considered cowpea breeding lines: ‘17-61’, ‘17-86’, ‘Early Scarlet’, and ‘ARBlackeye #1’ as tolerant to water with-holding state. A similar study was conducted by (Ravelombola et al., 2020a) who analyzed 331 cowpea lines from various nations, and a total of 21 cultivars were regarded to be tolerant to drought. Regarding tomato, (Rahman et al., 1998) evaluated sixteen cultivars from different regions of the world, and identified one cultivar, TM 0126 as the most drought tolerant cultivar. Later, (Wahb-Allah et al., 2011) conducted a similar study using four commercial lines and one drought-tolerant breeding line. The study found two drought tolerant cultivars, Pakmore VF and the breeding line L 03306. Another study investigated fourteen tomato cultivars from United States, Iran, Hungary, Italy, and Turkey, and three cultivars namely Early orbana, Roma and Cal-j were found to be more susceptible to drought (Aghaie et al., 2018). It is important to conduct further phenotypic evaluation of a large germplasm accession collection to identify more drought tolerant and susceptible tomato cultivars.

The focus of this study was to conduct evaluation of USDA tomato accessions in a greenhouse-controlled environment at a seedling stage to identify tomato genotypes with the ability to survive in dry conditions. The resistant tomato genotypes will be used in selection as parents for use in future tomato breeding programs.

Literature Review

Significance of Tomato

Tomato is one of the most extensively grown vegetable crops across the globe. China was the main producer (50.0 million tons), followed by India (17.5 million tons) and the USA (13.2 million tons) in 2012; these three nations attained 49.9% of the total global tomato production (Testa et al., 2014).Tomato has an impressive range of uses. It is regarded as beneficial for human health because of its beneficial vitamins and minerals. For instance, tomato is known to contain high amount of vitamin A, B, and C. Tomato crop is primarily grown for fresh consumption and industrial purposes (Hassan khan et al., 2015). It is a raw material for processing into paste, soup, juice, sauce, powder, and concentrate (Kahlau & Bock, 2008; Li et al., 2016; Quinet et al., 2019). Importantly, tomato has become one of the model plants for the study of fleshy fruit development (Quinet et al., 2019). Moreover, tomato is grown as a cash crop and the crop can be grown for the entire year on the African continent (Dhaliwal, 2001)**.**

Genetic Diversity in Tomato

Genetic diversity is the measure of genetic variability existing between individuals of a variety or a population within a species (Salgotra & Chauhan, 2023). Genetic diversity is important in the selection of individuals with desirable characteristics. The efficacy of selection is influenced by the type and extent of genetic variation present in a population, as well as the degree to which desirable traits are inherited (Kumar et al., 2013)**.** The process of selection involves identifying individuals with desirable traits and using them to produce offspring with those same traits. The success of this process depends on the level of genetic variability in the population and the degree to which those desirable traits are heritable. Several researchers have studied genetic diversity in tomato. For instance, (Kumar et al., 2013) evaluated twenty-six genotypes of tomato to find the nature and magnitude of variability and correlation between yield and yield-related traits including plant height, number of fruits per plant, yield per plant, and fruit weight. The study discovered high significant variation among all genotypes for the traits. Also, high heritability estimates and genetic gain were observed for plant height, number of fruits per plant, yield per plant, and fruit weight. The study also discovered a significant and positive correlation between yield and number of fruits per cluster.

Effect of Drought in Plants

Drought stresses affect plants in different ways and is one of the major causes of decreased crop productivity, leading to great social-economic and ecological damage. (Chandra Rai et al.,

2012) stressed that severe drought stress causes a decline in world's grain production by approximately 5% and annual crop losses of about 17% in the tropics. Extreme water shortage inhibits normal growth and development of plants, resulting in yield reduction. In adequate water supply adversely affects the normal growth of plants and reduces yield, and it has a damaging influence on physiological, morphological, and anatomical features of tomato plants (Massimi, 2021). Reduced level of hormones such as cytokinins and gibberellic acid, reduced relative water content, reduced leaf size, reduced number and closure of stomata, and early leaf senescence are attributed to limited water conditions (Massimi, 2021). Consequently, enzymatic functions, and activities of the cell such as cell division, cell differentiation and organization, and cell turgidity are adversely impacted, resulting in reduced transpiration and decline in nutrients production and distribution (Chandra Rai et al., 2012).

As one of water demanding crops, tomato physiology and its food production machinery are hampered by inadequate water supply. (Liang et al., 2020; Zhou et al., 2017) reported significant lower net photosynthesis and sugars, reduction of stomata and pore length, and reduction of shoot fresh and dry weight, leaf area and relative water content in tomato plants exposed to drought situations.

Mechanisms for Drought Tolerance in Plant

Destructive environmental conditions such as salinity, drought, and extreme temperature cold, heat, flooding, nutrient deficiency, and high and low light intensities, including ultraviolet radiation are a threat to the developmental activities and productivity. They are likely to negatively affect crop performance, leading to approximately 50%-70% crop yield loss (Francini & Sebastiani, 2019). The plants experience various physio-morphological changes such as diminished transpiration and photosynthesis process, osmotic adjustments, reduced root and shoot development, excessive production of reactive oxygen species, altered stress signaling pathways, and senescence. These incidences cause permanent injury to the plant. Plants respond to stress depending on their adaptation ability. Some plants reduce photosynthetic activity and light-use efficiency to strengthen their tolerance to stress. Additionally, antioxidant networks are stimulated, and several enzymes produce metabolites to prevent cell injury (Francini & Sebastiani, 2019).

Water is a fundamental component of photosynthesis, and adequate water supply directly correlates with yield and quality (Francini & Sebastiani, 2019). Drought tolerance, plants' capability to tolerate low-tissue water content through adaptive traits (Pereira, 2016), is critical for the survival of plants growing under water deprived environments. The adaptive attributes include maintenance of cell turgor through osmotic modification and cellular elasticity and enhancing protoplasmic resistance. In response to drought stress, plants utilize stress-related hormones, manufacture osmolytes, eradicate reactive oxygen species (ROS) and accumulate stress protective proteins. Several plant hormones such as abscisic acid, cytokinin, gibberellic acid, auxin, and ethylene, control various activities thereby enhancing adaptation to water stress (Wilkinson et al., 2012). During drought stress, abscisic acid is manufactured in roots and transferred to the leaves to initiate stomatal closure and reduce plant growth (Wilkinson et al., 2012).

Stomatal closure reduces the inflow of carbon dioxide. This situation increases the concentration of oxygen into the leaves and accumulation of food production electrons, which have capacity to react with oxygen, leading to reactive oxygen species (ROS). ROS can be more reactive, leading to oxidation of proteins, lipids, DNA and RNA and eventually cause cell death (Carvalho, 2008; Pereira, 2016). Complex antioxidant molecules such as polyphenols and specific enzymes scavenge reactive oxygen species resulting in neutralization of ROS in the cells. (Carvalho, 2008; Huang et al., 2019; Liu et al., 2016).

Concentration of compatible solutes maintain osmotic regulation to sustain turgor pressure under extremely dry conditions. Osmolytic regulating molecules such as several ammonium containing complexes such as polyamines, glycine, and beta, or obtained from starch such as trehalose, mannitol, sorbitol, or amino acids such as proline are valuable in controlling osmosis to counter moisture stress (Conti et al., 2019; Yang et al., 2021; Yao et al., 2016).

Plants growing in extremely low moisture zones develop xeromorphic traits to minimize water loss through transpiration. Decreased water loss can also be accomplished by leaf shedding, decrease in leaf number, leaf size, and branching. Alternative mechanism against drought is formation of hard leaves that will withstand permanent wilting, and ability to be re-established to proper functionality when favorable conditions are recreated (Pereira, 2016).

Under mild drought conditions, root morphology is affected by reducing the growth of lateral roots through inactivation of the lateral root meristems. Plants respond through expression of root morphology associated enzymes such as xyloglucan endotransglucosylase while reducing production of structural proteins. These circumstances increase the surface area for water uptake (Pereira, 2016).

Screening for Drought Tolerance in Tomatoes

The development of water stress tolerant cultivars and breeding for tolerance to drought have been proposed to be more promising strategies to support sustainable production and yield under dry conditions in many crops (Taheri et al., 2022; Saqlan Naqvi et al., 2014). Characterization of crop genotypes grown under water deprived conditions has been emphasized to identify drought-tolerant cultivars in several crops (Conti et al., 2019; Ghebremariam et al., 2013; Ravelombola et al., 2020a). Comprehensive details on phenotypic evaluation of genotypes are important for successful development of drought tolerant cultivars.

Screening of genotypes for drought tolerance under greenhouse controlled and field conditions has been widely used to study tolerance or resistance to drought in many crops (Abdelhaleim et al., 2022; Conti et al., 2019; Cui et al., 2020b; Soleimani et al., 2014).

Screening for tolerance to drought stress is a serious problem encountering crop improvement experts worldwide. Choosing the best growth parameter for characterization of crop genotypes for their capacity to grow well under low moisture conditions has been the core aim of establishing phenotypic variation in relation to drought tolerance. Both physiological and morphological parameters have been used to screen tomato genotypes for drought tolerance. (Sousaraei et al., 2021) considered growth and morphological characteristics (height, leaf number, shoot dry weight, root volume, root fresh weight, root dry weight) and chlorophyll fluorescence during phenotyping for drought tolerance. (Kumar et al., 2017) evaluated tomato genotypes based on germination percentage and germination rate among other parameters. Another study by (Baret et al., 2018; Soleimani et al., 2014) assessed drought tolerance in maize and wheat genotypes based on leaf rolling along with canopy level measurements while other studies used a combination of leaf wilting and leaf rolling (Engelbrecht et al., 2007; Susanto et al., 2019).

Screening procedure also needs to be considered in analyzing tomato genotypes for water stress tolerance. Several studies used either a single or combined approach to screen tomato genotypes. For instance, (Kumar et al., 2017) characterized tomato genotypes for drought tolerance under laboratory conditions. The tomato genotypes were treated with varying concentrations (4%, 8%, 12% and 16%) of Polyethylene Glycol (PEG-6000) and distilled water. The results showed that an increase in concentrations of Polyethylene Glycol (PEG-6000) resulted in reduced germination percentage, germination rate, root length, shoot length, root dry weight, and shoot dry weight. Another study by (Wahb-Allah et al., 2011b) investigated drought tolerance in different tomato genotypes grown under greenhouse conditions where drip irrigation was used. Vegetative growth, flowering and yield traits were measured whereas water use efficiency was determined. The data indicated that an increase in low moisture levels led to considerable decline in vegetative and fruit traits. This study focused on the evaluation of phenotypic performance of tomato genotypes under water scarcity conditions to discover drought tolerant genotypes that may be used to supporting breeding for tolerance to drought in tomato.

Objectives of the study

The core focus of this study was to conduct phenotypic evaluation to discover drought tolerant genotypes of tomato that could be used in breeding programs to develop drought tolerant cultivars of tomato to support sustainable production of tomato in arid regions.

Materials and Methods

Plant material

Sixty-eight USDA tomato germplasm accessions were used for drought tolerance evaluation in this study. Out of 68 accessions, 14 (20.6%) were originally collected from United States; nine from Canada; five from Peru; and the left 40 from other 24 countries (Supplementary Table S1).

Evaluation for drought tolerance

Evaluation of tomato accessions was performed in a greenhouse at the Arkansas Agricultural Research and Extension Center, Fayetteville, AR (Fig 1 A) between January 2023 to February 2023. During the experiment, the greenhouse temperature and humidity were kept at 21^0C/18^0C in day/night and 73%, respectively. The screening procedure was followed as described in previous reports (Cardoso et al., 2022; Cui et al., 2020; Engelbrecht et al., 2007; Susanto et al., 2019) with slight modifications.

Five seeds of each tomato accession were sown in pots (8.5 cm-high, 8.5 cm-top diameter, and 5.8 cm-base diameter) placed in trays (52 cm-long, 26 cm-wide, and 6 cm-high). Each tray contained 12 pots filled with commercial compost (Berger, berger.ca, BM 6) up to 8 cm-high in one day before seeds were sown. Each pot was filled with 300mL (milliliters) of water, while each tray was filled with 2L (liters) of water soon after seed sowing. After the initial irrigation, the pots and trays were left unirrigated for a period of 7 days. Then 180 mL of water was maintained per pot every 3 days for 28 days before drought treatment.

180mL of liquid (0.5 teaspoon per gallon or 3.8L) fertilizer (Miracle-Gro Water Soluble All Purpose Plant Food 24-8-16) containing ammoniacal nitrogen (N) (3.5%), urea nitrogen (N) (20.5%), available phosphate (P_2O_5) (8%), soluble potash (K_2O) (16%), Boron (B) (0.02%), Water Soluble Copper (Cu) (0.07%), Chelated Iron (Fe) (0.15%), Manganese (Mn) (0.05%), Molybdenum (Mo) (0.0005), and Water Soluble zinc (Zn) (0.06%), was applied in liquid form per pot 10 days after seed sowing and every 14 days in subsequent applications before the plants were exposed to drought stress.

The experiment was a randomized complete block design (RCBD) with three blocks, organized in a split-plot manner, with the drought treatment as the main plot and the tomato accessions as the subplot. During the experiment, thinning was done in 15 days after planted. Three plants per pot were kept for each tomato accession in a block. The drought treatment was applied to the tomato plants in 35 days after seed sowing until susceptible genotypes were completely dead approximately 10 days without watering in this study, showing vulnerability to water scarcity conditions. The control treatment was maintained with 180 mL of tap water every 3 days constantly.

Fig 1. Drought tolerance treatment in greenhouse and measurement: A) tomato plants, B. 0-9 scale for leaf wilting; and C) 1-9 scale for leaf rolling.

Measurements

Measurements on plant height, leaf wilting, leaf rolling, and total leaf chlorophyll content (SPAD) were recorded. Plant height was measured from each plant per genotype in each replicate for the drought stressed and non-drought stressed plants in 10 days after drought stress initiated.

Table 1. Visual assessment of leaf wilting and leaf rolling on a scale of 0 to 9 and 1 to 9, respectively, in 68 tomato accessions assessed for drought tolerance.

Category[*]	Leaf wilting	Leaf rolling stage
0	Normal (not wilted)	
1	Slightly wilted	No symptom of leaf rolling
2	Slight wilting - minimal signs of leaf wilting, but overall plant health was relatively unaffected	Minimal leaf rolling: Slight curling of a few leaves
3	Wilted leaves, with loss of turgidity, but the plant remains moderately healthy	Mild leaf rolling: Some curling and folding of a small number of leaves
4	Moderate wilting - significant wilting observed in several leaves, indicating a moderate level of stress	Moderate leaf rolling: Noticeable curling and folding of several leaves.
5	Moderate to severe wilting - a substantial number of leaves wilted, indicating a higher level of stress	Significant leaf rolling: Extensive curling and folding of most leaves
6	Severe wilting - all leaves wilted, and the plant was under considerable stress	Significant leaf rolling: Extensive curling and folding of most leaves.
7	Extreme wilting - all leaves wilted, and the plant is severely stressed	Significant leaf rolling: Further increase in curling and folding, affecting a significant portion of leaves
8	Critical wilting - all leaves and stem dried, and the plant almost dead	Severe leaf rolling: Intense curling and folding of almost all leaves, potentially impacting plant health
9	Dead	Leaves tightly rolled (Severe leaf rolling: Maximum intensity of curling and folding, with nearly all leaves affected)
[*]0-4=drought tolerant; 5-6=moderately tolerant; 7-9=drought sensitive		

Visual assessment of leaf wilting and leaf rolling were performed based on a scale of 0 to 9 (Fig 1 B) and 1 to 9 (Fig 1 C), respectively (Table 1), with slight modifications based on the symptoms associated with leaf drying and folding (Cui et al., 2020b; Engelbrecht et al., 2007; Susanto et al., 2019).The scores were recorded for each plant of the genotypes in the drought treatment, and the average score in each accession was calculated to determine the drought tolerance response under drought treatment.

The SPAD chlorophyll content was measured from three regions of trifoliate leaves for all plants of each genotype per treatment (drought and without drought) using the using the SPAD-502 Plus Chlorophyll Meter (Spectrum Technologies, Inc., Plainfield, IL). The measurements for each region in the leaf were recorded, separately.

The following data were collected and computed (Ravelombola., 2021) (Table S1).

i. LW-d6: leaf wilting in day 7 after drought treatment based on 0 - 9 scale;
ii. LW-d10: leaf wilting in day 10 after drought treatment based on 0-9 scale;
iii. LR-d6: leaf rolling in day 7 after drought treatment based on 1-9 scale;
iv. LR-d10: leaf rolling in day 10 after drought treatment based on 1-9 scale;
v. SPAD_healthy: leaf chlorophyll content in healthy without drought stress, measured by the SPAD-502 Plus Chlorophyll Meter (Spectrum Technologies, Inc., Plainfield, IL);
vi. SPAD_stress: leaf chlorophyll content under drought stress condition.
vii. SPAD_AD: Absolute decrease in leaf chlorophyll content (SPAD_healthy - SPAD_stress);
viii. SPAD_II: Inhibition Index in leaf chlorophyll content = [100 * (SPAD_healthy - SPAD_stress) / SPAD_healthy].
ix. SPAD_RDT: Relative drought tolerance in leaf chlorophyll content measured = (100 * SPAD_stress / SPAD_healthy) = (100 - SPAD_II);
x. PlHt_healthy: Plant height in healthy without drought stress;
xi. PlHt_stress: Plant height under drought stress;
xii. PlHt_AD: Absolute decrease in plant height (PlHt_healthy - PlHt_stress)
xiii. PlHt_II: Inhibition Index in plant height = [100 * (PlHt_healthy - PlHt_stress)/ PlHt_healthy]; and
xiv. PlHt_RDT = Relative drought tolerance in plant height = [100 * (PlHt_stress/PlHt_healthy)] = (100 - PlHt_II).

xv. Broad sense Heritability (H^2)

xvi. Pearson's correlation analysis

Data analysis

Statistical model

The statistical model for ANOVA analysis was the following: $Yij = \mu + Bi + Gj + \mathcal{E}ij$ where i= 1, 2, 3 and j=1.….68, with μ representing the overall mean, and Yij representing the response from the jth accession (Gj) (fixed effect) at the ith block (Bi) (random effect), and eij representing the random error associated with the ijth observation.

ANOVA, distribution, descriptive statistics, and Pearson's correlation

The data were analyzed using JMP PRO 17. Analysis of variance (ANOVA) was performed using the general linear model (GLM) procedure. Mean separation was conducted using Student T-test at alpha =0.05. The distribution of the data was visualized using the 'Distribution'; Descriptive statistics were estimated using the 'Tabulate'; and Person's correlation coefficients and their P-values were calculated by 'Multivariate Methods' options of JMP PRO 17, respectively. The broad-sense heritability (H^2) was estimated, using the following formula (Holland et al., 2003). $H^2 = 100 * \sigma^2_G / [\sigma^2_G + (\sigma^2_{GE} / e) + (\sigma^2_E / re)]$, where σ^2_G is the total genetic variance, σ^2_{GE} is variance between genetic and environment (here: location) interaction; σ^2_E is the residual variance; e is the number of environment (block); and r is the number of replications. The estimates for σ^2_G, σ^2_{GE} and σ^2_E are $\sigma^2_E = MSE$; $\sigma^2_{GE} = (MSGE - MSE)/r$; and $\sigma^2_G = (MSG - MSGE)/re$.

Absolute decrease, inhibition index, and relative drought tolerance

To completely evaluate tomato accessions for tolerance to drought, absolute decrease (AD), Inhibition index (II) (%), and relative drought tolerance (RDT) (%) were estimated for plant height and SPAD chlorophyll content in Microsoft Excel.

The AD was a measure of the absolute change (decrease) in the plant height or SPAD chlorophyll content. The AD in plant height and chlorophyll content was achieved by subtracting the plant height or chlorophyll content for the drought stressed plants from those of well-watered plants (AD = the value in healthy without drought stress – the value under drought stress condition). The higher the AD value, the more likely a tomato accession had its height or chlorophyll content decreased more, showing high susceptibility of the accession to drought stress. Conversely, the lower the AD value, the accession had higher drought tolerance.

The II was a measure the inhibition percentage to drought tolerance {II = [100 * (the value in healthy – the value under drought stress) / the value in healthy under normal irrigation]}. As same as the AD value, the higher II percent for an accession, the plant height and SPAD chlorophyll content decreased more, showing the tomato accession had higher susceptibility under drought stress condition. Conversely, the lower the AD value, the higher the accession had drought tolerance.

On the other hand, RDT was a measure of the relative change (decrease) percentage in the plant height or SPAD chlorophyll content, estimated by dividing the value under drought stress by in healthy under proper irrigation. Conversely as AD and II, the higher RDT% for an accession, the plant height and SPAD chlorophyll content decreased less, showing the tomato accession had higher tolerance under drought stress but the lower RDT%, the higher susceptible an accession was.

Rank of drought tolerance in tomato accessions

The 68 tomato accessions were ranked from 1 to 68 for each of the 10 traits (LW-d6, LW-d10, LR-d6, LR-d10, SPAD_AD, SPAD_II, PlHt_AD, PlHt_II, PlHt_RDT, and SPAD_RDT), where 1 as the top associated with drought tolerance and 68 as the most vulnerable one. Because the value of II equals to 100 minus ADT value (II = 100-ADT), the rank of ADT was the exact same as the rank order of II and both PlHt_RDT, and SPAD_RDT were not listed.

DNA extraction, Genotyping by Sequencing (GBS) and SNP discovery

Genomic DNA was extracted from fresh leaves of tomato plants using the CTAB/SDS method. DNA sequencing was conducted using genotyping by sequencing (GBS) approach (Elshire et al., 2011) in Pair-end sequencing libraries are sequenced by Illumina NovaSeq. The short-read sequences data are implemented in a pipeline using TASSE_GBS (Glaubitz et al., 2014) and Stacks 2 (Rochette et al., 2019; https://catchenlab.life.illinois.edu/stacks/). A total of 392,496 SNPs were discovered across 287 tomato genotypes distributed on 12 chromosomes of tomato.

Principal Component Analysis (PCA) and Genetic Diversity

Principal components were analysed and Dendrogram was drawn by hierarchical cluster method using JMP Pro 17 based on either traits (LW-d6, LW-d10, LR-d6, LR-d10, SPAD_AD, SPAD_II, PlHt_AD, and PlHt_II) among the 68 tomato accessions. Genetic diversity was analysed, and a phylogenetic tree was generated using MEGA 11 based on 5,003 SNPs distributed on 12 chromosomes in 65 USDA GRIN tomato accessions except the three accessions, PI 365956, PI 438587, and PI 600901 out of the 68 accessions in Table S1. Because they had bad GBS sequencing data, the three accessions were filtered out (removed) from the genetic diversity analysis. The SNP set consisted of 5,003 SNPs across the 65 accessions, after filtered and keeping the SNPs with minor allele frequency (MAF) >1.5%, missing allele <15%, and heterogeneous rate <=35% in this study.

Results

Parameters and distributions of drought related traits

Leaf wilting

The leaf wilting scale of 0-9 varied among the 68 tomato accessions under 6 and 10 days of drought stress (Supplementary Table S1 & S2). A large range was observed: 7.0 for LW-d6 and 6.3 for LW-d10 (Table S2). The mean rate of 6.9, standard deviation (Std Dev) of 1.5, standard error (Std Err) of 0.18, and coefficient variation (CV) of 21.6% were observed for 6 days drought treatment (LW-d6), while the mean rate of 8.4, Std Dev of 1.39, Std Err of 0.17, and CV of 16.6% were noted under 10 days drought treatment (LW-d10) (Supplementary Table S2). These leaf wilting data reveal significant variation in tolerance response to drought stress among the 68 tomato accessions.

The distributions of leaf wilting scores for either 6-day (LW-d6) or 10-day (LW-d10) drought treatment were right-skewed (Figure 2 A&B), showing that most of the 68 tomato accessions were extreme susceptibility to drought stress, where the two accessions, PI647531 and PI634828 were highest susceptible with 8.9 and 9 (highest scale defined) in either LW-d6 and LW-d10, respectively, indicating they can be used as susceptible control in drought evaluation experiment or as susceptible parents in genetic study of QTL mapping of drought tolerance in tomato. PI365956, PI584456, PI390510, and PI370091 had average leaf wilting scores of less than 4 in both treatments (Supplementary Table S1 & S2), showing that they were the highest tolerance to drought stress and suggesting that the four accessions could be useful as parents in breeding elite cultivars of tomato for drought tolerance.

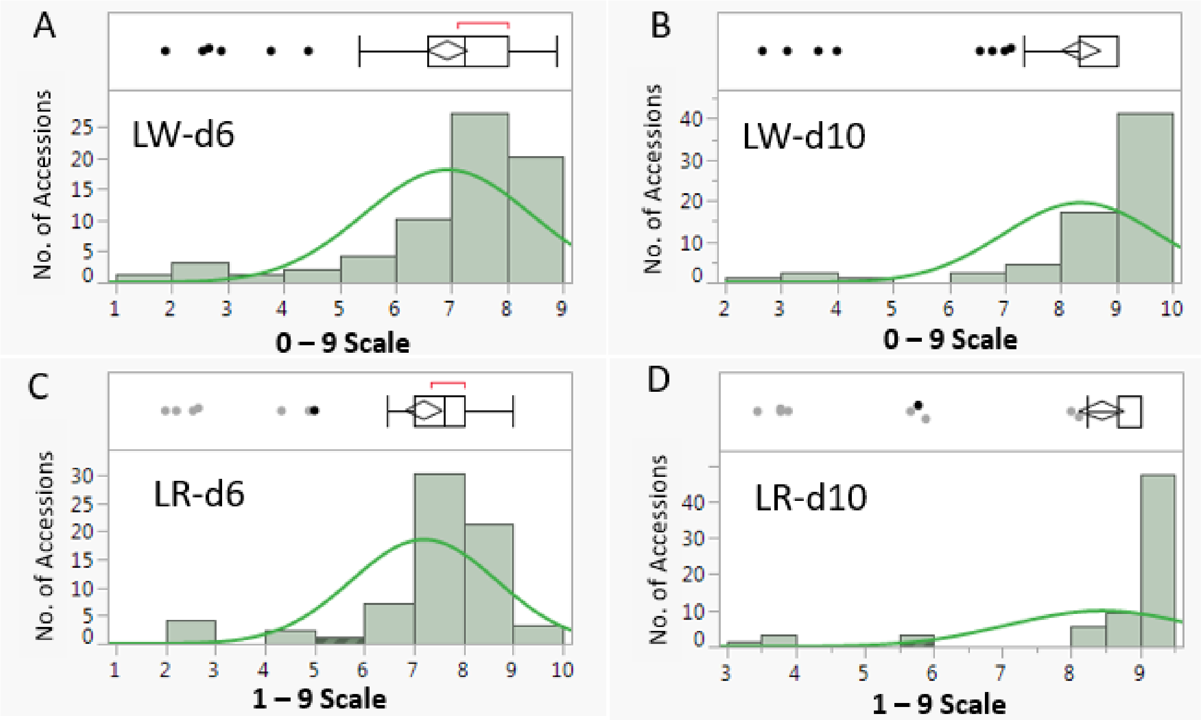


Fig 2. The four distributions of leaf wilting (LW) (A and B) and leaf rolling (LR) (C and D) in 68 tomato accessions: (A) and (C) in 6 days; and (B) and (D) in 10 days after drought treatment.

Leaf rolling

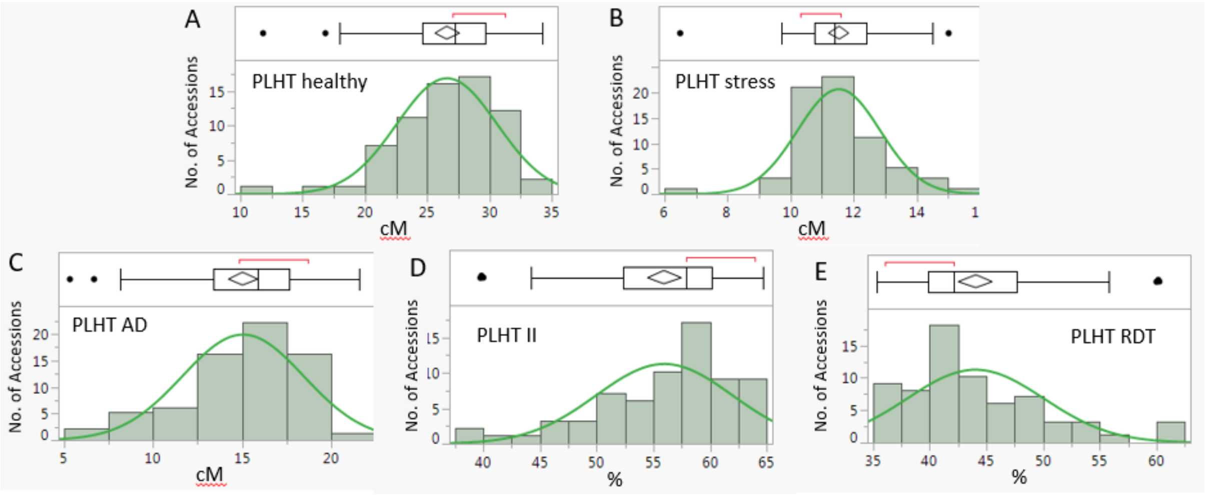
The average leaf rolling scores for 6-day (LR-d6) and 10-day (LR-D10) drought stress ranged from 2.0 to 9 and 3.4 to 9 (Supplementary Table S2), respectively, with a mean rate of 7.2, standard deviation (Std Dev) of 1.47, standard error (Std Err) of 0.18, and coefficient variation (CV) of 20.4% for 6 days drought treatment (LR-d6) and the mean rate of 8.4, standard Std Dev of 1.37, Std Err of 0.17, and CV of 16.3% under 10 days drought treatment (LR-10d) (Supplementary Table S2), showing significant differences and a large range (7.0 for LR-d6 and 5.6 for LR-d10) in reaction to drought stress among the 68 tomato accessions.

Distribution of leaf rolling scores for either 6-day (LR-d6) or 10-day (LR-d10) drought treatment were right-skewed (Figure 2 C&D), as same trend as those in leaf wilting, showing that most of the 68 tomato accessions were extreme susceptibility to drought stress, where the three accessions, PI 647531, PI 196297, and PI 634828 had the highest scale of 9 in both LR-d6 and LR-d10 (Table S1), indicating that the three accessions can be used as susceptible control in drought evaluation experiment or as susceptible parents in genetic study of QTL mapping of drought tolerance in tomato. The four accessions PI365956, PI584456, PI390510, and PI370091 as in the were found to have leaf rolling scores of less than 4, showing the lowest scales, as they were lowest leaf wilting scale values (Table S1), indicating that the four accessions were highest tolerance to drought stress and suggesting that the four accessions could be useful as parents in breeding elite cultivars of tomato for drought tolerance.

Plant height-related parameters

Plant height measurements were taken for 68 tomato accessions under both well-watered and drought-stressed conditions. For the well-watered plants, the average plant height (PlHt_healthy) ranged from 11.8 cm to 34.2 cm at 10-days with a near normal distribution skewed right side among the 68 accessions (Fig. 3 A), with a mean of 26.6 cm and a standard deviation (Std Dev) of 4.02 (Supplementary Table S2). PI 584456 was shortest with 11.8 cm and PI 433016 was the tallest with 34.2 cm (Table S1).

Fig 3. The five distributions of plant height related traits for drought tolerance in 68 tomato accessions.



*PlHt_healthy = Plant height in healthy without drought stress; PlHt_stress = Plant height under drought stress; PlHt_AD = Absolute decrease in plant height = PlHt_healthy - PlHt_stress; PlHt_II = Inhibition Index in plant height = [100 * (PlHt_healthy - PlHt_stress)/ PlHt_healthy]; and PlHt_RDT = Relative drought tolerance in plant height = [100 * (PlHt_stress/PlHt_healthy)] = (100 - PlHt_II).

Under drought-stressed conditions, the average plant height (PlHt_stress) ranged from 6.5 cm to 15.0 cm at 10-days (Fig 3 B), with a mean of 11.5 cm and a Std Dev of 1.31 (Supplementary Table S2). PI 584456 was still the shortest with 6.5 cm and PI 258478 was the tallest with 15.0 cm (Table S1).

The absolute decrease in average plant height (PlHt_AD) had a large range of 16.2 cm and ranged from 5.3 cm to 21.5 cm with a mean of 15.1 cm, a Std Dev of 3.41 cm, Std Err of 0.41 cm, and CV of 22.6 % (Fig 3 C, Supplementary Table S2), indicating that there was a large difference and variable of height decreased (AD) under drought stress among the 68 tomato accessions. PI 584456 showed the smallest with 5.3 cm plant height decreased (Table S2), indicating that PI 584456 was somewhat drought tolerant. PI 433016 was the greatest with 21.5 cm height decreased (Table S2), indicating that PI 433016 was drought susceptible.

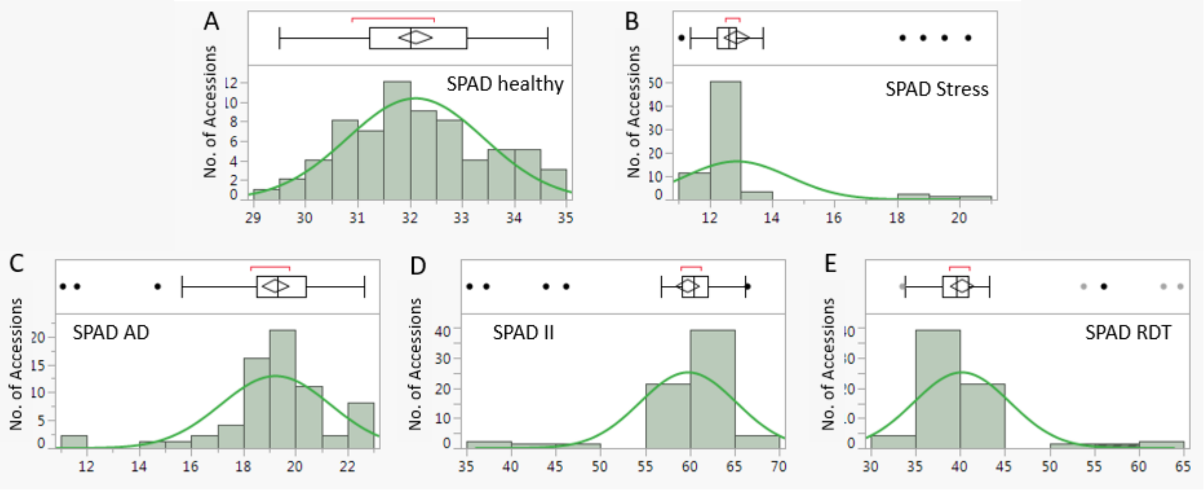
Inhibition index in plant height (PlHt_II), which represents the reduction in plant height of drought-stressed plants compared to well-watered plants, had a large range of 24.9% and ranged from 39.7% to 64.7% (Fig 3 D; Supplementary Table S2), with a mean of 56.0%, a Std Dev of 6.02%, Std Err of 0.73, and CV of 10.8% (Supplementary Table S2), indicating that there was a large difference and variable of plant height inhibition (tolerance) to drought tolerance among the 68 tomato accessions. The four PI 600906, PI 330725, PI 499370, and PI 451970 had the lowest II% of 39.7%, 39.8%, 40.0%, and 44.2% (Table S1), indicating the four accessions were highest drought tolerance in this study. PI 636277, PI 438859, PI 286255, PI 193399, and PI 644750 had the highest PlHt_II% with over 63% (Table S2), being the most drought susceptible.

Relative drought tolerance in plant height (PlHt_RDT), defined as the ability of a plant to maintain its height under drought stress compared to well-watered conditions, had a large range with 24.9% and ranged from 35.3% to 60.3% ((Fig 3 E, Supplementary Table S2), with a mean of 44.0%, a Std Dev of 6.02%, Std Err of 0.73, and CV of 13.7 (Supplementary Table S4), indicating that there were a large range and difference among the 68 accessions. The three accessions, PI 499370, PI 330725, and PI 600906 had the highest with >60% of RDT (Table S1) and showed the highest drought tolerance among the 68 accessions. PI 286255 (Moneymaker) and PI 644750 (Giant Tree) had the lowest RDT% with <36%, indicating the two accessions were susceptible to drought.

SPAD chlorophyll content

The SPAD chlorophyll content for well-watered plants (SPAD_healthy) ranged from 29.5 to 34.6 with a range of 5.1 and showed a near normal distribution among the 68 accessions (Fig 4 A, Supplementary Table S2), with a mean of 32.1; Std Dev of 1.31; Std Err of 0.16; and CV of 4.1 (Supplementary Table S2). Accessions with the highest SPAD chlorophyll content were PI 330342, PI 291337, and PI 258484 with 34.6, and the lowest were PI 451967, PI 127825, and PI 466917 with <30.0 (Supplementary Table S2).

Fig 4. The five distributions of leaf chlorophyll content related traits for drought tolerance in 68 tomato accessions.



*SPAD_healthy = leaf chlorophyll content in healthy without drought stress, measured by the SPAD-502 Plus Chlorophyll Meter (Spectrum Technologies, Inc., Plainfield, IL); SPAD_stress = leaf chlorophyll content under drought stress condition; SPAD_AD = Absolute decrease in leaf chlorophyll content (SPAD_healthy - SPAD_stress); SPAD_II = Inhibition Index in leaf chlorophyll content = [100 * (SPAD_healthy - SPAD_stress) / SPAD_healthy]; and SPAD_RDT = Relative drought tolerance in leaf chlorophyll content measured = [100 * SPAD_stress / SPAD_healthy] = (100 - SPAD_II).

For the plants under drought treatment, SPAD chlorophyll content (SPAD_stress) varied from 11.1 to 20.3, and the mean and standard deviation were 12.9 and 1.66, respectively (Supplementary Table S2). Distribution of SPAD chlorophyll data under drought stress among the 68 accessions were right skewed (Fig 4 B). Accessions with the highest SPAD chlorophyll content under stress were PI 365956 (LA 1373) (20.3), PI 584456 (19.5), PI 370091 (18.8), and PI 390510 (18.2) (Supplementary Table S1), indicating that these accessions were more tolerant to drought stress. The lowest SPAD chlorophyll values were recorded for PI 158760 and PI 438587 with less 11.5 (Supplementary Table S2), showing high sensitivity of the accessions to drought stress.

The absolute decrease in average SPAD chlorophyll content (SPAD_AD) had a large range of 11.5 and ranged from 11.1 to 20.3 with a mean of 19.2, a Std Dev of 2.10, Std Err of 0.25, and CV of 10.9% (Fig 4 C, Supplementary Table S2), indicating that there was a large difference and variable of chlorophyll content decreased (AD) under drought stress among the 68 tomato accessions. PI 584456 and PI 365956 showed the smallest with 11.1.and 11.6, respectively in chlorophyll content decreased (Table S2), indicating that PI 584456 and PI 365956 were somewhat drought tolerant. PI 645361 and PI 600906 were the greatest with 22.6 decreased (Table S2), indicating that the two accession were most drought susceptible.

Inhibition index in SPAD chlorophyll content (SPAD_II) had a large range of 31.1% and ranged from 35.4% to 66.4% (Fig 4 D; Supplementary Table S2), with a mean of 59.8%, a Std dev of 5.37%, Std Err of 0.65, and CV of 9.0% (Supplementary Table S2), indicating that there was a large difference and variable of SPAD chlorophyll content inhibition (tolerance) to drought tolerance among the 68 tomato accessions. The two accessions, PI 365956 and PI 584456 had the lowest SPAD_II values of <37.5% (Table S1), indicating the two accessions were highest drought tolerance in this study. PI 645361 and PI 158760 had the highest SPAD II% with over 66% (Table S2), being the most drought susceptible.

The relative drought tolerance in SPAD chlorophyll content (SPAD_RDT) varied from 33.6% to 64.6 with a large range of 31.1% (Fig 4 E, Supplementary Table S2). The mean and standard deviation shown were 40.2% and 5.37%, respectively (Supplementary Table S4), showing significant difference in drought tolerance among the 69 tomato accessions. The highest SPAD_II were observed in PI 365956 (64.6 %), PI 584456 (62.8%), and PI 390510 (53.8%), indicating the four accessions were highest tolerance to drought stress based on SPAD chlorophyll content. In contrast, PI 158760 (33.6%) and PI645361 (33.8%) showed the lowest relative drought tolerance values, indicating the extreme vulnerability to drought stress (Supplementary Table S1). Overview, four tomato accessions, PI 365956 (LA1373), PI 584456 (Allure), PI 370091 (Vision), and PI 390510 (W-C 1050) are drought tolerant with a scale of <4 in leaf wilting and leaf rolling, decreasing <16 in absolute SPAD chlorophyll content and <47% in SPAD chlorophyll inhibition index (II), decreasing < 18 cm in absolute plant height and <62% in plant height inhibition index (II).

Table 2. Top four tomato accessions with the highest drought tolerance based eight traits.

Accession	NAME	TAXONOMY	ORIGIN	LW-d6	LW-d10	LR-d6	LR-d10	SPAD_AD	SPAD_II	PlHt_AD	PlHt_II
PI 365956	LA1373	Solanum peruvianum L.	Lima, Peru	1.9	2.7	2.0	3.9	11.1	35.4	13.7	50.3
PI 584456	Allure	Solanum lycopersicum L.	United States	2.7	3.1	2.2	3.8	11.6	37.2	5.3	45.1
PI 370091	Vision	Solanum lycopersicum L.	Canada	2.6	4.0	2.6	3.4	14.7	43.9	17.7	61.7
PI 390510	W-C 1050	Solanum lycopersicum L. var. cerasiforme (Alef.) Voss	Ecuador	2.9	3.7	2.7	3.8	15.6	46.2	16.1	56.4

Pearson’s correlation analysis

Table 3. Correlation coefficients (r-value) and their probability (P-value) among eight-drought tolerance related traits in 68 tomato accessions.

Correlation coefficients (r-value)	LW-d6	LW-d10	LR-d6	LR-d10	SPAD_AD	SPAD_II	PlHt_AD
LW-d10	0.85						
LR.d6	0.95	0.90					
LR.d10	0.87	0.92	0.93				
SPAD_AD	0.60	0.68	0.69	0.67			
SPAD_II	0.71	0.84	0.80	0.81	0.93		
PlHt_AD	0.15	0.24	0.14	0.15	0.04	0.11	
PlHt_II	0.15	0.25	0.14	0.15	0.07	0.11	0.90

Probability (P-Value)	LW-d6	LW-d10	LR-d6	LR-d10	SPAD_AD	SPAD_II	PlHt_AD
LW-d10	1.75E-20						
LR-d6	8.99E-34	6.54E-25					
LR-d10	4.64E-22	7.61E-28	3.85E-31				
SPAD_AD	5.16E-08	1.30E-10	1.06E-10	3.87E-10			
SPAD_II	1.29E-11	2.22E-19	1.95E-16	5.68E-17	1.09E-30		
PlHt_AD	0.22	0.05	0.26	0.24	0.77	0.39	
PlHt_II	0.24	0.04	0.27	0.22	0.59	0.38	3.68E-26

The correlation coefficients (r-value) among the eight-drought tolerance related traits in 68 tomato accessions were also showed in figure 5. A clear linear was observed each pair among the six traits, LW-d6, LW-d10, LR-d6, LR-d10, SPAD_AD, and SPAD_II, and between PlHt_AD and PlHt_II with a high r-value, indicating high correlations.

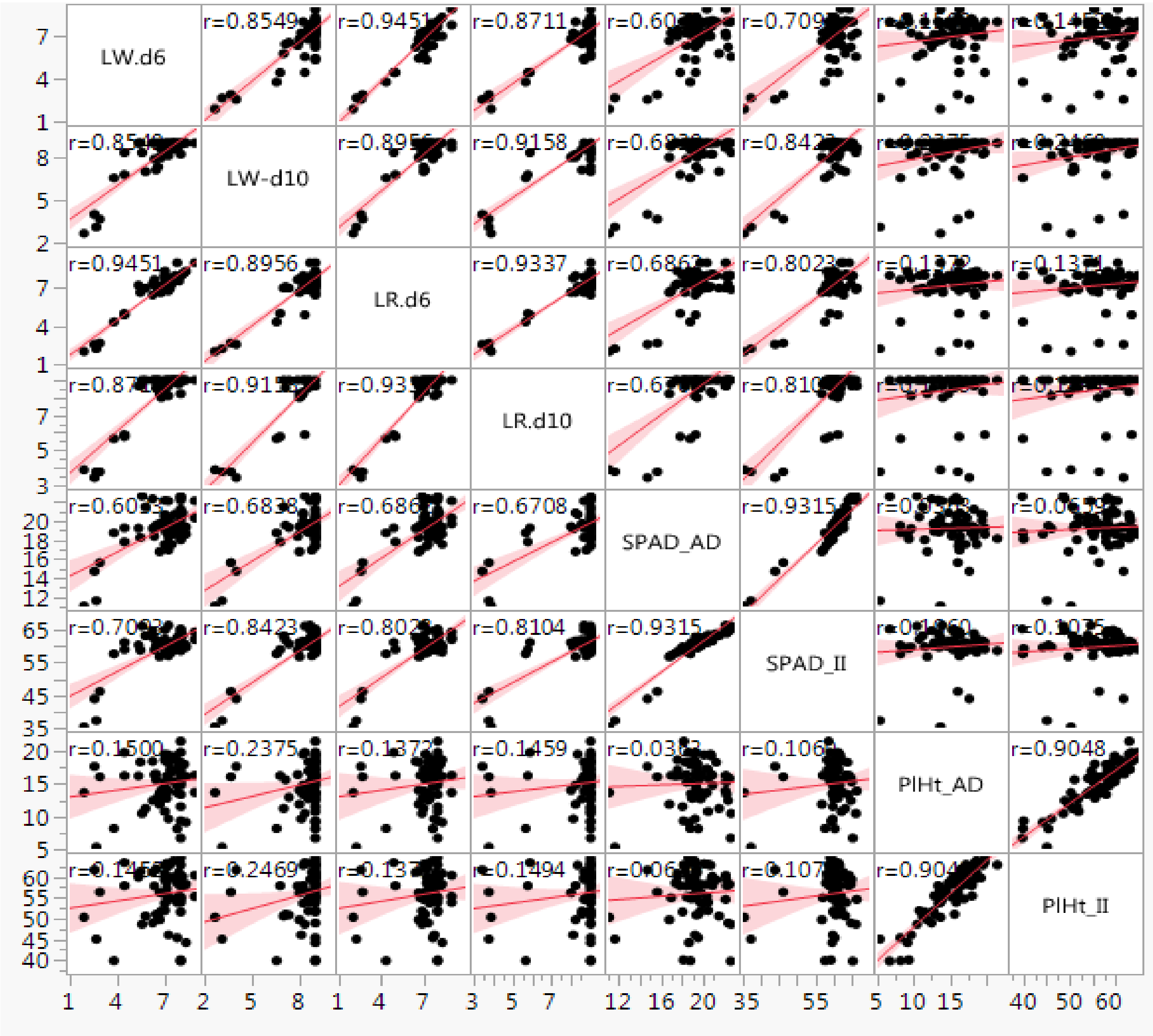


Fig 5. Correlation coefficients (r-value) among eight-drought tolerance related traits in 68 tomato accessions.

ANOVA and broad sense heritability

ANOVA for the parameters of drought tolerance and board sense heritability were estimated for all 14 traits (LW-d6, LW-d10, LR-d6, LR-d10, SPAD_healthy, SPAD_stress, SPAD_AD, SPAD_II, PlHt_healthy, PlHt_stress, PlHt_AD, PlHt_II, PlHt_RDT, and SPAD_RDT) in the 68 tomato accessions (Table S4). The Genotype (accession) had a significant effect at P=0.05 level for all 14 traits except SPAD_healthy. The significant effect of interaction between Genotype (Accession) and Block was also observed for PlHt_healthy, PlHt_stress, PlHt_AD, PlHt_II, PlHt_RDT, SPAD_stress, SPAD_II, and SPAD_RDT at P=0.05 level, but not for LW-d6, LW-d10, LR-d6, LR-d10, SPAD_healthy, and SPAD_AD (Table S4), indicating the stability of the traits.

The broad sense heritability (H%) was calculated for each of the 14 traits and they are 52.2%, 89.2%, 69.3%, 90.4% 64.1%, 62.4%, 94.1%, 70.3%, 70.3%, 25.4%, 72.2%, 48.5%, 73.5%, and 73.5% for LW-d6, LW-d10, LR-d6, LR-d10, PlHt_healthy, PlHt_stress, PlHt_AD, PlHt_II, PlHt_RDT, SPAD_healthy, SPAD_stress, SPAD_AD, SPAD_II, and SPAD_RDT,respectively (Table S4), showing that all 14 traits had high heritability H% >60% up to 94.1% except LW-d6 (52.2%), SPAD_healthy (25.4%) and SPAD_AD (48.5%) and indicating the drought tolerance can be heritable.

Ranking of accessions

In this study, tomato accessions were ranked based on multiple parameters used for assessing drought tolerance using 1 to 68 for each of the 68 tomato accessions where 1 as the best of the drought tolerance and 68 as the most susceptible. The values of PlHt_healthy, PlHt_stress, SPAD_healthy, and SPAD_stress in each tomato accessions are determined by the genetic background of the tomato genotypes (accessions) themselves and their interaction with the environment, and but are not directly associated with drought tolerance, therefore, they were removed for ranking drought tolerance. Each of the ten traits, LW-d6, LW-d10, LR-d6, LR-d10, PlHt_AD, PlHt_II, PlHt_RDT, SPAD_AD, SPAD_II, and SPAD_RDT was ranked from 1 to 68 (Table S5). In addition, two overall rankings of drought tolerance were used to rank the 68 accessions for their drought tolerance. Due to PlHt_RDT = 100 - PlHt_II, it will have the exact same ranking order as PlHt_II and was removed from the overall ranking. The SPAD_RDT was also removed due it had same ranking order as the SPAD_II. The first overall ranking was created by the eight traits, LW-d6, LW-d10, LR-d6, LR-d10, PlHt_AD, PlHt_II, SPAD_AD, and SPAD_II defined as Rank (8) (Table S5). Based on the correlation analysis, the plant height related to drought tolerance may have different mechanisms due to low r values between plant height related traits and others (Table 3 & S3, Fig 5), therefore, second overall ranking was formed using the six traits, LW-d6, LW-d10, LR-d6, LR-d10, SPAD_AD, and SPAD_II (Table S5). The four accessions with drought tolerance in Table 2, PI 365956, PI 584456, PI 370091, and PI 390510 were also listed as the top four drought tolerance ranked based on Rank(6) and each of six traits LW-d6, LW-d10, LR-d6, LR-d10, SPAD_AD, and SPAD_II individually (Table S5), indicating that the four accessions were highest drought tolerance from this study and they can be used in tomato breeding program as parents to develop drought tolerant cultivars. Besides the four drought tolerant accessions, the three accessions, PI 330725, PI 193400, and PI 127825 were ranked highly (Table S5), suggesting as intermediate drought tolerance.

PCA and genetic diversity

Principal components were analyzed among the 68 accessions based on the eight traits, LW-d6, LW-d10, LR-d6, LR-d10, PlHt_AD, PlHt_II, SPAD_AD, and SPAD_II. Four clusters (groups) were formed (Fig. 6). The four accessions with top drought tolerance in Table 2 and S5, PI 365956, PI 584456, PI 370091, and PI 390510 were grouped into the same cluster I based on hierarchical clustering analysis (Fig. 6), indicating that they had similar drought tolerance. The two out of three accessions in cluster II, PI 330725, and PI 193400 (Fig. 6) were also tolerant to drought stress (Table S1) and ranked among top 6 (Table S5), indicating they had similar response to drought stress in mediate level. Among the eight traits, there were two clusters: PlHt_AD and PlHt_II clustered together as I, and other six as cluster II, which was further divided into two groups: SPAD_AD and SPAD_II in the same group and the other four as another group. If furtherly divided, LW-d6 and LW-d10 together, and LR-d6 and LR-d10 as a pair (Fig. 6 bottom), indicating that leaf wilting and leaf rolling had similar results for drought tolerance, close to the results of SPAD chlorophyll content, but a little different from those of plant height related.

The Bioplot showed that LW-d6, LW-d10, LR-d6, LR-d10, SPAD_AD, and SPAD_II had same trend with tightly close each other; PlHt_AD and PlHt_II were close to each other, but far away from the others (Fig. 7 A), indicating that LW-d6, LW-d10, LR-d6, LR-d10, SPAD_AD, and SPAD_II were highly association but not associated with PlHt_AD and PlHt_II. The Scree plot (Fig. 7 B) and PCA plot (Fig 7 C) showed that there were four clusters among the 68 accessions.

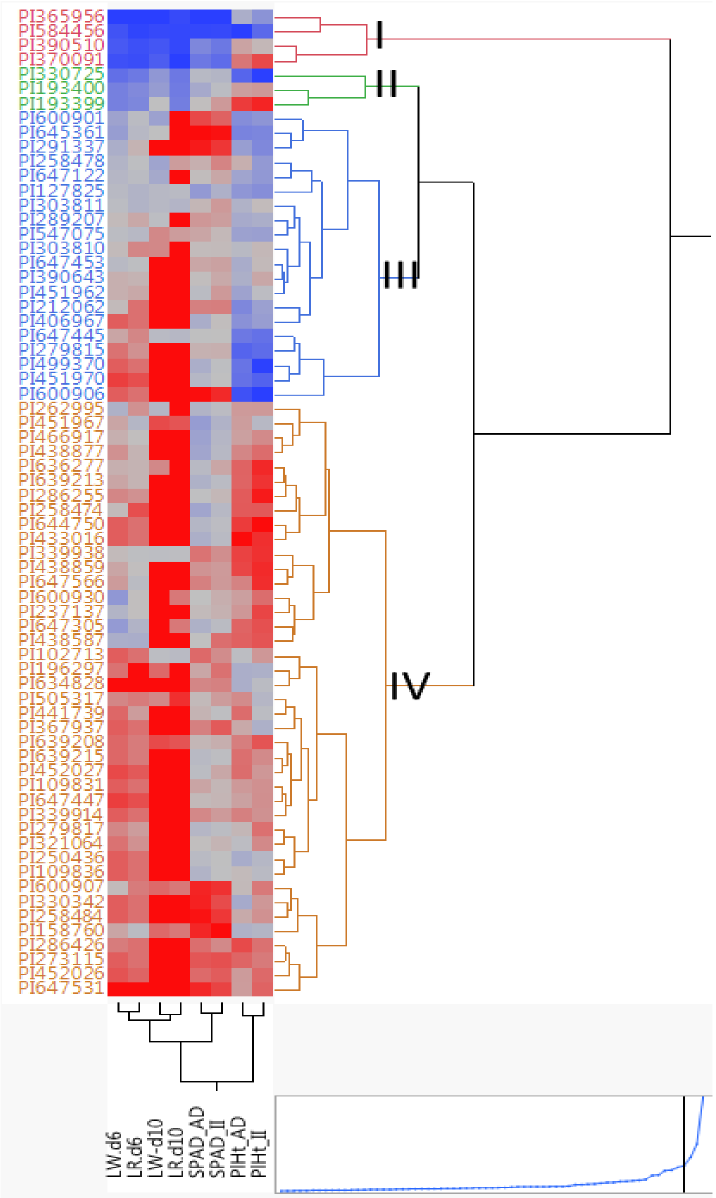


Fig 6. Two-way dendrogram in 68 tomato accessions by hierarchical cluster analysis in JMP Pro 17 based on eight drought tolerance related traits, LW-d6, LW-d10, LR-d6, LR-d10, SPAD_AD, SPAD_II, PlHt_AD, and PlHt_II, where the top four drought tolerant accessions were grouped into one cluster I (top).

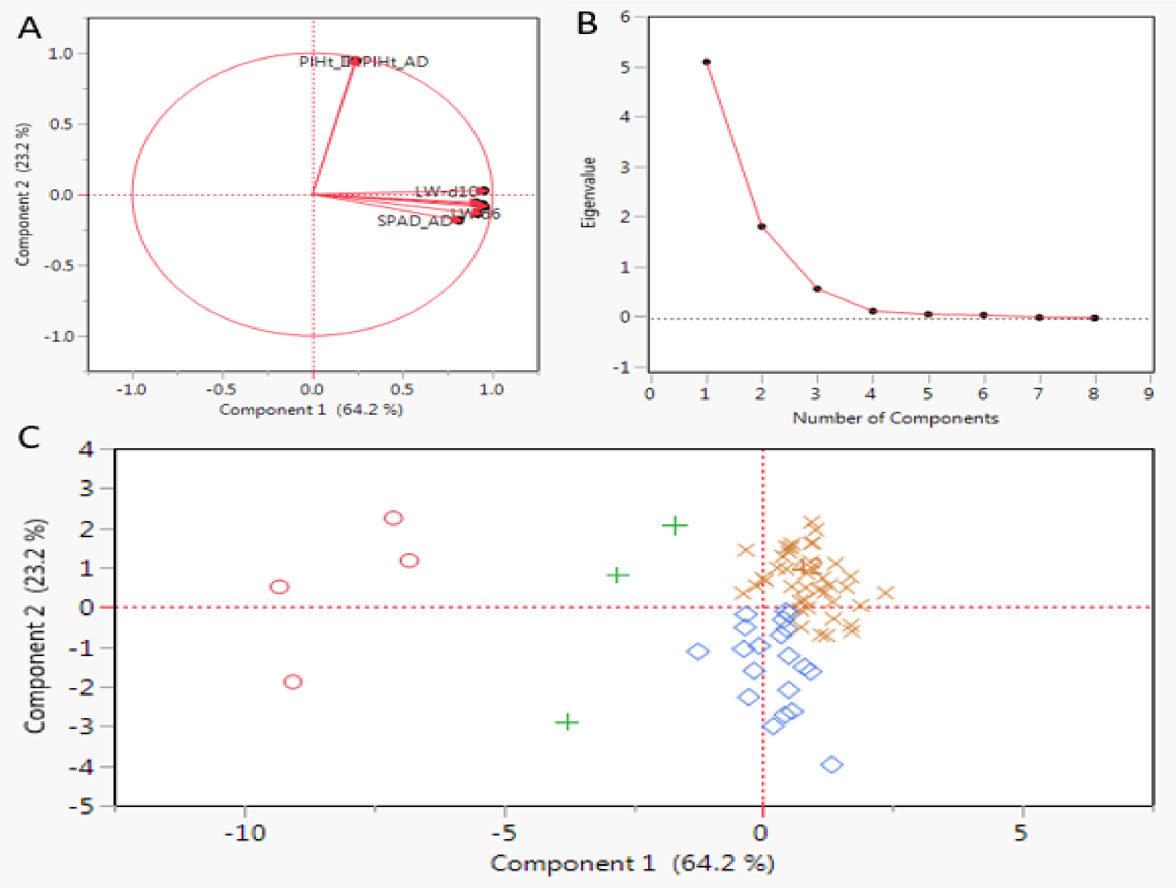


Fig 7. Principal component analysis (PCA) in 68 tomato accessions by JMP Genomics based on eight drought tolerance related traits, LW-d6, LW-d10, LR-d6, LR-d10, SPAD_AD, SPAD_II, PlHt_AD, and PlHt_II: (A) Bioplot, (B) Scree plot, and (C) PCA with 4-clusters.

From the phylogenetic tree among 65 tomato accessions which did not include the three accessions, PI 365956, PI 438587, and PI 600901 out of the 68 accessions in Table S1, the six drought tolerant accessions, PI 584456, PI 370091, PI 390510, PI 330725, PI 193400, and PI 127825 were arranged into different locations (parts) in the phylogenetic tree (Fig, 8), indicating that they have different genetic base (background) and are good drought tolerance resources.


PI250436 Q2 CentralBohemia CzechRepublic
PI639213 Q2 France
PI262995 Q2 Netherlands
PI286255 Q2 UnitedKingdom
PI636277 Q2 Argentina
PI109836 Q2 France
PI289207 Q2 Hungary
PI367937 Q2 MinasGerais Brazil
PI286426 Q2 Nepal
PI647531 Q2 Germany
PI639215 Q2 Italy
PI193399 Q2 Ohio UnitedStates
PI303810 Q2 UnitedStates
PI291337 Q2 China
PI339938 Q2 Spain
PI634828 Q2 Missouri UnitedStates
PI109831 Q2 France
🟥 PI193400 Q2 Ohio United States.drought.T
PI438877 Q2 Mexico
PI452026 Q2 Mexico
PI237137 Q2 Italy
PI258484 Q2 Peru
PI2731151 Q2
PI438859 Q2 Mexico
PI441739 Q2 Brazil
PI452027 Q2 Mexico
PI212062 Q2 CostaRica
🟥 PI127825 Q2 Peru drought.T
PI258478 Q2 Peru
PI196297 Q2 Nicaragua
🟥 PI390510 Q2 Ecuador drought.T
PI258474 Q2 Ecuador
PI158760 Q2 China
PI644750 Q2 Virginia UnitedStates
PI499370 Q2 Former SovietUnion
PI406967 Q2 Nicaragua
🟥 PI330725 Q2 UnitedStates drought T
PI102713 Q2 Former SovietUnion
PI639208 Q2 Tula RussianFederation
🟥 PI370091 Q2 Canada Drought.T
PI451962 Q2 Canada
PI466917 Q2 Bulgaria
PI279815 Q2 Canada
PI339914 Q2 Ontario Canada
PI451967 Q2 Canada
PI451970 Q2 Canada
PI547075 Q2 NorthCarolina UnitedStates
PI303811 Q2 UnitedStates
PI279817 Q2 Canada
PI321064 Q2 Hungary
PI647447 Q2 Bolivia
PI647122 Q2 Canada
PI647305 Q2 Spain
PI330342 Q2 Australia
PI647453 Q2 Bulgaria
PI390643 Q2 Peru
Q2
Q2
🟥 PI584456 Q1 UnitedStates drought.T
PI600930 Q1 UnitedStates
PI433016 Q1 China
PI647445 Q1 China
PI505317 Q1 Colombia
PI645361 Q1 Ontario Canada
PI647566 Q1 UnitedStates
PI600906 Q1 NorthCarolina UnitedStates
PI600907 Q1 NorthCarolina UnitedStates
Q1
0.05

Fig 8. Phylogenetic tree created by MEGA 11 based on 5,003 SNPs distributed on 12 chromosomes in 65 USDA GRIN tomato accessions.

Discussion

Drought tolerance of crops is related to a few factors that may contribute to tolerance, making studies on drought tolerance difficult. Numerous mechanisms of drought tolerance in several crops depend on the conditions, crop variety, and growth stages. As a result, many researchers have used multiple indicators to assess drought tolerance in comprehensive and integrated manner, which can provide more accurate and realistic information of drought tolerance in crops and can help researchers discover and select drought tolerant cultivars for cultivation and breeding. Inadequate information on drought tolerance in tomato has compromised the development of drought-tolerant cultivars. This study screened germplasm collection of tomato using multiple parameters and generated valuable information on drought tolerance in tomato by supplying reactions of various tomato accessions to drought stress.

Drought-associated parameters

Leaf wilting

The results of the drought tolerance study based on leaf wilting showed significant genetic variation among tomato accessions for tolerance to water stress. The results were consistent with past studies that have reported genetic variation in tomato for drought tolerance (Bose et al., 2019; Kumar et al., 2019). Finding genetic variation and developing high drought-tolerant cultivars is critical for sustainable agriculture, as drought is a major environmental stress that affects crop productivity and quality worldwide (Kumar et al., 2018). This study identified tomato accessions PI365956, PI584456, PI390510, and PI370091 imported from Peru, United States, Ecuador, and Canada (Supplementary Table S1; Table 2), respectively, to exhibit slow wilting under dry conditions, showing greater tolerance to drought stress. (Cardoso et al., 2022b; Pathan et al., 2014; J. Zhou et al., 2020) conducted a similar experiment and concluded that plant genotypes of tomato and soybean that maintained slow-wilting trait and less yield loss were drought-tolerant. The highly drought tolerant tomato accessions identified in this study might have drought tolerance associated genes that could be important in developing drought tolerant cultivars of tomato and could be useful in molecular and physiological studies to enhance mechanisms accountable for improving yield under water scarcity environments.

Leaf rolling

Leaf rolling is caused by dehydration of various sections across the leaf, which minimizes the leaf surface area for sunlight penetration and transpiration, leading to stomatal closure and reduced photosynthesis (Kadioglu et al., 2012; Kadioglu & Terzi, 2007; Baret et al., 2018). Leaf rolling is a significant indicator of drought tolerance in plants, as described by (Baret et al., 2018; Chandra & Dubey, 2009). The use of leaf rolling as an indicator of drought tolerance in breeding programs could facilitate the selection of more drought-tolerant cultivars of crops (Baret et al., 2018). (Baret et al., 2018) recently phenotyped maize genotypes in the field and reported the occurrence of leaf rolling in water-stressed plants at flowering stage even during the first day of exposure to drought. This study found significant variation in leaf rolling or folding among the 69 tomato accessions, indicating the importance of this trait to the overall drought tolerance level in tomato plants. Tomato accessions PI370091, PI390510, PI584456, and PI365956 were identified to exhibit high tolerance to drought stress based on leaf rolling scores (Supplementary Table S1; Table 2), showing that they could be utilized for selection as parental lines for successful breeding with focus on developing more drought-tolerant tomato cultivars.

Plant height

The impact of drought stress on tomato plants was studied by assessing the response of 69 tomato accessions with a focus on plant height as an indicator of drought tolerance. Drought stress is known to cause diminished plant growth due to impaired mitosis and loss of turgor (Farooq et al., 2009). The results of this study showed significant reduced plant growth in drought stressed plants, as previously observed in drought tolerance studies of other crops (Cui et al., 2020; Pervez et al., 2009; Ravelombola et al., 2020; Sakya et al., 2018; Singh, 2021; Zhang et al., 2020; Llugany et al., 2021). (Su et al., 2019) evaluated water stress tolerance in maize genotypes and concluded that even drought tolerant genotypes of maize had lower plant height. The results of this study showed significant variations in plant height among the accessions under both well-watered and drought-stressed conditions, with a mean absolute decrease of 19.2 cm (Supplementary Table S2; Table 2) across the accessions under drought stress. The inhibition index and relative drought tolerance were calculated, recognizing accessions PI365956, PI584456, PI370091, and PI390510 to have high inhibition index and relative drought tolerance, indicating that they may be drought tolerant. These drought tolerant accessions were noted to be better adapted to water deprived conditions than the others.

SPAD chlorophyll content

Dry conditions minimize photosynthesis by reducing leaf expansion, weaken photosynthetic system, early leaf ageing and associated reduction in chlorophyll content (Farooq et al., 2009). (Sakya et al., 2018; Sepehri & Reza Golparvar, 2011). Several previous studies reported decreased chlorophyll content for plants exposed to either severe drought stress in crops such as cowpea (Cui et al., 2020; Ravelombola et al., 2020). Leaf chlorophyll content is shown to increase during early stage of water stress and decrease gradually with increasing water stress (Abdelhaleim et al., 2022). The results of this study showed that leaf chlorophyll content was greatly reduced in drought-stressed tomato plants, indicating that water stress negatively affected chlorophyll synthesis as illustrated by (Sakya et al., 2018; Sepehri & Reza Golparvar, 2011). Interestingly, some tomato accessions were able to maintain slightly higher levels of chlorophyll content under drought stress as compared to others, indicating potential differences in drought tolerance among the accessions. (Alidu et al., 2019; Cardoso et al., 2022b) also reported moderately higher leaf chlorophyll content in drought tolerant cowpea recombinant inbred line and tomato genotypes, respectively, subjected to water stress. In the present study, the accessions with the highest relative drought tolerance based on chlorophyll content were PI365956, PI584456, PI370091, and PI390510 (Supplementary Table S1; Table 2), which all showed over 50% retention of chlorophyll content under drought stress. These results imply that chlorophyll content could be a suitable trait for detecting tomato accessions with higher drought tolerance and for breeding programs aimed at improving water stress tolerance in tomato plants.

Pearson’s Correlations Analysis

The strong positive correlations among leaf wilting, leaf rolling, and SPAD chlorophyll content parameters were found in this study (Supplementary Table S3). (O’Toole & Moya, 1978)discovered that leaf rolling, and leaf tip drying were highly correlated with maintenance of leaf water potential. (Baret et al., 2018) stressed that over a longer period of water stress, leaf rolling may be associated with a decrease in chlorophyll content because of the reduction of leaf area exposed to the sunlight. Another study on drought tolerance in cowpea showed strong correlation between leaf wilting and relative water content (Pungulani et al., 2013). On the other hand, weak correlations were observed between plant height-related parameters and the other traits (Supplementary Table S3; Table 3; Figure 5). Weak correlations between plant height and leaf chlorophyll content (chl. *a*) were found in a drought tolerance study in rice by (Ahmadikhah & Marufinia, 2016).

The outcomes of this research are significant for crop breeding programs focusing on improving drought tolerance. Selecting high correlated traits such as leaf wilting, leaf rolling, and SPAD chlorophyll content as illustrated in this study could help breeders develop crops with high adaptation to dry environments. Additionally, the weak correlations between plant height-related parameters and the other traits propose that the breeders may require to explore various set of traits to select for enhanced plant height under water limited conditions.

Conclusion

This study focused on finding drought-tolerant tomato accessions to improve crop yields in drought vulnerable areas. A fast-screening method was used to categorize 68 USDA tomato accessions into three groups: drought-tolerant, moderately drought-tolerant, and drought-sensitive. PI365956 was ranked as the best drought-tolerant accession, with PI584456, PI370091, and PI390510 also identified as highly tolerant. These accessions could be valuable parental lines for breeding programs to develop drought-tolerant tomato cultivars. Fast screening methods are significant for efficient identification of promising accessions. Developing drought-tolerant tomato cultivars can contribute to increased food production and food security in drought-prone regions.

References

Abdelhaleim, M. S., Rahimi, M., & Okasha, S. A. (2022). Assessment of drought tolerance indices in faba bean genotypes under different irrigation regimes. *Open Life Sciences*, *17*(1), 1462–1472. https://doi.org/10.1515/biol-2022-0520

Aghaie, P., Hosseini Tafreshi, S. A., Ebrahimi, M. A., & Haerinasab, M. (2018). Tolerance evaluation and clustering of fourteen tomato cultivars grown under mild and severe drought conditions. *Scientia Horticulturae*, *232*, 1–12. https://doi.org/10.1016/j.scienta.2017.12.041

Ahmadikhah, A., & Marufinia, • Amir. (n.d.). *Effect of reduced plant height on drought tolerance in rice*. https://doi.org/10.1007/s13205-016-0542-3

Albrecht, T., Wimmer, V., Auinger, H. J., Erbe, M., Knaak, C., Ouzunova, M., Simianer, H., & Schön, C. C. (2011). Genome-based prediction of testcross values in maize. *Theoretical and Applied Genetics*, *123*(2), 339–350. https://doi.org/10.1007/s00122-011-1587-7

Alidu, M. S., Asante, I. K., Tongoona, P., Ofori, K., Danquah, A., & Padi, F. K. (2019). Development and screening of cowpea recombinant inbred lines for seedling drought tolerance. *Journal of Plant Breeding and Crop Science*, *11*(1), 1–10. https://doi.org/10.5897/jpbcs2018.0768

Alves-Santos, F. M., Cordeiro-Rodrigues, L., Sayagués, J. M., Martín-Domínguez, R., García-Benavides, P., Crespo, M. C., Díaz-Mínguez, J. M., & Eslava, A. P. (2002). Pathogenicity and race characterization of Fusarium oxysporum f. sp. phaseoli isolates from Spain and Greece. *Plant Pathology*, *51*(5), 605–611. https://doi.org/10.1046/j.1365-3059.2002.00745.x

Arie, T. (2019). Fusarium diseases of cultivated plants, control, diagnosis, and molecular and genetic studies. *Journal of Pesticide Science*, *44*(4). https://doi.org/10.1584/JPESTICS.J19-03

Assefa, T., Assibi Mahama, A., Brown, A. V., Cannon, E. K. S., Rubyogo, J. C., Rao, I. M., Blair, M. W., & Cannon, S. B. (2019). A review of breeding objectives, genomic resources, and marker-assisted methods in common bean (Phaseolus vulgaris L.). In *Molecular Breeding* (Vol. 39, Issue 2). Springer Netherlands. https://doi.org/10.1007/s11032-018-0920-0

Bao, Y., Vuong, T., Meinhardt, C., Tiffin, P., Denny, R., Chen, S., Nguyen, H. T., Orf, J. H., & Young, N. D. (2014). Potential of Association Mapping and Genomic Selection to Explore PI 88788 Derived Soybean Cyst Nematode Resistance. *The Plant Genome*, *7*(3). https://doi.org/10.3835/plantgenome2013.11.0039

Baret, F., Madec, S., Irfan, K., Lopez, J., Comar, A., Hemmerlé, M., Dutartre, D., Praud, S., & Tixier, M. H. (2018). Leaf-rolling in maize crops: from leaf scoring to canopy-level measurements for phenotyping. *Journal of Experimental Botany*, *69*(10), 2705–2716. https://doi.org/10.1093/jxb/ery071

Barili, L. D., Vale, N. M. do, Silva, F. F. e, Carneiro, J. E. de S., Oliveira, H. R. de, Vianello, R. P., Valdisser, P. A. M. R., & Nascimento, M. (2018). Genome prediction accuracy of common bean via Bayesian models. *Ciência Rural*, *48*(8). https://doi.org/10.1590/0103-8478cr20170497

Barone, A., Chiusano, M. L., Ercolano, M. R., Giuliano, G., Grandillo, S., & Frusciante, L. (2008). Structural and Functional Genomics of Tomato. *International Journal of Plant Genomics*, *12*. https://doi.org/10.1155/2008/820274

Bartoli, C., & Roux, F. (2017). Genome-wide association studies in plant pathosystems: Toward an ecological genomics approach. In *Frontiers in Plant Science* (Vol. 8). Frontiers Media S.A. https://doi.org/10.3389/fpls.2017.00763

Batista, R. O., Silva, L. C., Moura, L. M., Souza, M. H., Carneiro, P. C. S., Filho, J. L. S. C., & de Souza Carneiro, J. E. (2017). Inheritance of resistance to fusarium wilt in common bean. *Euphytica*, *213*(7). https://doi.org/10.1007/s10681-017-1925-1

Blair, M. W. (2013). Mineral biofortification strategies for food staples: The example of common bean. In *Journal of Agricultural and Food Chemistry* (Vol. 61, Issue 35, pp. 8287–8294). https://doi.org/10.1021/jf400774y

Bradbury, P. J., Zhang, Z., Kroon, D. E., Casstevens, T. M., Ramdoss, Y., & Buckler, E. S. (2007). TASSEL: Software for association mapping of complex traits in diverse samples. *Bioinformatics*, *23*(19), 2633–2635. https://doi.org/10.1093/bioinformatics/btm308

Brick, M. A., Byrne, P. F., Schwartz, H. F., Ogg, J. B., Otto, K., Fall, A. L., & Gilbert, J. (2006). Reaction to three races of fusarium wilt in the Phaseolus vulgaris core collection. *Crop Science*, *46*(3), 1245–1252. https://doi.org/10.2135/cropsci2005.06-0102

Burton-Freeman, B., & Reimers, K. (2011). Tomato Consumption and Health: Emerging Benefits. In *American Journal of Lifestyle Medicine* (Vol. 5, Issue 2, pp. 182–191). https://doi.org/10.1177/1559827610387488

Cardoso, J., Silva, T. R., Abboud, A. C. de S., Finatto, T., Woyann, L. G., & Vargas, T. de O. (2022a). Selection of drought-tolerant tomato during the vegetative stage. *COLLOQUIUM AGRARIAE*, *18*(2), 42–53. https://doi.org/10.5747/ca.2022.v18.n2.a487

Cardoso, J., Silva, T. R., Abboud, A. C. de S., Finatto, T., Woyann, L. G., & Vargas, T. de O. (2022b). Selection of drought-tolerant tomato during the vegetative stage. *COLLOQUIUM AGRARIAE*, *18*(2). https://doi.org/10.5747/ca.2022.v18.n2.a487

Carolina, A., Galdino, S., De Freitas, M. B., De Borba, M. C., & Stadnik, M. J. (n.d.). *Phenolic and flavonoid content in roots and hypocotyls of resistant and susceptible bean plants (Phaseolus vulgaris L.) during early stage of colonization by Fusarium oxysporum f. sp. phaseoli*. https://doi.org/10.1007/s40858-021-00440-6/Published

Chandra, A., & Dubey, A. A. (2009). *Assessment of ploidy level on stress tolerance of Cenchrus species based on leaf photosynthetic characteristics*. https://doi.org/10.1007/s11738-009-0317-0

Chandra Rai, A., Singh, M., & Shah, K. (2012). Effect of water withdrawal on formation of free radical, proline accumulation and activities of antioxidant enzymes in ZAT12-transformed transgenic tomato plants. *Plant Physiology and Biochemistry*, *61*, 108–114. https://doi.org/10.1016/j.plaphy.2012.09.010

Conti, V., Mareri, L., Faleri, C., Nepi, M., Romi, M., Cai, G., & Cantini, C. (2019). Drought stress affects the response of italian local tomato (solanum lycopersicum L.) varieties in a genotype-dependent manner. *Plants*, *8*(9). https://doi.org/10.3390/plants8090336

Cross, H., Brick, M. A., Schwartz, H. F., Panella, L. W., & Byrne, P. F. (2000). Inheritance of resistance to fusarium wilt in two common bean races. *Crop Science*, *40*(4), 954–958. https://doi.org/10.2135/cropsci2000.404954x

Crossa, J., Pérez-Rodríguez, P., Cuevas, J., Montesinos-López, O., Jarquín, D., de los Campos, G., Burgueño, J., González-Camacho, J. M., Pérez-Elizalde, S., Beyene, Y., Dreisigacker, S., Singh, R., Zhang, X., Gowda, M., Roorkiwal, M., Rutkoski, J., & Varshney, R. K. (2017). Genomic Selection in Plant Breeding: Methods, Models, and Perspectives. In *Trends in Plant Science* (Vol. 22, Issue 11, pp. 961–975). Elsevier Ltd. https://doi.org/10.1016/j.tplants.2017.08.011

Cruz De Carvalho, M. H. (2008). Plant Signaling & Behavior Drought stress and reactive oxygen species production, scavenging and signaling. *Plant Signaling & Behavior*, *3*(3), 156–165. https://doi.org/10.4161/psb.3.3.5536

Cui, Q., Xiong, H., Yufeng, Y., Eaton, S., Imamura, S., Santamaria, J., Ravelombola, W., Mason, R. E., Wood, L., Mozzoni, L. A., & Shi, A. (2020a). Evaluation of drought tolerance in Arkansas Cowpea lines at seedling stage. *HortScience*, *55*(7), 1132–1143. https://doi.org/10.21273/HORTSCI15036-20

Cui, Q., Xiong, H., Yufeng, Y., Eaton, S., Imamura, S., Santamaria, J., Ravelombola, W., Mason, R. E., Wood, L., Mozzoni, L. A., & Shi, A. (2020b). Evaluation of drought tolerance in Arkansas Cowpea lines at seedling stage. *HortScience*, *55*(7), 1132–1143. https://doi.org/10.21273/HORTSCI15036-20

De Ron, A. M., González, A. M., Rodiño, A. P., Santalla, M., Godoy, L., & Papa, R. (2016). History of the common bean crop: Its evolution beyond its areas of origin and domestication. *Arbor*, *192*(779). https://doi.org/10.3989/arbor.2016.779n3007

Deng, Y., Ning, Y., Yang, D. L., Zhai, K., Wang, G. L., & He, Z. (2020). Molecular Basis of Disease Resistance and Perspectives on Breeding Strategies for Resistance Improvement in Crops. *Molecular Plant*, *13*(10), 1402–1419. https://doi.org/10.1016/J.MOLP.2020.09.018

Dhaliwal, M. S. (n.d.). *AVRDC tomato in sub-Saharan Africa Resistance Breeding View project Breeding for CMS lines of chilli and their utilization in hybrids development View project*. https://www.researchgate.net/publication/261062446

Diagnostic manual for plant diseases in Vietnam. (n.d.).

Diaz, L. M., Arredondo, V., Ariza-Suarez, D., Aparicio, J., Buendia, H. F., Cajiao, C., Mosquera, G., Beebe, S. E., Mukankusi, C. M., & Raatz, B. (2021). Genetic Analyses and Genomic Predictions of Root Rot Resistance in Common Bean Across Trials and Populations. *Frontiers in Plant Science*, *12*. https://doi.org/10.3389/fpls.2021.629221

Divina De Toledo-Souza, E., Marques Da Silveira, P., Corrêa Café-Filho, A., & Lobo, M. (n.d.). Fusarium wilt incidence and common bean yield according to the preceding crop and the soil tillage system. In *Pesq. agropec. bras* (Issue 8).

Dufayard, J. F., Bettembourg, M., Fischer, I., Droc, G., Guiderdoni, E., Périn, C., Chantret, N., & Diévart, A. (2017). New insights on Leucine-Rich repeats receptor-like kinase orthologous relationships in angiosperms. *Frontiers in Plant Science*, *8*. https://doi.org/10.3389/fpls.2017.00381

Elshire, R. J., Glaubitz, J. C., Sun, Q., Poland, J. A., Kawamoto, K., Buckler, E. S., & Mitchell, S. E. (2011). A robust, simple genotyping-by-sequencing (GBS) approach for high diversity species. *PLoS ONE*, *6*(5). https://doi.org/10.1371/journal.pone.0019379

Engelbrecht, B. M. J., Tyree, M. T., & Kursar, T. A. (2007). Printed in the United Kingdom SHORT COMMUNICATION Visual assessment of wilting as a measure of leaf water potential and seedling drought survival. *Journal of Tropical Ecology*, *23*, 497–500. https://doi.org/10.1017/S026646740700421X

Fall, A. L., Byrne, P. F., Jung, G., Coyne, D. P., Brick, M. A., & Schwartz, H. F. (2001a). Detection and mapping of a major locus for fusarium wilt resistance in common bean. *Crop Science*, *41*(5), 1494–1498. https://doi.org/10.2135/cropsci2001.4151494x

Fall, A. L., Byrne, P. F., Jung, G., Coyne, D. P., Brick, M. A., & Schwartz, H. F. (2001b). Detection and mapping of a major locus for fusarium wilt resistance in common bean. *Crop Science*, *41*(5), 1494–1498. https://doi.org/10.2135/cropsci2001.4151494x

Farooq, M., Wahid, A., Kobayashi, N., Fujita, D., & Basra, S. M. A. (2009). Plant drought stress: Effects, mechanisms and management. In *Agronomy for Sustainable Development* (Vol. 29, Issue 1, pp. 185–212). https://doi.org/10.1051/agro:2008021

Francini, A., & Sebastiani, L. (2019). *horticulturae Abiotic Stress Effects on Performance of Horticultural Crops*. https://doi.org/10.3390/horticulturae5040067

FUSARIUM WILT (YELLOWS). (n.d.).

Gerik, J. S., & Hanson, B. D. (2011). Drip application of methyl bromide alternative chemicals for control of soilborne pathogens and weeds. *Pest Management Science*, *67*(9), 1129–1133. https://doi.org/10.1002/ps.2162

Ghebremariam, K. M., Liang, Y., Li, C., Li, Y., & Qin, L. (2013). Screening of Tomato Inbred-Lines for Drought Tolerance at Germination and Seedling Stage. *Journal of Agricultural Science*, *5*(11). https://doi.org/10.5539/jas.v5n11p93

Glaubitz, J. C., Casstevens, T. M., Lu, F., Harriman, J., 1¤, R. J. E., Sun, Q., & Buckler, E. S. (2014). *TASSEL-GBS: A High Capacity Genotyping by Sequencing Analysis Pipeline*. https://doi.org/10.1371/journal.pone.0090346

González-Guerrero, M., Grusak, M. A., De Ron, A. M., Mendoza-Cozatl, D. G., Valdés-López, O., Castro-Guerrero, N. A., & Isidra-Arellano, M. C. (2016). *Common Bean: A Legume Model on the Rise for Unraveling Responses and Adaptations to Iron, Zinc, and Phosphate Deficiencies*. https://doi.org/10.3389/fpls.2016.00600

Gordon, T. R. (2017). Fusarium oxysporum and the Fusarium Wilt Syndrome. *Https://Doi.Org/10.1146/Annurev-Phyto-080615-095919*, *55*, 23–39. https://doi.org/10.1146/ANNUREV-PHYTO-080615-095919

Handy, S. M., Demir, E., Hutchins, D. A., Portune, K. J., Whereat, E. B., Hare, C. E., Rose, J. M., Warner, M., Farestad, M., Cary, S. C., & Coyne, K. J. (2008). Using quantitative real-time PCR to study competition and community dynamics among Delaware Inland Bays harmful algae in field and laboratory studies. *Harmful Algae*, *7*(5), 599–613. https://doi.org/10.1016/j.hal.2007.12.018

Hassan khan, S., Hassan Khan, S., Khan, A., Litaf, U., Sattar Shah, A., Ali Khan, M., Bilal, M., & Usman Ali, M. (2015). Effect of Drought Stress on Tomato cv. *Bombino. J Food Process Technol*, *6*, 465. https://doi.org/10.4172/2157-7110.1000465

Holland, J. B., Carolina, N., Nyquist, W. E., & Lafayette, W. (2003). Estimating and Interpreting Heritability for Plant Breeding : An Update. In *Plant Breeding* (Vol. 22).

Huang, H., Ullah, F., Zhou, D. X., Yi, M., & Zhao, Y. (2019). Mechanisms of ROS regulation of plant development and stress responses. In *Frontiers in Plant Science* (Vol. 10). Frontiers Media S.A. https://doi.org/10.3389/fpls.2019.00800

Huang, M., Liu, X., Zhou, Y., Summers, R. M., & Zhang, Z. (2019a). BLINK: A package for the next level of genome-wide association studies with both individuals and markers in the millions. *GigaScience*, *8*(2). https://doi.org/10.1093/gigascience/giy154

Huang, M., Liu, X., Zhou, Y., Summers, R. M., & Zhang, Z. (2019b). BLINK: A package for the next level of genome-wide association studies with both individuals and markers in the millions. *GigaScience*, *8*(2). https://doi.org/10.1093/gigascience/giy154

Iqbal, M. J., Mamidi, S., Ahsan, R., Kianian, S. F., Coyne, C. J., Hamama, A. A., Narina, S. S., & Bhardwaj, H. L. (2012). Population structure and linkage disequilibrium in Lupinus albus L. germplasm and its implication for association mapping. *Theoretical and Applied Genetics*, *125*(3), 517–530. https://doi.org/10.1007/s00122-012-1850-6

Jha, U. C., Bohra, A., Pandey, S., & Parida, S. K. (2020). Breeding, Genetics, and Genomics Approaches for Improving Fusarium Wilt Resistance in Major Grain Legumes. In *Frontiers in Genetics* (Vol. 11). Frontiers Media S.A. https://doi.org/10.3389/fgene.2020.01001

Kadioglu, A., Terzi, R., Saruhan, N., & Saglam, A. (2012). Current advances in the investigation of leaf rolling caused by biotic and abiotic stress factors. *Plant Science*, *182*(1), 42–48. https://doi.org/10.1016/J.PLANTSCI.2011.01.013

Kahlau, S., & Bock, R. (n.d.). *Plastid Transcriptomics and Translatomics of Tomato Fruit Development and Chloroplast-to-Chromoplast Differentiation: Chromoplast Gene Expression Largely Serves the Production of a Single Protein W OA*. https://doi.org/10.1105/tpc.107.055202

Kaler, A. S., Gillman, J. D., Beissinger, T., Purcell, L. C., Maccaferri, M., Uptmoor, R., & Cannon, S. B. (2020). *Comparing Different Statistical Models and Multiple Testing Corrections for Association Mapping in Soybean and Maize*. *10*, 1. https://doi.org/10.3389/fpls.2019.01794

Kamanga, R. M. (2020). Screening and differential physiological responses of tomato (Solanum lycopersicum L.) to drought stress. In *Plant Physiology Reports* (Vol. 25, Issue 3, pp. 472–482). Springer. https://doi.org/10.1007/s40502-020-00532-6

Karavidas, I., Ntatsi, G., Vougeleka, V., Karkanis, A., Ntanasi, T., Saitanis, C., Agathokleous, E., Ropokis, A., Sabatino, L., Tran, F., Iannetta, P. P. M., & Savvas, D. (2022). Agronomic Practices to Increase the Yield and Quality of Common Bean (Phaseolus vulgaris L.): A Systematic Review. In *Agronomy* (Vol. 12, Issue 2). MDPI. https://doi.org/10.3390/agronomy12020271

Kumar, D., Kumar, R., Kumar, S., Bhardwaj, M. L., Thakur, M. C., Kumar, R., Thakur, K. S., Dogra, B. S., Vikram, A., Thakur, A., & Kumar, P. (2013). Genetic Variability, Correlation and Path Coefficient Analysis in Tomato. *International Journal of Vegetable Science*, *19*(4), 313–323. https://doi.org/10.1080/19315260.2012.726701

Kumar, P. A., Reddy, N. N., & Lakshmi, N. J. (2017). PEG Induced Screening for Drought Tolerance in Tomato Genotypes. *International Journal of Current Microbiology and Applied Sciences*, *6*(7), 168–181. https://doi.org/10.20546/ijcmas.2017.607.020

Kuzay, S., Hamilton-Conaty, P., Palkovic, A., & Gepts, P. (2020). Is the USDA core collection of common bean representative of genetic diversity of the species, as assessed by SNP diversity? *Crop Science*, *60*(3), 1398–1414. https://doi.org/10.1002/csc2.20032

Legarra, A., Robert-Granié, C., Croiseau, P., Guillaume, F., & Fritz, S. (2011). Improved Lasso for genomic selection. *Genetics Research*, *93*(1), 77–87. https://doi.org/10.1017/S0016672310000534

Leitao, S. T., Malosetti, M., Song, Q., Van Eeuwijk, F., Rubiales, D., & Vaz Patto, M. C. (2020). Natural variation in Portuguese common bean germplasm reveals new sources of resistance against fusarium oxysporum f. sp. phaseoli and resistance-associated candidate genes. *Phytopathology*, *110*(3), 633–647. https://doi.org/10.1094/PHYTO-06-19-0207-R

Li, J., Xiaoya, 1☯, 1☯, T., Li, L., Mao, L., Luo, Z., Ullah Khan, Z., & Ying, T. (2016). *Comprehensive RNA-Seq Analysis on the Regulation of Tomato Ripening by Exogenous Auxin*. https://doi.org/10.1371/journal.pone.0156453

Liang, G., Liu, J., Zhang, J., & Guo, J. (2020). Effects of drought stress on photosynthetic and physiological parameters of tomato. *Journal of the American Society for Horticultural Science*, *145*(1), 12–17. https://doi.org/10.21273/JASHS04725-19

Lipka, A. E., Tian, F., Wang, Q., Peiffer, J., Li, M., Bradbury, P. J., Gore, M. A., Buckler, E. S., & Zhang, Z. (2012). GAPIT: Genome association and prediction integrated tool. *Bioinformatics*, *28*(18), 2397–2399. https://doi.org/10.1093/bioinformatics/bts444

Liu, X., Huang, M., Fan, B., Buckler, E. S., & Zhang, Z. (2016). Iterative Usage of Fixed and Random Effect Models for Powerful and Efficient Genome-Wide Association Studies. *PLoS Genetics*, *12*(2). https://doi.org/10.1371/journal.pgen.1005767

Lombardi, M., Materne, M., Cogan, N. O. I., Rodda, M., Daetwyler, H. D., Slater, A. T., Forster, J. W., & Kaur, S. (2014). Assessment of genetic variation within a global collection of lentil (Lens culinaris Medik.) cultivars and landraces using SNP markers. *BMC Genetics*, *15*(1). https://doi.org/10.1186/s12863-014-0150-3

Massimi, M. (2021). Tomato (Lycopersicon esculentum Mill.) anatomical, physiological, biochemical and production responses to drought stress - A mini-review essay. *International Journal of Horticultural Science*, *27*. https://doi.org/10.31421/ijhs/27/2021/8439

McClean, P. E., Terpstra, J., McConnell, M., White, C., Lee, R., & Mamidi, S. (2012). Population structure and genetic differentiation among the USDA common bean (Phaseolus vulgaris L.) core collection. *Genetic Resources and Crop Evolution*, *59*(4), 499–515. https://doi.org/10.1007/s10722-011-9699-0

Meuwissen, T. H. E., Hayes, B. J., & Goddard, M. E. (2001). *Prediction of Total Genetic Value Using Genome-Wide Dense Marker Maps*. https://academic.oup.com/genetics/article/157/4/1819/6048353

Meyers, B. C., Kozik, A., Griego, A., Kuang, H., & Michelmore, R. W. (2003). Genome-wide analysis of NBS-LRR-encoding genes in Arabidopsis. *Plant Cell*, *15*(4), 809–834. https://doi.org/10.1105/tpc.009308

Mihajlovic, M., Rekanovic, E., Hrustic, J., Grahovac, M., & Tanovic, B. (2021). In vitro and in vivo toxicity of fungicides and biofungicides for the control of verticillium and fusarium wilt of pepper. *Pesticidi i Fitomedicina*, *36*(1), 23–34. https://doi.org/10.2298/pif2101023m

Mokhtar, M. M. E.-M. N. S. (2014). *Bio-compost Application for Controlling Soil-borne Plant Pathogens –A Review*. *4*(1).

Monteiro, A. L. R., Pantaleão, A. S. L., Badel, J. L., Soares, P. H. M., Carneiro, V. Q., Carneiro, P. C. S., & Carneiro, J. E. S. (2021). Genome-wide association study (GWAS) of Phaseolus vulgaris resistance to Xanthomonas citri pv. fuscans. *Plant Pathology*, *70*(7), 1733–1744. https://doi.org/10.1111/ppa.13399

Mou, B., Ravelombola, W., Shi, A., Qin, J., Weng, Y., Bhattarai, G., Zia, B., & Zhou, W. (2018). Investigation on various aboveground traits to identify drought tolerance in cowpea seedlings. *HortScience*, *53*(12), 1757–1765. https://doi.org/10.21273/HORTSCI13278-18

Nasar, S., Shaheen, H., Murtaza, G., Tinghong, T., Arfan, M., & Idrees, M. (2023). Socioeconomic Evaluation of Common Bean (Phaseolus vulgaris L.) Cultivation in Providing Sustainable Livelihood to the Mountain Populations of Kashmir Himalayas. *Plants*, *12*(1). https://doi.org/10.3390/plants12010213

Nay, M. M., Souza, T. L. P. O., Raatz, B., Mukankusi, C. M., Pastor-Corrales, M. A., Abreu, A. F. B., & Melo, L. C. (2019). A review of angular leaf spot resistance in common bean. In *Crop Science* (Vol. 59, Issue 4, pp. 1376–1391). Crop Science Society of America. https://doi.org/10.2135/cropsci2018.09.0596

Okungbowa, F. I., & Shittu, H. (2012). *Fusarium Wilts: An Overview In vitro screening of some selected nanoparticles against phytopathogens View project 1. Multiple drug resistant bacteria and integron gene as a contributory factor to multiple drug resistance and production of bio-pharmaceutics and industrial proteins in plants and other expression systems. View project*. https://www.researchgate.net/publication/292243135

Oliveira Batista, R., Cruz E Oliveira, A. M., Lennon, J., Silva, O., Nicoli, A., Crescêncio, P., Carneiro, S., Eustáquio De Sousa Carneiro, J., Júnior, P., & Vieira De Queiroz, M. (2016). Resistance to Fusarium wilt in common bean ARTICLE. *Crop Breeding and Applied Biotechnology*, *16*, 226–233. https://doi.org/10.1590/1984

O'Toole, J. C., & Moya, T. B. (1978). Genotypic Variation in Maintenance of Leaf Water Potential in Rice1. *Crop Science*, *18*(5), 873–876. https://doi.org/10.2135/CROPSCI1978.0011183X001800050050X

Pang, Y., Wu, Y., Liu, C., Li, W., St. Amand, P., Bernardo, A., Wang, D., Dong, L., Yuan, X., Zhang, H., Zhao, M., Li, L., Wang, L., He, F., Liang, Y., Yan, Q., Lu, Y., Su, Y., Jiang, H., … Liu, S. (2021). High-resolution genome-wide association study and genomic prediction for disease resistance and cold tolerance in wheat. *Theoretical and Applied Genetics*, *134*(9), 2857–2873. https://doi.org/10.1007/s00122-021-03863-6

Panth, M., Hassler, S. C., & Baysal-Gurel, F. (2020). Methods for management of soilborne diseases in crop production. In *Agriculture (Switzerland)* (Vol. 10, Issue 1). MDPI AG. https://doi.org/10.3390/agriculture10010016

Pathan, S. M., Lee, J. D., Sleper, D. A., Fritschi, F. B., Sharp, R. E., Carter, T. E., Nelson, R. L., King, C. A., Schapaugh, W. T., Ellersieck, M. R., Nguyen, H. T., & Shannon, J. G. (2014). Two soybean plant introductions display slow leaf wilting and reduced yield loss under drought. *Journal of Agronomy and Crop Science*, *200*(3), 231–236. https://doi.org/10.1111/jac.12053

Pathania, A., Sharma, S. K., & Sharma, P. N. (2014a). Common bean. In *Broadening the Genetic Base of Grain Legumes* (pp. 11–50). Springer India. https://doi.org/10.1007/978-81-322-2023-7_2

Pathania, A., Sharma, S. K., & Sharma, P. N. (2014b). Common bean. In *Broadening the Genetic Base of Grain Legumes* (pp. 11–50). Springer India. https://doi.org/10.1007/978-81-322-2023-7_2

Paulino, J. F. de C., de Almeida, C. P., Bueno, C. J., Song, Q., Fritsche-Neto, R., Carbonell, S. A. M., Chiorato, A. F., & Benchimol-Reis, L. L. (2021). Genome-wide association study reveals genomic regions associated with fusarium wilt resistance in common bean. *Genes*, *12*(5). https://doi.org/10.3390/genes12050765

Pedrosa-Harand, A., Kami, J., Gepts, P., Geffroy, V., & Schweizer, D. (2009). Cytogenetic mapping of common bean chromosomes reveals a less compartmentalized small-genome plant species. *Chromosome Research*, *17*(3), 405–417. https://doi.org/10.1007/s10577-009-9031-4

Pereira, A. (2016). *F1000Research*. https://doi.org/10.12688/f1000research.7678.1

Perseguini, J. M. K. C., Oblessuc, P. R., Rosa, J. R. B. F., Gomes, K. A., Chiorato, A. F., Carbonell, S. A. M., Garcia, A. A. F., Vianello, R. P., & Benchimol-Reis, L. L. (2016). Genome-Wide Association Studies of Anthracnose and Angular Leaf Spot Resistance in Common Bean (Phaseolus vulgaris L.). *PLoS ONE*, *11*(3). https://doi.org/10.1371/journal.pone.0150506

Pervez, M. A., Ayub, C. M., Khan, H. A., Shahid, M. A., & Ashraf, I. (2009). EFFECT OF DROUGHT STRESS ON GROWTH, YIELD AND SEED QUALITY OF TOMATO (Lycopersicon esculentum L.). *Pak. J. Agri. Sci*, *46*(3).

Pungulani, L. L. M., Millner, J. P., Williams, W. M., & Banda, M. (2013). Improvement of leaf wilting scoring system in cowpea (Vigna unguiculata (L) Walp.): From qualitative scale to quantitative index. *Australian Journal of Crop Science*, *7*(9).

Quinet, M., Angosto, T., Yuste-Lisbona, F. J., Blanchard-Gros, R., Bigot, S., Martinez, J. P., & Lutts, S. (2019). Tomato Fruit Development and Metabolism. In *Frontiers in Plant Science* (Vol. 10). Frontiers Media S.A. https://doi.org/10.3389/fpls.2019.01554

Rahman, M. Z., Ahmad, K., Kutawa, A. B., Siddiqui, Y., Saad, N., Geok Hun, T., Hata, E. M., & Hossain, M. I. (2021). Biology, diversity, detection and management of fusarium oxysporum f. Sp. niveum causing vascular wilt disease of watermelon (citrullus lanatus): A review. In *Agronomy* (Vol. 11, Issue 7). MDPI AG. https://doi.org/10.3390/agronomy11071310

Rahman, S. M. L., Nawata, E., & Sakuratani, T. (1998). Evaluation of Drought Tolerance of Tomato Cultivars. In *Jpn. J. Trop. Agr* (Vol. 42, Issue 1).

Ranjan, A., Ichihashi, Y., & Sinha, N. R. (2012). The tomato genome: Implications for plant breeding, genomics and evolution. *Genome Biology*, *13*(8). https://doi.org/10.1186/gb-2012-13-8-167

Ravelombola, W., Dong, L., Barickman, T. C., Xiong, H., Olaoye, D., Bhattarai, G., Zia, B., Alshaya, H., Alatawi, I., & Shi, A. (2021). Evaluation of salt tolerance in cowpea at seedling stage. *Euphytica*, *217*(6). https://doi.org/10.1007/s10681-021-02832-w

Ravelombola, W. S., Qin, J., Shi, A., Nice, L., Bao, Y., Lorenz, A., Orf, J. H., Young, N. D., & Chen, S. (2019). Genome-wide association study and genomic selection for soybean chlorophyll content associated with soybean cyst nematode tolerance. *BMC Genomics*, *20*(1). https://doi.org/10.1186/s12864-019-6275-z

Ravelombola, W., Shi, A., Chen, S., Xiong, H., Yang, Y., Cui, Q., Olaoye, D., & Mou, B. (2020a). Evaluation of cowpea for drought tolerance at seedling stage. *Euphytica*, *216*(8). https://doi.org/10.1007/s10681-020-02660-4

Ravelombola, W., Shi, A., Chen, S., Xiong, H., Yang, Y., Cui, Q., Olaoye, D., & Mou, B. (2020b). Evaluation of cowpea for drought tolerance at seedling stage. *Euphytica*, *216*(8). https://doi.org/10.1007/s10681-020-02660-4

Ravelombola, W., Shi, A., & Huynh, B. L. (2021). Loci discovery, network-guided approach, and genomic prediction for drought tolerance index in a multi-parent advanced generation intercross (MAGIC) cowpea population. *Horticulture Research*, *8*(1). https://doi.org/10.1038/s41438-021-00462-w

Reinprecht, Y., Schram, L., Dé Ric Marsolais, F., Smith, T. H., Hill, B., Pauls, K. P., Mastrorilli, M., Abdelhamid, M. T., & Saia, S. (2020). *Effects of Nitrogen Application on Nitrogen Fixation in Common Bean Production*. *11*. https://doi.org/10.3389/fpls.2020.01172

Rendón-Anaya, M., Montero-Vargas, J. M., Saburido-Álvarez, S., Vlasova, A., Capella-Gutierrez, S., Ordaz-Ortiz, J. J., Aguilar, O. M., Vianello-Brondani, R. P., Santalla, M., Delaye, L., Gabaldón, T., Gepts, P., Winkler, R., Guigó, R., Delgado-Salinas, A., & Herrera-Estrella, A. (2017). Genomic history of the origin and domestication of common bean unveils its closest sister species. *Genome Biology*, *18*(1). https://doi.org/10.1186/s13059-017-1190-6

Ripoll, J., Urban, L., Staudt, M., Lopez-Lauri, F., Bidel, L. P. R., & Bertin, N. (2014). Water shortage and quality of fleshy fruits-making the most of the unavoidable. In *Journal of*

Experimental Botany (Vol. 65, Issue 15, pp. 4097–4117). Oxford University Press. https://doi.org/10.1093/jxb/eru197

Rochette, N. C., Rivera-Colón, A. G., & Catchen, J. M. (2019). Stacks 2: Analytical methods for paired-end sequencing improve RADseq-based population genomics. *Molecular Ecology*, *28*(21). https://doi.org/10.1111/mec.15253

Romeroetal.2013-2. (n.d.).

Roux, F., & Frachon, L. (2022). A Genome-Wide Association study in Arabidopsis thaliana to decipher the adaptive genetics of quantitative disease resistance in a native heterogeneous environment. *PLoS ONE*, *17*(10 October). https://doi.org/10.1371/journal.pone.0274561

Sahu, V., & Chandel, G. (2016). *Assessment of genetic diversity in Cherry tomato (Solanum lycopersicum L. var. Ceraslforme) genotypes using SSR markers*. https://www.researchgate.net/publication/316506944

Sakya, A. T., Sulistyaningsih, E., Indradewa, D., & Purwanto, B. H. (2018). Physiological characters and tomato yield under drought stress. *IOP Conference Series: Earth and Environmental Science*, *200*(1). https://doi.org/10.1088/1755-1315/200/1/012043

Salgado, M. O., Schwartz, H. F., & Brick, M. A. (1995). Inheritance of resistance to a Colorado race of Fusarium oxysporum f. sp. phaseoli in common beans. *Plant Disease*, *79*(3). https://doi.org/10.1094/PD-79-0279

Salgotra, R. K., & Chauhan, B. S. (2023). Genetic Diversity, Conservation, and Utilization of Plant Genetic Resources. In *Genes* (Vol. 14, Issue 1). MDPI. https://doi.org/10.3390/genes14010174

Saqlan Naqvi, S. M., Athar, H., & Waheed, A. (2014). Screening and selection of tomato genotypes/cultivars for drought tolerance using multivariate analysis Role of Salicylic Acid in regulating salinity induced stress in Raphanus sativus View project Development of Salt Tolerance in Lentil and chickpea View project SEE PROFILE. In *Article in Pakistan Journal of Botany*. https://www.researchgate.net/publication/281673958

Schwartz, H., Panella, L., Brick, M., & Byrne, P. (n.d.). *Fusarium Wilt & Yellows of Sugar Beet & Dry Bean*. https://doi.org/10.1111/j/1365-3059.2010.02394.x

Sepehri, A., & Reza Golparvar, A. (2011). The Effect of Drought Stress on Water Relations, Chlorophyll Content and Leaf Area in Canola Cultivars (Brassica napus L.). *Electronic Journal of Biology*, *7*(3), 49–53.

Shahinnia, F., Geyer, M., Schürmann, F., Rudolphi, S., Holzapfel, J., Kempf, H., Stadlmeier, M., Löschenberger, F., Morales, L., Buerstmayr, H., Isidro Sánchez, J., Akdemir, D., Mohler, V., Lillemo, M., Hartl, L., Shahinnia FahimehShahinnia, F., & Hartl LorenzHartl, L. (2022). *Genome-wide association study and genomic prediction of resistance to stripe rust in current Central and Northern European winter wheat germplasm*. *135*, 3583–3595. https://doi.org/10.1007/s00122-022-04202-z

Shi, A., Bhattarai, G., Xiong, H., Avila, C. A., Feng, C., Liu, B., Joshi, V., Stein, L., Mou, B., Du Toit, L. J., & Correll, J. C. (2022). Genome-wide association study and genomic prediction of white rust resistance in USDA GRIN spinach germplasm. *Horticulture Research*, *9*. https://doi.org/10.1093/hr/uhac069

Silva, É. D. B. da, Xavier, A., & Faria, M. V. (2021). Impact of Genomic Prediction Model, Selection Intensity, and Breeding Strategy on the Long-Term Genetic Gain and Genetic Erosion in Soybean Breeding. *Frontiers in Genetics*, *12*. https://doi.org/10.3389/fgene.2021.637133

Singh, R. (2021). Deciphering the Impact of Water-stress on Plant Growth and Yield Attributes in Tomato Genotypes. *International Journal of Agriculture Environment and Biotechnology*, *14*(3). https://doi.org/10.30954/0974-1712.03.2021.23

Solankey, S. S., Singh, R. K., Baranwal, D. K., & Singh, D. K. (2014). Genetic expression of tomato for heat and drought stress tolerance: An overview. *International Journal of Vegetable Science*, *21*(5), 496–515. https://doi.org/10.1080/19315260.2014.902414

Soleimani, Z., Ramshini, H., Mohammad, S., Mortazavian, M., Fazelnajafabadi, M., & Foughi, B. (2014). Screening for drought tolerance in Iranian wheat genotypes (Triticum aestivum L.) using physiological traits evaluated under drought stress and normal condition. In *200 AJCS* (Vol. 8, Issue 2).

Song, Q., Hyten, D. L., Jia, G., Quigley, C. V., Fickus, E. W., Nelson, R. L., & Cregan, P. B. (2013). Development and Evaluation of SoySNP50K, a High-Density Genotyping Array for Soybean. *PLoS ONE*, *8*(1). https://doi.org/10.1371/journal.pone.0054985

Sousaraei, N., Mashayekhi, K., Mousavizadeh, S. J., Akbarpour, V., Medina, J., & Aliniaeifard, S. (2021). Screening of tomato landraces for drought tolerance based on growth and chlorophyll fluorescence analyses. *Horticulture Environment and Biotechnology*, *62*(4), 521–535. https://doi.org/10.1007/s13580-020-00328-5

Su, Y., Wu, F., Ao, Z., Jin, S., Qin, F., Liu, B., Pang, S., Liu, L., & Guo, Q. (n.d.). *Evaluating maize phenotype dynamics under drought stress using terrestrial lidar*. https://doi.org/10.1186/s13007-019-0396-x

Susanto, U., Rohaeni, W. R., & Sasmita, P. (2019). Selecting Traits for Drought Tolerance Screening in Rice. *IOP Conference Series: Earth and Environmental Science*, *383*(1). https://doi.org/10.1088/1755-1315/383/1/012049

Taheri, S., Gantait, S., Azizi, P., & Mazumdar, P. (2022). Drought tolerance improvement in Solanum lycopersicum: an insight into “OMICS” approaches and genome editing. In *3 Biotech* (Vol. 12, Issue 3). Springer Science and Business Media Deutschland GmbH. https://doi.org/10.1007/s13205-022-03132-3

Tameling, W. I. L., Vossen, J. H., Albrecht, M., Lengauer, T., Berden, J. A., Haring, M. A., Cornelissen, B. J. C., & Takken, F. L. W. (2006). Mutations in the NB-ARC domain of I-2 that impair ATP hydrolysis cause autoactivation. *Plant Physiology*, *140*(4), 1233–1245. https://doi.org/10.1104/pp.105.073510

Testa, R., di Trapani, A. M., Sgroi, F., & Tudisca, S. (2014). Economic sustainability of Italian greenhouse cherry tomato. *Sustainability (Switzerland)*, *6*(11), 7967–7981. https://doi.org/10.3390/su6117967

Uffelmann, E., Huang, Q. Q., Munung, N. S., de Vries, J., Okada, Y., Martin, A. R., Martin, H. C., Lappalainen, T., & Posthuma, D. (2021). Genome-wide association studies. In *Nature Reviews Methods Primers* (Vol. 1, Issue 1). Springer Nature. https://doi.org/10.1038/s43586-021-00056-9

van Esse, H. P., Reuber, T. L., & van der Does, D. (2020). Genetic modification to improve disease resistance in crops. In *New Phytologist* (Vol. 225, Issue 1, pp. 70–86). Blackwell Publishing Ltd. https://doi.org/10.1111/nph.15967

Wahb-Allah, M. A., Alsadon, A., Alsadon, A. A., & Ibrahim, A. A. (2011a). Drought Tolerance of Several Tomato Genotypes Under Greenhouse Conditions CoCooN project View project Natural control of endogenous ethylene biosynthesis in fresh climacteric produce View project Drought Tolerance of Several Tomato Genotypes Under Greenhouse Conditions. *World Applied Sciences Journal*, *15*(7), 933–940. https://www.researchgate.net/publication/265974299

Wahb-Allah, M. A., Alsadon, A., Alsadon, A. A., & Ibrahim, A. A. (2011b). Drought Tolerance of Several Tomato Genotypes Under Greenhouse Conditions CoCooN project View project Natural control of endogenous ethylene biosynthesis in fresh climacteric produce View project Drought Tolerance of Several Tomato Genotypes Under Greenhouse Conditions. *World Applied Sciences Journal*, *15*(7), 933–940. https://www.researchgate.net/publication/265974299

Wang, J., Zhou, Z., Zhang, Z., Li, H., Liu, D., Zhang, Q., Bradbury, P. J., Buckler, E. S., & Zhang, Z. (2018). Expanding the BLUP alphabet for genomic prediction adaptable to the genetic architectures of complex traits. *Heredity*, *121*(6), 648–662. https://doi.org/10.1038/s41437-018-0075-0

Wang, M. C., Gong, M., Zang, H. B., Hua, X. M., Yao, J., Pang, Y. J., & Yang, Y. H. (2006). Effect of methamidophos and urea application on microbial communities in soils as determined by microbial biomass and community level physiological profiles. *Journal of Environmental Science and Health - Part B Pesticides, Food Contaminants, and Agricultural Wastes*, *41*(4), 399–413. https://doi.org/10.1080/03601230600616155

Wen, L., Chang, H. X., Brown, P. J., Domier, L. L., & Hartman, G. L. (2019). Genome-wide association and genomic prediction identifies soybean cyst nematode resistance in common bean including a syntenic region to soybean Rhg1 locus. *Horticulture Research*, *6*(1). https://doi.org/10.1038/s41438-018-0085-3

Wilkinson, S., Kudoyarova, G. R., Veselov, D. S., Arkhipova, T. N., & Davies, W. J. (2012). Plant hormone interactions: innovative targets for crop breeding and management. *Journal of Experimental Botany*, *63*(9), 3499–3509. https://doi.org/10.1093/jxb/ers148

Wu, J., Zhu, J., Wang, L., & Wang, S. (2017). Genome-wide association study identifies NBS-LRR-encoding genes related with anthracnose and common bacterial blight in the common bean. *Frontiers in Plant Science*, *8*. https://doi.org/10.3389/fpls.2017.01398

Xavier, A., Muir, W. M., & Rainey, K. M. (2016). *Assessing Predictive Properties of Genome-Wide Selection in Soybeans*. https://doi.org/10.1534/g3.116.032268

Yang, X., Lu, M., Wang, Y., Wang, Y., Liu, Z., & Chen, S. (2021). Response mechanism of plants to drought stress. In *Horticulturae* (Vol. 7, Issue 3). MDPI AG. https://doi.org/10.3390/horticulturae7030050

Yao, X., Yang, R., Zhao, F., Wang, S., Li, C., & Zhao, W. (2016). An analysis of physiological index of differences in drought tolerance of tomato rootstock seedlings. *Journal of Plant Biology*, *59*(4), 311–321. https://doi.org/10.1007/s12374-016-0071-y

Yi, H., Breheny, P., Imam, N., Liu, Y., Hoeschele, I., & Yi, H. (2015). Penalized multimarker vs. single-marker regression methods for genome-wide association studies of quantitative traits. *Genetics*, *199*(1), 205–222. https://doi.org/10.1534/genetics.114.167817

Zeng, J., Pszczola, M., Wolc, A., Strabel, T., Fernando, R. L., Garrick, D. J., & Dekkers, J. C. (2012). Genomic breeding value prediction and QTL mapping of QTLMAS2011 data using Bayesian and GBLUP methods. *BMC Proceedings*, *6*(SUPPL. 2). https://doi.org/10.1186/1753-6561-6-S2-S7

Zhang, H., Zhao, Y., & Zhu, J. K. (2020). Thriving under Stress: How Plants Balance Growth and the Stress Response. In *Developmental Cell* (Vol. 55, Issue 5, pp. 529–543). Cell Press. https://doi.org/10.1016/j.devcel.2020.10.012

Zhou, D., Jing, T., Chen, Y., Wang, F., Qi, D., Feng, R., Xie, J., & Li, H. (2019). Deciphering microbial diversity associated with Fusarium wilt-diseased and disease-free banana rhizosphere soil. *BMC Microbiology*, *19*(1). https://doi.org/10.1186/s12866-019-1531-6

Zhou, J., Zhou, J., Ye, H., Ali, M. L., Nguyen, H. T., & Chen, P. (2020). Classification of soybean leaf wilting due to drought stress using UAV-based imagery. *Computers and Electronics in Agriculture*, *175*. https://doi.org/10.1016/J.COMPAG.2020.105576

Zhou, R., Yu, X., Ottosen, C. O., Rosenqvist, E., Zhao, L., Wang, Y., Yu, W., Zhao, T., & Wu, Z. (2017). Drought stress had a predominant effect over heat stress on three tomato cultivars subjected to combined stress. *BMC Plant Biology*, *17*(1). https://doi.org/10.1186/s12870-017-0974-x

Zhou, R., Yu, X., Ottosen, C.-O., Rosenqvist, E., Zhao, L., Wang, Y., Yu, W., Zhao, T., & Wu, Z. (n.d.). *BMC Plant Biology*. https://doi.org/10.1186/s12870-017-0974-x

Zia, B., Shi, A., Olaoye, D., Xiong, H., Ravelombola, W., Gepts, P., Schwartz, H. F., Brick, M. A., Otto, K., Ogg, B., & Chen, S. (2022). Genome-Wide Association Study and Genomic Prediction for Bacterial Wilt Resistance in Common Bean (Phaseolus vulgaris) Core Collection. *Frontiers in Genetics*, *13*. https://doi.org/10.3389/fgene.2022.853114

List of Tables

List of Figures

Figure 1. Drought tolerance treatment in greenhouse and measurement: A) tomato plants, B. 0-9 scale for leaf wilting; and C) 1-9 scale for leaf rolling

Figure 2. The four distributions of leaf wilting (LW) (A and B) and leaf rolling (LR) (C and D) in 68 tomato accessions: (A) and (C) in 6 days; and (B) and (D) in 10 days after drought treatment.

Figure 3. The five distributions of plant height related traits for drought tolerance in 68 tomato accessions

Figure 4. The five distributions of leaf chlorophyll content related traits for drought tolerance in 68 tomato accessions.

Figure 5. Correlation coefficients (r-value) among eight-drought tolerance related traits in 68 tomato accessions.

Figure 6. Two-way dendrogram in 68 tomato accessions by hierarchical cluster analysis in JMP Pro 17 based on eight drought tolerance related traits, LW-d6, LW-d10, LR-d6, LR-d10, SPAD_AD, SPAD_II, PlHt_AD, and PlHt_II, where the top four drought tolerant accessions were grouped into one cluster I (top).

Figure 7. Principal component analysis (PCA) in 68 tomato accessions by JMP Genomics based on eight drought tolerance related traits, LW-d6, LW-d10, LR-d6, LR-d10, SPAD_AD, SPAD_II, PlHt_AD, and PlHt_II: (A) Bioplot, (B) Scree plot, and (C) PCA with 4-clusters.

Figure 8. Phylogenetic tree created by MEGA 11 based on 5,161 SNPs distributed on 11 chromosomes in 65 USDA GRIN tomato accessions.

CHAPTER 2. GENOME-WIDE ASSOCIATION STUDY AND GENOMIC PREDICTION OF FUSARIUM WILT RESISTANCE IN COMMON BEAN CORE COLLECTION

Abstract

Common bean (*Phaseolus vulgaris* L.) is one of the important leguminous crops being cultivated worldwide. Several studies have indicated that Fusarium wilt, caused by *Fusarium oxysporum f. sp. phaseoli (Fop)*, is one of the important diseases that cause substantial production loss in common bean. Cultivation of disease resistant cultivars has been suggested as an effective approach to manage Fusarium wilt in common bean. Identification of potential parents and single nucleotide polymorphism (SNP) markers associated with resistance to Fusarium wilt pathogen is useful in the breeding for resistance to Fusarium wilt in common bean. The objective of this study was to identify SNP markers associated with resistance and discover possible accessions of common bean as sources of Fusarium oxysporum resistance in a common bean core collection. 157 USDA accession of common bean were phenotyped for Fusarium wilt resistance under greenhouse conditions. 21 common bean accessions were identified to be highly resistant to Fusarium wilt. Genome-wide association study (GWAS) was performed in 157 common bean accessions using TASSEL 5 and GAPIT 3, phenotyped with Fop race 1 and race 4 and genotyped with 4,740 SNPs of BARCBean6K_3 Infinium BeadChips. The GWAS analysis identified 16 SNP markers on chromosome *Pv*04, *Pv*05, *Pv*07, *Pv*8, and *Pv*09 to be associated with Fop race 1 resistance; 23 SNP markers on chromosome *Pv*03, *Pv*04, *Pv*05, *Pv*07, *Pv*09, *Pv*10, and *Pv*11 to be associated with Fop race 4 resistance; and 7 SNP markers on chromosome *Pv*04 and *PV*09 to be associated with both Fop race 1 and race 4 resistances. A total of 17 candidate genes were identified for Fusarium wilt resistance situated on chromosomes *Pv*03, *Pv*04, *Pv*05, *Pv*07, *Pv*08, *Pv*09, and *Pv*10. Genomic prediction (GP) was performed for Fop race 1 and race 4 resistances and the prediction accuracy (PA) fluctuated from 0.26 to 0.55 for both Fop race resistances. The identified Fusarium wilt resistant accessions can be utilized as parental lines in breeding programs, and the SNP markers associated with resistance, along with high prediction accuracy, can provide valuable information for breeders to improve common bean varieties using marker-assisted selection (MAS) and genomic selection (GS) techniques.

Introduction

Common bean (*Phaseolus vulgaris* L.) is ranked third among widely cultivated leguminous crops across the globe (De Ron et al., 2016). It is reported to be native to Mexico approximately 8000 years ago and extended to Mesoamerica and the Andes several years ago (De Ron et al., 2016; Rendón-Anaya et al., 2017). Common bean belongs to Fabaceae family (De Ron et al., 2016). It is a diploid (2n = 2× = 22) plant species consisting of a haploid genome size of approximately 600-Mb(Pedrosa-Harand et al., 2009), annual, self-pollinating, and significant leguminous crop. Common beans are grown and mostly eaten as dry food legume because of high protein content of the dry grain, pulse (pods) and as well as vegetables (leaves)(Pathania et al., 2014a). However, in many regions of the world, tender and green fresh pod (snap bean) is mostly used. The consumption of this leguminous crop is increasing and makes an essential component of a healthy diet not only of the Africa region, but also of the Mediterranean and the USA. Apart from high protein content, consumption of the common bean is known to help reduce risk of obesity, diabetes, cardiovascular diseases and colon, and prostate and breast cancer due to fiber and antioxidants (phenolic) contents of the grain (Blair, 2013; De Ron et al., 2016; Karavidas et al., 2022). Additionally, common bean is known to have a long storage life, and they have ability to fix atmospheric nitrogen in the soil through nitrogen-fixing bacteria, making the common bean to be perceived to offer economic benefits as they help reduce the use of synthetic fertilizers (Assefa et al., 2019; Karavidas et al., 2022).

High prevalence of soil-borne diseases is among the major restrictive factors leading to low yield and significant losses of about 50-75% in crops including common bean (Mihajlovic et al., 2021; Panth et al., 2020). Soil-borne diseases do not only reduce performance and yield of crops, but also increase cost of production(Panth et al., 2020). In the United States, soil-dwelling plant pathogens are described to be accountable for approximately 90% of the 2000 main diseases of major crops. (Mokhtar, 2014) Fusarium wilt, a fungal disease cause by *Fusarium oxysporum* f. sp. *phaseoli* (*Fop*), is a common problem in the most common bean producing regions (Alves-Santos et al., 2002; Batista et al., 2017;), especially in zones where central pivotal irrigation system is used apart from poor production methods such as continuous cropping on the same land (De Ron et al., 2016; Oliveira Batista et al., 2016). Being a soil-borne plant pathogen, *Fusarium oxysporum* is apparently spread in the field by contaminated seed or farm equipment (Oliveira Batista et al., 2016). The major symptom of the Fusarium wilt attack is associated with discolouration of the vascular tissue system. Other manifested symptoms include loss of turgor and leaf chlorosis, beginning with the bottom leaves, occasionally followed by leaf abscission and plant death (De Ron et al., 2016;). The attack may arise even at the early stage of shoot growth, causing underdeveloped plants. Fusarium wilt is difficult to control because of the development of chlamydospores that remain active in the soil for many seasons(Fall et al., 2001a). The application of several methods such as chemical, cultural, and biological have been proved unreliable to control the disease(Fall et al., 2001a) for several reasons: increased and frequent use of chemicals inadvisable because they cause long-term negative effects such as reduce microbial growth and activities, reduced soil health, and productivity and enhancement of chemical resistance in the pathogens (Gerik & Hanson, 2011; van Esse et al., 2020; M. C. Wang et al., 2006). In addition, the application of synthetic chemical is challenged by strict regulations to reduce unwanted side effects (van Esse et al., 2020) besides being associated with increased production costs (Panth et al., 2020). Because of the numerous problems posed by chemical use to control diseases in the crops, cultivation of disease resistant cultivars and crop breeding to enhance agronomic performance of existing cultivars have been proposed to be reliable, effective, and sustainable long-term alternative control methods against soil-borne plant pathogens such as *Fusarium oxysporum* even in common bean (Panth et al., 2020; van Esse et al., 2020).

Thus, it is beneficial to identify potential parents of resistance to support production even in the presence of *Fusarium oxysporum* species and to allow breeding for resistance to the pathogen in common bean (Jha et al., 2020; Nay et al., 2019; Oliveira Batista et al., 2016). Phenotyping and genotypic methods are frequently used to characterize plant genotypes for their resistance to abiotic and biotic stresses. Testing a germplasm collection of common bean accessions for their ability to resist *Fop* strain has been done through inoculation approach (Brick et al., 2006; Paulino et al., 2021). Despite its usefulness in assessing the germplasm collection of plants, this approach may not be more effective as it relies on visual scoring of plants, making it difficult to understand molecular mechanisms triggering resistance against the pathogen in the plant. Therefore, an important advanced approach to determine genetic resistance of common bean to *Fop* through examining the genome-wide genetic variants across diverse genetic materials to understand the distribution and effects of resistance loci along with their relationships with molecular markers is required. Single nucleotide polymorphisms (SNP) markers are the most popular and high occurring molecular markers throughout the genome, and they are accountable for the variability in characteristics that exist among individuals (Bartoli & Roux, 2017). It is useful to identify SNP markers associated with Fusarium wilt resistance in a common bean.

Genome-wide association study (GWAS) and genomic prediction have emerged as powerful tools in plant breeding for the improvement of disease resistance in crops (Shahinnia et al., 2022). Diseases, caused by various pathogens such as fungi, bacteria, and viruses, pose significant challenges to crop production, resulting in substantial yield losses and economic impacts. Traditional breeding methods for disease resistance are time-consuming and labor-intensive, often requiring multiple cycles of phenotypic evaluations and selection (Deng et al., 2020). However, GWAS and genomic prediction have revolutionized the field of plant breeding by enabling the identification of specific genetic markers associated with disease resistance and facilitating the prediction of disease resistance in crops based on genomic information (Paulino et al., 2021; Zia et al., 2022).

GWAS is a powerful approach that involves the examination of countless genetic markers spanning the entire genome of a crop species to identify associations between genotypes and phenotypes, such as disease resistance (Bartoli & Roux, 2017; Uffelmann et al., 2021). By analyzing the genetic variations in large populations of crops with contrasting disease resistance levels, GWAS can identify genomic regions that are significantly associated with disease resistance traits (Bartoli & Roux, 2017; Uffelmann et al., 2021). These genomic regions, also known as quantitative trait loci (QTLs) (Bartoli & Roux, 2017; Pang et al., 2021; Roux & Frachon, 2022), can contain candidate genes or regulatory elements that are involved in the expression of disease resistance traits (Pang et al., 2021). GWAS can provide insights into the genetic basis of disease resistance, identify potential candidate genes or pathways involved in the resistance, and facilitate the development of marker-assisted selection (MAS) strategies for breeding crops with improved disease resistance (Pang et al., 2021; Roux & Frachon, 2022). GWAS approach has been used to discover SNP markers and their associated genes in several crops. Many methods such as Bayesian-information and Linkage-disequilibrium Iteratively Nested Keyway (BLINK), general linear model (GLM), mixed linear model (MLM), fixed and random model circulating probability unification (FarmCPU) FarmCPU, and single marker regression (SMR) (Huang et al., 2019; Kaler et al., 2020; Yi et al., 2015)

Genomic prediction (GP) is a rapidly growing tool that is revolutionizing plant breeding by enhancing efficiency and acceleration (Albrecht et al., 2011; Xavier et al., 2016). GP has gained widespread use in genetic studies of crops and plants to predict breeding values for multiple traits (Ravelombola et al., 2021; Zeng et al., 2012). Bayesian methods (Bayes A, Bayes B, Bayes LASSO, and Bayes ridge regression) and BLUP methods (RR-BLUP, gBLUP, and cBLUP) are commonly recommended for estimating genomic breeding values (Albrecht et al., 2011; Silva et al., 2021; Xavier et al., 2016). Previous reports indicate that the accuracy of GP is typically evaluated using prediction accuracy (PA), which measures the correlation between the predicted genomic breeding values and the observed phenotypic values for a given trait in a validation set. Pearson's correlation coefficient (r) is a common statistical measure used to describe PA. A higher correlation coefficient (r) indicates higher prediction accuracy (Zia et al., 2022), signifying a strong correlation between the genomic breeding values and the observed phenotypic values. GP has been widely embraced in various crops and plant species for predicting breeding values of multiple traits, leading to significant advancements in plant breeding by enabling more precise and efficient selection of superior plants based on their genomic information.

In this study, 157 common bean accessions were phenotyped with *Fop* race 1 and race 4 and genotyped with 4,740 SNPs of BARCBean6K_3 Infinium BeadChips. The BARCBean6K_3 BeadChip is significant in the study of many traits in common beans including Fusarium wilt. The focus of this study was to identify SNPs associated with resistance to *Fusarium oxysporum* in common bean and provide possible accessions as sources of *Fusarium oxysporum* resistance.

Literature Review

Economic Value of Common Bean

Common bean (*Phaseolus vulgarisL*) is one of the important crops being utilized by humans. Common bean is reported to contain high amount of protein, fiber, and minerals (Nasar et al., 2023; Romero et al., 2013). Apart from providing nutrition benefits, common bean is also known to have the ability to fix nitrogen in the soil (Reinprecht et al., 2020), making the soil more productive for cultivation of several crops while reducing the need for chemical fertilizers (González-Guerrero et al., 2016). Importantly, common bean has a short growth cycle with multiple uses such as pulse or vegetable (leaves and pods) (Pathania et al., 2014). Additionally, common bean has a long storage life (González-Guerrero et al., 2016) and can be used for a long time.

Fusarium Wilt Introduction and History

Fusarium wilt is one of the important soil-borne fungal diseases affecting production on many diseases in several countries (Okungbowa & Shittu, 2012). Fusarium species are filamentous and belong to the class Ascomycetes and Family Hypocreaceae. The (Okungbowa & Shittu, 2012). The diseases are introduced by a fungus known as Fusarium oxysporum, which adversely affects a variety of plants such as bananas, melons, cucumber, tomato, common bean, and ornamental plants (Okungbowa & Shittu, 2012). The disease is more devastative and can cause total plant death and decrease in yield and quality and is a major threat to crop production worldwide.

The Fusarium oxysporum pathogen persists in the soil for a long time, and spreads throughout the plant through the root system (Arie, 2019), hindering the movement of water and nutrients, and causing wilting and yellowing of the leaves (Rahman et al., 2021). In some instances, the disease may continue to spread, causing plant death within a short period of time (Arie, 2019; Rahman et al., 2021).

Disease Symptoms and Transmission

Being a soil-borne fungal disease caused by the fungus Fusarium oxysporum (Okungbowa & Shittu, 2012; Zhou et al., 2019), Fusarium wilt affects many plants including vegetables, fruits, and ornamental plants (Okungbowa & Shittu, 2012; Zhou et al., 2019). The pathogen infects the vascular system of the plants (Okungbowa & Shittu, 2012), stopping the flow of water and nutrients, causing destruction of leaves and other parts of the plants. The occurrence of symptoms of the Fusarium wilt disease can fluctuate based on the plant species and severity of infection, but the most observable signs include wilting and yellowing of leaves, stunted growth, and premature dropping of leaves and fruits (Okungbowa & Shittu, 2012). In some instances, the infected plants may die within a short period of time following the occurrence of the symptoms(Okungbowa & Shittu, 2012).

The fungus that causes Fusarium wilt disease can spread through various ways, including infected soil, contaminated tools or equipment, and infected seeds or transplants (Arie, 2019; Oliveira Batista et al., 2016). When the fungus penetrates the plant, it can reproduce quickly and spread throughout the vascular system of the plant (Arie, 2019), preventing the flow of water and nutrients (Rahman et al., 2021). The fungus can also produce spores (Gordon, 2017) that can be transferred by wind or water to infect neighboring plants. Once the disease is established in a field, it can be difficult to control, as fungus can survive in the soil for many years and can infect new plants. Preventive measures such as crop rotation, soil sterilization, and using disease-resistant varieties can help reduce the spread of Fusarium wilt disease.

Genetics of resistance to Fusarium wilt

Fusarium wilt is a fungal disease caused by Fusarium oxysporum that affects many plant species, including common beans (Phaseolus vulgaris). Previous reports have presented varying findings on the genetic inheritance of Fusarium oxysporum f. sp. phaseoli (Fop) resistance in common beans. For instance, (Cross et al., 2000; Salgado et al., 1995) suggested that resistance is controlled by either a single dominant gene, a few genes, or polygenic inheritance. However, (Fall et al., 2001) observed partial resistance to Fop race 4 in Recombinant Inbred Line (RIL) populations derived from lines A55 and Belneb-RR1 and identified Quantitative Trait Loci (QTL) that explained a significant proportion of the phenotypic variation. These findings suggest that the genetic basis of Fop resistance in common beans may be influenced by factors such as genetic background and population origin, and further research is needed to elucidate the complex mechanisms underlying this trait and guide breeding efforts for developing resistant cultivars.

Genome-Wide Association Study

Genome-wide association study (GWAS) and genomic prediction (GP) are powerful tools that are currently being explored in molecular plant breeding approach. GWAS has been extensively used to reveal molecular markers (SNPs) and candidate genes underlying resistance to major diseases in common bean. Recently, GWAS has been used to uncover molecular markers (SNPs) conferring resistance to Fusarium wilt in common bean. Numerous SNP markers associated with *Fop* strains were identified on chromosomes *Pv*01, *Pv*03, *Pv*04, *Pv*05, *Pv*07, *Pv*10, and *Pv*11 together with putative candidate genes related to nucleotide-binding sites and carboxy-terminal leucine-rich repeats in a 205 Mesoamerican Diversity Panel (MDP) (Paulino et al., 2021). Another study conducted by Zia et al. (2022) discovered a total of 14 SNP markers and 14 candidate genes on chromosomes *Pv*02, *Pv*04, *Pv*07, *Pv*08, and *Pv*09 associated with bacterial wilt isolates 528, 557, and 597 in a 168 USDA common bean core collection. Shi et al., (2021) used GWAS approach and detected 18 SNPs (6 SNPs associated with HG Type 2.5.7 resistance on *Pv* 01, 02, 03, and 07, and 12 SNPs with HG Type 1.2.3.5.6.7 resistance on *Pv* 01, 03, 06, 07, 09, 10, and 11) that were accountable for resistance to cyst nematode (SCN, *Heterodera glycines*) in 276 Soybean germplasm accessions.

Genomic Prediction

Genomic prediction (GP) for genomic selection (GS) has also been established to predict quantitative traits that are costly phenotype and has been proved to be a promising tool in accelerating genetic gain in plant breeding(Crossa et al., 2017; Meuwissen et al., 2001). GP has been recognized to have powerful features compared to conventional marker-assisted selection (MAS) in understanding complex traits (Bao et al., 2014). GP has been used to study many diseases in common bean. Some previous reports indicate genomic prediction accuracy (PA) of resistance to root rot disease ranging from 0.7 to 0.8(Diaz et al., 2021), from 0.30 to 0.56 for resistance to bacteria wilt (Zia et al., 2022), and from 0.41 to 0.52 for resistance to two soybean cyst nematode HG types in common bean (Wen et al., 2019).

Objectives of the study

The main aim of this study was to conduct genome-wide association study and genomic prediction to understand genetic resistances against the Fusarium wilt pathogen in common bean. This dissertation research was designed to discover common bean genotypes with high resistance to Fusarium wilt disease and Fusarium wilt resistance associated single nucleotide polymorphism (SNP) markers and candidate genes.

Materials and Method

Plant material and phenotyping

The evaluation of 157 accession core collection of common bean from 10 countries (Supplementary Table S1) for Fusarium wilt resistance was performed and reported in 2006(Brick et al., 2006). The 157 accessions of the common bean (*Phaseolus vulgaris L.*) obtained from the USDA/ARS Western Regional Plant Introduction Station, Pullman, WA were evaluated for resistance to *Fusarium oxysporum* races 1,4, and 5 in Fort Collins, CO in a controlled greenhouse (Brick et al., 2006) (Supplementary Table S1). The accessions were characterized based on their origin. Seedlings from each accession were screened by the root dip inoculation procedure. The greenhouse condition was maintained at approximately 16/32^{0}C night/day with additional lighting maintained 13h of light. Twenty-one days following inoculation, the plants were evaluated for reaction to *Fop* using CIAT disease severity scale. The scale rated the plants according to percentage of leaf tissue with disease symptoms, such as drying, wilting or chlorosis, as follows: 1= no disease symptoms and completely healthy; 3=10% of the leaf surface area showing disease symptoms; 5=25% of the leaf surface showing disease symptoms, as well as some whole plant stunting; 7=disease symptoms on 50% of leaves, and severely stunted; and 9=plant death. The plant was considered resistant if it scored 1 to 3, intermediate if scored 4 to 6, and susceptible if scored 7 to 9 on the CIAT disease severity score. Eight to 10 seedlings from each accession were evaluated. The mean for each accession of all plants evaluated was reported as the average severity index (ASI). In all experiments, inoculated resistant and susceptible checks were used to evaluate pathogenicity of the test and to confirm disease classification of known resistant and susceptible lines. The check entries were cultivar UI 114 and the line Lef-2RB that consistently rated susceptible (ASI>8) and resistant (ASI<3), respectively. In addition, two non-inoculated plants from each accession were grown to evaluate the pathogenicity of the inoculum with the inoculated plants and determine the phenotype of each accession in the absence of disease symptoms.

Genotyping and SNP selection

A set of 157 common bean accessions was genotyped using BARCBean6K_3 Infinium BeadChips (Song et al., 2013)and SNPs across the 157 accessions were downloaded from the SNP dataset at (https://datadryad.org/stash/dataset/doi:10.25338/B8KP45). SNPs were filtered with exclusion of SNPs; data missing rate >20%, heterogeneous >10%, and MAF (minor allele frequency) <5%**.** After filtering, 4,740 SNPs distributed on the 11 chromosomes (Supplementary Figure S1) were used for GWAS of *Fop* resistance in this study.

Phenotypic data analysis and estimation of plant distribution for *Fusarium oxysporum* races

The phenotypic data analysis for the two *Fop* races was conducted using ANOVA functions in JMP Genomics 7 (Handy et al., 2008). The parameters were estimated for the mean (X), variance

(V), standard deviation (SD), and standard error (SE). These parameters were evaluated using the “Tabulate” function in JMP Genomics 7, and Distribution function was used to graphically present the phenotypic data for each of the *Fop* races.

Principle component analysis (PCA) and genetic diversity

The principal component analysis (PCA) and genetic diversity analysis were performed using 4,740 SNPs in GAPIT 3 (Genomic Association and Prediction Integration Tool version 3) by setting PCA = 2 to 10 and NJ tree = 2 to 10, and phylogenetic trees were drawn using the neighbor-joining (NJ) method (Lipka et al., 2012). Phylogenetic trees were drawn by using neighbor-joining (NJ) method. Genetic diversity was also assessed, and phylogenetic trees were drawn using MEGA 11 based on the Maximum Likelihood tree method.

Genome-wide association study and SNP marker identification

Genome-wide association mapping of phenotypic and genotypic data from the 157 accessions of common bean was performed using the Bayesian-information and Linkage-disequilibrium Iteratively Nested Keyway (BLINK), mixed linear model (MLM), general linear model (GLM), Fixed and random model Circulating Probability Unification (FarmCPU) in GAPIT 3 (M. Huang et al., 2019b; Lipka et al., 2012; Liu et al., 2016), and single marker regression (SMR), generalized linear model (GLM), mixed linear model (MLM) methods in TASSEL 5 (Bradbury et al., 2007). A threshold –[log10(p)] {we defined –[log10(p)] as LOD (logarithm of odds) in this study} >=2.0 as the Bonferroni correction of P-value was used to select significant SNP markers associated with resistance to the *Fop* race 1 and race 4. In addition, the SNP marker having LOD >2.0 in three or more out of the seven GWAS models was also selected as significant associated markers in this study. The Manhattan and QQ plots for all association models were generated using GAPIT3 and

TASSEL 5. The squared correlation coefficient (R^2) was used to calculate the linkage disequilibrium (LD) between the markers.

Candidate gene estimation

All SNP loci significantly associated with either *Fop* race 1 or race 4 were subjected to candidate gene prediction for the discovery of candidate genes covering the 50 kb (50 kb on each side of SNP) regions. The Andean whole-genome reference sequence *Pvulgaris* 442_v2.1 presented on the Phytozome website (https://phytozome.jgi.doe.gov/pz/portal.html) was explored to retrieve the candidate genes from the reference annotation of the common bean genome.

Genomic prediction for genomic selection of Fusarium wilt resistance

GP was performed to analyze the effect of the SNP markers identified in the association analysis using five different models (best linear unbiased prediction (BLUP) rrBLUP; Bayesian models: Bayes A (BA), Bayes B (BB), Bayes ridge regression (BRR), and Bayes LASSO (BL) (Supplementary Table S7).

The GP was conducted using the unbiased prediction in the rrBLUP (J. Wang et al., 2018) package to predict for GS using the R software version 3.5.0 (https://www.r-project.org) .The PA was calculated using Pearson Correlation Coefficient (r) using the observed values for resistance to each *Fop* race pathogen. Prominently, Bayesian models: BA, BB (Barili et al., 2018), BRR, and BL (Legarra et al., 2011)were used to evaluate GP. Each combination of GP had multiple cycles and statistical parameters (mean (X), standard error (SE), and (r) values) were calculated. Three sets of SNPs, 1_m32 (32 associated SNP markers), 2_r32 (randomly selected 32 SNPs), and 3_4740 (all 4740 SNPs), were used along with the five models. The distribution plots were generated using RStudio (R version 4.2.2) package.

Results

Phenotypic variation

The 1-9 score of the resistance to *Fop* race 1 and race 4 was observed in each of the 157 common bean accessions (Supplementary Table S1). The mean rate was 7.0 for *Fop* race 1 and 6.8 for race 4; the standard deviation (std) was 2.01 for race 1 and 2.10 for race 4; the standard error (SE) was 0.16 for race 1 and 0.17 for race 4; and the coefficient variation (CV) were 28.80% and 30.83% for races 1 and race 4, respectively, showing that there were genetic differences in respect to resistance to the *Fop* races among the 157 common bean accessions (Supplementary Table S2).

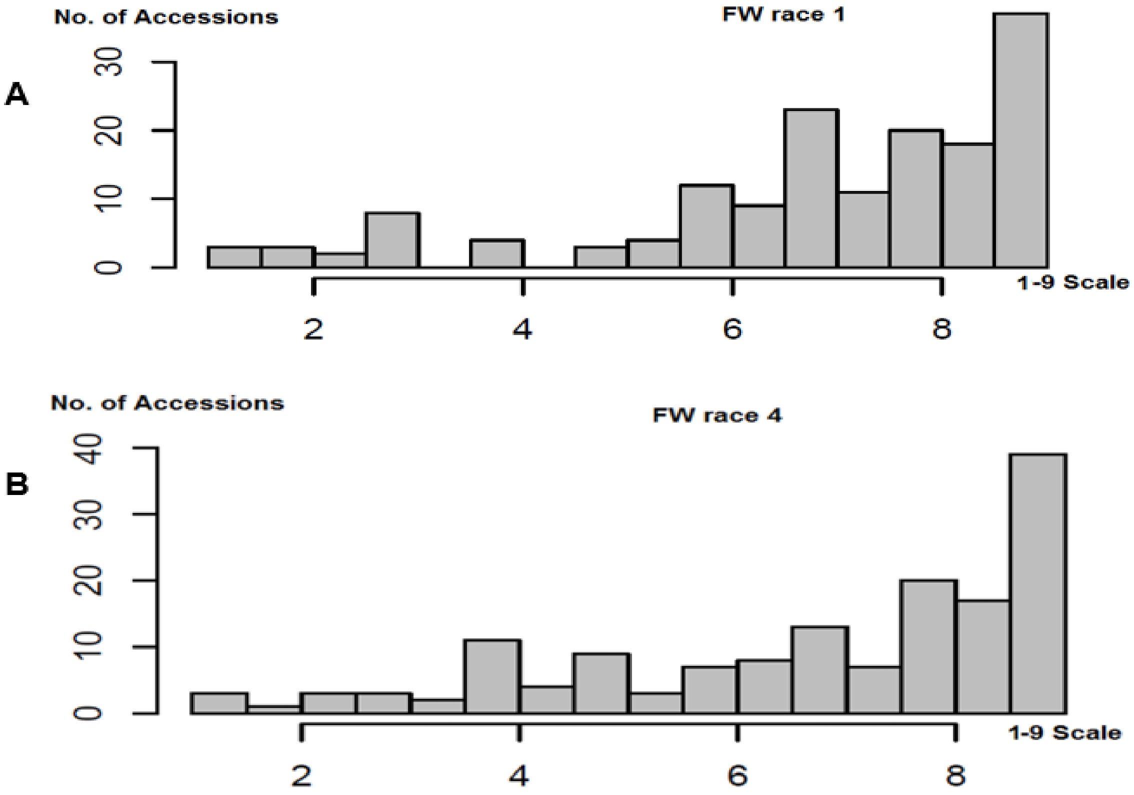


Figure 1. Distribution of Fusarium wilt disease (1-9 scale) in 157 common bean accessions.

The distribution of either *Fop* race 1 or race 4 scores among the 157 accessions was right-skewed (Figure 1 A&B), indicating that there were more susceptible accessions in the panel. Twenty-one accessions had score <= 3.0 either in race 1 or race 4 (Table 1), indicating that the 21 accessions are resistant to either race 1 or race 4. Sixteen out of 21 accessions were identified as highly resistant to race 1 with a disease severity score >= 3 (Table 1). Among the16 accessions, PI 311853 from Guatemala had the lowest score of 1 followed by PI 288016 from Nicaragua and PI309877 from Costa Rica with scores of 1.3 and 1.4, respectively, showing that the three accessions were the highest resistance to the *Fop* race 1 pathogen (Table 1). Likewise, 10 out of the 21 accessions were highly resistant to race 4 with scores >= 3 (Table 1). The accessions, PI 209482 and PI 308908 from Costa Rica, and PI 310778 from Guatemala had the lowest score of 1 and PI 288016 had a score of 1.7, were highest resistance to *Fop* race 4 pathogen (Table 1). The accessions, PI 209482, PI 308908, PI 309877, PI 288016 and PI 310842 from Cota Rica and Nicaragua were the top five accessions with highest resistance to both *Fop* race 1 and race 4 (Table 1). The resistant accessions can be used as parental lines in common bean breeding programs to improve Fusarium wilt resistance.

TABLE 1 |Top 21 common bean accessions with high ressitance to both Fusarium wilt race 1 and race 4

PI_accession	PI_name	Origin.country	Race1_2006_ disease_rate	Race4_2006_ disease_rate	rate <=3 either race 1 or race 4 or both
PI260418	PV-3	Bolivia	3	9	race1<=3
PI387865	W-941d	Bolivia	2.7	5	race1<=3
PI207207	Z-#4	Colombia	6.8	2.7	race4<=3
PI207279	Chiapas 36-3	Colombia	3	7	race1<=3
PI207336	Jalisco 31-1	Colombia	2.3	3.7	race1<=3
PI313572	Antioquia 12	Colombia	3	4	race1<=3
PI313598	Cauca 38	Colombia	2.7	4.3	race1<=3
PI209482	G16837	Costa Rica	2	1	race1&4<=3
PI209498	G1363	Costa Rica	1.7	6.3	race1<=3
PI308898	Line 7	Costa Rica	3	3.3	race1<=3
PI308908	Criollo blanco No. 2	Costa Rica	3	1	race1&4<=3
PI309877	Col. No. 20670, lot #33	Costa Rica	1.4	2.3	race1&4<=3
PI313693	Col. No.	Ecuador	6.3	3	race4<=3
PI307788	S-219-R	El Salvador	7	2.5	race4<=3
PI310761	G2022	Guatemala	2.5	9	race1<=3
PI310778	G2031	Guatemala	5	1	race4<=3
PI311843	Frijol de gato	Guatemala	1.7		race1<=3
PI311853	Colorado del suelo	Guatemala	1	8.7	race1<=3
PI451917		Guatemala	6	3	race4<=3
PI288016	Negro Nicaraguense	Nicaragua	1.3	1.7	race1&4<=3
PI310842	G2084	Nicaragua	3	2.3	race1&4<=3

The correlation of scores of resistances to both Fop race 1 and race 4 was moderately high with r = 0.51, indicating that there were accessions with the resistance to both *Fop* races controlled by same resistance alleles.

Population structure

The 157 accessions were divided into two clusters (sub-populations) with red (Q1) and blue (Q2) colors (Figure 2). The Supplementary Figure S2 showed the two clusters with detailed and viewable accessions. The Q1 sub-population is the majority one with 63.7% of accessions (Figure 2).

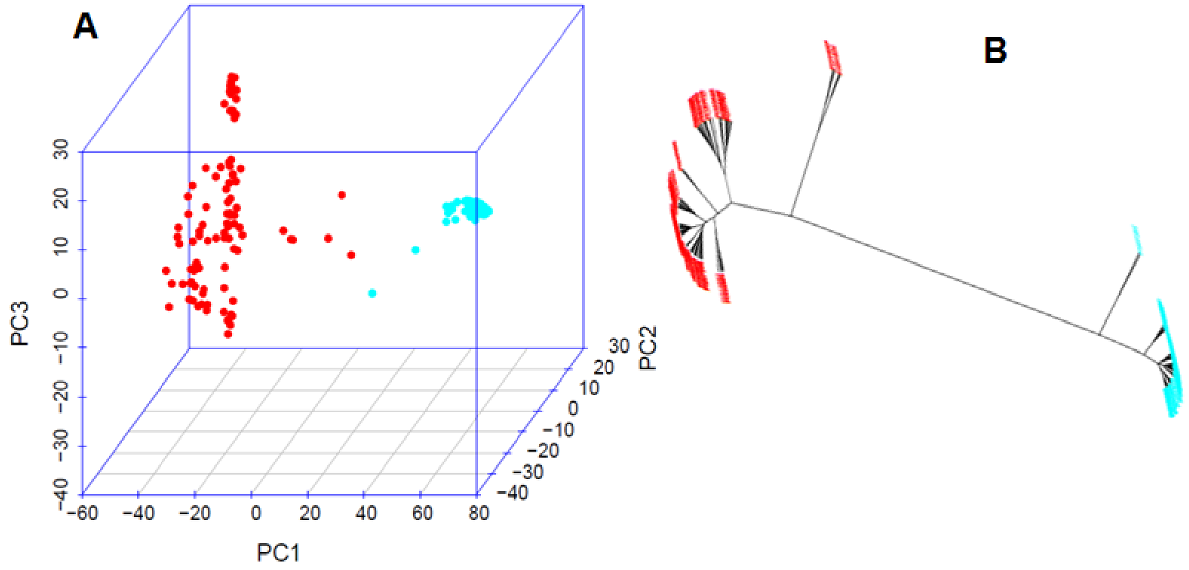


Figure 2. Model-based population structure for the 157 common bean panel. The 3D graphical plot of the principal component analysis (PCA) (A) and phylogenetic trees were created using the neighbor-joining (NJ) method in two subpopulations (B) created using GAPIT 3. The distribution of the accessions to different populations is indicated by the color code (Q1: red and Q2: blue).

Association analysis and SNP marker identification

When the 4,740 SNPs were used in combination with the four models (Blink, FarmCPU, GLM, and MLM) in GAPIT 3 and three models (SMR, GLM, and MLM) in TASSEL 5, 16 and 23 SNP markers were associated with *Fop* race 1 and race 4 resistances, respectively (Supplementary Table S3 & S4). Each SNP associated with either race 1 or race 4 with a LOD value >=4.98 in one or more of the seven models (Supplementary Table S3 & S4). Seven SNP markers were associated with both race 1 and race 4 based on the seven models. The LOD values for each SNP marker from *t*-test, together with their beneficial allele, special for *Fop* resistance allele and un-beneficial allele for susceptible allele, were also listed in Supplementary Table S3 and Table S4. The highest associated SNP markers were listed in Table 2. The Manhattan plots and QQ-plot the four models (Blink, FarmCPU, GLM, and MLM) in GAPIT 3 and three models (SMR, GLM, and MLM) in TASSEL 5 were shown in the supplementary Figures 3-9. The example of Manhattan and QQ plots of BLINK model for Fop race 1 resistance and GLM model for race 4 resistance by GAPIT 3 was shown in Figure 3. All QQ-plots between the observed and expected LOD values unveiled deviation from the linear models (Figure 3, S3-S9 right), and a dozen of SNPs with large LOD (-log(P)) values >4.98 (Bonferroni correction threshold) or LOD >4.0 were observed in several models (Figure 3, S3-S9 left), indicating that there were SNPs associated with either *Fop* race 1 or race 4 resistance.

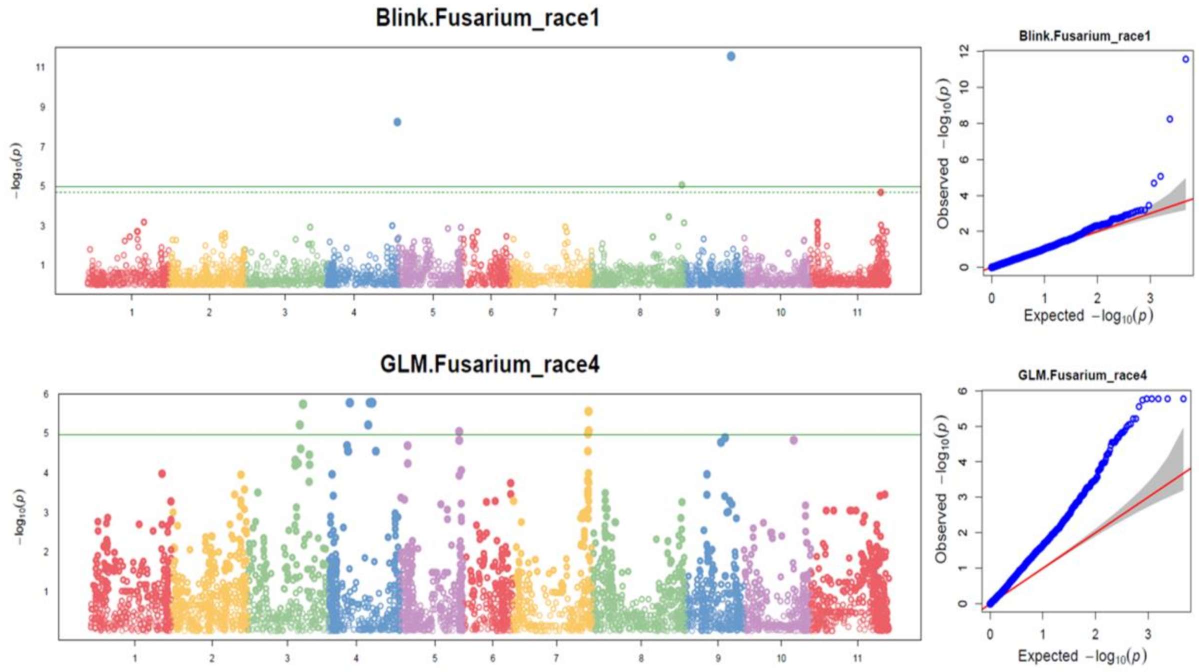


Figure 3. The Manhattan (Left) and QQ (Right) plots of BLINK model for Fusarium wilt race 1 resistance and GLM model for Fusarium wilt race 4 resistances by GAPIT 3. The vertical and horizontal axes represent observed vs expected logarithm of odds (LOD or -log(P-value).

SNP marker for *Fusarium oxysporum* race 1 resistance

Sixteen SNP markers were associated with *Fop* race 1 resistance, consisting of 8, 1, 2, 2, and 3 SNPs on chromosomes, *Pv*04, 05, 07, 08, and 09 respectively (Table S3). Six SNP markers, ss715650990_Chr04_26314820, ss715647361_Chr04_45301836, ss715647824_Chr05_275140, ss715645682_Chr07_517953, ss715646092_Chr08_57870335, and ss715646367_Chr09_29788600 were chosen as the highly associated with race 1 resistance, located at 26,314,820 bp and 45,301,836 bp on *Pv*04; 2,75,140 bp on *Pv*05; 517,953 bp on *Pv*07; 57,870,335 bp on *Pv*08, and 29,788,600 bp on *Pv*09, respectively (Table 3). Among the six SNP markers in Table 3 or 16 SNPs in Table S3, ss715646367_Chr09_29788600 had the largest LOD value of 11.56 based on BLINK model and it had LOD >5 across five models, indicating that there was a QTL region for race 1 resistance, located near the SNP at *Pv*09. The second highest SNP was ss715647361_Chr04_45301836 having a LOD = 8.24 based on BLINK model, but it had low LOD values (< 2.0) in five models, indicating that the SNP was not identified as a stable or reliable marker. The SNP, ss715645682_Chr07_517953 had LOD >4.98 (Bonferroni correction threshold) in two models and LOD >4.8 across four models (Table 3) and another SNP ss715645685_Chr07_606814 nearby had same LOD values across the seven models and also had a high LOD (10.08) in *t*-test (Table S3), indicating that there was a QTL region for race 1 resistance, located at the two SNP region at *Pv*07. The SNP ss715650990_Chr04_26314820 (Table 3) and other three SNPs, ss715650115_Chr04_27464228, ss715650468_Chr04_27690714, and ss715649688_Chr04_27781623 located at a 1.5 Mbp region from 26,314,820 bp to 27,690,714 bp on *Pv*04 had a LOD >4.8 across four models, their R^2 were low with 2.5% in the MLM model (Table S3), indicating that there was a QTL in the region with a low effect. Other SNPs had a LOD >4.89 in one or more model or LOD >4.0 in two or more models (Table 3 & S3), indicating these SNPs were associated with Race 1 resistance.

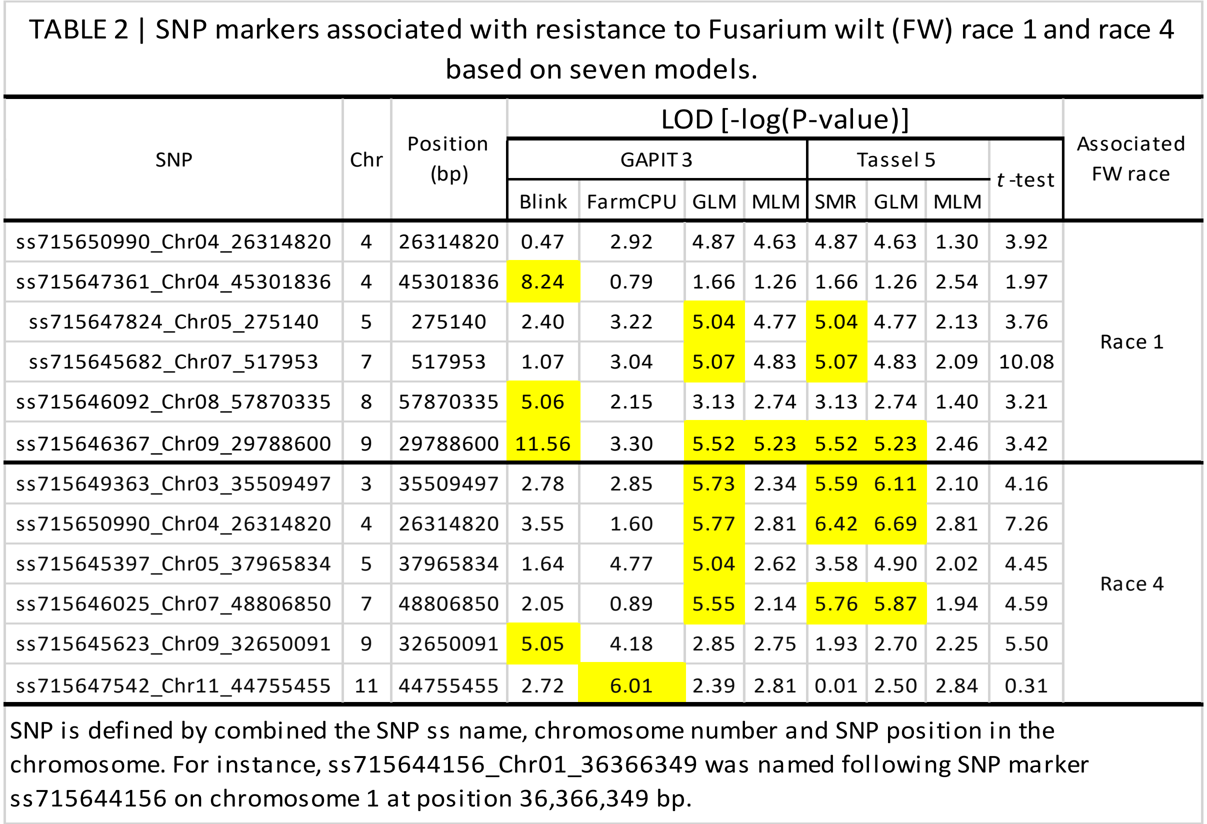


TABLE 2 | SNP markers associated with resistance to Fusarium wilt (FW) race 1 and race 4 based on seven models.

SNP	Chr	Position (bp)	LOD [-log(P-value)]								Associated FW race
			GAPIT 3				Tassel 5			*t*-test	
			Blink	FarmCPU	GLM	MLM	SMR	GLM	MLM		
ss715650990_Chr04_26314820	4	26314820	0.47	2.92	4.87	4.63	4.87	4.63	1.30	3.92	Race 1
ss715647361_Chr04_45301836	4	45301836	8.24	0.79	1.66	1.26	1.66	1.26	2.54	1.97	
ss715647824_Chr05_275140	5	275140	2.40	3.22	5.04	4.77	5.04	4.77	2.13	3.76	
ss715645682_Chr07_517953	7	517953	1.07	3.04	5.07	4.83	5.07	4.83	2.09	10.08	
ss715646092_Chr08_57870335	8	57870335	5.06	2.15	3.13	2.74	3.13	2.74	1.40	3.21	
ss715646367_Chr09_29788600	9	29788600	11.56	3.30	5.52	5.23	5.52	5.23	2.46	3.42	
ss715649363_Chr03_35509497	3	35509497	2.78	2.85	5.73	2.34	5.59	6.11	2.10	4.16	Race 4
ss715650990_Chr04_26314820	4	26314820	3.55	1.60	5.77	2.81	6.42	6.69	2.81	7.26	
ss715645397_Chr05_37965834	5	37965834	1.64	4.77	5.04	2.62	3.58	4.90	2.02	4.45	
ss715646025_Chr07_48806850	7	48806850	2.05	0.89	5.55	2.14	5.76	5.87	1.94	4.59	
ss715645623_Chr09_32650091	9	32650091	5.05	4.18	2.85	2.75	1.93	2.70	2.25	5.50	
ss715647542_Chr11_44755455	11	44755455	2.72	6.01	2.39	2.81	0.01	2.50	2.84	0.31	

SNP is defined by combined the SNP ss name, chromosome number and SNP position in the chromosome. For instance, ss715644156_Chr01_36366349 was named following SNP marker ss715644156 on chromosome 1 at position 36,366,349 bp.

SNP markers for *Fusarium oxysporum* race 4 resistance

Twenty-three SNP markers were associated with *Fop* race 2 resistance, consisting of 3, 10, 2, 3, 3, 1, and 1 SNPs on chromosomes, *Pv*,03, 04, 05, 07, 09, 10, and 11 respectively (Table S4). Six SNP markers, ss715649363_Chr03_35509497, ss715650990_Chr04_26314820, ss715645397_Chr05_37965834, ss715646025_Chr07_48806850, ss715645623_Chr09_32650091, and ss715647542_Chr11_44755455, located at 35,509,497 bp on *Pv*03; 26,314,820 bp 0n *Pv*04, 37,965,834 bp on *Pv*05; 48,806,850 bp 0n *Pv*07; 32,650,091 bp on *Pv*09; and 44,755,455 bp on *Pv*11 were chosen as highly associated SNP markers for race 4 resistance (Table 3). Based on BLINK, only one SNP ss715645623_Chr09_32650091 had LOD >4.98 (Bonferroni correction threshold) (Table 3 & S3), indicating the SNP was associated with *Fop* race 4. Based on FarmCPU, only ss715647542_Chr11_44755455 had LOD >4.98 (Bonferroni correction threshold) (Table 3 & S3), indicating the SNP was associated with *Fop* race

4. The ss715649363_Chr03_35509497 had LOD >4.98 across three models (Table 3); nearly, two SNPs ss715650616_Chr03_32369163 and ss715647848_Chr03_33503791 had LOD values >4.98 and >4.0 in two models; the three SNPs extended 3.15 Mbp length from 32,369,163 bp to 35,509,497 bp on *Pv*03 (Table S4), indicating there was a QTL on *Pv*03 for race 4 resistance. Four SNPs, ss715651182_Chr04_11640123, ss715648302_Chr04_12157925, ss715648999_Chr04_12447195, and ss715649810_Chr04_13397055 extended 1.76 Mbp length from 11,640,123 bp to 13,397,055 bp on *Pv*04 had LOD >4.5 across three models (Table S4), indicating there was a QTL on *Pv*43 for race 4 resistance in the region. Second QTL region on *Pv*04 for race 4 resistance had ss715650115_Chr04_27464228, ss715650468_Chr04_27690714, and ss715649688_Chr04_27781623, extended 320 Kb from 27,464,228 bp to 27,781,623 bp with LOD >5.7 in three models (Table S4). The SNP, ss715646025_Chr07_48806850 (Table 3) plus near two SNPs, ss715648570_Chr07_48450279 and ss715646020_Chr07_48927436, extended 478 Kb from 48,450,279 bp to 48,927,436 bp on *Pv*07 had LOD >=4.98 in two or three models (Table S4), indicating there was a QTL in the region on *Pv*07 for race 4 resistance. Other SNPs in Table 3 & S4 had LOD >4.98 one or more models, suggesting there were QTL for race 4 resistance nearby.

SNP markers for resistance to both *Fusarium oxysporum* race 1 and race 4

Seven SNP markers, including five SNP markers on *Pv*04 and two SNPs on *Pv*09 were associated simultaneously with the resistance to both *Fop* race 1 and race 4 pathogen (Supplementary Table S5), suggesting that the presence of QTL associated both race-resistance. Four of the five SNPs, ss715650990_Chr04_26314820, ss715650115_Chr04_27464228, ss715650468_Chr04_27690714, and ss715649688_Chr04_27781623 extended a 1.5 Mbp from 26,314,820 bp to 27,781,623 bp on *Pv*04 had LOD >4.6 across four models, indicating that a QTL existed in the region of *Pv*04. The two SNPs, ss715648883_Chr09_22785976 and ss715646055_Chr09_25385192 located at a region of 2.6 Mbp from 22,785,976 bp to 25,385,192 bp on *Pv*09 had LOD >=4.0 across four models (Table S5), indicating that there was a QTL in the region of *Pv*09.

Candidate genes for Fusarium wilt resistance

153 genes were found to be located at within 50 kb distance from the 16 associated SNP markers for Fop race1 resistance in Table S3 and 23 SNP markers for race 4 resistance in Table S4 (Supplementary Table S6). Among the 163 genes, 10 genes were identified for *Fop* race 1 resistance and 7 genes for race 4 resistance. whereby 5 genes were found on 0kb, 3 genes within <1kb, 5 genes within <2kb, 1 gene within <3kb, 1 gene within <5kb, 1 gene within <10kb, and 1 gene at <30kb, respectively (Table 3). Among the 17 gene models, a single gene model Phvul.004G016532 found on chromosome *Pv*04 contained NB-ARC domain-containing disease resistance protein and was close to the SNP marker,

TABLE 3 | Seventeen candidate genes within 3 kb distance and four disease gene analogs within 30 kb distance from the associated SNP markers, where 10 genes for Fusarium wilt race 1 resistance and 7 genes for race 4 resistance.

Gene	Chr	Gene_ start	Gene_ end	Arabi-defline	distance-to -start (bp)	distance to end (bp)	Closest SNP marker	Chr	Position	Associated FW race	Comment
Phvul.004G016532	4	1795047	1799504	NB-ARC domain-containing disease resistance protein	32616	28159	ss715647806_Chr04_1827663	4	1827663	race1	<30kb
Phvul.004G016800	4	1839577	1845525	HD domain-containing metal-dependent phosphohydrolase family protein	6012	64	ss715647808_Chr04_1845589	4	1845589		<1kb
Phvul.004G151100	4	45295935	45302841	zinc finger (Ran-binding) family protein	5901	-1005	ss715647361_Chr04_45301836	4	45301836		0
Phvul.005G003400	5	276370	278458	SNARE-like superfamily protein	-1230	-3318	ss715647824_Chr05_275140	5	275140		<2kb
Phvul.007G007100	7	512875	516186	Nitrilase/cyanide hydratase and apolipoprotein N-acyltransferase family protein	5078	1767	ss715645682_Chr07_517953	7	517953		<2kb
Phvul.007G008400	7	607208	609910	Peroxidase superfamily protein	-394	-3096	ss715645685_Chr07_606814	7	606814		<1kb
Phvul.007G008300	7	601126	604961	Pre-mRNA-splicing factor 3	5688	1853					<2kb
Phvul.008G228500	8	57867269	57871407	Protein of Unknown Function (DUF239)	3066	-1072	ss715646092_Chr08_57870335	8	57870335		0
Phvul.009G153600	9	22783004	22790439	amino acid permease 2	2972	-4463	ss715648883_Chr09_22785976	9	22785976		0
Phvul.009G195900	9	29776401	29778968	Leucine-rich repeat protein kinase family protein	12199	9632	ss715646367_Chr09_29788600	9	29788600		<10kb
Phvul.003G129400	3	32362269	32364947	Leucine-rich repeat protein kinase family protein	6894	4216	ss715650616_Chr03_32369163	3	32369163	race4	<5kb
Phvul.004G073900	4	12159333	12172638	Polynucleotidyl transferase, ribonuclease H fold protein with HRDC domain	-1408	-14713	ss715648302_Chr04_12157925	4	12157925		<2kb
Phvul.005G045400	5	4810890	4813123	P-loop containing nucleoside triphosphate hydrolases superfamily protein	-2186	-4419	ss715650411_Chr05_4808704	5	4808704		<3kb
Phvul.005G137400	5	37959124	37963889	carbamoyl phosphate synthetase B	6710	1945	ss715645397_Chr05_37965834	5	37965834		<2kb
Phvul.009G153600	9	22783004	22790439	amino acid permease 2	2972	-4463	ss715648883_Chr09_22785976	9	22785976		0
Phvul.009G216500	9	32631124	32649380	binding;RNA binding	18967	711	ss715645623_Chr09_32650091	9	32650091		<1kb
Phvul.010G071766	10	32132142	32138589	Nucleotidyltransferase family protein	949	-5498	ss715650855_Chr10_32133091	10	32133091		0

ss715647806_Chr04_1827663 within 30 kb distance, which was associated with *Fop* race 1 resistance. The two gene models Phvul.009G195900 and Phvul.009G195901 on chromosomes *Pv*09 and *Pv*03, respectively, were close to the two SNPs, ss715646367_Chr09_29788600 and ss715650616_Chr03_32369163, respectively, contained Leucine-rich repeat protein kinase family protein, and the two gene models showed to be associated with *Fop* race 1 and race 4 resistance, respectively. The gene Phvul.004G151100, close to SNP s715647361_Chr04_45301836 on *Pv*04, contained Zinc finger (Ran-binding) family protein, may be responsible for *Fop* race 1 resistance (Table 3). The 17 gene models found in this study need further assessment to validate their association to Fusarium wilt resistance.

Genomic prediction for genomic selection using various models and GWAS-derived SNP markers

The GP used five models in combination with three sets of SNPs. The PA (r_{100}_value) varied from 0.26 to 0.29 for the set of all 4740 SNPs and 0.42 to 0.47 for the GWAS-derived 32 associated SNPs as opposed to the low PA (r_{100}_value) from 0.01 to 0.14 for the randomly selected 32 SNPs for the *Fop* race 1 resistance across the five models (Figure 4 left, Supplementary Table S7). Correspondingly, the PA ranged from 0.31 to 0.34 for all 4740 SNPs and 0.53 to 0.55 for the 32 associated SNPs as compared to a low PA (r_{100}-value) of 0.05 to 0.24 for the 32 randomly selected SNPs for the *Fop* race 4 resistance (Figure 4 right, Supplementary Table S7).

The five GP models had similar PA (r100_value) in each of the three SNP sets (Table S7), indicating each of the five GP model can be used in GS to select *Fop* resistance.

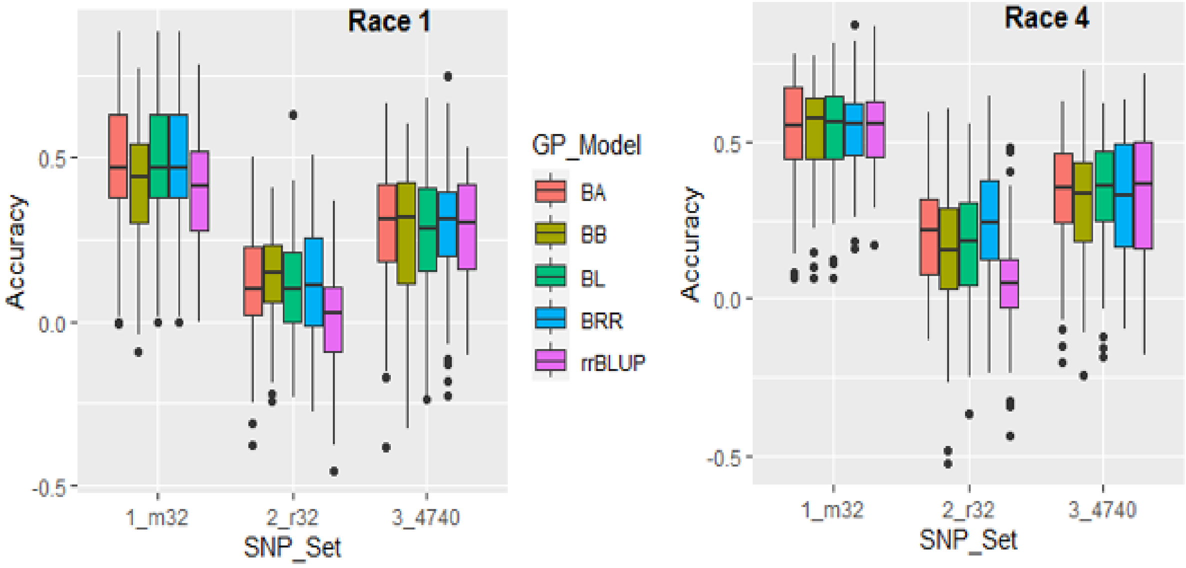


Figure 4. Genomic prediction (r-value) for resistance to Fusarium wilt race 1 and race 4 in 157 common bean accessions estimated by five genomic prediction (GP) models, BA, BB, BL, BRR, and rrBLUP on three SNP sets, 1_m32 (32 associated SNP markers), 2_r32 (randomly selected 32 SNPs), and 3_4740 (all 4740 SNPs).

Among the three SNP sets, the set “m32” of the GWAS-derived 32 associated SNPs had the highest PA (r_{100}-value) with a mean of 0.45 for *Fop* race 1 and 0.54 for race 4 resistance estimated from five models; The “4740SNP” of all 4740 SNPs was the second with a mean of 0.28 for *Fop* race 1 and 0.32 for race 4 resistance; and the “r32” set of randomly selected 32 SNPs was the lowest a mean of 0.10 for *Fop* race 1 and 0.0.16 for race 4 resistance (Figure 4, Table S7), showing that the GWAS derived markers can be utilized in GS for selecting Fusarium wilt resistance in common bean.

The genetic diversity among Fusarium wilt resistant accessions

From the 157 common bean accessions, 21 accessions displayed high *Fop* resistance with a low disease severity rate of less than 3 (Table 1), showing that the 21 common bean accessions can be used as parents in breeding program to develop new common bean cultivars or lines for Fusarium wilt resistance.

The genetic diversity analysis among the 21 Fusarium resistant accessions demonstrated that there were two clusters (groups), and those accessions of the same origin were mostly aligned next to each other with smaller genetic distance within the group (Figure 5), indicating the similar genetic background. Additionally, the accessions were grouped into two distinct clusters in which the larger cluster consisted of 15 resistant accessions and the smaller contained 6 resistant accessions (Figure 5). The genetic diversity analysis showed some variation among the resistant accessions, indicating that the accessions can be used in breeding for improving Fusarium wilt resistance in common bean.

Discussion

Genetic diversity and population structure for the common bean germplasm

Information of genetic diversity and associations among common bean accessions is valuable for breeding projects through selection of genotypes as parental lines to develop new and improve gene pools for better agronomic performance in varied cultivation systems(Iqbal et al., 2012; Lombardi et al., 2014). The genetic diversity and population structure results presented in this study demonstrated the existence of two subpopulations (Q1 and Q2) among the examined accessions (Figure 2 & S2). Previous studies on genetic diversity of USDA common bean demonstrated two different subpopulations for the Andean and Mesoamerican pool and the subpopulations consisted of some common bean accessions from Colombia, Ecuador, Bolivia, and Guatemala (McClean et al., 2012). The occurrence of common bean accessions in the two subpopulations as indicated in this study from the regions substantiates the presence of Andean and Mesoamerican gene pool (Table 1; Figure 5). Hence, we can conclude that our tested germplasm is composed of diverse accessions and belongs to the original two gene pools.

Phenotypic variation

Genetic resistance is by far the most reliable and economical method against low yield caused by Fusarium wilt. The characterization of plant germplasm collections for their ability to resist plant-pathogen interaction and understanding their genetic basis is the first step towards successful breeding of elite common bean cultivars with high resistance to Fusarium wilt. Fusarium wilt is caused by *Fusarium oxysporum* (*Fop*), a soil-borne pathogen that attacks the roots making it more challenging to screen a large common bean germplasm for resistance to it. Recently, studies have been conducted to optimize the procedure in the field and greenhouse conditions to characterize and identify Fusarium wilt-resistant common bean accessions at large scale (Brick et al., 2006). The results of this study have been used to perform GWAS to identify SNP markers associated with the Fusarium wilt resistance. According to the phenotypic variation results, out of 157 accessions, 21 accessions demonstrated high resistance to *Fop* race 1 and race 4 (scale of 3.0 or less) (Supplementary Table S1; Table 1; Figure 5). These identified high resistant common bean accessions would provide useful information for selection of genotypes as parents for developing Fusarium wilt-resistant cultivars of common bean.

Genome-wide association study and SNP markers identification

The focus of this study was to identify SNP markers responsible for resistance to the two *Fop* races of Fusarium wilt in common bean core collection. Four models (Blink, FarmCPU, GLM, and MLM) in GAPIT3 and three models (SMR, GLM and MLM) in TASSEL 5 were used to conduct

GWAS analysis for Fop race 1 and race 4 using phenotypic and genotypic information from the 157 accessions of the common bean. Sixteen SNP markers were identified for resistance to *Fop* race 1 and 23 to race 4 (Supplementary Table S3 & S4). These SNP markers were distributed on chromosomes *Pv*03, *Pv*04, *Pv*05, *Pv*07, *Pv*08, *Pv*09, *Pv*10 and *Pv*11. Additionally, seven SNP markers were discovered on chromosomes *Pv*04 and *Pv*09 to be simultaneously associated with resistance to both *Fop* race 1 and race 4. The Fusarium resistance associated regions identified in this study are similar to those reported by (Paulino et al., 2021) who performed GWAS of Fusarium resistance in 205 common bean core collection obtained from the germplasm bank (BAG) of the Agronomic Institute (IAC, Campinas, SP, Brazil). However, (Paulino et al., 2021) identified additional SNPs on *Pv*01 for *Fop* resistance. Also, (Leitao et al., 2020) performed association mapping using a 162 Portuguese genotypes of common bean and identified nine significant Fusarium wilt-resistance associated SNP markers on chromosomes *Pv*04, *Pv*05, *Pv*07, and *Pv*08. Interestingly, QTLs were reported to be associated with other diseases of common bean in same chromosomes. For instance, (Perseguini et al., 2016) identified significant associations for resistances to anthracnose and angular leaf spot on chromosomes *Pv*03, *Pv*04, and *Pv*08. Another study by (Zia et al., 2022) found fourteen SNP associations for resistance to bacteria wilt resistance in common bean on chromosome *Pv*02, *Pv*04, *Pv*07, *Pv*08, *Pv*10, and *Pv*11. Further, the GWAS analysis by (Monteiro et al., 2021) indicated ten SNPs on chromosomes *Pv*01, *Pv*03, *Pv*06, *Pv*07, *Pv*08, *Pv*09, *Pv*10, and *Pv*01 to be associated with resistance to *Xanthomonas citri* Pv. *Fuscans in Phaseolus vulgaris*. These SNP associations reported in previous studies and those found in this study illustrate that these associations provide resistance against a wide range of pathogens. The discovered significant SNPs regulating Fusarium wilt resistance will be valuable for the improvement of elite cultivars through marker-assisted selection breeding programs.

Candidate gene for Fusarium wilt resistance

The characterization of genes aids in understanding disease resistance mechanisms in plants. This study identified seventeen candidate genes (Table 3). Few identified candidate genes such as Phvul.004G016532, Phvul.004G151100 contained receptors such as NB-ARC domain-containing disease resistance protein, zinc finger (Ran-binding) family protein, and leucine-rich repeat protein kinase family protein, respectively, on chromosomes *Pv*03, *Pv*04 and *Pv*09 (Table 3). Many plant disease resistances associated genes are reported to have a nucleotide-binding site and leucine-rich repeat (NBS-LRR) and Zinc finger domains (Paulino et al., 2021; Shi et al., 2022; Wu et al., 2017) and are comparable to the candidate genes found in this study. The NBS-LRR domain is known to be directly involved in the transduction of disease resistance signal in coordination with ATP or GTP and it has Kinase 1, Kinase 2, and Kinase 3, which are essential in recognizing pathogen effects on host cells (Meyers et al., 2003; Tameling et al., 2006).(Dufayard et al., 2017) also indicated that Leucine-rich repeat protein kinase family protein are significant mediators of interaction among cells to transmit developmental signals and environmental stimuli or to trigger defense or resistance against pathogens. Similarly, Zinc finger family proteins found in this study were previously reported to be useful in various metabolic pathways and are thought to provide stress response and defense against pathogens in plants and to be accountable for Jasmonic acid (JA)-dependent pathway (Paulino et al., 2021). The model genes with their SNPs established in this study will increase the number of useful markers to enable marker-assisted breeding in common bean to be successful.

Genomic prediction for genomic selection of Fusarium Wilt resistance

GP was performed in three SNP sets (m32, r32, and 4740SNP) by five GP models (rrBLUP, BA, BB, BRR, and BL) in this study. The randomly selected 32 SNP set had the lowest PA value. The highest PA values were obtained when the 32 GWAS-derived associated SNP markers were used followed by all 4740 SNP markers for both *Fop* race resistances. When examining the five models used, a similar trend PA was observed for both *Fop* race 1 and race 4 resistances (Supplementary Table S7; Figure 4), indicating the GWAS-derived SNP set would increase the PA values and the more SNP number would also increase the PA value. The similar trend was previously reported for other traits in different plants (W. S. Ravelombola et al., 2019; Shi et al., 2022). (W. S. Ravelombola et al., 2019) reported that the highest PA (r-value) of >0.5 (50%) was observed in the set of GWAS-derived SNPs for reduced soybean chlorophyll content associated with soybean cyst nematode tolerance. (Shi et al., 2022) also reported that the GWAS-derived SNP set had PA (r-value) greater than 0.7 for white rust resistance in USDA GRIN spinach germplasm.

Conclusion

In this study, GWAS was performed for Fusarium wilt resistance in 157 USDA common bean accessions based on phenotypic data reported by (Brick et al., 2006) and genotyped using BARCBean6K_3 Infinium BeadChips (Kuzay et al., 2020; Song et al., 2013). Twenty-one accessions were observed to be highly resistant to either *Fop* race 1 or race 4 with a score of 3 or less. Five common bean accessions, PI 209482, PI 308908, PI 309877, PI 288016, and PI 310842 were resistant to both races, showing their importance as parents in the common bean breeding program to develop Fusarium wilt resistant lines. Thirty-nine SNP markers on chromosome *Pv*03, *Pv*04, *Pv*05, *Pv*07, *Pv*08, *Pv*9, *Pv*10 and *Pv*11 and 17 candidate genes were identified for Fop resistance. GP was performed for *Fop* race 1 and race 4 resistance and the PA (r_{100}_value) ranging from 0.26 to 0.55 was observed. The SNP markers and associated genes for *Fop* races can be used to enhance Fusarium wilt resistance in common bean.

References

Abdelhaleim, M. S., Rahimi, M., & Okasha, S. A. (2022). Assessment of drought tolerance indices in faba bean genotypes under different irrigation regimes. *Open Life Sciences*, *17*(1), 1462–1472. https://doi.org/10.1515/biol-2022-0520

Aghaie, P., Hosseini Tafreshi, S. A., Ebrahimi, M. A., & Haerinasab, M. (2018). Tolerance evaluation and clustering of fourteen tomato cultivars grown under mild and severe drought conditions. *Scientia Horticulturae*, *232*, 1–12. https://doi.org/10.1016/j.scienta.2017.12.041

Ahmadikhah, A., & Marufinia, • Amir. (n.d.). *Effect of reduced plant height on drought tolerance in rice*. https://doi.org/10.1007/s13205-016-0542-3

Albrecht, T., Wimmer, V., Auinger, H. J., Erbe, M., Knaak, C., Ouzunova, M., Simianer, H., & Schön, C. C. (2011). Genome-based prediction of testcross values in maize. *Theoretical and Applied Genetics*, *123*(2), 339–350. https://doi.org/10.1007/s00122-011-1587-7

Alidu, M. S., Asante, I. K., Tongoona, P., Ofori, K., Danquah, A., & Padi, F. K. (2019). Development and screening of cowpea recombinant inbred lines for seedling drought tolerance. *Journal of Plant Breeding and Crop Science*, *11*(1), 1–10. https://doi.org/10.5897/jpbcs2018.0768

Alves-Santos, F. M., Cordeiro-Rodrigues, L., Sayagués, J. M., Martín-Domínguez, R., García-Benavides, P., Crespo, M. C., Díaz-Mínguez, J. M., & Eslava, A. P. (2002). Pathogenicity and race characterization of Fusarium oxysporum f. sp. phaseoli isolates from Spain and Greece. *Plant Pathology*, *51*(5), 605–611. https://doi.org/10.1046/j.1365-3059.2002.00745.x

Arie, T. (2019). Fusarium diseases of cultivated plants, control, diagnosis, and molecular and genetic studies. *Journal of Pesticide Science*, *44*(4). https://doi.org/10.1584/JPESTICS.J19-03

Assefa, T., Assibi Mahama, A., Brown, A. V., Cannon, E. K. S., Rubyogo, J. C., Rao, I. M., Blair, M. W., & Cannon, S. B. (2019). A review of breeding objectives, genomic resources, and marker-assisted methods in common bean (Phaseolus vulgaris L.). In *Molecular Breeding* (Vol. 39, Issue 2). Springer Netherlands. https://doi.org/10.1007/s11032-018-0920-0

Bao, Y., Vuong, T., Meinhardt, C., Tiffin, P., Denny, R., Chen, S., Nguyen, H. T., Orf, J. H., & Young, N. D. (2014). Potential of Association Mapping and Genomic Selection to Explore PI 88788 Derived Soybean Cyst Nematode Resistance. *The Plant Genome*, *7*(3). https://doi.org/10.3835/plantgenome2013.11.0039

Baret, F., Madec, S., Irfan, K., Lopez, J., Comar, A., Hemmerlé, M., Dutartre, D., Praud, S., & Tixier, M. H. (2018). Leaf-rolling in maize crops: from leaf scoring to canopy-level measurements for phenotyping. *Journal of Experimental Botany*, *69*(10), 2705–2716. https://doi.org/10.1093/jxb/ery071

Barili, L. D., Vale, N. M. do, Silva, F. F. e, Carneiro, J. E. de S., Oliveira, H. R. de, Vianello, R. P., Valdisser, P. A. M. R., & Nascimento, M. (2018). Genome prediction accuracy of common bean via Bayesian models. *Ciência Rural*, *48*(8). https://doi.org/10.1590/0103-8478cr20170497

Barone, A., Chiusano, M. L., Ercolano, M. R., Giuliano, G., Grandillo, S., & Frusciante, L. (2008). Structural and Functional Genomics of Tomato. *International Journal of Plant Genomics*, *12*. https://doi.org/10.1155/2008/820274

Bartoli, C., & Roux, F. (2017). Genome-wide association studies in plant pathosystems: Toward an ecological genomics approach. In *Frontiers in Plant Science* (Vol. 8). Frontiers Media S.A. https://doi.org/10.3389/fpls.2017.00763

Batista, R. O., Silva, L. C., Moura, L. M., Souza, M. H., Carneiro, P. C. S., Filho, J. L. S. C., & de Souza Carneiro, J. E. (2017). Inheritance of resistance to fusarium wilt in common bean. *Euphytica*, *213*(7). https://doi.org/10.1007/s10681-017-1925-1

Blair, M. W. (2013). Mineral biofortification strategies for food staples: The example of common bean. In *Journal of Agricultural and Food Chemistry* (Vol. 61, Issue 35, pp. 8287–8294). https://doi.org/10.1021/jf400774y

Bradbury, P. J., Zhang, Z., Kroon, D. E., Casstevens, T. M., Ramdoss, Y., & Buckler, E. S. (2007). TASSEL: Software for association mapping of complex traits in diverse samples. *Bioinformatics*, *23*(19), 2633–2635. https://doi.org/10.1093/bioinformatics/btm308

Brick, M. A., Byrne, P. F., Schwartz, H. F., Ogg, J. B., Otto, K., Fall, A. L., & Gilbert, J. (2006). Reaction to three races of fusarium wilt in the Phaseolus vulgaris core collection. *Crop Science*, *46*(3), 1245–1252. https://doi.org/10.2135/cropsci2005.06-0102

Burton-Freeman, B., & Reimers, K. (2011). Tomato Consumption and Health: Emerging Benefits. In *American Journal of Lifestyle Medicine* (Vol. 5, Issue 2, pp. 182–191). https://doi.org/10.1177/1559827610387488

Cardoso, J., Silva, T. R., Abboud, A. C. de S., Finatto, T., Woyann, L. G., & Vargas, T. de O. (2022a). Selection of drought-tolerant tomato during the vegetative stage. *COLLOQUIUM AGRARIAE*, *18*(2), 42–53. https://doi.org/10.5747/ca.2022.v18.n2.a487

Cardoso, J., Silva, T. R., Abboud, A. C. de S., Finatto, T., Woyann, L. G., & Vargas, T. de O. (2022b). Selection of drought-tolerant tomato during the vegetative stage. *COLLOQUIUM AGRARIAE*, *18*(2). https://doi.org/10.5747/ca.2022.v18.n2.a487

Carolina, A., Galdino, S., De Freitas, M. B., De Borba, M. C., & Stadnik, M. J. (n.d.). *Phenolic and flavonoid content in roots and hypocotyls of resistant and susceptible bean plants (Phaseolus vulgaris L.) during early stage of colonization by Fusarium oxysporum f. sp. phaseoli*. https://doi.org/10.1007/s40858-021-00440-6/Published

Chandra, A., & Dubey, A. A. (2009). *Assessment of ploidy level on stress tolerance of Cenchrus species based on leaf photosynthetic characteristics*. https://doi.org/10.1007/s11738-009-0317-0

Chandra Rai, A., Singh, M., & Shah, K. (2012). Effect of water withdrawal on formation of free radical, proline accumulation and activities of antioxidant enzymes in ZAT12-transformed transgenic tomato plants. *Plant Physiology and Biochemistry*, *61*, 108–114. https://doi.org/10.1016/j.plaphy.2012.09.010

Conti, V., Mareri, L., Faleri, C., Nepi, M., Romi, M., Cai, G., & Cantini, C. (2019). Drought stress affects the response of italian local tomato (solanum lycopersicum L.) varieties in a genotype-dependent manner. *Plants*, *8*(9). https://doi.org/10.3390/plants8090336

Cross, H., Brick, M. A., Schwartz, H. F., Panella, L. W., & Byrne, P. F. (2000). Inheritance of resistance to fusarium wilt in two common bean races. *Crop Science*, *40*(4), 954–958. https://doi.org/10.2135/cropsci2000.404954x

Crossa, J., Pérez-Rodríguez, P., Cuevas, J., Montesinos-López, O., Jarquín, D., de los Campos, G., Burgueño, J., González-Camacho, J. M., Pérez-Elizalde, S., Beyene, Y., Dreisigacker, S., Singh, R., Zhang, X., Gowda, M., Roorkiwal, M., Rutkoski, J., & Varshney, R. K. (2017). Genomic Selection in Plant Breeding: Methods, Models, and Perspectives. In *Trends in Plant Science* (Vol. 22, Issue 11, pp. 961–975). Elsevier Ltd. https://doi.org/10.1016/j.tplants.2017.08.011

Cruz De Carvalho, M. H. (2008). Plant Signaling & Behavior Drought stress and reactive oxygen species production, scavenging and signaling. *Plant Signaling & Behavior*, *3*(3), 156–165. https://doi.org/10.4161/psb.3.3.5536

Cui, Q., Xiong, H., Yufeng, Y., Eaton, S., Imamura, S., Santamaria, J., Ravelombola, W., Mason, R. E., Wood, L., Mozzoni, L. A., & Shi, A. (2020a). Evaluation of drought tolerance in Arkansas Cowpea lines at seedling stage. *HortScience*, *55*(7), 1132–1143. https://doi.org/10.21273/HORTSCI15036-20

Cui, Q., Xiong, H., Yufeng, Y., Eaton, S., Imamura, S., Santamaria, J., Ravelombola, W., Mason, R. E., Wood, L., Mozzoni, L. A., & Shi, A. (2020b). Evaluation of drought tolerance in Arkansas Cowpea lines at seedling stage. *HortScience*, *55*(7), 1132–1143. https://doi.org/10.21273/HORTSCI15036-20

De Ron, A. M., González, A. M., Rodiño, A. P., Santalla, M., Godoy, L., & Papa, R. (2016). History of the common bean crop: Its evolution beyond its areas of origin and domestication. *Arbor*, *192*(779). https://doi.org/10.3989/arbor.2016.779n3007

Deng, Y., Ning, Y., Yang, D. L., Zhai, K., Wang, G. L., & He, Z. (2020). Molecular Basis of Disease Resistance and Perspectives on Breeding Strategies for Resistance Improvement in Crops. *Molecular Plant*, *13*(10), 1402–1419. https://doi.org/10.1016/J.MOLP.2020.09.018

Dhaliwal, M. S. (n.d.). *AVRDC tomato in sub-Saharan Africa Resistance Breeding View project Breeding for CMS lines of chilli and their utilization in hybrids development View project*. https://www.researchgate.net/publication/261062446

Diagnostic manual for plant diseases in Vietnam. (n.d.).

Diaz, L. M., Arredondo, V., Ariza-Suarez, D., Aparicio, J., Buendia, H. F., Cajiao, C., Mosquera, G., Beebe, S. E., Mukankusi, C. M., & Raatz, B. (2021). Genetic Analyses and Genomic Predictions of Root Rot Resistance in Common Bean Across Trials and Populations. *Frontiers in Plant Science*, *12*. https://doi.org/10.3389/fpls.2021.629221

Divina De Toledo-Souza, E., Marques Da Silveira, P., Corrêa Café-Filho, A., & Lobo, M. (n.d.). Fusarium wilt incidence and common bean yield according to the preceding crop and the soil tillage system. In *Pesq. agropec. bras* (Issue 8).

Dufayard, J. F., Bettembourg, M., Fischer, I., Droc, G., Guiderdoni, E., Périn, C., Chantret, N., & Diévart, A. (2017). New insights on Leucine-Rich repeats receptor-like kinase orthologous relationships in angiosperms. *Frontiers in Plant Science*, *8*. https://doi.org/10.3389/fpls.2017.00381

Elshire, R. J., Glaubitz, J. C., Sun, Q., Poland, J. A., Kawamoto, K., Buckler, E. S., & Mitchell, S. E. (2011). A robust, simple genotyping-by-sequencing (GBS) approach for high diversity species. *PLoS ONE*, *6*(5). https://doi.org/10.1371/journal.pone.0019379

Engelbrecht, B. M. J., Tyree, M. T., & Kursar, T. A. (2007). Printed in the United Kingdom SHORT COMMUNICATION Visual assessment of wilting as a measure of leaf water potential and seedling drought survival. *Journal of Tropical Ecology*, *23*, 497–500. https://doi.org/10.1017/S026646740700421X

Fall, A. L., Byrne, P. F., Jung, G., Coyne, D. P., Brick, M. A., & Schwartz, H. F. (2001a). Detection and mapping of a major locus for fusarium wilt resistance in common bean. *Crop Science*, *41*(5), 1494–1498. https://doi.org/10.2135/cropsci2001.4151494x

Fall, A. L., Byrne, P. F., Jung, G., Coyne, D. P., Brick, M. A., & Schwartz, H. F. (2001b). Detection and mapping of a major locus for fusarium wilt resistance in common bean. *Crop Science*, *41*(5), 1494–1498. https://doi.org/10.2135/cropsci2001.4151494x

Farooq, M., Wahid, A., Kobayashi, N., Fujita, D., & Basra, S. M. A. (2009). Plant drought stress: Effects, mechanisms and management. In *Agronomy for Sustainable Development* (Vol. 29, Issue 1, pp. 185–212). https://doi.org/10.1051/agro:2008021

Francini, A., & Sebastiani, L. (2019). *horticulturae Abiotic Stress Effects on Performance of Horticultural Crops*. https://doi.org/10.3390/horticulturae5040067

FUSARIUM WILT (YELLOWS). (n.d.).

Gerik, J. S., & Hanson, B. D. (2011). Drip application of methyl bromide alternative chemicals for control of soilborne pathogens and weeds. *Pest Management Science*, *67*(9), 1129–1133. https://doi.org/10.1002/ps.2162

Ghebremariam, K. M., Liang, Y., Li, C., Li, Y., & Qin, L. (2013). Screening of Tomato Inbred-Lines for Drought Tolerance at Germination and Seedling Stage. *Journal of Agricultural Science*, *5*(11). https://doi.org/10.5539/jas.v5n11p93

Glaubitz, J. C., Casstevens, T. M., Lu, F., Harriman, J., 1¤, R. J. E., Sun, Q., & Buckler, E. S. (2014). *TASSEL-GBS: A High Capacity Genotyping by Sequencing Analysis Pipeline*. https://doi.org/10.1371/journal.pone.0090346

González-Guerrero, M., Grusak, M. A., De Ron, A. M., Mendoza-Cozatl, D. G., Valdés-López, O., Castro-Guerrero, N. A., & Isidra-Arellano, M. C. (2016). *Common Bean: A Legume Model on the Rise for Unraveling Responses and Adaptations to Iron, Zinc, and Phosphate Deficiencies*. https://doi.org/10.3389/fpls.2016.00600

Gordon, T. R. (2017). Fusarium oxysporum and the Fusarium Wilt Syndrome. *Https://Doi.Org/10.1146/Annurev-Phyto-080615-095919*, *55*, 23–39. https://doi.org/10.1146/ANNUREV-PHYTO-080615-095919

Handy, S. M., Demir, E., Hutchins, D. A., Portune, K. J., Whereat, E. B., Hare, C. E., Rose, J. M., Warner, M., Farestad, M., Cary, S. C., & Coyne, K. J. (2008). Using quantitative real-time PCR to study competition and community dynamics among Delaware Inland Bays harmful algae in field and laboratory studies. *Harmful Algae*, *7*(5), 599–613. https://doi.org/10.1016/j.hal.2007.12.018

Hassan khan, S., Hassan Khan, S., Khan, A., Litaf, U., Sattar Shah, A., Ali Khan, M., Bilal, M., & Usman Ali, M. (2015). Effect of Drought Stress on Tomato cv. *Bombino. J Food Process Technol*, *6*, 465. https://doi.org/10.4172/2157-7110.1000465

Holland, J. B., Carolina, N., Nyquist, W. E., & Lafayette, W. (2003). Estimating and Interpreting Heritability for Plant Breeding : An Update. In *Plant Breeding* (Vol. 22).

Huang, H., Ullah, F., Zhou, D. X., Yi, M., & Zhao, Y. (2019). Mechanisms of ROS regulation of plant development and stress responses. In *Frontiers in Plant Science* (Vol. 10). Frontiers Media S.A. https://doi.org/10.3389/fpls.2019.00800

Huang, M., Liu, X., Zhou, Y., Summers, R. M., & Zhang, Z. (2019a). BLINK: A package for the next level of genome-wide association studies with both individuals and markers in the millions. *GigaScience*, *8*(2). https://doi.org/10.1093/gigascience/giy154

Huang, M., Liu, X., Zhou, Y., Summers, R. M., & Zhang, Z. (2019b). BLINK: A package for the next level of genome-wide association studies with both individuals and markers in the millions. *GigaScience*, *8*(2). https://doi.org/10.1093/gigascience/giy154

Iqbal, M. J., Mamidi, S., Ahsan, R., Kianian, S. F., Coyne, C. J., Hamama, A. A., Narina, S. S., & Bhardwaj, H. L. (2012). Population structure and linkage disequilibrium in Lupinus albus L. germplasm and its implication for association mapping. *Theoretical and Applied Genetics*, *125*(3), 517–530. https://doi.org/10.1007/s00122-012-1850-6

Jha, U. C., Bohra, A., Pandey, S., & Parida, S. K. (2020). Breeding, Genetics, and Genomics Approaches for Improving Fusarium Wilt Resistance in Major Grain Legumes. In *Frontiers in Genetics* (Vol. 11). Frontiers Media S.A. https://doi.org/10.3389/fgene.2020.01001

Kadioglu, A., Terzi, R., Saruhan, N., & Saglam, A. (2012). Current advances in the investigation of leaf rolling caused by biotic and abiotic stress factors. *Plant Science*, *182*(1), 42–48. https://doi.org/10.1016/J.PLANTSCI.2011.01.013

Kahlau, S., & Bock, R. (n.d.). *Plastid Transcriptomics and Translatomics of Tomato Fruit Development and Chloroplast-to-Chromoplast Differentiation: Chromoplast Gene Expression Largely Serves the Production of a Single Protein W OA*. https://doi.org/10.1105/tpc.107.055202

Kaler, A. S., Gillman, J. D., Beissinger, T., Purcell, L. C., Maccaferri, M., Uptmoor, R., & Cannon, S. B. (2020). *Comparing Different Statistical Models and Multiple Testing Corrections for Association Mapping in Soybean and Maize*. *10*, 1. https://doi.org/10.3389/fpls.2019.01794

Kamanga, R. M. (2020). Screening and differential physiological responses of tomato (Solanum lycopersicum L.) to drought stress. In *Plant Physiology Reports* (Vol. 25, Issue 3, pp. 472–482). Springer. https://doi.org/10.1007/s40502-020-00532-6

Karavidas, I., Ntatsi, G., Vougeleka, V., Karkanis, A., Ntanasi, T., Saitanis, C., Agathokleous, E., Ropokis, A., Sabatino, L., Tran, F., Iannetta, P. P. M., & Savvas, D. (2022). Agronomic Practices to Increase the Yield and Quality of Common Bean (Phaseolus vulgaris L.): A Systematic Review. In *Agronomy* (Vol. 12, Issue 2). MDPI. https://doi.org/10.3390/agronomy12020271

Kumar, D., Kumar, R., Kumar, S., Bhardwaj, M. L., Thakur, M. C., Kumar, R., Thakur, K. S., Dogra, B. S., Vikram, A., Thakur, A., & Kumar, P. (2013). Genetic Variability, Correlation and Path Coefficient Analysis in Tomato. *International Journal of Vegetable Science*, *19*(4), 313–323. https://doi.org/10.1080/19315260.2012.726701

Kumar, P. A., Reddy, N. N., & Lakshmi, N. J. (2017). PEG Induced Screening for Drought Tolerance in Tomato Genotypes. *International Journal of Current Microbiology and Applied Sciences*, *6*(7), 168–181. https://doi.org/10.20546/ijcmas.2017.607.020

Kuzay, S., Hamilton-Conaty, P., Palkovic, A., & Gepts, P. (2020). Is the USDA core collection of common bean representative of genetic diversity of the species, as assessed by SNP diversity? *Crop Science*, *60*(3), 1398–1414. https://doi.org/10.1002/csc2.20032

Legarra, A., Robert-Granié, C., Croiseau, P., Guillaume, F., & Fritz, S. (2011). Improved Lasso for genomic selection. *Genetics Research*, *93*(1), 77–87. https://doi.org/10.1017/S0016672310000534

Leitao, S. T., Malosetti, M., Song, Q., Van Eeuwijk, F., Rubiales, D., & Vaz Patto, M. C. (2020). Natural variation in Portuguese common bean germplasm reveals new sources of resistance against fusarium oxysporum f. sp. phaseoli and resistance-associated candidate genes. *Phytopathology*, *110*(3), 633–647. https://doi.org/10.1094/PHYTO-06-19-0207-R

Li, J., Xiaoya, 1☯, 1☯, T., Li, L., Mao, L., Luo, Z., Ullah Khan, Z., & Ying, T. (2016). *Comprehensive RNA-Seq Analysis on the Regulation of Tomato Ripening by Exogenous Auxin*. https://doi.org/10.1371/journal.pone.0156453

Liang, G., Liu, J., Zhang, J., & Guo, J. (2020). Effects of drought stress on photosynthetic and physiological parameters of tomato. *Journal of the American Society for Horticultural Science*, *145*(1), 12–17. https://doi.org/10.21273/JASHS04725-19

Lipka, A. E., Tian, F., Wang, Q., Peiffer, J., Li, M., Bradbury, P. J., Gore, M. A., Buckler, E. S., & Zhang, Z. (2012). GAPIT: Genome association and prediction integrated tool. *Bioinformatics*, *28*(18), 2397–2399. https://doi.org/10.1093/bioinformatics/bts444

Liu, X., Huang, M., Fan, B., Buckler, E. S., & Zhang, Z. (2016). Iterative Usage of Fixed and Random Effect Models for Powerful and Efficient Genome-Wide Association Studies. *PLoS Genetics*, *12*(2). https://doi.org/10.1371/journal.pgen.1005767

Lombardi, M., Materne, M., Cogan, N. O. I., Rodda, M., Daetwyler, H. D., Slater, A. T., Forster, J. W., & Kaur, S. (2014). Assessment of genetic variation within a global collection of lentil (Lens culinaris Medik.) cultivars and landraces using SNP markers. *BMC Genetics*, *15*(1). https://doi.org/10.1186/s12863-014-0150-3

Massimi, M. (2021). Tomato (Lycopersicon esculentum Mill.) anatomical, physiological, biochemical and production responses to drought stress - A mini-review essay. *International Journal of Horticultural Science*, *27*. https://doi.org/10.31421/ijhs/27/2021/8439

McClean, P. E., Terpstra, J., McConnell, M., White, C., Lee, R., & Mamidi, S. (2012). Population structure and genetic differentiation among the USDA common bean (Phaseolus vulgaris L.) core collection. *Genetic Resources and Crop Evolution*, *59*(4), 499–515. https://doi.org/10.1007/s10722-011-9699-0

Meuwissen, T. H. E., Hayes, B. J., & Goddard, M. E. (2001). *Prediction of Total Genetic Value Using Genome-Wide Dense Marker Maps*. https://academic.oup.com/genetics/article/157/4/1819/6048353

Meyers, B. C., Kozik, A., Griego, A., Kuang, H., & Michelmore, R. W. (2003). Genome-wide analysis of NBS-LRR-encoding genes in Arabidopsis. *Plant Cell*, *15*(4), 809–834. https://doi.org/10.1105/tpc.009308

Mihajlovic, M., Rekanovic, E., Hrustic, J., Grahovac, M., & Tanovic, B. (2021). In vitro and in vivo toxicity of fungicides and biofungicides for the control of verticillium and fusarium wilt of pepper. *Pesticidi i Fitomedicina*, *36*(1), 23–34. https://doi.org/10.2298/pif2101023m

Mokhtar, M. M. E.-M. N. S. (2014). *Bio-compost Application for Controlling Soil-borne Plant Pathogens –A Review*. *4*(1).

Monteiro, A. L. R., Pantaleão, A. S. L., Badel, J. L., Soares, P. H. M., Carneiro, V. Q., Carneiro, P. C. S., & Carneiro, J. E. S. (2021). Genome-wide association study (GWAS) of Phaseolus vulgaris resistance to Xanthomonas citri pv. fuscans. *Plant Pathology*, *70*(7), 1733–1744. https://doi.org/10.1111/ppa.13399

Mou, B., Ravelombola, W., Shi, A., Qin, J., Weng, Y., Bhattarai, G., Zia, B., & Zhou, W. (2018). Investigation on various aboveground traits to identify drought tolerance in cowpea seedlings. *HortScience*, *53*(12), 1757–1765. https://doi.org/10.21273/HORTSCI13278-18

Nasar, S., Shaheen, H., Murtaza, G., Tinghong, T., Arfan, M., & Idrees, M. (2023). Socioeconomic Evaluation of Common Bean (Phaseolus vulgaris L.) Cultivation in Providing Sustainable Livelihood to the Mountain Populations of Kashmir Himalayas. *Plants*, *12*(1). https://doi.org/10.3390/plants12010213

Nay, M. M., Souza, T. L. P. O., Raatz, B., Mukankusi, C. M., Pastor-Corrales, M. A., Abreu, A. F. B., & Melo, L. C. (2019). A review of angular leaf spot resistance in common bean. In *Crop Science* (Vol. 59, Issue 4, pp. 1376–1391). Crop Science Society of America. https://doi.org/10.2135/cropsci2018.09.0596

Okungbowa, F. I., & Shittu, H. (2012). *Fusarium Wilts: An Overview In vitro screening of some selected nanoparticles against phytopathogens View project 1. Multiple drug resistant bacteria and integron gene as a contributory factor to multiple drug resistance and production of bio-pharmaceutics and industrial proteins in plants and other expression systems. View project*. https://www.researchgate.net/publication/292243135

Oliveira Batista, R., Cruz E Oliveira, A. M., Lennon, J., Silva, O., Nicoli, A., Crescêncio, P., Carneiro, S., Eustáquio De Sousa Carneiro, J., Júnior, P., & Vieira De Queiroz, M. (2016). Resistance to Fusarium wilt in common bean ARTICLE. *Crop Breeding and Applied Biotechnology*, *16*, 226–233. https://doi.org/10.1590/1984

O'Toole, J. C., & Moya, T. B. (1978). Genotypic Variation in Maintenance of Leaf Water Potential in Rice1. *Crop Science*, *18*(5), 873–876. https://doi.org/10.2135/CROPSCI1978.0011183X001800050050X

Pang, Y., Wu, Y., Liu, C., Li, W., St. Amand, P., Bernardo, A., Wang, D., Dong, L., Yuan, X., Zhang, H., Zhao, M., Li, L., Wang, L., He, F., Liang, Y., Yan, Q., Lu, Y., Su, Y., Jiang, H., … Liu, S. (2021). High-resolution genome-wide association study and genomic prediction for disease resistance and cold tolerance in wheat. *Theoretical and Applied Genetics*, *134*(9), 2857–2873. https://doi.org/10.1007/s00122-021-03863-6

Panth, M., Hassler, S. C., & Baysal-Gurel, F. (2020). Methods for management of soilborne diseases in crop production. In *Agriculture (Switzerland)* (Vol. 10, Issue 1). MDPI AG. https://doi.org/10.3390/agriculture10010016

Pathan, S. M., Lee, J. D., Sleper, D. A., Fritschi, F. B., Sharp, R. E., Carter, T. E., Nelson, R. L., King, C. A., Schapaugh, W. T., Ellersieck, M. R., Nguyen, H. T., & Shannon, J. G. (2014). Two soybean plant introductions display slow leaf wilting and reduced yield loss under drought. *Journal of Agronomy and Crop Science*, *200*(3), 231–236. https://doi.org/10.1111/jac.12053

Pathania, A., Sharma, S. K., & Sharma, P. N. (2014a). Common bean. In *Broadening the Genetic Base of Grain Legumes* (pp. 11–50). Springer India. https://doi.org/10.1007/978-81-322-2023-7_2

Pathania, A., Sharma, S. K., & Sharma, P. N. (2014b). Common bean. In *Broadening the Genetic Base of Grain Legumes* (pp. 11–50). Springer India. https://doi.org/10.1007/978-81-322-2023-7_2

Paulino, J. F. de C., de Almeida, C. P., Bueno, C. J., Song, Q., Fritsche-Neto, R., Carbonell, S. A. M., Chiorato, A. F., & Benchimol-Reis, L. L. (2021). Genome-wide association study reveals genomic regions associated with fusarium wilt resistance in common bean. *Genes*, *12*(5). https://doi.org/10.3390/genes12050765

Pedrosa-Harand, A., Kami, J., Gepts, P., Geffroy, V., & Schweizer, D. (2009). Cytogenetic mapping of common bean chromosomes reveals a less compartmentalized small-genome plant species. *Chromosome Research*, *17*(3), 405–417. https://doi.org/10.1007/s10577-009-9031-4

Pereira, A. (2016). *F1000Research*. https://doi.org/10.12688/f1000research.7678.1

Perseguini, J. M. K. C., Oblessuc, P. R., Rosa, J. R. B. F., Gomes, K. A., Chiorato, A. F., Carbonell, S. A. M., Garcia, A. A. F., Vianello, R. P., & Benchimol-Reis, L. L. (2016). Genome-Wide Association Studies of Anthracnose and Angular Leaf Spot Resistance in Common Bean (Phaseolus vulgaris L.). *PLoS ONE*, *11*(3). https://doi.org/10.1371/journal.pone.0150506

Pervez, M. A., Ayub, C. M., Khan, H. A., Shahid, M. A., & Ashraf, I. (2009). EFFECT OF DROUGHT STRESS ON GROWTH, YIELD AND SEED QUALITY OF TOMATO (Lycopersicon esculentum L.). *Pak. J. Agri. Sci*, *46*(3).

Pungulani, L. L. M., Millner, J. P., Williams, W. M., & Banda, M. (2013). Improvement of leaf wilting scoring system in cowpea (Vigna unguiculata (L) Walp.): From qualitative scale to quantitative index. *Australian Journal of Crop Science*, *7*(9).

Quinet, M., Angosto, T., Yuste-Lisbona, F. J., Blanchard-Gros, R., Bigot, S., Martinez, J. P., & Lutts, S. (2019). Tomato Fruit Development and Metabolism. In *Frontiers in Plant Science* (Vol. 10). Frontiers Media S.A. https://doi.org/10.3389/fpls.2019.01554

Rahman, M. Z., Ahmad, K., Kutawa, A. B., Siddiqui, Y., Saad, N., Geok Hun, T., Hata, E. M., & Hossain, M. I. (2021). Biology, diversity, detection and management of fusarium oxysporum f. Sp. niveum causing vascular wilt disease of watermelon (citrullus lanatus): A review. In *Agronomy* (Vol. 11, Issue 7). MDPI AG. https://doi.org/10.3390/agronomy11071310

Rahman, S. M. L., Nawata, E., & Sakuratani, T. (1998). Evaluation of Drought Tolerance of Tomato Cultivars. In *Jpn. J. Trop. Agr* (Vol. 42, Issue 1).

Ranjan, A., Ichihashi, Y., & Sinha, N. R. (2012). The tomato genome: Implications for plant breeding, genomics and evolution. *Genome Biology*, *13*(8). https://doi.org/10.1186/gb-2012-13-8-167

Ravelombola, W., Dong, L., Barickman, T. C., Xiong, H., Olaoye, D., Bhattarai, G., Zia, B., Alshaya, H., Alatawi, I., & Shi, A. (2021). Evaluation of salt tolerance in cowpea at seedling stage. *Euphytica*, *217*(6). https://doi.org/10.1007/s10681-021-02832-w

Ravelombola, W. S., Qin, J., Shi, A., Nice, L., Bao, Y., Lorenz, A., Orf, J. H., Young, N. D., & Chen, S. (2019). Genome-wide association study and genomic selection for soybean chlorophyll content associated with soybean cyst nematode tolerance. *BMC Genomics*, *20*(1). https://doi.org/10.1186/s12864-019-6275-z

Ravelombola, W., Shi, A., Chen, S., Xiong, H., Yang, Y., Cui, Q., Olaoye, D., & Mou, B. (2020a). Evaluation of cowpea for drought tolerance at seedling stage. *Euphytica*, *216*(8). https://doi.org/10.1007/s10681-020-02660-4

Ravelombola, W., Shi, A., Chen, S., Xiong, H., Yang, Y., Cui, Q., Olaoye, D., & Mou, B. (2020b). Evaluation of cowpea for drought tolerance at seedling stage. *Euphytica*, *216*(8). https://doi.org/10.1007/s10681-020-02660-4

Ravelombola, W., Shi, A., & Huynh, B. L. (2021). Loci discovery, network-guided approach, and genomic prediction for drought tolerance index in a multi-parent advanced generation intercross (MAGIC) cowpea population. *Horticulture Research*, *8*(1). https://doi.org/10.1038/s41438-021-00462-w

Reinprecht, Y., Schram, L., Dé Ric Marsolais, F., Smith, T. H., Hill, B., Pauls, K. P., Mastrorilli, M., Abdelhamid, M. T., & Saia, S. (2020). *Effects of Nitrogen Application on Nitrogen Fixation in Common Bean Production*. *11*. https://doi.org/10.3389/fpls.2020.01172

Rendón-Anaya, M., Montero-Vargas, J. M., Saburido-Álvarez, S., Vlasova, A., Capella-Gutierrez, S., Ordaz-Ortiz, J. J., Aguilar, O. M., Vianello-Brondani, R. P., Santalla, M., Delaye, L., Gabaldón, T., Gepts, P., Winkler, R., Guigó, R., Delgado-Salinas, A., & Herrera-Estrella, A. (2017). Genomic history of the origin and domestication of common bean unveils its closest sister species. *Genome Biology*, *18*(1). https://doi.org/10.1186/s13059-017-1190-6

Ripoll, J., Urban, L., Staudt, M., Lopez-Lauri, F., Bidel, L. P. R., & Bertin, N. (2014). Water shortage and quality of fleshy fruits-making the most of the unavoidable. In *Journal of Experimental Botany* (Vol. 65, Issue 15, pp. 4097–4117). Oxford University Press. https://doi.org/10.1093/jxb/eru197

Rochette, N. C., Rivera-Colón, A. G., & Catchen, J. M. (2019). Stacks 2: Analytical methods for paired-end sequencing improve RADseq-based population genomics. *Molecular Ecology*, *28*(21). https://doi.org/10.1111/mec.15253

Romeroetal.2013-2. (n.d.).

Roux, F., & Frachon, L. (2022). A Genome-Wide Association study in Arabidopsis thaliana to decipher the adaptive genetics of quantitative disease resistance in a native heterogeneous environment. *PLoS ONE*, *17*(10 October). https://doi.org/10.1371/journal.pone.0274561

Sahu, V., & Chandel, G. (2016). *Assessment of genetic diversity in Cherry tomato (Solanum lycopersicum L. var. CerasIforme) genotypes using SSR markers*. https://www.researchgate.net/publication/316506944

Sakya, A. T., Sulistyaningsih, E., Indradewa, D., & Purwanto, B. H. (2018). Physiological characters and tomato yield under drought stress. *IOP Conference Series: Earth and Environmental Science*, *200*(1). https://doi.org/10.1088/1755-1315/200/1/012043

Salgado, M. O., Schwartz, H. F., & Brick, M. A. (1995). Inheritance of resistance to a Colorado race of Fusarium oxysporum f. sp. phaseoli in common beans. *Plant Disease*, *79*(3). https://doi.org/10.1094/PD-79-0279

Salgotra, R. K., & Chauhan, B. S. (2023). Genetic Diversity, Conservation, and Utilization of Plant Genetic Resources. In *Genes* (Vol. 14, Issue 1). MDPI. https://doi.org/10.3390/genes14010174

Saqlan Naqvi, S. M., Athar, H., & Waheed, A. (2014). Screening and selection of tomato genotypes/cultivars for drought tolerance using multivariate analysis Role of Salicylic Acid in regulating salinity induced stress in Raphanus sativus View project Development of Salt Tolerance in Lentil and chickpea View project SEE PROFILE. In *Article in Pakistan Journal of Botany*. https://www.researchgate.net/publication/281673958

Schwartz, H., Panella, L., Brick, M., & Byrne, P. (n.d.). *Fusarium Wilt & Yellows of Sugar Beet & Dry Bean*. https://doi.org/10.1111/j/1365-3059.2010.02394.x

Sepehri, A., & Reza Golparvar, A. (2011). The Effect of Drought Stress on Water Relations, Chlorophyll Content and Leaf Area in Canola Cultivars (Brassica napus L.). *Electronic Journal of Biology*, *7*(3), 49–53.

Shahinnia, F., Geyer, M., Schürmann, F., Rudolphi, S., Holzapfel, J., Kempf, H., Stadlmeier, M., Löschenberger, F., Morales, L., Buerstmayr, H., Isidro Sánchez, J., Akdemir, D., Mohler, V., Lillemo, M., Hartl, L., Shahinnia FahimehShahinnia, F., & Hartl LorenzHartl, L. (2022). *Genome-wide association study and genomic prediction of resistance to stripe rust in current Central and Northern European winter wheat germplasm*. *135*, 3583–3595. https://doi.org/10.1007/s00122-022-04202-z

Shi, A., Bhattarai, G., Xiong, H., Avila, C. A., Feng, C., Liu, B., Joshi, V., Stein, L., Mou, B., Du Toit, L. J., & Correll, J. C. (2022). Genome-wide association study and genomic prediction of white rust resistance in USDA GRIN spinach germplasm. *Horticulture Research*, *9*. https://doi.org/10.1093/hr/uhac069

Silva, É. D. B. da, Xavier, A., & Faria, M. V. (2021). Impact of Genomic Prediction Model, Selection Intensity, and Breeding Strategy on the Long-Term Genetic Gain and Genetic Erosion in Soybean Breeding. *Frontiers in Genetics*, *12*. https://doi.org/10.3389/fgene.2021.637133

Singh, R. (2021). Deciphering the Impact of Water-stress on Plant Growth and Yield Attributes in Tomato Genotypes. *International Journal of Agriculture Environment and Biotechnology*, *14*(3). https://doi.org/10.30954/0974-1712.03.2021.23

Solankey, S. S., Singh, R. K., Baranwal, D. K., & Singh, D. K. (2014). Genetic expression of tomato for heat and drought stress tolerance: An overview. *International Journal of Vegetable Science*, *21*(5), 496–515. https://doi.org/10.1080/19315260.2014.902414

Soleimani, Z., Ramshini, H., Mohammad, S., Mortazavian, M., Fazelnajafabadi, M., & Foughi, B. (2014). Screening for drought tolerance in Iranian wheat genotypes (Triticum aestivum L.) using physiological traits evaluated under drought stress and normal condition. In *200 AJCS* (Vol. 8, Issue 2).

Song, Q., Hyten, D. L., Jia, G., Quigley, C. V., Fickus, E. W., Nelson, R. L., & Cregan, P. B. (2013). Development and Evaluation of SoySNP50K, a High-Density Genotyping Array for Soybean. *PLoS ONE*, *8*(1). https://doi.org/10.1371/journal.pone.0054985

Sousaraei, N., Mashayekhi, K., Mousavizadeh, S. J., Akbarpour, V., Medina, J., & Aliniaeifard, S. (2021). Screening of tomato landraces for drought tolerance based on growth and chlorophyll fluorescence analyses. *Horticulture Environment and Biotechnology*, *62*(4), 521–535. https://doi.org/10.1007/s13580-020-00328-5

Su, Y., Wu, F., Ao, Z., Jin, S., Qin, F., Liu, B., Pang, S., Liu, L., & Guo, Q. (n.d.). *Evaluating maize phenotype dynamics under drought stress using terrestrial lidar*. https://doi.org/10.1186/s13007-019-0396-x

Susanto, U., Rohaeni, W. R., & Sasmita, P. (2019). Selecting Traits for Drought Tolerance Screening in Rice. *IOP Conference Series: Earth and Environmental Science*, *383*(1). https://doi.org/10.1088/1755-1315/383/1/012049

Taheri, S., Gantait, S., Azizi, P., & Mazumdar, P. (2022). Drought tolerance improvement in Solanum lycopersicum: an insight into “OMICS” approaches and genome editing. In *3 Biotech* (Vol. 12, Issue 3). Springer Science and Business Media Deutschland GmbH. https://doi.org/10.1007/s13205-022-03132-3

Tameling, W. I. L., Vossen, J. H., Albrecht, M., Lengauer, T., Berden, J. A., Haring, M. A., Cornelissen, B. J. C., & Takken, F. L. W. (2006). Mutations in the NB-ARC domain of I-2 that impair ATP hydrolysis cause autoactivation. *Plant Physiology*, *140*(4), 1233–1245. https://doi.org/10.1104/pp.105.073510

Testa, R., di Trapani, A. M., Sgroi, F., & Tudisca, S. (2014). Economic sustainability of Italian greenhouse cherry tomato. *Sustainability (Switzerland)*, *6*(11), 7967–7981. https://doi.org/10.3390/su6117967

Uffelmann, E., Huang, Q. Q., Munung, N. S., de Vries, J., Okada, Y., Martin, A. R., Martin, H. C., Lappalainen, T., & Posthuma, D. (2021). Genome-wide association studies. In *Nature Reviews Methods Primers* (Vol. 1, Issue 1). Springer Nature. https://doi.org/10.1038/s43586-021-00056-9

van Esse, H. P., Reuber, T. L., & van der Does, D. (2020). Genetic modification to improve disease resistance in crops. In *New Phytologist* (Vol. 225, Issue 1, pp. 70–86). Blackwell Publishing Ltd. https://doi.org/10.1111/nph.15967

Wahb-Allah, M. A., Alsadon, A., Alsadon, A. A., & Ibrahim, A. A. (2011a). Drought Tolerance of Several Tomato Genotypes Under Greenhouse Conditions CoCooN project View project Natural control of endogenous ethylene biosynthesis in fresh climacteric produce View project Drought Tolerance of Several Tomato Genotypes Under Greenhouse Conditions. *World Applied Sciences Journal*, *15*(7), 933–940. https://www.researchgate.net/publication/265974299

Wahb-Allah, M. A., Alsadon, A., Alsadon, A. A., & Ibrahim, A. A. (2011b). Drought Tolerance of Several Tomato Genotypes Under Greenhouse Conditions CoCooN project View project Natural control of endogenous ethylene biosynthesis in fresh climacteric produce View project Drought Tolerance of Several Tomato Genotypes Under Greenhouse Conditions. *World Applied Sciences Journal*, *15*(7), 933–940. https://www.researchgate.net/publication/265974299

Wang, J., Zhou, Z., Zhang, Z., Li, H., Liu, D., Zhang, Q., Bradbury, P. J., Buckler, E. S., & Zhang, Z. (2018). Expanding the BLUP alphabet for genomic prediction adaptable to the genetic architectures of complex traits. *Heredity*, *121*(6), 648–662. https://doi.org/10.1038/s41437-018-0075-0

Wang, M. C., Gong, M., Zang, H. B., Hua, X. M., Yao, J., Pang, Y. J., & Yang, Y. H. (2006). Effect of methamidophos and urea application on microbial communities in soils as determined by microbial biomass and community level physiological profiles. *Journal of Environmental Science and Health - Part B Pesticides, Food Contaminants, and Agricultural Wastes*, *41*(4), 399–413. https://doi.org/10.1080/03601230600616155

Wen, L., Chang, H. X., Brown, P. J., Domier, L. L., & Hartman, G. L. (2019). Genome-wide association and genomic prediction identifies soybean cyst nematode resistance in common bean including a syntenic region to soybean Rhg1 locus. *Horticulture Research*, *6*(1). https://doi.org/10.1038/s41438-018-0085-3

Wilkinson, S., Kudoyarova, G. R., Veselov, D. S., Arkhipova, T. N., & Davies, W. J. (2012). Plant hormone interactions: innovative targets for crop breeding and management. *Journal of Experimental Botany*, *63*(9), 3499–3509. https://doi.org/10.1093/jxb/ers148

Wu, J., Zhu, J., Wang, L., & Wang, S. (2017). Genome-wide association study identifies NBS-LRR-encoding genes related with anthracnose and common bacterial blight in the common bean. *Frontiers in Plant Science*, *8*. https://doi.org/10.3389/fpls.2017.01398

Xavier, A., Muir, W. M., & Rainey, K. M. (2016). *Assessing Predictive Properties of Genome-Wide Selection in Soybeans*. https://doi.org/10.1534/g3.116.032268

Yang, X., Lu, M., Wang, Y., Wang, Y., Liu, Z., & Chen, S. (2021). Response mechanism of plants to drought stress. In *Horticulturae* (Vol. 7, Issue 3). MDPI AG. https://doi.org/10.3390/horticulturae7030050

Yao, X., Yang, R., Zhao, F., Wang, S., Li, C., & Zhao, W. (2016). An analysis of physiological index of differences in drought tolerance of tomato rootstock seedlings. *Journal of Plant Biology*, *59*(4), 311–321. https://doi.org/10.1007/s12374-016-0071-y

Yi, H., Breheny, P., Imam, N., Liu, Y., Hoeschele, I., & Yi, H. (2015). Penalized multimarker vs. single-marker regression methods for genome-wide association studies of quantitative traits. *Genetics*, *199*(1), 205–222. https://doi.org/10.1534/genetics.114.167817

Zeng, J., Pszczola, M., Wolc, A., Strabel, T., Fernando, R. L., Garrick, D. J., & Dekkers, J. C. (2012). Genomic breeding value prediction and QTL mapping of QTLMAS2011 data using Bayesian and GBLUP methods. *BMC Proceedings*, *6*(SUPPL. 2). https://doi.org/10.1186/1753-6561-6-S2-S7

Zhang, H., Zhao, Y., & Zhu, J. K. (2020). Thriving under Stress: How Plants Balance Growth and the Stress Response. In *Developmental Cell* (Vol. 55, Issue 5, pp. 529–543). Cell Press. https://doi.org/10.1016/j.devcel.2020.10.012

Zhou, D., Jing, T., Chen, Y., Wang, F., Qi, D., Feng, R., Xie, J., & Li, H. (2019). Deciphering microbial diversity associated with Fusarium wilt-diseased and disease-free banana rhizosphere soil. *BMC Microbiology*, *19*(1). https://doi.org/10.1186/s12866-019-1531-6

Zhou, J., Zhou, J., Ye, H., Ali, M. L., Nguyen, H. T., & Chen, P. (2020). Classification of soybean leaf wilting due to drought stress using UAV-based imagery. *Computers and Electronics in Agriculture*, *175*. https://doi.org/10.1016/J.COMPAG.2020.105576

Zhou, R., Yu, X., Ottosen, C. O., Rosenqvist, E., Zhao, L., Wang, Y., Yu, W., Zhao, T., & Wu, Z. (2017). Drought stress had a predominant effect over heat stress on three tomato cultivars subjected to combined stress. *BMC Plant Biology*, *17*(1). https://doi.org/10.1186/s12870-017-0974-x

Zhou, R., Yu, X., Ottosen, C.-O., Rosenqvist, E., Zhao, L., Wang, Y., Yu, W., Zhao, T., & Wu, Z. (n.d.). *BMC Plant Biology*. https://doi.org/10.1186/s12870-017-0974-x

Zia, B., Shi, A., Olaoye, D., Xiong, H., Ravelombola, W., Gepts, P., Schwartz, H. F., Brick, M. A., Otto, K., Ogg, B., & Chen, S. (2022). Genome-Wide Association Study and Genomic Prediction for Bacterial Wilt Resistance in Common Bean (Phaseolus vulgaris) Core Collection. *Frontiers in Genetics*, *13*. https://doi.org/10.3389/fgene.2022.853114

Overall conclusion

In conclusion, the characterization of tomato accessions for drought tolerance discovered that four accessions (PI 365956, PI 584456, PI 390510, and PI 370091) demonstrated high tolerance to dry conditions. This valuable information can be utilized in tomato breeding programs to develop drought-resistant elite cultivars, thereby mitigating the adverse effects of water scarcity on tomato production.

Similarly, in the case of common bean, the identification of 21 highly resistant accessions to Fusarium wilt, along with the discovery of 46 SNP markers associated with resistance, presents a great opportunity to improve disease management strategies. Furthermore, the identification of candidate genes related to Fusarium wilt resistance on various chromosomes adds to our understanding of the genetic basis underlying the ability of the plants to combat this pathogen.

These findings collectively emphasize the significance of employing advanced genomic tools, such as genome-wide association studies (GWAS) and genomic prediction (GP), to accelerate crop improvement efforts. By harnessing the genetic diversity present in crop germplasm, breeders can advance the development of drought-tolerant tomato varieties and disease-resistant common bean cultivars. Incorporating marker-assisted selection (MAS) and genomic selection (GS) techniques into breeding programs can substantially accelerate the development of high-performing and resilient plant varieties, ensuring sustainable and stable agricultural production in the face of changing environmental conditions.

List of Tables

List of Figures

Figure 1. Distribution of Fusarium wilt disease (1-9 scale) in 157 common bean accessions.

Figure 2. Model-based population structure for the 157 common bean panel. The 3D graphical plot of the principal component analysis (PCA) (A) and phylogenetic trees were created using the neighbor-joining (NJ) method in two subpopulations (B) created using GAPIT 3. The distribution of the accessions to different populations is indicated by the color code (Q1: red and Q2: blue).

Figure 3. The Manhattan (Left) and QQ (Right) plots of BLINK model for Fusarium wilt race 1 resistance and GLM model for Fusarium wilt race 4 resistances by GAPIT 3. The vertical and horizontal axes represent observed vs expected logarithm of odds (LOD or -log(P-value).

Figure 4. Genomic prediction (r-value) for resistance to Fusarium wilt race 1 and race 4 in 157 common bean accessions estimated by five genomic prediction (GP) models, BA, BB, BL, BRR, and rrBLUP on three SNP sets, 1_m32 (32 associated SNP markers), 2_r32 (randomly selected 32 SNPs), and 3_4740 (all 4740 SNPs).