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Breeding for yield and quality improvement in tomato (*Solanum lycopersicum*) using genetic variability and modern genomic tools

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Abstract

Tomato (*Solanum lycopersicum* L.) is one of the most important horticultural crops in the world, but its production continually grapples with difficulty of improving yield without compromising fruit quality. To achieve, this balance requires breeders to make full use of the wide genetic diversity present in cultivated varieties, landraces, and wild relatives. This review synthesises current knowledge on global production trends, genetic basis of key agronomic and quality characteristics, and central role of diversity in sustaining breeding progress. Traditional breeding approaches, such as mass selection, pedigree breeding, backcrossing, and hybrid development have long supported tomato improvement, but their impact has grown significantly with the integration of molecular tools. Advances in QTL mapping, marker-assisted selection, genomic selection, multi-omics technologies, and CRISPR-based editing now make it easier to carefully study complex traits and adjust them with greater accuracy and control. These tools also help broaden the narrow genetic base created by domestication bottlenecks, allowing beneficial alleles from wild germplasm to be reintroduced into elite lines. Looking ahead, climate-smart breeding, high-throughput phenotyping, pangenomics, and farmer-participatory approaches offer promising pathways for developing cultivars that combine high yield, superior flavour and nutrition, and resilience to environmental stresses. Sustained exploitation of genetic variability therefore remains the foundation for meeting future productivity and quality demands in tomatoes.

Key words: QTL mapping, CRISPR/Cas9, Pangenome, Heterosis, *Genomics*, High-throughput phenotyping

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Tomato (*Solanum lycopersicum* Linn., 2n = 2x = 24) is an annual, predominantly self-fertilising species that is widely recognized as one of the most important fruit vegetables worldwide (Waiba *et al.,* 2021). It represents about 16% of total vegetable production, generates an estimated market value of $58 billion, underscoring its immense economic importance (Villanueva Gutierrez, 2018). According to the *World Food and Agriculture – Statistical Yearbook 2024,* the production of tomato reached about 192 million tonnes globally, occupying nearly five million hectares worldwide (World Food and Agriculture, 2024). Tomato serves as an excellent source of essential vitamins and provitamins, including pro-vitamin A, folate, β-carotene and vitamin C, along with important minerals, such as potassium (Avdikos *et al.,* 2021; W. Liu *et al.,* 2022).

Despite its economic and nutritional prominence, tomato production faces serious challenges worldwide. Climate change has increased the frequency and severity of abiotic stresses, including drought, elevated temperatures, and irregular rainfall patterns, while biotic factors such as pests and diseases continue to constrain crop productivity (Sánchez-Bermúdez *et al.,* 2022). Additionally, post-harvest losses, which can exceed 30% in some regions, further constrain the profitability and sustainability of tomato cultivation. In Ghana, these issues are exacerbated by low productivity and a high dependence on imports. In Ghana, the estimated annual demand for tomatoes is approximately 1,048,000 metric tons, whereas local production is only about 500,000–510,000 metric tons, creating a significant supply deficit that compels reliance on imports (Business Ghana, 2024). To offset the domestic production shortfall, Ghana imports the majority of its fresh tomatoes from Burkina Faso, accounting for nearly 90 % of the nation's fresh tomato imports. Additionally imports substantial quantities of processed tomato products such as paste and concentrate from China, Italy, and other European countries. These imports are estimated at 78,000 tonnes of tomato paste annually, equivalent to 500,000 tonnes of fresh tomatoes (HortiDaily, 2024; RVO Netherlands, 2023). Tomato farming in Ghana is dominated by smallholder producers working on limited plots. In a recent survey, almost 90% of farmers operated on less than 2 ha (~5 acres), with many cultivating around 1–2 acres (~0.4–0.8 ha.) (Melomey *et al.,* 2022).

To meet these challenges, how can genetic variability be effectively harnessed to improve yield and quality of

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tomato under diverse and changing environments? The extensive genetic diversity within *Solanum lycopersicum* and its wild relatives provides the foundation to develop improved varieties resilient to environmental stresses to achieve high yield with superior quality fruits (Bhandari *et al.,* 2017; Niehoff *et al.,* 2024). This review examines the role of genetic variability in tomato breeding for improving yield and fruit quality. It summarizes findings on key genetic parameters, including genotypic and phenotypic variation, heritability, genetic advance, correlation, and genotype × environment interactions, and their importance in selection. The review also emphasizes combining genomic tools with conventional breeding to accelerate the development of resilient, high-yielding, and nutritious tomato cultivars.

Tomato Production and Breeding

Global and regional production trends

Tomatoes are one of the most commonly grown and valuable vegetables worldwide. Global production has expanded dramatically over the past half-century – roughly sevenfold since 1960 – reaching the order of 186–192 million tonnes per year in the early 2020s (W. Li *et al.,* 2023). According to FAO data, world tomato output in 2020 was 186.8 million tonnes (worth about US $92.8 billion) (World Food and Agriculture, 2024). Major producers include China (by far the largest, 68–70 Mt), India (20–21 Mt), Turkey (13 Mt), the United States (12 Mt) and Egypt (6.2 Mt) (World Food and Agriculture, 2024). China alone accounts for one-third of the global output. Tomatoes rank among the top five crops worldwide by production volume with a substantial global market value (on the order of $100 billion annually), making tomatoes a key agricultural commodity (w. Li *et al.,* 2023).

Tomatoes have a major economic impact in developing regions. The fourth most valued food crop after rice, sugarcane and wheat grown in low and middle-income countries is the tomato (Schreinemachers *et al.,* 2022) . Every African country grows tomatoes, and its crop provides vital income and nutrition. Tomato and onion make the key ingredients in many traditional dishes eaten daily in West Africa (Awan *et al.,* 2012). In Africa, production is led by Egypt (with high yields and a large processing industry) and Nigeria (the largest producer by volume). (Schreinemachers *et al.,* 2022.).

Production (in tonnes) for major tomato-producing countries (China, India, USA, Brazil, Russia) showing long-term increases, especially the rapid growth in China since the 1990s.

Data source: Food and Agriculture Organization of the United Nations (FAO), accessed via *Our World in Data* (2025).

Tomatoes in Ghana

Ghana is classified as one of the major tomato-growing countries in West Africa. Recent FAO estimates put Ghana's production at 0.32–0.38 million tonnes annually (ca. 300–375 kt/year from 2009–2023) (Melomey *et al.,* 2022). This accounts for roughly 0.2% of the world output (Ghana ranked ~50th globally in 2023). Tomatoes are deeply important in the Ghanaian diet and economy: surveys report that tomato constitutes about 35% of a typical household's vegetable expenditure. It is estimated that some 90,000 smallholder farmers grow tomatoes and over 300,000 Ghanaians are linked to the tomato value chain nationwide (Awan *et al.,* 2012). However, Ghana relies heavily on imports of processed tomato paste to meet demand, reflecting gaps in domestic production and processing capacity.

Domestication history of tomato

Tomato has a well-documented domestication history. The wild progenitor is *S. pimpinellifolium*, a small-fruited species native to coastal Peru and Ecuador. Domestication commenced in the Andean region, South America and later ended in Mesoamerica (Mexico) (w. Li *et al.,* 2023). Intermediate forms include *S. lycopersicum* var. *cerasiforme* (a semi-domesticated cherry tomato found in the Andes). Over thousands of years, indigenous peoples selected larger and less-acidic fruits, leading to the ancestral cultivated tomato (Razifard *et al.,* 2020). This domestication "bottleneck" – followed by modern breeding – profoundly reduced genetic diversity. Studies show that cultivated tomatoes retain only a portion of the variation found in wild ancestors (Alatawi *et al.,* 2025; W. Li *et al.,* 2023). Indeed, traditional cultivars suffered a loss of diversity as varieties spread from the New World to Europe and Asia, and as intensive selection fixed preferred traits. For example, while wild

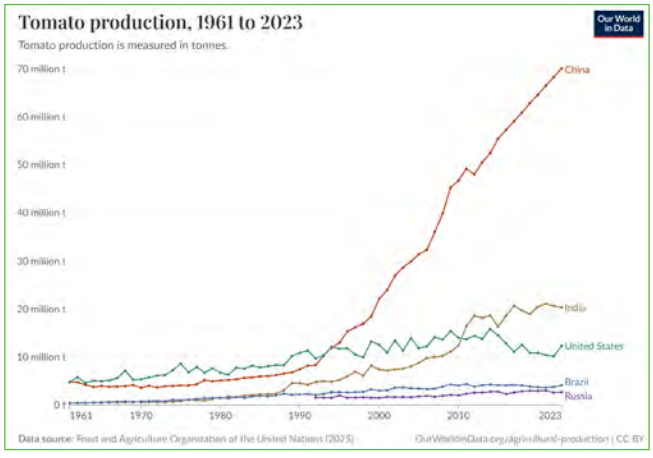

Fig. 1: Global tomato production trends from 1961 to 2023.

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S. pimpinellifolium populations harbour rich variability in fruit colour, flavour and stress tolerance, much of that diversity was lost in early *S. lycopersicum* varieties (Li *et al.,* 2023).

Modern genomic analyses confirm this genetic narrowing. Cultivated tomato shows a clear bottleneck signal: many gene loci are fixed or low in diversity compared to wild relatives. This has implications for breeding: reduced allelic variation can limit the ability to improve traits. In response, breeders now recognize the need to tap wild and landrace germplasm. Wild relatives (like *S. pimpinellifolium, S. habrochaites, S. peruvianum* etc.) offer an "immense gene pool" of useful alleles (Alatawi *et al.,* 2025). For instance, disease-resistant genes such as *Pto* (against bacterial speck) and *Ph-3* (late blight resistant) were introduced into cultivated lines through the germplasms from the wild *S. pimpinellifolium (W. Li et al., 2023).*

Genetic Variability

Genetic variability refers to differences in DNA sequences and phenotypic variation in traits among conspecifics (Rasheed *et al.,* 2023). In tomato (*Solanum lycopersicum* L.), genetic variability is the cornerstone of programmes on breeding because it provides the raw material necessary to select desirable traits such as higher yield, improved fruit quality, tolerance to stress and resistance to disease(Rasheed *et al.,* 2023). Without sufficient variability, breeding progress becomes severely limited, as the scope for introducing beneficial traits is constrained (Jorgensen, 2012).

Sources of genetic variation

Genetic variation in tomato arises from multiple sources(FAO, 2019). Natural populations of wild species such as *S. pimpinellifolium*, *S. peruvianum*, and *S. habrochaites* harbour extensive allelic diversity, particularly for traits related to abiotic stress tolerance, disease resistance, and fruit quality (Lin *et al.,* 2014). Landraces, which are locally adapted, traditional varieties maintained by farmers, contribute additional variability, often containing alleles nonexistent in modern cultivars (Blanca *et al.,* 2015; Lin *et al.,* 2014). In addition, induced mutations, created through chemical mutagens, radiation, or modern genome editing techniques expand the genetic base and allow breeders to introduce novel alleles for characteristic, such as the shape of fruit, colour, and ripening rate (Li *et al.,* 2018, 2019; Tiwari *et al.,* 2023). Collectively, these sources provide a diverse pool of alleles that can be harnessed for targeted breeding (Li *et al.,* 2018, 2019; Tiwari *et al.,* 2023).

Assessment of genetic diversity

Assessing the extent of genetic variation is essential for effective breeding (Temesgen and Temesgen, 2024) . Traditionally, morphological traits such as shape, size of fruit, colour, and anatomy of plant have been used to evaluate variability among genotypes (Kumar Kundu, 2021). While informative, conditions of the environment affect these traits and may not fully reflect underlying genetic differences (Bauchet and Causse, 2012). To complement phenotypic assessment, biochemical markers such as isozyme and protein polymorphisms have been employed, revealing additional hidden variation at the molecular level (El-Sitiny *et al.,* 2022).

In modern breeding, molecular markers have become indispensable (Yali, 2022). Simple Sequence Repeats (SSR), Single Nucleotide Polymorphisms (SNPs), and Amplified Fragment Length Polymorphisms (AFLPs) enable precise genotyping, allowing breeders to assess population structure, track inheritance of target alleles, and perform marker-assisted selection (Chen *et al.,* 2025; W. Xu *et al.,* 2024; Yongsuwan *et al.,* 2024).

Traits Influencing Yield

Tomato yield is a complex trait influenced by multiple component characteristics that altogether influence the overall productivity of a genotype (Tsutsumi-Morita *et al.,* 2021). Yield is not a single attribute but rather a function of several interrelated factors, including fruit number per plant, fruit size, flowering behaviour, plant architecture, and resource-use efficiency.

Yield component traits

Fruit number is a major contributor to tomato yield and is influenced by flower production, pollination success, hormonal balance, environmental conditions, and plant's capacity to sustain fruit development (Azzi



Fig. 2: Genetic variability in tomato fruit: a variety of shapes (round, elongated, lobed), sizes (from cherry to beefsteak), and colours.

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et al., 2015; Dinesh *et al.,* 2025). Fruit size contributes significantly to total yield, especially in market-driven production systems where uniform and large fruits are preferred. Fruit size is regulated by genes controlling cell division and expansion, such as FW2.2, FW3.2, and FW11.3, which have been linked to specific quantitative trait loci (QTLs) affecting fruit weight (Roohanitaziani *et al.,* 2020).

Heterosis and hybrid breeding

Hybrid breeding exploiting heterosis has been instrumental in increasing tomato productivity. Crosses between genetically diverse parents often produce F_1 hybrids with superior yield, uniformity, and stress resilience compared to either parent (Felföldi *et al.,* 2021; Z. Liu *et al.,* 2021). Hybrids are particularly needed for commercial fresh-market and processing tomatoes, where consistency in size, shape, and production duration is critical.

Trade-offs Between Yield and Stress Adaptability

While selection for high yield has historically driven productivity gains, trade-offs exist. Genotypes optimized for maximum yield under ideal conditions may be less adaptable to stress environments such as drought, heat, salinity, or pathogen pressure (Cirillo *et al.,* 2025; Graci and Barone, 2023; Meza *et al.,* 2020). Breeders must balance yield stability with adaptability, ensuring varieties perform consistently across environments while maintaining high fruit quality Modern breeding strategies integrate stress-tolerant alleles from wild relatives and landraces to mitigate these trade-offs, leveraging genomic selection and high-throughput phenotyping to identify resilient genotypes. Such varieties perform consistently across environments while maintaining high fruit quality (Tyagi *et al.,* 2024). Yield in tomato is a multi-component, quantitatively controlled trait shaped by genetics, physiology, and environment. Breeding programmes that integrate knowledge of component traits, polygenic control, QTLs, and heterosis, while accounting for trade-offs under stress, are key to sustaining and improving tomato productivity globally.

Genetic Basis of Fruit Quality Traits

Fruit quality in tomato is a multidimensional trait encompassing physical, nutritional, and sensory features that determine acceptance by consumers, market value, and nutritional benefits (Zhang *et al.,* 2023). Physical quality attributes include shape, fruit size, colour, and firmness, while nutritional quality encompasses lycopene content, vitamin C, sugars, and organic acids. Sensory quality is evaluated through flavour, aroma, and texture, which together influence the overall eating experience (Zhang *et al.,* 2023). The genetic control of these traits is complex, often polygenic, and tightly intertwined with biochemical pathways and environmental influences, making their improvement a central challenge in tomato breeding (Emmanuel Umeohia and Adekunle Olapade, 2024; Zhang *et al.,* 2023).

Breeding Approaches for Yield and Quality Improvement

Traditional breeding methods

Traditional breeding methods remain foundational in tomato improvement, each with unique strengths and limitations. Mass selection involves choosing the best-performing plants based on phenotype and bulking their seeds, which is simple, low-cost, and preserves existing cultivar traits, but improvement is slow and incremental (Abewoy Fentik, 2017; Sharma *et al.,* 2019). Pedigree breeding advances progeny through successive generations by selecting superior individuals from defined crosses, allowing trait combination and ancestry tracking; it accelerates cultivar development but is labour-intensive and may reduce genetic diversity over time (Abewoy Fentik, 2017; Sharma *et al.,* 2019). Backcross breeding transfers specific traits from donor lines into elite cultivars, precise for single-gene traits like disease resistance, though linkage drag can prolong programmes and introduce unwanted alleles (Chitwood-Brown *et al.,* 2021; Sharma *et al.,* 2019; Tripodi *et al.,* 2020). Finally, hybrid breeding exploits heterosis and uniformity, improving stability of yield and quality of fruits; however, heterosis in tomato is modest, and developing hybrid varieties requires extensive selfing, selection, and controlled crosses, making the process more laborious and costly (Z. Liu *et al.,* 2021; Soresa *et al.,* 2020) These traditional approaches complement each other, with choice depending on breeding objectives, available resources, and trait of interest.

Modern breeding methods

Modern breeding methods have significantly accelerated tomato improvement by enabling precise, rapid, and genome-informed selection (Cappetta *et al.,* 2020). Marker-assisted selection (MAS) uses DNA markers linked to target genes or QTL to identify desirable seedlings early, reducing phenotyping time and improving accuracy (Collard and Mackill, 2008). QTL mapping and genome-wide association studies (GWAS) have mapped numerous loci controlling yield, fruit size, soluble solids, colour and quality traits in biparental populations and diverse tomato panels, providing breeders with genomic

Table 1: Comparison of traditional tomato breeding methods, their strengths, limitations, and specific applications

Breeding Method	Key Features/Strengths	Limitations	Reference/Applications in Tomato
Mass selection	Low cost, preserves existing traits	Slow progress, relies on visible traits	Open-pollinated varieties (Abewoy Fentik, 2017; Sharma *et al.,* 2019)
Pedigree breeding	Combines multiple traits, tracks ancestry	Labor-intensive, may reduce diversity	Cultivar development programmes (Abewoy Fentik, 2017; Sharma *et al.,* 2019)
Backcross breeding	Precise introgression of specific traits	Linkage drag, time-consuming	Introgression of disease resistance genes from wild Solanum (Sharma *et al.,* 2019; Tripodi *et al.,* 2020; Chitwood-Brown *et al.,* 2021)
Hybrid breeding	Exploits heterosis, uniformity, yield stability	Modest heterosis, complex and costly parental line maintenance	Processing and F1 hybrids (z. Liu *et al.,* 2021; Soresa *et al.,* 2020)

targets for the improvement of traits (Causse *et al.,* 2004; Tripodi *et al.,* 2020). Genomic selection (GS) also improves the breeding pipeline by using genome-wide markers to predict breeding values, allowing early selection for traits that are highly polygenic such as yield and fruit quality, and thus accelerating genetic gain (Cappetta *et al.,* 2020). Genetic engineering and genome editing tools, including CRISPR/Cas, offer precise modification of genes controlling ripening, disease resistance, shelf life, and nutrition (Tiwari *et al.,* 2023). These methods bypass linkage drag and enable phenotypes unattainable through classical breeding, although regulatory and consumer acceptance issues remain (Abewoy Fentik, 2017; Vu *et al.,* 2020). Together, modern breeding methods provide high-resolution genomic insight and selection power, forming the core of contemporary tomato improvement programmes.

Integrating conventional and modern breeding

Modern tomato breeding increasingly merges classical and advanced methods to accelerate genetic gain. Instead of using each approach in isolation, breeders now stack technologies in tandem. For example, major disease and quality genes discovered by QTL mapping can be immediately fixed in elite lines by MAS, while genomic selection optimises polygenic traits. Indeed, Cappetta et al. (2020) emphasize that GS can be incorporated "in elite line selection, and descendant and backcross schemes" to boost gain. In practice, one might introgress a useful allele by MAS or CRISPR, then use GS on the segregating population to rapidly capture background improvements.

The CRISPR/Cas is the latest tool in this integrated toolbox. Alleles lost during domestication (for flavour nutrition, stress resistance) have traditionally been reintroduced by lengthy backcrossing with wild relatives. New genome-editing strategies, however, can "accelerate allele introgression" or even perform genome-wide gene stacking in one generation. For instance, the concept of de novo domestication exploits CRISPR to create "ideal" forms of wild tomato that carry multiple domesticated traits at once (Fernie and Yan, 2019). The edited plants can then enter conventional breeding programmes already far along, effectively leaping generations. This integration of precision editing with normal crosses could cut years off breeding time.

Role of Genetic Variability in Breeding Success

Genetic variability is the cornerstone of plant breeding programmes that have been a success (Temesgen and Temesgen, 2024).

Exploiting wild relatives for trait improvement

Wild relatives of cultivated tomatoes are invaluable sources of genetic diversity. Species such as *S.*

Table 2: Comparison of modern tomato breeding methods, their strengths, limitations, and specific applications

Modern Breeding Method	Key Features/Strengths	Limitations	Applications/References in Tomato
Marker-Assisted Selection (MAS)	Early DNA-based selection; speeds introgression; high accuracy	Requires reliable markers; limited for highly polygenic traits	Introgression of quality and resistance genes (Collard & Mackill, 2008; Lecomte *et al.,* 2004; Vu *et al.,* 2020)
QTL Mapping	Identifies genomic regions controlling traits	Low resolution; limited to biparental variation	*S. pennellii* ILs mapping fruit traits (Causse *et al.,* 2004)
GWAS	High-resolution mapping using natural diversity	Requires large diversity panels; susceptible to false positives	Loci for fruit size, shape, colour soluble solids (Tripodi *et al.,* 2021)
Genomic Selection (GS)	Predicts breeding value using genome-wide markers; ideal for polygenic traits	Requires large training populations and computational models	Enhanced prediction for yield and quality (Cappetta *et al.,* 2020)
Genetic Engineering & CRISPR	Precise gene modification; bypasses linkage drag; introduces novel traits	Regulatory restrictions; public acceptance issues	Flavr Savr tomato, virus resistance, shelf-life modification (Abewoy Fentik, 2017; Vu *et al.,* 2020)

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pimpinellifolium, *S. habrochaites*, and *S. pennellii* harbour alleles for traits largely absent or diminished in modern cultivars due to the genetic bottleneck imposed by domestication(Mata-Nicolás *et al.,* 2020). These alleles have without fail been introgressed into elite cultivars to enhance both disease resistance and the quality of fruits (Barrantes *et al.,* 2016; Celik *et al.,* 2017).

Genetic diversity, adaptability, and sustainability

Broad genetic variability underpins both short-term breeding success and long-term sustainability. Diverse germplasm provides alleles that allow breeders to respond to emerging biotic stresses (new pathogens or pest strains) and abiotic stresses (drought, salinity, heat). For instance, the introgression of multiple disease resistance genes from wild relatives not only improved current cultivars but also provided genetic "insurance" against pathogen evolution (A. Kaur and Sangha, 2023). This dynamic adaptability is critical as climate change introduces novel stress patterns and expands cultivation into marginal environments (Causse *et al.,* 2013; Kapazoglou *et al.,* 2023; Rose *et al.,* 2025).

The importance of wild and exotic germplasm is further highlighted in long-term sustainability of plant breeding (Kapazoglou *et al.,* 2023). Landraces and wild relatives act as reservoirs for traits that may not be immediately needed but become critical under changing environments or pathogen pressures. Programmes that systematically conserve, characterize, and utilize these resources—such as the Tomato Genetics Resource Center (TGRC) and IL collections—illustrate how broad genetic variability is a practical necessity for sustained genetic gain (Bai ans Lindhout, 2007; Hussain *et al.,* 2025).

The evidence is clear: genetic variability is fundamental to breeding success in tomato. Wild relatives and landraces provide alleles for disease resistance, stress tolerance, and fruit quality that are largely absent in modern cultivars (Kapazoglou *et al.,* 2023).

Challenges and Future Prospects in Tomato Breeding

Tomato improvement has achieved remarkable progress over the last century, yet the crop continues to face complex genetic, environmental, and market-driven pressures that constrain breeding efficiency. Many of these challenges stem from long-term domestication, modern production demands, and the increasing unpredictability of climate stressors. Addressing them requires not only access to broad genetic diversity but also the integration of cutting-edge technologies and innovative breeding approaches that align yield, quality, and resilience goals (Du *et al.,* 2025).

Ongoing challenges

Genetic erosion and narrow breeding pools

One of the most persistent challenges is *genetic erosion*—the loss of allelic diversity in cultivated tomato due to domestication, modern selection, and widespread commercialization of uniform hybrids. The process of domestication and repeated selective breeding has greatly reduced genetic diversity compared to wild relatives, leaving breeders with only a limited number of alleles for complex traits like flavour, hardiness, and nutrient content (Lin *et al.,* 2014).

Limited germplasm exchange

Although wild relatives contain valuable alleles, *access and exchange of germplasm* remain constrained by regulatory barriers, intellectual property rights, and insufficient international collaborations. Many breeding programmes rely on a small subset of accessible lines, while vast collections maintained in gene banks remain underutilized due to poor characterization or lack of molecular data (Ebert *et al.,* 2023; Nguyen & Norton, 2020).

Consumer-driven uniformity

Modern supply chains and consumer markets demand *uniform fruit shape, colour ripening behaviour, and shelf life*. These expectations lead breeders to prioritize appearance and firmness over broader variation in flavour and nutritional composition. Over time, this has reinforced selection for a narrow set of phenotypes that meet commercial needs, often at the expense of flavour aroma, and micronutrient diversity (G. Kaur *et al.,* 2023; Nie *et al.,* 2024; Tieman *et al.,* 2017).

Climate change and stress interactions

Rising temperatures, erratic rainfall, high salinity, and emerging pest complexes pose new challenges for tomato production. Many elite cultivars lack broad-based tolerance, and stress interactions such as heat combined with drought are rarely addressed in traditional breeding (Bai *et al.,* 2018; Fernández-Crespo *et al.,* 2022; Roșca *et al.,* 2023).

Technological opportunities to overcome these challenges

Despite the constraints, recent advances in genomics and phenotyping offer unprecedented opportunities to expand usable variability and accelerate genetic gain.

Pangenomics and structural variant discovery

The tomato *pangenome is* constructed from multiple cultivated and wild accessions which capture genomic

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regions absent from the reference genome. Pangenomic studies reveal structural variations, presence–absence variants, and hidden allelic diversity that were previously undetectable. These new insights allow breeders to target novel genes affecting quality of fruit, resistance to disease, and abiotic stress tolerance (Gao *et al.,* 2019).

High-throughput phenotyping (HTP)

High-throughput phenotyping (HTP) has rapidly evolved thanks to advances in imaging systems, drones, hyperspectral sensors, and automated greenhouse platforms (Xu & Li, 2022). These technologies allow breeders to precisely measure complex, traits such as canopy temperature (a proxy for water or heat stress), biomass accumulation, plant architecture, and even biochemical features of fruit across different environments and time points. By integrating computer vision, machine learning, and frequent imagery, HTP dramatically reduces the labour and cost associated with traditional, manual measurements (Aono *et al.,* 2021; R. Xu and Li, 2022).

Multi-omics integration

Modern breeding increasingly relies on multi-omics integration which combines genomics, transcriptomics, metabolomics, and proteomics and these help to unravel the complex biochemical networks that underlie traits like flavour, lycopene synthesis, sugar–acid balance, and stress responses(Pascual *et al.,* 2025). For instance, systems biology studies in tomato using transcriptomic, proteomic, and metabolomic layers have revealed how key ripening regulators such as NOR and RIN coordinate metabolic shifts in sugars, organic acids, and cell-wall compounds (Osorio *et al.,* 2011). Multi-omics approaches have also shown how cold storage reprograms secondary metabolism: low-temperature treatment dramatically alters flavonoid and phenylpropanoid metabolites, and this correlates with the structural genes expression and factors of trascription like *SlCHS* as well as *MYB70* (Liu *et al.,* 2023). In stress studies, integration of transcriptome and metabolome data under combined abiotic stresses uncovered regulatory hubs involving amino-acid, sugar, and hormone pathways, highlighting candidate genes and metabolites that might be key to climate resilience breeding (Pascual *et al.,* 2025).

Bioinformatics and AI-driven breeding

Machine learning and AI algorithms are revolutionising how breeders interpret complex data and make breeding decisions. These models can predict genotype performance under different environmental conditions, forecast how alleles will interact, and simulate how specific crossing designs will perform. AI-driven platforms help breeders identify favourable haplotypes, optimise parent selection, and prioritise crosses, especially when working with highly polygenic traits (e.g. yield, flavour, stress resilience). By integrating genomic, phenotypic, and environmental datasets, these tools accelerate decision-making and increase breeding program efficiency ultimately decreasing the time and cost needed to deliver improved tomato varieties (Farooq *et al.,* 2024; Gerakari *et al.,* 2025).

Strengthening pre-breeding and participatory approaches

Pre-breeding to unlock wild diversity

Pre-breeding is a crucial step in modern tomato breeding, allowing the transfer of valuable alleles from wild relatives — such as *S. pennellii*, *S. habrochaites*, and *S. pimpinellifolium* — into intermediate lines while minimizing linkage drag (A. Kaur and Sangha, 2023). These intermediate lines act as a bridge, expanding the usable genetic base and making wild alleles (Lecomte *et al.,* 2004)more accessible for integration into elite cultivars. Through pre-breeding, researchers have successfully identified QTLs associated with important traits, such as soluble solids content, disease resistance (e.g. resistance to bacterial speck, nematodes, and viruses), and abiotic stress tolerance, which can then be directly exploited in commercial breeding programmes. This approach not only widens the genetic diversity available for selection but also speeds the development of high-performing, resilient, and quality-focused tomato varieties (Thapa *et al.,* 2015; Zsögön *et al.,* 2018) .

Participatory breeding

Participatory breeding is a deeply empowering process that brings farmers, processors, consumers, and scientists into the same conversation, not just as recipients of new varieties, but as active decision-makers. In smallholder-dominated regions in Africa and Asia, this matters a great deal: farmers know their land, their climate, and their market conditions intimately, and when they help select and breed crops, the resulting varieties are more likely to combine productivity with resilience and the traits people truly value (such as taste, cooking quality, or post-harvest features). By enriching the breeding environment with local voices, participatory breeding helps develop cultivars that suit real-life conditions rather than ideal research station plots, accelerating adoption, boosting biodiversity, and building trust between researchers and communities. Studies in Ethiopia, for example, show that involving farmers in bean breeding leads to selection based on 40+ criteria,

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from drought tolerance to cooking colour and results in varieties farmers are more likely to grow and maintain (Al-Tawaha *et al.,* 2005). Similarly, participatory programmes in maize across Sub-Saharan Africa have shown that farmer-preferred traits often diverge from breeder-only priorities (Worku *et al.,* 2020). This inclusive approach also strengthens social capital, as farmers gain new skills and take ownership of seed systems, and it contributes to food sovereignty by preserving and enhancing locally adapted genetic diversity (Greenberg, 2018).

Climate-smart breeding

Climate-smart breeding strategies intentionally build resilience into new varieties so they can withstand rising temperatures, erratic water availability, and soil salinity while still producing high-quality fruit. For instance, breeders are selecting for heat-tolerant flowering and stable fruit set under stress using Quantitative Trait Loci (QTL) associated with yield and soluble solids under heat stress (Cappetta *et al.,* 2021; Elazazi *et al.,* 2024). At the same time, they pyramid multiple stress-tolerance genes *via* marker-assisted selection (MAS) or genomic selection, which leverages genome-wide markers to predict performance under combined stress environments (Cappetta *et al.,* 2021). *A*dditionally, grafting onto vigorous rootstocks derived from wild relatives like *Solanum pimpinellifolium* and *S. habrochaites* is increasingly used to boost tolerance to salinity and maintain nutrient balance under salt stress (Aydin, 2024). Together, these strategies align breeding with future climate scenarios, ensuring new cultivars remain both productive and resilient, and helping farmers sustain yields even as growing conditions change.

Vision for Future: Precision and Resilient Tomato Improvement

The future of tomato breeding lies in combining broad genetic diversity with precision tools that allow breeders to sculpt phenotypes with unprecedented accuracy (Yali, 2022). Pangenomic resources, multi-omics insights, CRISPR-mediated editing, and genomic prediction models will enable targeted improvement of traits previously considered too complex or polygenic(Cappetta *et al.,* 2021; Fernie & Aharoni, 2019; Gao *et al.,* 2019; Pascual *et al.,* 2025; Rönspies *et al.,* 2021; Yeon *et al.,* 2024; Zhou *et al.,* 2022).

A resilient future tomato cultivar will be one that:

- draws from the broadest possible genetic base
- withstands multiple stress combinations
- satisfies consumer demand for flavour, nutrition, and shelf life
- performs predictably across diverse environments
- is developed through data-driven, farmer-inclusive breeding
- leverages precision breeding tools to accelerate genetic gain

CONCLUSION

Sustainable enhancement of tomato yield and fruit quality ultimately depends on the continuous exploration, conservation, and strategic use of genetic variability. The collective evidence demonstrates that broadening the genetic base through wild relatives, landraces, pre-breeding, and modern genomic tools is essential for unlocking new alleles that support resilience, nutritional improvement, and long-term productivity. Traditional breeding strategies continue to provide a reliable foundation, but their power increases substantially when integrated with advanced genomic, transcriptomic, metabolomic, and genome-editing technologies. These tools not only accelerate selection but also enable precise manipulation of complex traits previously limited by narrow diversity and long breeding cycles. Moving forward, a holistic breeding paradigm that merges classical knowledge with cutting-edge biotechnology, data-driven prediction, and climate-smart strategies will be critical. Such integration will ensure the development of tomato cultivars that meet global expectations for yield, flavour, nutrition, and environmental adaptability. Maintaining and expanding genetic diversity is therefore not optional, it is the defining requirement for future tomato improvement and for securing both productivity and nutritional security in an increasingly unstable climate.

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