Genetic Variability Studies on *Solanum Lycopersicum*

Victor I. Ajie[1]
[1] Department of Plant Science and Biotechnology,
Rivers State University, Npkolu-Orowuroko, Port-Harcourt, Rivers State, Nigeria
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Abstract
Genetic variability is essential for improving crop species and forms the foundation of effective tomato breeding programs. Tomatoes exhibit extensive phenotypic and genotypic diversity across traits like fruit size, shape, color, yield, and stress resistance. This review synthesizes current research on tomato genetic variability, integrating traditional morphological assessments with advanced molecular tools like DNA markers, genome-wide association studies (GWAS), and transcriptomics. Statistical techniques such as variability coefficients, correlation analysis, and principal component analysis are highlighted for data interpretation. Modern technologies, including CRISPR-Cas9 and machine learning, are explored for their role in unlocking hidden genetic potential. By consolidating knowledge, the review emphasizes the importance of genetic variability in breeding high-yielding, stress-tolerant, and nutritionally enhanced tomatoes. It provides insights for developing sustainable production systems and addressing global challenges related to food security and climate change. This comprehensive analysis aims to guide future strategies in tomato improvement.

Keywords: *Genetic variability, Solanum lycopersicum, tomato breeding, quantitative traits, molecular techniques, sustainable agriculture*

Introduction

Tomato (*Solanum lycopersicum* Linn., $2n = 2x = 24$) is a self-pollinating annual crop, and one of the most important fruit vegetables in the world. Tomatoes are a rich source of essential vitamins and pro-vitamins, including vitamin C, pro-vitamin A, β-carotene, and folate, as well as minerals like potassium. They also contain significant secondary metabolites such as lycopene, flavonoids, phytosterols, and polyphenols (Beecher, 1998; Luthria *et al*., 2006). These bioactive compounds possess diverse physiological properties, such as anti-inflammatory, anti-allergenic, antimicrobial, vasodilatory, antithrombotic, cardioprotective, and antioxidant effects (Raiola *et al*., 2014). Approximately 182.3 million tons of tomato fruits are produced on 4.85 million ha each year (FAOSTAT, 2019). Tomato consumption is highest in regions such as China, India, North Africa, the Middle East, the United States, and Brazil, with per capita consumption ranging from 61.9 kg to 198.9 kg. (FAOSTAT, 2019). Recognizing the vital role of *Solanum lycopersicum* in global agriculture highlights the need to explore genetic variability.

Genetic variability is fundamental for crop improvement as it provides the raw material for selection and improvement. In *Solanum lycopersicum*, genetic diversity enables the development new varieties that can adapt to changing environmental conditions and exhibit enhanced traits such as disease resistance, yield, and fruit quality (Bhandari *et al*., 2017). The presence of diverse alleles allows for the identification of beneficial traits that can be combined

to create superior cultivars. Moreover, studying genetic variability helps in understanding the inheritance of important traits and facilitates the application of molecular markers for precise breeding (Rasheed *et al*. 2023). Advances in genomics and phenotyping have further enriched our ability to explore and exploit genetic diversity effectively (Udriște *et al*., 2022). Thus, maintaining and studying genetic variability in tomatoes is crucial for addressing both current and future challenges in crop production.

The primary objectives of genetic variability studies in tomatoes are to identify and utilize genetic differences that can lead to significant crop improvements. Enhancing yield potential is a key goal, as breeders aim to develop varieties that produce higher and more consistent harvests (Rasheed *et al*. 2023). Another crucial objective is improving disease resistance, which reduces the reliance on chemical control measures and promotes sustainable farming practices (Mugao *et al*., 2023). Genetic studies also focus on increasing drought tolerance, enabling tomato crops to thrive in water-scarce environments and adapt to climate change (Ilakiya *et al*., 2022). Additionally, presence of variability facilitates the improvement of nutritional content, such as elevating levels of vitamins, antioxidants, and other beneficial compounds (Debnath *et al*., 2021), as well as the development of tomatoes with desirable traits like extended shelf life and better flavour (Tranchida-Lombardo *et al*., 2019). Overall, these studies drive the creation of resilient, high-quality tomato varieties that meet both consumer preferences and agricultural demands.

Overcoming the challenges associated with cultivating *Solanum lycopersicum* (Dube *et al*., 2020) necessitates thorough genetic variability studies to identify and utilize advantageous traits. Such efforts could enhance breeding programs and facilitate the development of improved, resilient tomato varieties capable of withstanding both biotic and abiotic stresses. This review seeks to compile and analyze current research findings on genetic variability in tomatoes and underscore their significance for breeding strategies.

Genetic Diversity and Variability in Tomato

It is a misconception to consider genetic variability and genetic diversity as synonymous terms. Genetic diversity refers to the total number of genetic characteristics present within a species or population, providing a broad measure of the genetic health and adaptability of a group. Genetic variability, on the other hand, describes the tendency of genetic traits to differ within and between populations, emphasizing the potential for variation that can be leveraged for adaptation and selection of advantageous traits (Bhandari *et al*., 2017). High genetic diversity is essential because it increases the likelihood of identifying traits that contribute to improved yield, disease resistance, and environmental stress tolerance (Swarup *et al*., 2021). By tapping into this genetic reservoir, breeders can develop tomato varieties that are more resilient and better suited to changing agricultural conditions.

Solanum sect. *Lycopersicon* comprises 13 closely related taxa, including the domesticated and feral forms of *Solanum lycopersicum*. The section also includes 12 wild species: *S. arcanum*, *S. cheesmaniae*, *S. chilense*, *S. chmielewskii*, *S. corneliomulleri*, *S. galapagense*, *S. habrochaites*, *S. huaylasense*, *S. neorickii*, *S. pennellii*, *S. peruvianum*, and *S. pimpinellifolium* (Peralta *et al*. 2008). *Solanum pimpinellifolium* is the closest wild relative with a divergence of only 0.6% nucleotide base pairs (Tomato Genome Consortium, 2012). The genetic distance and polymorphism observed in wild tomato relatives, such as *S. peruvianum*, *S. pennellii*, and

S. hirsutum, have been found to be notably high (Passam *et al*., 2007). Wild relatives of *Solanum lycopersicum* therefore provide a rich reservoir of genetic diversity, harboring unique alleles that are often absent in cultivated varieties.

Landraces, traditional locally adapted cultivars, are vital sources of genetic variability due to their adaptation to specific environments and cultural practices. Analysis of 16 Southern Italian tomato landraces using (GATA)4 DNA fingerprinting revealed variability in one-third of the landraces, a link between fruit type and landrace clusters, and a low frequency of admixed genotypes (Caramante et al., 2024). This underscores the importance of assessing genetic variability to prevent diversity loss and enhance breeding programs (Caramante et al., 2024). Similarly, five "Piennolo" tomato landraces from Southern Italy exhibited high °Brix values, acidity, and significant levels of lycopene, ascorbic acid, and polyphenols, contributing to their quality as fresh produce. Notably, polyphenols correlated positively with antioxidant activity, while lycopene showed a negative correlation, revealing unique interrelationships among these components (Fratianni et al., 2020). Landraces often possess resilience traits absent in commercial varieties. A study on 17 Iranian tomato landraces and two hybrids under drought stress highlighted reduced growth and photosynthetic efficiency but increased electrolyte leakage and energy dissipation. The landraces were grouped by tolerance, with drought-adapted ones exhibiting higher resilience. Principal component analysis identified eight key parameters as indicators of drought impact (Sousaraei et al., 2021).

Induced mutants generated through chemical, radiation, or transposon mutagenesis introduce novel genetic variations for developing superior cultivars. Gamma radiation's impact on genetic variability in *Solanum lycopersicum* revealed significant variability in traits such as seed germination, seedling survival, plant height, and flower and fruit numbers. Higher doses (450 Gy and 300 Gy) were detrimental, while 150 Gy caused minimal damage and induced maximum variability (Zafar et al., 2022). Similarly, the chemical mutagen ethyl methanesulfonate (EMS) was used to induce mutations, revealing changes in six of nine target genes and producing diverse phenotypic variants, including amino acid sequence alterations (Yong et al., 2021). DNA methylation also contributes to genetic variability by regulating gene expression and adaptation. CRISPR-Cas9-mediated SlCMT4 mutants in *Solanum lycopersicum* showed developmental abnormalities such as smaller, thicker leaves, increased lateral buds, and defective reproductive structures. These mutants also exhibited hormonal imbalances, irregular pollen development, and reduced fruit and seed size, emphasizing SlCMT4's critical role in tomato development and maturation (Guo et al., 2022).

One of the primary challenges faced in capturing and utilizing genetic diversity in *Solanum lycopersicum* breeding programs lies in the narrow genetic base of modern commercial tomato cultivars, which limits breeders' ability to develop crops with improved stress resistance and adaptive traits (Gao *et al*., 2019). Landraces and wild relatives hold untapped reservoirs of genetic variation, but integrating these traits often involves overcoming barriers such as linkage drag and poor compatibility with cultivated varieties (Schmidt *et al*., 2022; Chitwood-Brown *et al*., 2021). Advanced genomic tools and molecular markers offer opportunities to identify and introduce beneficial alleles more efficiently, enhancing the precision of breeding efforts. The advent of CRISPR-Cas9 and other gene-editing technologies permits the bypassing of traditional breeding constraints and directly modify specific genes associated with desired traits (Guo *et al*., 2022; Tran *et al*., 2023). However, the need for comprehensive germplasm characterization and the protection of intellectual property rights complicate access to diverse

genetic resources. Germplasm evaluation often faces two main challenges: genotype-by-environment interaction (GEI) for specific traits and unfavorable correlations among key traits and their relationships in different genotypes (Yan & Frégeau-Reid, 2018). El-Aziz et al. (2016) highlighted that while the selection of high-performing tomato genotypes across various spatial environments has been explored, consistent performance in certain quantitative traits across different temporal environments has not been extensively studied.

Methodologies for Assessing Genetic Variability

Assessing genetic variability in *Solanum lycopersicum* involves several key methodologies to ensure comprehensive analysis. Some of such methodologies include:

Morphological Analysis

Morphological analysis is a foundational method for evaluating genetic variability in *Solanum lycopersicum* by assessing observable traits within tomato populations. Morphological traits provide valuable initial insights into the extent of diversity present among genotypes and can be used to identify unique or superior phenotypes suited for breeding purposes. Roohanitaziani *et al*. (2020) evaluated a core collection of 122 tomato accessions, including landraces, cultivars, and wild relatives, for variation in plant growth, yield, and fruit quality traits, with genotypic analysis focusing on key mutations. Cultivated varieties exhibited higher fruit number and weight, while wild accessions had higher Brix values; known mutations in genes related to fruit size, shape, and color explained much of the phenotypic diversity observed (Roohanitaziani *et al*., 2020). Another study conducted at the Bangladesh Agricultural Research Institute evaluated 22 tomato inbred lines for 27 morphological traits, highlighting significant variation in 21 qualitative and 6 quantitative traits (Salim et al., 2020). Key diagnostic traits such as hypocotyl color, leaf type, and fruit cross-sectional shape were identified as valuable for distinguishing genotypes, though no single trait was sufficient for complete differentiation (Salim *et al*., 2020). The findings emphasize the importance of morphological characterization in enhancing tomato diversity, aiding in the selection of genotypes with desirable traits for future variety development.

The International Plant Genetic Resources Institute (IPGRI, 1996) has developed descriptors for quantitative as well as qualitative characters to ensure precise, accurate and uniform identification of genotypes. Twenty-four IPGRI phenotypic traits were used in evaluating 10 landrace accessions of Cypriot tomato germplasm (Athinodorou *et al*., 2021). The study revealed valuable diversity for breeding by highlighting variation in fruit morphology, including flattened, heart-shaped, rounded, and highly rounded types, with morphological grouping of accessions reflecting distinct fruit shapes and sizes (Athinodorou *et al*., 2021). Similarly, the International Union for the Protection of New Varieties of Plants (UPOV) was established in 1961 by the International Convention for the Protection of New Varieties of Plants. UPOV aim is to provide and promote an effective system of plant variety protection, in order to encourage the development of new cultivars of plants, for the benefit of society (UPOV, 2001). IPGRI and UPOV descriptors were used to characterize 228 hybrid samples of the tomato type "Beef" and 11 standard varieties using 24 quantitative and 2 qualitative traits to reveal phenotypic diversity (Ünal *et al*., 2021). Significant variability was observed among genotypes, with high broad-sense heritability for traits like fruit number, firmness, and plant height. However, the accuracy and consistency of morphological evaluations are often

influenced by environmental factors, leading to genotype-by-environment interactions that can obscure true genetic differences. To mitigate this, replicated trials across different environments are used to better capture trait stability and adaptability.

Molecular Markers

A DNA marker or molecular marker is typically derived from a small region or fragments of DNA that shows sequence variation that can be used in detecting polymorphism between individuals within or between species (Foolad, 2007). Such fragments are associated with a genomic locus and discerns the chromosomal trait it may represent (Barcaccia *et al.,* 2000). DNA markers allow a more complete evaluation of the genome and are little affected by the environment, hence they are a widely used technique in characterizing genetic diversity (Ansari *et al*., 2016). A good genetic marker for the assessment of diversity is defined by high variability and its ability to create multi-locus information from the genome (Anne, 2006). Different types of molecular markers have been developed and evolved, including, but not limited to, randomly amplified polymorphic DNAs (RAPDs) (Williams *et al*., 1990), simple sequence repeats (SSRs or microsatellites) (He *et al*., 2003) and single-nucleotide polymorphisms (SNPs) (Landegren *et al.,* 1998).

Random Amplified Polymorphic DNA (RAPD)

Random Amplified Polymorphic DNA (RAPD) markers, generated by amplifying random DNA segments using short, arbitrary primers in a polymerase chain reaction, are useful for assessing genetic diversity (Reshma and Das, 2020). RAPD markers were applied to evaluate genetic diversity among 30 tomato breeding lines, revealing polymorphic bands across all genotypes. However, the overall genetic diversity was narrow, with a genetic diversity index of 0.1981 and Shannon's information index of 0.1764 (Ghosh et al., 2019). While large sample sizes are generally preferred for capturing broader genetic variation and enhancing statistical power, small sample sizes can still uncover significant diversity if the varieties represent distinct genetic backgrounds. Conversely, larger sample sizes may exhibit low diversity if varieties share a narrow genetic pool. In a recent study, genetic diversity among five tomato varieties was analyzed using seven RAPD primers (Almiahy et al., 2023). The primer OPE12 produced the highest number of polymorphic bands, while OPH13 produced the least. Genetic analysis grouped the varieties into two main clusters, illustrating distinct genetic relationships among them (Almiahy et al., 2023).

Random Amplified Polymorphic DNA (RAPD) markers have also been utilized in the study of genetic variability in plants under abiotic stress conditions by identifying genetic polymorphisms that correlate with stress tolerance. This helps uncover genetic markers associated with traits, aiding in the selection of stress-tolerant varieties. In 2024, the genetic diversity among 12 tomato genotypes in Bangladesh was examined under heat stress conditions using seven RAPD markers (Anwar *et al*., 2024). Results showed that RAPD markers effectively differentiated the genotypes, with specific genotypes like BARI Hybrid Tomato 4, BARI Hybrid Tomato 8, A12, D13, and RHS1 identified as promising candidates for further breeding programs. The analysis highlighted the genetic relationships and potential common ancestry among the genotypes, emphasizing the utility of RAPD markers in heat-stress tolerance research (Anwar *et al*., 2024).

Combining multiple molecular markers, provides a comprehensive analysis of genetic variability by capturing different types of genetic variation across the genome. This approach enhances the resolution of genetic diversity studies, allowing for more accurate identification of genetic relationships and potential markers for breeding programs. In Nigeria, chloroplast DNA (cpDNA) and RAPD markers revealed a low genetic variability among 35 tomato varieties (Onwukwe *et al*., 2023). Both cpDNA and RAPD analyses identified a narrow gene pool, with accessions clustering into two groups, indicating high homogeneity and limited genetic variability. The findings highlight the risks of inbreeding depression and emphasize the need for incorporating wild cultivars to enhance genetic diversity and adaptability in tomato breeding programs (Onwukwe *et al*., 2023).

Ahang *et al*. (2024) assessed the genetic diversity of ten Iranian tomato cultivars using RAPD and ISSR molecular markers. The analysis revealed significant genetic variation, with Hengam exhibiting the highest diversity and Raha and JS12 showing minimal diversity. ISSR markers were found to be more effective than RAPD in determining genetic diversity among the cultivars (Ahang *et al*., 2024). This may be because ISSR markers target highly polymorphic microsatellite regions, providing greater specificity, reproducibility, and discriminatory power. Additionally, ISSR markers are less influenced by experimental conditions, ensuring more consistent and reliable results (Tonk *et al*., 2014). This is also in agreement with El-Mansy et al. (2021), who reported that ISSR markers demonstrated the highest polymorphism percentage and efficiency when used alongside RAPD and SCoT markers to assess six tomato lines (G1–G6) under heat stress.

Simple Sequence Repeats (SSRs or microsatellites)

Simple sequence repeats (SSRs), or microsatellites, are DNA sequences comprising repeated nucleotide motifs of 1 to 6 base pairs, with variations in type and frequency across species and genomic locations (Hancock, 1999; Jarvis et al., 2008). In Kazakhstan, 10 SSR markers were used to analyze genetic diversity in 49 tomato cultivars and hybrids. Polymorphism was detected in six markers, with notable genetic diversity between outdoor and greenhouse types. High polymorphic SSR markers (PIC > 0.5) associated with fruit traits were identified as effective tools for marker-assisted selection to enhance breeding efficiency and yield (Genievskaya et al., 2024). DNA fingerprinting, a molecular technique for analyzing unique genetic patterns, aids in assessing genetic diversity and relationships among accessions (Poets et al., 2020). This method characterized the genetic profiles of 121 traditional Umbrian tomato landraces using 19 SSR markers, identifying 60 alleles with moderate diversity and an average PIC of 0.38. Unique fingerprinting codes were developed for each landrace, and a QR code-based system was proposed to facilitate conservation and management of these genetic resources (Castellana et al., 2020). These findings emphasize the importance of SSR markers in genetic studies and resource conservation, highlighting their potential in breeding programs.

Techniques like SSR have advanced the detection of genetic diversity in stress-responsive traits, supporting the development of resilient crop varieties. Drought, a major challenge in regions like North Africa, reduces crop productivity and threatens food security (Nie et al., 2021). In Egypt, drought tolerance was assessed in six tomato genotypes, including *Solanum pimpinellifolium* (LA:411), five cultivated varieties, and their 15 crosses, using 10 SSR primers. Genetic diversity ranged from 0.485 to 0.947, with a high similarity (0.999) observed in crosses involving Super Marmande. LA:411 and Edkawi were identified as key drought-

tolerant resources for tomato breeding (Sheded et al., 2022). Tomato Spotted Wilt Virus (TSWV) and Fusarium Wilt (FW), major tomato diseases, cause severe yield losses through viral and fungal pathogen attacks. Resistance to TSWV and FW was analyzed in 48 tomato genotypes using 84 polymorphic SSR markers, identifying seven genotypes with the *Sw-5* gene for TSWV resistance and nine with the *I-2* gene for FW resistance, validated phenotypically (Pidigam et al., 2021). The study detected 195 alleles, with PIC values ranging from 0.12 to 0.93, and revealed significant correlations between fruit weight and yield, highlighting SSR markers' role in disease resistance and trait improvement (Pidigam et al., 2021).

Combining morphological markers with molecular markers enables the capture of both visible trait variations and underlying genetic differences, providing a more accurate and reliable assessment of genetic resources. Morphological and molecular variability of 40 tomato accessions were evaluated using both field experiments and molecular analysis (Olawuyi and Ajie, 2023). Significant variation was observed in growth and yield traits. Accessions NGB/05081, NGB/00714, and Hausa excelled in growth and yield, while Tp 124 and Tp 121 primers were highly polymorphic with high gene diversity (Olawuyi and Ajie, 2023). Also, Popescu et al. (2022) analyzed the morphological and molecular diversity of 13 tomato genotypes to assess their distinctiveness and suitability for cultivation. Genetic diversity was evaluated using 8 SSR markers, revealing 81.5% polymorphic bands, a mean of 6.62 scorable bands per marker, and a polymorphism information content of 0.764. Cluster analysis grouped the genotypes based on growth type and parental origin, further confirming that combining morphological and molecular methods is an effective approach for characterizing tomato genotypes.

Single nucleotide polymorphism (SNP)

Single nucleotide polymorphism (SNP) markers are among the most widely used molecular tools for genetic studies due to their abundance, stability, and ease of detection across the genome (Dwiningsih *et al*., 2020). These markers represent single base pair variations at specific loci, making them ideal for assessing genetic variability, population structure, and trait association in diverse crops (Morgil *et al*., 2020), including *Solanum lycopersicum* (tomato). Wang *et al*. (2019) compared the effectiveness of SNP and InDel markers in assessing genetic diversity and relatedness among 191 tomato inbred lines, including cherry tomato, traditional varieties, and contemporary lines. SNPs demonstrated higher genetic diversity and resolution than InDels, with greater expected heterozygosity (He) and polymorphic information content (PIC), particularly for traditional varieties. While SNPs were better for distinguishing closely related lines, InDels proved more effective for differentiating genotypes across gene pools, highlighting their complementary roles in tomato population genetics (Wang *et al*., 2019).

Exploring genetic diversity among tomato germplasm has revealed significant variation in key flavor-related traits (Wang and Seymour, 2017), offering opportunities to identify novel alleles that can be leveraged for enhancing fruit quality. Genetic diversity and functional polymorphism study in five key genes (LIN5, ALMT9, AAT1, CXE1, and LoxC) that influence tomato fruit flavor revealed a high genetic diversity, including novel haplotypes, across *Solanum pimpinellifolium*, *S. lycopersicum cerasiforme*, and *S. lycopersicum* (Pereira *et al*., 2021). There was a notable duplication at the *LoxC* locus linked to reduced volatile accumulation in some accessions. The identification of functional polymorphisms, such as those affecting volatile accumulation and metabolite levels, underscores the importance of

integrating genetic and metabolic data to refine cultivation approaches. Moreover, leveraging the genetic diversity within wild and semi-domesticated tomato species provides a valuable reservoir of alleles for enhancing flavor-related traits in modern cultivars.

Extending this framework of genetic diversity, integrating advanced molecular tools with traditional evaluation methods offers a robust approach to characterizing and utilizing genetic resources in tomato. A high consistency was observed between using both SNP fingerprinting and DUS (Distinctness, Uniformity, and Stability) testing in identifying tomato varieties (Zhang *et al*., 2023). Furthermore, a new set of 16 core SNPs and 18 core DUS traits was developed, showing improved efficiency and convenience for variety identification. Strong linear correlation between SNP markers and DUS traits underscores the potential of combining these approaches for effective and reliable discrimination of tomato varieties. More recently, a core collection of 137 tomato accessions was developed from 484 cultivated accessions using phenotypic traits and SNP markers (Chen *et al*., 2025). Genetic diversity analysis revealed high variability, with correlations among quantitative traits, and population structure analysis identified four subpopulations (Chen *et al*., 2025). The inclusion of highly polymorphic SNP markers enabled precise differentiation among accessions, showing the genetic uniqueness of each subpopulation.

Genomic and Transcriptomic Approaches

Advances in genomic and transcriptomic technologies have transformed variability studies in crops, providing deeper insights into genetic makeup and functional gene expression. Genomic approaches like whole-genome sequencing and genome-wide association studies (GWAS) offer comprehensive understanding of structural and functional variations in tomato germplasm (Tiwari et al., 2022). These methods enable the identification of genetic markers (Kim et al., 2018), analysis of population structure (Yongsuwan et al., 2024), and discovery of loci associated with key agronomic traits (Tranchida-Lombardo et al., 2018). Transcriptomic techniques, including RNA sequencing (RNA-seq) and gene expression profiling, further allow dynamic analysis of gene expression under various conditions (Chaudhary et al., 2019). The integration of genomic and transcriptomic tools links genetic variations to phenotypic traits, providing a robust framework for identifying genetic diversity and improving traits such as yield, stress tolerance, and fruit quality in tomato.

Whole-genome Sequencing

The genome of the inbred tomato cultivar 'Heinz 1706' was sequenced and assembled in 2012 using a combination of Sanger and next-generation sequencing technologies, providing a foundational reference for tomato genetics (Tomato Genome Consortium, 2012). This reference genome has facilitated studies on domestication, breeding, and trait evolution. High-quality sequencing of *Solanum pimpinellifolium* accession LA2093 identified over 92,000 structural variants (SVs) compared to Heinz 1706. Analysis of these SVs in approximately 600 tomato accessions revealed alleles selected during domestication and breeding, particularly those regulating traits such as fruit weight and lycopene content (Wang et al., 2020). Structural variants represent large genomic changes like deletions, duplications, and inversions, while smaller variations, such as SNPs and InDels, typically constitute polymorphisms. Genomic analysis of the *Solanum lycopersicum* cultivar Caimanta and *S. pimpinellifolium* accession LA0722 identified 1,397,518 polymorphisms relative to the Heinz 1706 reference genome

(Cambiaso et al., 2019). These polymorphisms were linked to key traits, including the resistant allele for *Rx4/Xv3*, and used to develop InDel markers for constructing a genetic linkage map (Cambiaso et al., 2019). This underscores the value of whole-genome sequencing in elucidating phenotypic traits and advancing genetic characterization in tomatoes.

Subsequent resequencing efforts have identified genetic variations across diverse tomato accessions, aiding in the improvement of cultivated varieties. These variations have been linked to key traits such as yield, disease resistance, and fruit quality. The identification of specific alleles has provided valuable targets for marker-assisted breeding. The genomes of Corbarino (COR) and Lucariello (LUC) tomato landraces, known for traits like water deficit adaptation, extended shelf life, and high fruit quality, were re-sequenced using the Reconstructor pipeline (Tranchida-Lombardo *et al*., 2019). Novel genomic regions and significant variations, including SNPs affecting genes related to fruit quality, shelf life, and stress tolerance, were identified, with similarities to *Solanum pimpinellifolium* and *Solanum pennellii*. The findings highlighted candidate genes, particularly in ethylene response pathways, that may explain the unique phenotypes of these landraces (Tranchida-Lombardo *et al*., 2019). Furthermore, whole-genome resequencing of 150 Japanese large-sized fresh-market tomato cultivars revealed how breeding selection from the 1940s to 2000s shaped their genomes (Yamamoto *et al*., 2024). Trends showed increased fruit sugar content but decreased yield, with selection signatures detected across all chromosomes, including the introgression of the *Tm-2* resistance gene. (Yamamoto *et al*., 2024). This underlines how breeding priorities have shaped the genetic makeup and agronomic traits of Japanese tomatoes, providing a genomic framework for future efforts to balance yield, quality, and disease resistance.

Whole-genome sequencing (WGS) offers a comprehensive approach to understanding the genetic variability associated with disease resistance in plants, aiding in the identification of key resistance genes and variants. This facilitates development of crops with improved resistance profiles through marker-assisted breeding. Whole-genome sequencing data from six Tomato bacterial wilt (BW)-resistant and nine susceptible tomato lines revealed 27,046 SNPs and 5,975 indels affecting 385 genes, with a significant variant on chromosome 3 linked to the resistance gene *Asc* within the Bwr-3 locus (Barchenger *et al*., 2022). The identification of loci contributing to disease resistance in tomato lines offers a foundation for investigating genes that may confer resistance to multiple pathogens. Genetic variability uncovered through whole-genome sequencing can as such be leveraged to identify resistance-associated loci across different pathogens and crops. Udriște *et al*. (2022) analysed genetic variability in eight Romanian tomato varieties, focusing on the Ve1 and Ve2 loci linked to resistance against Verticillium species. Genotypes carrying the Ve1 gene were pinpointed as prospective donors for breeding Verticillium race 1-resistant varieties (Udriște *et al*., 2022), emphasizing the importance of targeted genomic analysis in identifying valuable resistance traits for crop improvement. This may be achieved by incorporating such genotypes into breeding programs, making it possible to enhance disease resilience and ensure sustainable tomato production.

Genome-Wide Association Studies (GWAS)

Genome-Wide Association Studies (GWAS) are powerful tools for uncovering genetic factors underlying phenotypic variability in plants, offering high-resolution mapping of quantitative trait loci (QTL). In tomatoes, GWAS has revealed that single nucleotide polymorphisms (SNPs) and transposable elements (TEs) significantly contribute to genetic diversity,

influencing traits such as fruit size, flavor, stress resistance, and agronomic performance (Dominguez *et al*., 2020; Tripodi *et al*., 2021; Wang *et al*., 2024). TEs, often located near genes involved in environmental responses, drive diversity in tomato as revealed by whole-genome resequencing of 602 cultivated and wild accessions (Lin *et al*., 2014; Tieman *et al*., 2017; Aflitos *et al*., 2014). A genome-wide association study (GWAS) identified 6,906 TE insertion polymorphisms (TIPs), many of which were associated with key agronomic traits and secondary metabolites (Dominguez *et al*., 2020). These transposable element insertion polymorphisms (TIPs) were predominantly located near genes involved in environmental responses and often escaped detection by traditional SNP-based analyses. This suggests their significant role in trait adaptation and emphasizes their unique contribution to tomato genetic variability (Dominguez *et al*., 2020).

Knowledge of variation in important traits like yield, fruit quality, and abiotic stress tolerance in tomatoes is essential for improving crop performance and addressing global food security challenges. Identifying genetic factors underlying these traits enables fosters the development of high-yielding, resilient tomato varieties with enhanced nutritional and market value. An exploration into genetic variations influencing yield in U.S. fresh-market tomatoes integrated phenotypic data from 68 core inbred lines and whole-genome resequencing of 8,289,741 SNPs (Bhandari *et al*., 2023). Genome-wide association (GWA) mapping identified 18 significant signals, including 10 novel loci unrelated to previously reported regions for fruit size/shape, and demonstrated the utility of SNP-driven genomic estimated breeding values (GEBVs) for predicting yield traits (Bhandari *et al*., 2023). The use of such regularization methods further enhanced the accuracy of GEBVs, particularly for traits like extra-large and small fruit yields, revealing the potential for refined marker-assisted selection. Building on this approach, other studies have leveraged diverse genomic datasets and GWAS methodologies to uncover genetic loci associated with a broader range of traits under varied environmental conditions. For example, loci influencing agronomic, fruit quality, and root architecture traits were mapped using 37,300 SNPs from dd-RADseq in 244 traditional and improved tomato accessions. GWAS identified 59 significant loci, including novel genes related to flower and fruit characteristics, with key associations near SUN, OVATE, and MYB gene families (which regulate key traits such as fruit shape, size, and color) (Tripodi *et al*., 2021). Such insights are instrumental in developing targeted breeding strategies aimed at improving tomato productivity and quality across diverse cultivation systems.

Tomato flavor evolution during domestication was elucidated through a meta-analysis of genome-wide association studies (GWAS) using 775 accessions and 2,316,117 SNPs (Zhao *et al*., 2019). A total of 305 significant associations for sugars, acids, amino acids, and flavor-related volatiles were identified, proving that domestication strongly influenced citrate and malate contents while sugar content faced less stringent selection (Zhao *et al*., 2019). This detailed analysis highlights the impact of domestication on specific metabolic pathways, emphasizing how human selection pressures have shaped key quality traits in tomatoes. Beyond flavor, domestication has also influenced other critical stress-related traits, such as salt tolerance, which reflects the genetic trade-offs associated with modern breeding efforts. In investigating the reduction in salt tolerance in tomatoes due to domestication and genetic variability between wild ancestors and contemporary breeding accessions, genome-wide association studies identified a key variation in the KSB1 gene's promoter region, associated with survival rates and Na+/K+ ratios under salt stress (Wang *et al*., 2024). The findings further

highlight the role of SlHY5-KSB1-KSL1 module in maintaining ion homeostasis, shedding light on the genetic basis of salt tolerance in tomatoes (Wang et al., 2024). Leveraging such knowledge, key genetic modules like SlHY5-KSB1-KSL1 can be targeted to enhance salt tolerance in modern tomato cultivars without sacrificing yield or quality.

Expanding the understanding of stress resilience, genome-wide association studies have also been instrumental in uncovering genetic mechanisms underlying resistance to other biotic stresses in tomatoes. For instance, bacterial wilt (BW) resistance in tomatoes was investigated using genome-wide association studies (GWAS) on 191 varieties genotyped with 38,541 SNPs from the 51 K Axiom® tomato array (Nguyen *et al*., 2021). GWAS identified eight significant marker-trait associations, including major QTL on chromosomes 4 (Bwr-4) and 12 (Bwr-12) that explained 8.36–18.28% of phenotypic variation and were validated in two disease assays, along with Bwr-6 on chromosome 6 and environment-specific QTL (Nguyen *et al*., 2021). The environment-specific QTLs and the significant association of Bwr-6 on chromosome 6 provide further insights into the complex genetic architecture of BW resistance, offering new targets for precise breeding strategies in diverse growing conditions. The SlPP2C gene family in tomato is involved in regulating stress responses, including resistance to bacterial wilt, through phytohormone signaling pathways like ABA (Li *et al*., 2022). A comprehensive genome-wide analysis of the SlPP2C gene family in tomato identified 92 genes distributed across 11 chromosomes, all containing type 2C phosphatase domains (Qiu et al., 2022). Type 2C phosphatase domains play a crucial role in biotic stress signaling by modulating plant responses to pathogen attack (Hong et al., 2016). Through regulating phosphatase activity, these genes participate in key signaling pathways that affect disease resistance, including responses to bacterial wilt and other pathogens.

Transcriptomic Methods

Transcriptomic techniques, including RNA sequencing (RNA-Seq) and microarrays, enable the identification of differentially expressed genes across diverse tomato accessions or under varying environmental conditions. This facilitates the identification of candidate genes and elucidates regulatory networks underlying traits like fruit size, shape, color, flavor, and stress tolerance. This capability has been applied in specific studies to explore the genetic basis of important traits in *Solanum lycopersicum.* For instance, apart from finding high genetic diversity and novel haplotypes for key genes influencing tomato fruit flavour, gene expression analysis revealed increased activity during fruit ripening, with expression patterns varying between accessions without a direct correlation to metabolite levels (Pereira *et al*., 2021). This reflects the complexity of gene expression regulation and its influence on key traits among tomato accessions. Broader transcriptomic analyses have provided further insights into how both natural and artificial selection have shaped the tomato transcriptome variation, influencing traits such as stress resistance and fruit quality. Using a pan-transcriptome constructed from RNA-seq data of 399 tomato accessions, Dan et al. (2020) identified 7,181 genes absent in the reference genome, including resistance genes and those influencing fruit traits. This showed that both natural and artificial selection have led to reduction of TSS content in modern cultivars and enhancement of resistance to abiotic and biotic stresses (Dan *et al*., 2020). As such, this has resulted in tomato cultivars that are better equipped to withstand environmental challenges and pathogens. Consequently, modern breeding practices have successfully prioritized resilience alongside other desirable traits in tomatoes, in a bid to ensure a robust and sustainable crop.

Integrating transcriptomic data with phenotypic and genomic information enhances the identification of quantitative trait loci (QTLs) and marker-assisted selection. Key genomic regions responsible for bacterial spot (BS) resistance in tomato were revealed through shared resistance QTLs on chromosome 11 between resistant genotypes (Shi and Panthee, 2020). Resistant genotypes showed more differentially expressed genes (834) than the susceptible genotype (714), which exhibited significant downregulation of defense genes, including an R gene (Shi and Panthee, 2020). In contrast to this, differential expression analysis for transcriptomic responses in resistant (Sp-R) and susceptible (Sp-S) tomato accessions to *phytophthora parasitica* identified 2657 and 3079 DEGs in Sp-R and Sp-S, respectively (Naveed *et al*., 2018). However, 1173 DEGs unique to Sp-R were located, including key defense-related genes such as protease inhibitors, chitinases, and PR-1. This underscores the extensive transcriptional changes that occur in tomato genotypes when they resist or succumb to various pathogens, indicating the depth of genetic reprogramming involved in defense mechanisms against different diseases.

Abiotic stresses significantly reduce tomato yield and quality, posing a major challenge for sustainable tomato cultivation. Tomato plants experience notable changes at both the phenotypic and molecular levels when subjected to stresses such as water deficit (WD) stress, leading to compromised growth and fruit quality. RNA sequencing of leaves and fruits from eight tomato accessions under varying irrigation revealed 14,065 differentially expressed genes (DEGs), with notable genotype- and organ-specific expression, and stronger transcriptome variations in leaves (Diouf *et al*., 2020). This gives emphasis to the importance of genetic makeup and the interaction between genotype and watering conditions in determining how tomatoes respond to drought conditions (Diouf *et al*., 2020). Similarly, RNA sequencing of tolerant and sensitive tomato genotypes was done to investigate molecular response to potassium (K)-deficiency stress (Zhao *et al*., 2018). A total of 1936 differentially expressed genes (DEGs) were identified, with significant changes in transcription factors, transporters, kinases, oxidative stress proteins, and hormone signaling pathways, particularly involving 110 oxidative stress-related genes and 19 ethylene response factors. The study confirmed 20 DEGs influencing root configuration and proposed a cross-talk between phytohormone signaling and reactive oxygen species (ROS) as a key mechanism for low-K+ tolerance in tomatoes, offering insights for improving K efficiency (Zhao *et al*., 2018). In suggesting a complex regulatory network utilized by tomato to adapt to low potassium conditions, valuable insights into the intricate gene interactions and signaling pathways that confer tolerance are provided, pinpointing potential targets for breeding potassium-efficient tomato varieties.

Statistical Methods

Statistical methods are a collection of mathematical techniques and principles used for collecting, analyzing, interpreting, and presenting data. They help in making sense of data by identifying patterns, relationships, and trends, enabling informed decision-making (Balzarini et al., 2011). These methods allow the dissection the genetic basis of various traits and assess the potential for improvement through breeding. One of such methods is the analysis of variance, which shows significant differences between genotypes (Mishra *et al*., 2019), leading to insights into genetic diversity. This method proves particularly useful in assessing a wide range of traits across different genotypes, offering a comprehensive understanding of the genetic landscape. Highly significant mean squares for characters suggest significant

variability among the studied traits under study and hence ample scope for selection (Dwary *et al*., 2023).

Genotypic and Phenotypic Coefficients of Variability (GCV and PCV) measure the extent of variation within a population, identifying traits with high genetic variability. The main difference between genotypic coefficient of variation (GCV) and phenotypic coefficient of variation (PCV) is that GCV is caused by genetic variations, while PCV is the result of both genetic and environmental variations (Patel *et al*., 2021). Similarly, heritability estimates provide insight into the potential for genetic improvement by assessing the proportion of phenotypic variance attributed to genetic variance. High heritability values indicate that a large portion of the observed variation is genetic and this helps in identifying traits that are likely to respond well to selection (Foroud *et al*., 2021). Cholin and Raghavendra (2021) found that environmental factors significantly influenced trait expression, with higher phenotypic than genotypic coefficient of variation for most traits, while high heritability was noted for several important fruit characteristics. Kumari et al. (2020) observed that genotypic coefficient of variation (GCV) was higher than phenotypic coefficient of variation (PCV) for eighteen tomato traits, with high GCV, PCV, and heritability reported for multiple agronomic and quality traits, including plant height, fruit characteristics, and yield. Rasheed et al. (2023) found high GCV and PCV values for yield per plant, number of fruits per cluster, number of flowers per cluster, and single fruit weight, indicating effective selection potential, with higher heritability for the number of flowers per cluster, single fruit weight, and yield per plant. These indicate significant genetic variability in tomatoes, with high genotypic and phenotypic coefficients of variation and heritability estimates for key traits, indicating strong potential for genetic improvement through selective breeding.

Correlation and path coefficient analyses reveal relationships between different traits, aiding in the identification of key selection criteria. This facilitates understanding the relationships and influence of different traits on key characteristics, thus allowing for the identification of traits that significantly impact desired outcomes (Alishah *et al*., 2008). Quispe-Choque and Huanca-Alanoca (2023) found that fruit yield in tomatoes was significantly correlated best with fruit weight per plant followed by polar diameter, with the number of fruits per plant having the highest positive direct effect, followed by fruit weight and polar diameter. From another combined study of correlation and path analysis, polar diameter, number of primary branches and equatorial diameter found to be most important selection criteria in crop improvement of tomato (Basfore *et al*., 2020). These suggest that selecting for these traits, such as polar diameter, can significantly improve tomato yield, but breeders must be cautious of undesirable trait associations that may arise. Identifying and mitigating such negative linkages is essential to ensure that improvements in one trait do not inadvertently cause reductions in other important characteristics. Gamma radiation's effect on tomato genetic variability revealed that higher doses, particularly 450 Gy, disrupted trait associations and reduced the contribution of independent variables to the variability in yield (Zafar *et al*., 2022). This disruption, caused by gamma radiation, underscores the potential of mutagenesis in breaking undesirable linkages and creating new genetic combinations that could be beneficial for breeding programs.

Cluster analysis classifies variables based on shared characteristics, aiding crop conservation, breeding, and understanding evolution by identifying distinct genetic groups (Mohammadi and Prasanna. 2003). Principal component analysis (PCA) simplifies complex datasets by transforming numerous correlated variables into a smaller set of uncorrelated components

(Ahmed *et al*., 2019). According to Seymen et al. (2019), PCA can be used effectively when the first two components explain more than 25% of the variation in the studies. A collection of 589 tomato accessions from the National Plant Gene Bank of Iran was grouped into nine clusters using hierarchical cluster analysis (Marefatzadeh-Khameneh *et al*., 2021) and seven PCA components explained over 83% of the data variation, with the first two components accounting for 50%. PCA highlighted fruit shape index and proximal/distal fruit end shape as major contributors to diversity. By the same token, PCA identified fruit weight, size, diameter, total soluble solids, and moisture content as key contributors to variability when fruit quality indices were used to scrutinize genetic diversity among 64 tomato accessions from Iraqi Kurdistan Region (Rasul and Tahir, 2024). Both studies demonstrate the effectiveness of PCA in identifying key traits that contribute to genetic diversity in tomato accessions, with fruit shape and weight being significant factors in tomato variability.

Applications in Breeding and Crop Improvement

As shown so far, genetic variability studies are important in understanding the diverse traits within a species. By assessing the extent of genetic diversity, desirable traits, such as disease resistance, yield potential, and stress tolerance, can be identified for selection in breeding populations. Diversity studies help in the identification of elite genotypes that possess superior characteristics, which can serve as parents for hybridization (Sivakumar *et al*., 2023). Furthermore, genetic variability enables the assessment of potential for genetic improvement, ensuring that novel traits are incorporated into breeding lines. The use of molecular markers in variation analysis provides more precise tools for selection, enabling the tracking of specific alleles linked to beneficial traits (Ansari *et al*., 2016). Additionally, the identification of germplasm with high genetic diversity contributes to the development of more resilient tomato cultivars capable of adapting to changing environmental conditions (Kulus, 2022). Altogether, genetic variability studies are integral to ensuring the long-term success of breeding programs focused on enhancing the quality, yield, and adaptability of *Solanum lycopersicum*.

As tomato breeding aims to address challenges like climate change, pests, and diseases, understanding genetic variation is essential for improving overall productivity and sustainability (Ferrero *et al*., 2020). A diverse genetic pool allows for the selection of varieties that can thrive under various environmental stresses, such as increased temperatures, water scarcity, and fluctuating growing conditions. As climate change accelerates, access to genetically diverse tomato germplasm ensures the development of varieties with better tolerance to heat, drought, and other abiotic stresses. Additionally, genetic diversity provides a broader range of resistance to pests and diseases, reducing the reliance on chemical control methods and improving sustainable agricultural practices (Swarup *et al*., 2021). Varieties with resistance to diseases like bacterial wilt (Kumar *et al*., 2018), tomato mosaic virus (Grozeva *et al*., 2020), and late blight (Copati *et al*., 2024) can be developed, minimizing crop losses and reducing the need for pesticides. The ongoing evolution of pests and pathogens demands the continuous exploration of genetic variation (Lahlali *et al*., 2024), enabling the introduction of new traits that confer resistance to emerging threats. Finally, maintaining genetic diversity in tomato cultivars contributes to food security by providing a pool of adaptable varieties that can withstand environmental unpredictability (Zsögön *et al*., 2022).

Challenges and Future Directions

One of the primary challenges in discerning genetic variability in *Solanum lycopersicum* is the limited access to diverse germplasm, particularly for underrepresented tomato varieties and landraces from different geographical regions (Kulus, 2022). Many breeding programs struggle to obtain germplasm with unique traits due to restrictions on seed exchange, intellectual property concerns, or insufficiently curated gene banks. The high cost of advanced molecular techniques, such as next-generation sequencing and genotyping-by-sequencing, further complicates the study of genetic diversity, making it difficult for resource-limited institutions to conduct comprehensive analyses. Additionally, the complexity and time-intensive nature of processing large genomic datasets pose challenges, as not all breeding programs have the necessary computational infrastructure or expertise (Mondal *et al*., 2023). Another challenge is the insufficient characterization of the functional relevance of genetic markers, which limits the ability to effectively link molecular variation to desirable phenotypic traits. In some cases, the lack of standardized protocols and data sharing hinders collaboration and the exchange of critical genetic information. Furthermore, climate change introduces an additional layer of complexity to genetic variability studies, as genetic adaptation to evolving environmental pressures requires continuous and dynamic analysis of diverse germplasm (Ferrero *et al*., 2020). These challenges underscore the need for investment in accessible technologies, improved data-sharing practices, and expanded germplasm collections

Gene-editing tools like CRISPR-Cas9 allow precise modifications of specific genes, enabling the creation of novel traits such as improved stress tolerance, disease resistance, and enhanced fruit quality (Razzaq *et al*., 2022; Tyagi *et al*., 2021; Xu *et al*., 2020). These technologies can complement traditional breeding methods by introducing targeted genetic variation without the need for extensive hybridization and selection cycles. Moreover, multiplex gene editing offers the potential to simultaneously modify multiple genes, paving the way for more efficient improvement of complex traits governed by polygenic interactions (Yang *et al*., 2023). Combining CRISPR with high-throughput phenotyping and genomic data will further enable the identification and manipulation of key genes associated with desirable traits. Optimized prime editing tools have overcome inefficiencies in dicots like tomatoes, enabling precise, heritable, and multiplex genome modifications with high accuracy, paving the way for transformative advancements in breeding and functional genomics (Vu *et al*., 2024). Another promising direction in the face of climate change, is the application of CRISPR to enhance the adaptability of tomatoes to climate change by engineering traits like heat tolerance and water-use efficiency (Yu et al., 2019; Li et al., 2020).

Bioinformatics and machine learning are poised to revolutionize the analysis of large-scale genetic data in tomato breeding programs by enabling more efficient and accurate interpretation of complex datasets. These technologies can streamline the identification of key genetic markers associated with desirable traits such as yield, disease resistance, and abiotic stress tolerance (Bostan, 2015). Machine learning algorithms, such as random forests and neural networks, can predict trait outcomes based on genotype-phenotype associations, accelerating the selection of superior breeding lines (Yoosefzadeh Najafabadi *et al*., 2023). Bioinformatics tools facilitate the integration of genomic, transcriptomic, and proteomic data, offering a holistic understanding of genetic variability in *Solanum lycopersicum* (Xia, 2018). Additionally, machine learning models can uncover hidden patterns in data, providing insights into polygenic traits that are traditionally challenging to analyse (Cheng and Wang, 2024). By automating the processing of high-throughput sequencing data, these technologies reduce the

time and cost associated with genetic variability studies. Furthermore, predictive models can be used to simulate breeding scenarios, aiding in the design of targeted and efficient breeding strategies. The combination of bioinformatics and machine learning promises to enhance the precision and speed of genetic improvement, ensuring the development of resilient and high-performing tomato varieties for future agricultural challenges.

Conclusion

Genetic variability plays a pivotal role in improving *Solanum lycopersicum* by providing the foundation for improvement of traits. The continuous exploration and characterization of genetic resources, including landraces, wild relatives, and underutilized germplasm, are essential to expand the genetic base of cultivated tomatoes. Advances in molecular tools, bioinformatics, and machine learning have revolutionized the study of genetic variability, enabling precise identification and utilization of key traits for breeding. As climate change and emerging pests and diseases pose growing challenges, leveraging genetic diversity becomes critical for developing resilient and sustainable tomato varieties. Studies focusing on genetic variability not only advance our understanding of tomato genetics but also inform targeted breeding strategies for future demands. Integrating traditional and modern techniques will ensure that genetic resources are conserved and utilized effectively. Ultimately, genetic variability studies will continue to play a transformative role in securing the productivity and adaptability of *Solanum lycopersicum* in the face of evolving agricultural challenges.

References

Aflitos S, Schijlen E, De Jong H. Exploring genetic variation in the tomato (Solanum section Lycopersicon) clade by whole-genome sequencing. The Plant Journal. 2014;80:136-148.

Ahang B, Pashapour S, Ghasemi A, Zabihi A. Investigating the genetic diversity of several varieties of Iranian tomato (Solanum lycopersicum) using RAPD and ISSR molecular markers. Food Health. 2024;6(4):18. doi: 10.53388/FH2024018.

Ahmed HGM-D, Sajjad M, Li M, Azmat MA, Rizwan M, Maqsood RH, Khan SH. Selection Criteria for Drought-Tolerant Bread Wheat Genotypes at Seedling Stage. Sustainability. 2019;11(9):2584. doi:10.3390/su11092584.

Alishah O, Bagherieh-Najjar MB, Fahmideh L. Correlation, path coefficient and factor analysis of some quantitative and agronomic traits in cotton (Gossypium hirsutum L.).

Almiahy FH, Al-Jaf IH. Detection of genetic diversity for five varieties of tomato (Lycopersicon esculentum Mill) using the RAPD-PCR technique. Int J Agricult Stat Sci. 2023;19(1):1421-1425.

Anne C. Choosing the Right Molecular Genetic Markers for Studying Biodiversity: from Molecular Evolution to Practical Aspects. Genetica. 2006;127:101-120.

Ansari A, Sikarwar P, Lade S, Yadav H, Ranade SH. Genetic diversity clusters in germplasm of Cluster Bean (Cyamopsis tetragonoloba L., Taub), an important food and an industrial legume crop. J Agric Sci Technol. 2016;18:1407-1418.

Anwar A, Roy S, Islam MN. Genetic variability analysis of tomato varieties using RAPD markers under heat stress. Bangladesh J Bot. 2024;53(1):91-100.

Athinodorou F, Foukas P, Tsaniklidis G, Kotsiras A, Chrysargyris A, Delis C, Kyratzis AC, Tzortzakis N, Nikoloudakis N. Morphological Diversity, Genetic Characterization, and Phytochemical Assessment of the Cypriot Tomato Germplasm. Plants. 2021;10(8):1698. doi:10.3390/plants10081698.

Balzarini M, Teich I, Bruno C, Peña A. Making genetic biodiversity measurable: a review of statistical multivariate methods to study variability at gene level. Rev Fac Cienc Agrarias. 2011;43(1):261-275.

Barcaccia G, Albertini E, Rosellini D, Tavoletti S, Veronesi F. Inheritance and mapping of 2n-egg production in diploid alfalfa. Genome. 2000;43(3):528-537.

Barchenger DW, Hsu YM, Ou JY, Lin YP, Lin YC, Balendres MAO, et al. Whole genome resequencing and complementation tests reveal candidate loci contributing to bacterial wilt (Ralstonia sp.) resistance in tomato. Sci Rep. 2022;12(1):8374.

Basfore S, Sikder S, Das B, KV M, Chatterjee R. Genetic variability, character associations and path coefficient studies in tomato (Solanum lycopersicum L.) grown under terai region of West Bengal. IJCS. 2020;8(2):569-573.

Beecher GR. Nutrient content of tomatoes and tomato products. Proc Soc Exp Biol Med. 1998;218:98-100.

Bhandari HR, Bhanu AN, Srivastava K, Singh MN, Shreya HA. Assessment of genetic diversity in crop plants-an overview. Adv Plants Agric Res. 2017;7(3):279-286.

Bhandari P, Kim J, Lee TG. Genetic architecture of fresh-market tomato yield. BMC Plant Biol. 2023;23(1):18.

Bostan H. Bioinformatics strategies for genomics: examples and approaches for tomato.

Brewer MT, Lang L, Fujimura K, Dujmovic N, Gray S, van der Knaap E. Development of a controlled vocabulary and software application to analyze fruit shape variation in tomato and other plant species. Plant Physiol. 2006;141(1):15-25.

Cambiaso V, Pratta GR, da Costa JHP, Zorzoli R, Francis DM, Rodríguez GR. Whole genome re-sequencing analysis of two tomato genotypes for polymorphism insight in cloned genes and a genetic map construction. Scientia Horticulturae. 2019;247:58-66.

Caramante M, Rouphael Y, Corrado G. Genetic diversity among and within tomato (Solanum lycopersicum L.) landraces grown in Southern Italy. Genet Resour Crop Evol. 2024;71(1):157-166.

Castellana S, Ranzino L, Beritognolo I, Cherubini M, Luneia R, Villani F, Mattioni C. Genetic characterization and molecular fingerprint of traditional Umbrian tomato (Solanum lycopersicum L.) landraces through SSR markers and application for varietal identification. Genet Resour Crop Evol. 2020;67(7):1807-1820.

Chaudhary J, Khatri P, Singla P, Kumawat S, Kumari A, Vikram A, Deshmukh R. Advances in omics approaches for abiotic stress tolerance in tomato. Biology. 2019;8(4):90.

Chen X, Liu YY, Zheng FS, Cheng GX, Guo M, Li JS, Wang XM. Construction of a core collection of tomato (Solanum lycopersicum) germplasm based on phenotypic traits and SNP markers. Scientia Horticulturae. 2025;339:113855.

Cheng Q, Wang X. Machine Learning for AI Breeding in Plants. Genomics Proteomics Bioinformatics. 2024;22(4):qzae051.

Chitwood-Brown J, Vallad GE, Lee TG, Hutton SF. Characterization and elimination of linkage-drag associated with Fusarium wilt race 3 resistance genes. Theor Appl Genet. 2021;134:2129-2140.

Cholin S, Raghavendra S. Assessment of genetic variability in tomato (Solanum lycopersicum L.) for yield and yield attributing traits. Pharm Innov J. 2021;10:399-403.

Copati MG, Pessoa HP, Dariva FD, Castro Filho MND, Nick C. Tomato families possessing resistance to late blight also display high-quality fruit. Acta Scientiarum Agron. 2024;46:e66790.

Dan LIU, Liang YANG, Zhang JZ, Zhu GT, Lü HJ, Lü YQ, Wu YY. Domestication and breeding changed tomato fruit transcriptome. J Integr Agric. 2020;19(1):120-132.

Darrigues A, Hall J, van der Knaap E, Francis DM, Dujmovic N, Gray S. Tomato analyzer-color test: a new tool for efficient digital phenotyping. J Am Soc Hortic Sci. 2008;133(4):579-586.

Debnath A, Kumar R, Prasad SK, Sharma N. Genetic variation and character association study among morphological and biochemical traits of tomato (Solanum lycopersicum L.) genotypes. The Bioscan. 2021;16(1):69-76.

Diouf I, Albert E, Duboscq R, Santoni S, Bitton F, Gricourt J, Causse M. Integration of QTL, transcriptome and polymorphism studies reveals candidate genes for water stress response in tomato. Genes. 2020;11(8):900.

Domínguez M, Dugas E, Benchouaia M, Leduque B, Jiménez-Gómez JM, Colot V, Quadrana L. The impact of transposable elements on tomato diversity. Nat Commun. 2020;11(1):4058.

Dube J, Ddamulira G, Maphosa M. Tomato breeding in sub-Saharan Africa-Challenges and opportunities: A review. Afr Crop Sci J. 2020;28(1):131-140.

Dwary S, Dukpa P, Gaikwad M, Thapa U, Kumar P, Yeasmin S. Genetic Variability, Heritability and Genetic Advance Studies in Diverse Genotypes of Tomato (Solanum lycopersicum L.). Int J Plant Soil Sci. 2023;35(22):441-446.

Dwiningsih Y, Rahmaningsih M, Alkahtani J. Development of single nucleotide polymorphism (SNP) markers in tropical crops. Adv Sustain Sci Eng Technol. 2020;2(2):343558.

El-Aziz MA, Farid S, Elkomey S. Evaluation of molecular and phenotypic diversity in relation to heterosis in some tomato lines under different climatic conditions. J Agric Chem Biotechnol. 2016;7(5):141-151. doi: 10.21608/JACB.2016.40796.

El-Mansy AB, Abd El-Moneim D, ALshamrani SM, Safhi FA, Abdein MA, Ibrahim AA. Genetic diversity analysis of tomato (Solanum lycopersicum L.) with morphological, cytological, and molecular markers under heat stress. Horticulturae. 2021;7(4):65.

FAOSTAT. FAOSTAT. 2019. Available at: http://www.fao.org/faostat/en/#home [Accessed April 15, 2019].

Ferrero V, Baeten L, Blanco-Sánchez L, Planelló R, Díaz-Pendón JA, Rodríguez-Echeverría S, de la Peña E. Complex patterns in tolerance and resistance to pests and diseases underpin the domestication of tomato. New Phytol. 2020;226(1):254-266.

Foolad MR. Genome mapping and molecular breeding of tomato. Int J Plant Genomics. 2007;10:1-52.

Foroud GN, Mousavizadeh SJ, Akbarpour V, Mashayekhi K. Fruit heritability and the effect of pollen on fruit set of some tomato (Solanum esculentum Mill.) accessions. J Crop Breed. 2021;13(39):77-86.

Fratianni F, Cozzolino A, Nazzaro F, Riccardi R, Spigno P. Qualitative Aspects of Some Traditional Landraces of the Tomato "Piennolo" (Solanum lycopersicum L.) of the Campania Region, Southern Italy. Antioxidants. 2020;9(7):565. doi:10.3390/antiox9070565.

Gajera HP, Tomar RS, Patel SV, Viradia RR, Golakiya BA. Comparison of RAPD and ISSR markers for genetic diversity analysis among different endangered Mangifera indica genotypes of Indian Gir forest region. J Plant Biochem Biotechnol. 2011;20:217-223.

Gao L, Gonda I, Sun H, Ma Q, Bao K, Tieman DM, Burzynski-Chang EA, Fish TL, Stromberg KA, Sacks GL, et al. The tomato pan-genome uncovers new genes and a rare allele regulating fruit flavor. Nat Genet. 2019;51:1044-1051.

Genievskaya Y, Jantasov S, Nurbayeva E, Turuspekov Y. SSR-based assessment of genetic diversity in tomato cultivars and lines grown in Kazakhstan. Eurasian J Appl Biotechnol. 2024;(2):3-15.

Ghosh TK, Hossen BN, Islam SN, Hasan MM, Tareq MZ. RAPD Marker Based Genetic Diversity Analysis of Some Tomato Breeding Lines. Int J Bus Soc Sci Res. 2019;7(2):29-36.

Guo X, Zhao J, Chen Z, Qiao J, Zhang Y, Shen H, Hu Z. CRISPR/Cas9-targeted mutagenesis of SlCMT4 causes changes in plant architecture and reproductive organs in tomato. Horticult Res. 2022;9:uhac081.

Hancock JM. Microsatellites and other simple sequences: Genomic context and mutational mechanisms. In: Goldstein DB, Schlötterer C, editors. Microsatellites: Evolution and applications. Oxford: Oxford University Press; 1999. p. 1–9.

He C, Poysa V, Yu K. Development and characterization of simple sequence repeat (SSR) markers and their use in determining relationships among *Lycopersicon esculentum* cultivars. Theor Appl Genet. 2003;106(2):363–373.

Hong Y, Zhao J, Guo L, Kim SC, Deng X, Wang G, et al. Plant phospholipases D and C and their diverse functions in stress responses. Prog Lipid Res. 2016;62:55-74.

Ilakiya T, Premalakshmi V, Arumugam T, Sivakumar T. Variability analysis in tomato (*Solanum lycopersicum* L.) crosses under drought stress. J Appl Nat Sci. 2022;14(SI):49–52.

IPGRI. Genetic Resources of Tomatoes and Wild Relatives – a Global Report. Esquinas-Alcazar JT, editor. Rome: IBPGR Secretariat; 1996. 65 p.

Jarvis D, Kopp O, Jellen E. Simple sequence repeat marker development and genetic mapping in quinoa (*Chenopodium quinoa* Willd.). J Genet. 2008;87:39–51.

Kim B, Hwang IS, Lee HJ, Lee JM, Seo E, Choi D, Oh CS. Identification of a molecular marker tightly linked to bacterial wilt resistance in tomato by genome-wide SNP analysis. Theor Appl Genet. 2018;131:1017-1030.

Kulus D. Genetic diversity for breeding tomato. In: Cash Crops: Genetic Diversity, Erosion, Conservation and Utilization. p. 505-521; 2022.

Kumari K, Akhtar S, Kumari S, Kumar M, Kumari K, Singh NK, Ranjan A. Genetic variability and heritability studies in diverse tomato genotypes. J Pharm Phytochem. 2020;9(3):1011–1014.

Lahlali R, Taoussi M, Laasli SE, Gachara G, Ezzouggari R, Belabess Z, et al. Effects of climate change on plant pathogens and host-pathogen interactions. Crop Environ. 2024;3(3):159–170.

Landegren U, Nilsson M, Kwok PY. Reading bits of genetic information: Methods for single-nucleotide polymorphism analysis. Genome Res. 1998;8(8):769–776.

Lee U, Chang S, Putra GA, Kim H, Kim DH. An automated, high-throughput plant phenotyping system using machine learning-based plant segmentation and image analysis. PLoS One. 2018;13(4):e0196615.

Li S, Zhang J, Liu L, Wang Z, Li Y, Guo L, et al. SlTLFP8 reduces water loss to improve water-use efficiency by modulating cell size and stomatal density via endoreduplication. Plant Cell Environ. 2020;43(11):2666–2679.

Li Y, Zhang X, Jiang J, Zhao T, Xu X, Yang H, Li J. Virus-induced gene silencing of SlPYL4 decreases the drought tolerance of tomato. Hortic Plant J. 2022;8(3):361–368.

Lin T, Zhu G, Zhang J, Xu X, Yu Q, Zheng Z, et al. Genomic analyses provide insights into the history of tomato breeding. Nat Genet. 2014;46(11):1220–1226.

Luthria DL, Sudarsan M, Krizek DT, Krizek DT. Content of total phenolics and phenolic acids in tomato (*Lycopersicon esculentum* Mill.) fruits as influenced by cultivar and solar UV radiation. J Food Compos Anal. 2006;19:77-83.

M Sheded N, M Salim T, M Ahmed S, H Refaat M, M Bekhit M. Genetic diversity analysis of tomato (*Solanum lycopersicum* L.) hybrids under drought tolerant stress using SSR markers. Benha J Appl Sci. 2022;7(5):219-225.

Marefatzadeh-Khameneh M, Fabriki-Ourang S, Sorkhilalehloo B, Abbasi-Kohpalekani J, Ahmadi J. Genetic diversity in tomato (*Solanum lycopersicum* L.) germplasm using fruit variation implemented by tomato analyzer software based on high throughput phenotyping. Genet Resour Crop Evol. 2021;68:2611–2625.

Mishra P, Singh U, Pandey CM, Mishra P, Pandey G. Application of student's t-test, analysis of variance, and covariance. Ann Card Anaesth. 2019;22(4):407–411.

Mohammadi SA, Prasanna BM. Analysis of Genetic Diversity in Crop Plants—Salient Statistical Tools and Considerations. Crop Sci. 2003;43:1235–1248.

Mondal R, Kumar A, Gnanesh BN. Crop germplasm: Current challenges, physiological-molecular perspective, and advance strategies towards development of climate-resilient crops. Heliyon. 2023;9(1).

Morgil H, Gercek YC, Tulum I. Single nucleotide polymorphisms (SNPs) in plant genetics and breeding. In: The Recent Topics in Genetic Polymorphisms. p. 825-400; 2020.

Mugao L. Morphological and molecular variability of *Alternaria solani* and *Phytophthora infestans* causing tomato blights. Int J Microbiol. 2023;2023(1):8951351.

Nankar AN, Tringovska I, Grozeva S, Ganeva D, Kostova D. Tomato phenotypic diversity determined by combined approaches of conventional and high-throughput tomato analyzer phenotyping. Plants. 2020;9(2):197.

Naveed ZA, Ali GS. Comparative transcriptome analysis between a resistant and a susceptible wild tomato accession in response to *Phytophthora parasitica*. Int J Mol Sci. 2018;19(12):3735.

Nguyen TT, Le NT, Sim SC. Genome-wide association study and marker development for bacterial wilt resistance in tomato (*Solanum lycopersicum* L.). Scientia Horticulturae. 2021;289:110418.

Nie W, Kumar SV, Arsenault KR, Peters-Lidard CD, Mladenova IE, Bergaoui K, et al. Towards effective drought monitoring in the Middle East and North Africa (MENA) region: implications from assimilating leaf area index and soil moisture into the Noah-MP land surface model for Morocco. Hydrol Earth Syst Sci Discuss. 2021;1-36.

Olawuyi OJ, Ajie VI. Diverse morphological and molecular patterns of tomato (*Solanum lycopersicum* Linn.) accessions. Plant Gene. 2023;34:100423.

Onwukwe AA, Falusi AO, Onyenekwe PC. Genetic diversity of tomato (*Solanum lycopersicum*) accessions using chloroplast DNA and random amplified polymorphic DNA markers. Afr J Food Agric Nutr Dev. 2023;23(5):23425–23447.

Passam HC, Karapanos IC, Bebeli PJ, Savvas D. A review of recent research on tomato nutrition, breeding and post-harvest technology with reference to fruit quality. Eur J Plant Sci Biotechnol. 2007;1:1–21.

Patel RR, Sharma D, Das BK, Mondal S, Sahu PK, Vishwakarma G, Khute IK. Study of coefficient of variation (GCV & PCV), heritability and genetic advance in advanced generation mutant line of rice (*Oryza sativa* L.). The Pharma Innovation J. 2021;10(10):784–787.

Peralta IE, Spooner DM, Knapp S. Taxonomy of wild tomatoes and their relatives (Solanum sections Lycopersicoides, Juglandifolia, Lycopersicon; Solanaceae). Syst Bot Monogr. 2008;84:1–186.

Pereira L, Sapkota M, Alonge M, Zheng Y, Zhang Y, Razifard H, van Der Knaap E. Natural genetic diversity in tomato flavor genes. Front Plant Sci. 2021;12:642828.

Pidigam S, Thuraga V, Munnam SB, Amarapalli G, Kuraba G, Pandravada SR, et al. Genetic diversity, population structure and validation of SSR markers linked to Sw-5 and I-2 genes in tomato germplasm. Physiol Mol Biol Plants. 2021;27(8):1695–1710. doi:10.1007/s12298-021-01037-8.

Poets A, Silverstein K, Pardey PG, Hearne S, Stevenson J. DNA fingerprinting for crop varietal identification: Fit-for-purpose protocols, their costs and analytical implications.

Popescu CF, Bădulescu A, Manolescu AE, Dumitru AM, Sumedrea DI. Morphological characterization and genetic variability assessment with SSR markers in several tomato genotypes. Sci Pap Ser B Hortic. 2022;66(1).

Qiu J, Ni L, Xia X, Chen S, Zhang Y, Lang M, et al. Genome-wide analysis of the protein phosphatase 2C genes in tomato. Genes. 2022;13(4):604.

Quispe-Choque G, Huanca-Alanoca N. Correlation analysis and path coefficients for yield components in nine experimental tomato lines. J Selva Andina Res Soc. 2023;14(2):26–35.

Raiola A, Rigano MM, Calafiore R, Frusciante L, Barone A. Enhancing the health-promoting effects of tomato fruit for biofortified food. Mediators Inflamm. 2014. doi: 10.1155/2014/139873.

Rasheed A, Ilyas M, Khan TN, Mahmood A, Riaz U, Chattha MB, et al. Study of genetic variability, heritability, and genetic advance for yield-related traits in tomato (Solanum lycopersicon MILL.). Front Genet. 2023;13:1030309.

Rasul KS, Tahir NAR. Response of different tomato accessions to biotic and abiotic stresses. arXiv preprint arXiv:2403.17030. 2024.

Razzaq MK, Akhter M, Ahmad RM, Cheema KL, Hina A, Karikari B, et al. CRISPR-Cas9 based stress tolerance: New hope for abiotic stress tolerance in chickpea (Cicer arietinum). Mol Biol Rep. 2022;49(9):8977-8985.

Reshma RS, Das D. Molecular markers and its application in animal breeding. Adv Anim Genomics. 2020;123-140. doi:10.1016/B978-0-12-820595-2.00009-6.

Roohanitaziani R, De Maagd RA, Lammers M, Molthoff J, Van Kaauwen MP, Finkers R, et al. Exploration of a resequenced tomato core collection for phenotypic and genotypic variation in plant growth and fruit quality traits. Genes. 2020;11(11):1278. doi:10.3390/genes11111278.

Salim MM, Rashid MH, Hossain MM, Zakaria M. Morphological characterization of tomato (Solanum lycopersicum L.) genotypes. J Saudi Soc Agric Sci. 2020;19(3):233-240. doi:10.1016/j.jssas.2018.11.001.

Schmidt W, Effgen S, Le DB, Wang Y, Adly Mohd Zaidan MW, Huettel B, Schouten HJ, Usadel B, Underwood CJ. A chromosome scale tomato genome built from complementary PacBio and Nanopore sequences alone reveals extensive linkage drag during breeding. Plant J. 2022;110(2):572-588. doi:10.1111/tpj.15690.

Seymen M, Yavuz D, Dursun A, Kurtar ES, Türkmen Ö. Identification of drought-tolerant pumpkin (Cucurbita pepo L.) genotypes associated with certain fruit characteristics, seed yield, and quality. Agric Water Manag. 2019;221:150-159.

Shi R, Panthee DR. Transcriptome-based analysis of tomato genotypes resistant to bacterial spot (Xanthomonas perforans) race t4. Int J Mol Sci. 2020;21(11):4070.

Sivakumar J, Sridhar Reddy M, Sergeant K, Hausman JF, ShaValli Khan PS, Osman Basha P. Principal component analysis-assisted screening and selection of salt-tolerant tomato genotypes. Plant Physiol Rep. 2023;28(2):272-288.

Sousaraei N, Mashayekhi K, Mousavizadeh SJ, Akbarpour V, Medina J, Aliniaeifard S. Screening of tomato landraces for drought tolerance based on growth and chlorophyll fluorescence analyses. Hortic Environ Biotechnol. 2021;62:521-535.

Swarup S, Cargill EJ, Crosby K, Flagel L, Kniskern J, Glenn KC. Genetic diversity is indispensable for plant breeding to improve crops. Crop Sci. 2021;61(2):839-852.

Tieman D, Zhu G, Resende Jr MF, Lin T, Nguyen C, Bies D, et al. A chemical genetic roadmap to improved tomato flavor. Science. 2017;355(6323):391-394.

Tiwari JK, Yerasu SR, Rai N, Singh DP, Singh AK, Karkute SG, et al. Progress in marker-assisted selection to genomics-assisted breeding in tomato. Crit Rev Plant Sci. 2022;41(5):321-350.

Tomato Genome Consortium. The tomato genome sequence provides insights into fleshy fruit evolution. Nature. 2012;485(7400):635–641.

Tonk FA, Tosun M, Ilker E, Istipliler D, Tatar O. Evaluation and comparison of ISSR and RAPD markers for assessment of genetic diversity in triticale genotypes. Bulg J Agric Sci. 2014;20(6):1413-1420.

Tran MT, Son GH, Song YJ, Nguyen NT, Park S, Thach TV, et al. CRISPR-Cas9-based precise engineering of SlHyPRP1 protein towards multi-stress tolerance in tomato. Front Plant Sci. 2023;14:1186932.

Tranchida-Lombardo V, Aiese Cigliano R, Anzar I, Landi S, Palombieri S, Colantuono C, et al. Whole-genome re-sequencing of two Italian tomato landraces reveals sequence variations in genes associated with stress tolerance, fruit quality and long shelf-life traits. DNA Res. 2018;25(2):149-160.

Tranchida-Lombardo V, Mercati F, Avino M, Punzo P, Fiore MC, Poma I, Grillo S. Genetic diversity in a collection of Italian long storage tomato landraces as revealed by SNP markers array. Plant Biosyst. 2019;153(2):288-297.

Tripodi P, Soler S, Campanelli G, Díez MJ, Esposito S, Sestili S, et al. Genome wide association mapping for agronomic, fruit quality, and root architectural traits in tomato under organic farming conditions. BMC Plant Biol. 2021;21:1-22.

Tyagi S, Kumar R, Kumar V, Won SY, Shukla P. Engineering disease resistant plants through CRISPR-Cas9 technology. GM Crops Food. 2021;12(1):125-144.

Udriște AA, Iordachescu M, Ciceoi R, Bădulescu L. Next-generation sequencing of local Romanian tomato varieties and bioinformatics analysis of the Ve locus. Int J Mol Sci. 2022;23(17):9750.

Ünal A, Özbaş MO, Arslan D, İlbi H. Morphological and agronomical characterization of beef type tomato hybrids. Int J Agric Environ Food Sci. 2021;8(2):430-445.

UPOV. International Union for the Protection of New Varieties of Plants. 2001.

Vu TV, Nguyen NT, Kim J, Song YJ, Nguyen TH, Kim JY. Optimized dicot prime editing enables heritable desired edits in tomato and Arabidopsis. Nat Plants. 2024;10(10):1502-1513.

Wang D, Seymour GB. Tomato flavor: Lost and found?. Mol Plant. 2017;10(6):782-784.

Wang T, Li HT, Zhu H, Qi SY, Zhang YM, Zhang ZJ, et al. Comparative analyses of genetic variation in a tomato (Solanum lycopersicum L.) germplasm collection with single nucleotide polymorphism and insertion-deletion markers. Russ J Genet. 2019;55:204-211.

Wang X, Gao L, Jiao C, Stravoravdis S, Hosmani PS, Saha S, et al. Genome of Solanum pimpinellifolium provides insights into structural variants during tomato breeding. Nat Commun. 2020;11(1):5817.

Wang Z, Hong Y, Li D, Wang Z, Chao ZF, Yu Y, et al. Association analysis provides insights into molecular evolution in salt tolerance during tomato domestication. Plant Physiol. 2024;196(4):2721-2729.

Williams JGK, Kubelik AR, Livak KJ, Rafalski JA, Tingey SV. DNA polymorphisms amplified by arbitrary primers are useful as genetic markers. Nucleic Acids Res. 1990;18(22):6531-6535.

Xia X. Bioinformatics and the cell: modern computational approaches in genomics, proteomics and transcriptomics. Springer; 2018.

Xu X, Yuan Y, Feng B, Deng W. CRISPR/Cas9-mediated gene-editing technology in fruit quality improvement. Food Qual Saf. 2020;4(4):159-166.

Yamamoto E, Matsunaga H, Ohyama A, Nunome T, Yamaguchi H, Miyatake K, et al. Whole-genome resequencing of Japanese large-sized tomato cultivars provides insights into the history of modern breeding. Breed Sci. 2024;74(4):344-353.

Yan W, Frégeau-Reid J. Genotype by yield*trait (GYT) biplot: A novel approach for genotype selection based on multiple traits. Sci Rep. 2018;8(1):8242. doi:10.1038/s41598-018-26688-8.

Yang T, Ali M, Lin L, Li P, He H, Zhu Q, et al. Recoloring tomato fruit by CRISPR/Cas9-mediated multiplex gene editing. Horticult Res. 2023;10(1):uhac214.

Yong WTL, Aswandy AK, Cheong BE, Rodrigues KF. Mutagenic effects of ethyl methanesulfonate on nine protein coding genes in tomato (Solanum lycopersicum L.). Scientia Horticulturae. 2021;276:109739.

Yongsuwan A, Poncheewin W, Sastawittaya W, Somkul A, Thunnom B, Aesomnuk W, et al. Exploring the genomic landscape: A comprehensive analysis of the genetic diversity

and population structure of Thai tomato germplasm through whole-genome sequencing (WGS). Horticulturae. 2024;10(6):602.

Yoosefzadeh Najafabadi M, Hesami M, Eskandari M. Machine learning-assisted approaches in modernized plant breeding programs. Genes. 2023;14(4):777.

Yu W, Wang L, Zhao R, Sheng J, Zhang S, Li R, Shen L. Knockout of SlMAPK3 enhances tolerance to heat stress involving ROS homeostasis in tomato plants. BMC Plant Biol. 2019;19:1-13.

Zafar SA, Aslam M, Albaqami M, Ashraf A, Hassan A, Iqbal J, et al. Gamma rays induced genetic variability in tomato (Solanum lycopersicum L.) germplasm. Saudi J Biol Sci. 2022;29(5):3300-3307.

Zhang J, Ren J, Yang J, Fu S, Zhang X, Xia C, Zhao H, Yang K, Wen C. Evaluation of SNP fingerprinting for variety identification of tomato by DUS testing. Agric Commun. 2023;1(1):100006. doi:10.1016/j.agrcom.2023.100006.

Zhao J, Sauvage C, Zhao J, Bitton F, Bauchet G, Liu D, et al. Meta-analysis of genome-wide association studies provides insights into genetic control of tomato flavor. Nat Commun. 2019;10(1):1534.

Zhao X, Liu Y, Liu X, Jiang J. Comparative transcriptome profiling of two tomato genotypes in response to potassium-deficiency stress. Int J Mol Sci. 2018;19(8):2402.

Zsögön A, Peres LE, Xiao Y, Yan J, Fernie AR. Enhancing crop diversity for food security in the face of climate uncertainty. Plant J. 2022;109(2):402-414.