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REVIEW ARTICLE

Tomato: Breeding and Genomics

HC Prasanna[1], N. Rai[2], Zakir Hussain[3], Suresh R. Yerasu[2] and Jagesh K. Tiwari[2*]

Abstract

Tomato is an important vegetable of the human diet. In tomatoes, through conventional breeding methods, many cultivars with desirable traits have been developed. With the advancement in sequencing technologies combined with reducing cost per sample, high-throughput genotyping platforms and bioinformatics pipelines have revolutionized tomato improvement. After the tomato genome sequencing in 2012, thousands of cultivated and wild species have been sequenced with respect to studies on population structure, genetic diversity, high-density maps and structural variants analysis so on. Now, genomics-assisted research would aim to discover of QTLs/genes and associated SNP markers by genome-wide association studies (GWAS) using high-throughput genotyping (SNP array or genotyping-by-sequencing) for rapid breeding. Moreover, genome editing and genomics selection tools would increase breeding efficiency and higher genetic gain in tomatoes.

Keywords: Tomato, Genome sequencing, QTLs, SNP markers, Breeding, Genomics.

[1]ICAR-Indian Institute of Horticulture, Hessaraghatta, Karnataka, India

[2]ICAR-Indian Institute of Vegetable Research, Varanasi, Uttar Pradesh, India

[3]ICAR-Indian Agricultural Research Institute, PUSA, New Delhi, India

[*]**Corresponding author;** Email: jageshtiwari@gmail.com

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Introduction

In terms of acreage, productivity, economic worth, and human nutrition, the tomato (*Solanum lycopersicum* L.) has emerged as the most significant vegetable crop. Tomato is a tropical origin plant and is grown in almost every part of the world ranging from tropics and sub-tropics to parts of Arctic regions. It is grown in a wide range of diverse climatic conditions and requires adaptation to different abiotic environmental stress conditions (Chaudhary *et al.* 2019). In 2022, world tomato production reached to nearly 186.82 million tonnes from total area of 5 million hectares with an average productivity of 36.97 t/ha (FAOSTAT 2022). Worldwide, china (64.86 mt) is the top producer of tomatoes sharing nearly 34.72% of total tomato production and share (%) followed by India (20.57 mt, 11.01%), Turkey (13.20 mt, 7.06%) and USA (12.22 mt, 6.54%). In terms of coverage area under tomato, China (1.11 mha) is leading followed by India (0.81 mha), Turkey (0.18 mha) and USA (0.11 mha). The highest productivity of tomatoes was recorded in the USA (110.71 t/ha) followed by Spain (77.75 t/ha), Turkey (72.59 t/ha), Brazil (72.24 t/ha), Italy (62.61 t/ha) and China (58.35 t/ha) (FAOSTAT, 2022) (Table 1).

Tomato is an essential dietary component of our vegetables. Tomato is considered as a rich source of vitamins A and C, minerals and antioxidants (lycopene and beta-carotene) and other antioxidants. Tomato is therefore considered as functional food, which provides basic nutrition and health benefits (Causse *et al.*, 2016). Owing to

Table 1: Top ten tomato-producing countries

S. No.	Country/Region	Area (ha)	Production (tonnes)	Productivity (t/ha)	% of world production
Country					
	China	1 111 480	64 865 807	58.35	34.72
	India	812 000	20 573 000	25.33	11.01
	Turkey	181 879	13 204 015	72.59	7.06
	USA	110 439	12 227 402	110.71	6.54
	Egypt	170 862	6 731 220	39.39	3.60
	Italy	99 780	6 247 910	62.61	3.34
	Iran	129 058	5 787 094	44.84	3.09
	Spain	55 470	4 312 900	77.75	2.30
	Mexico	84 926	4 137 342	48.71	2.21
	Brazil	51 960	3 753 595	72.24	2.00
World region					
	Asia	2 683 606	116 993 632	43.59	62.62
	Americas	361 386	24 445 972	67.64	13.08
	Europe	424 449	22 810 698	53.74	12.20
	Africa	1 577 885	22228893	14.08	11.89
	Oceania	4 657	342 021	73.44	0.18
World total		5 051 983	186 821 216	36.97	100

Source: FAOSTAT 2022

high food values, nutrition, and high demand of fresh and processed tomatoes, it is necessary to rapidly breed cultivars for different purposes especially consumer and marker-specific cultivars at rapid scale. Despite much research advancement, this crop is affected by various diseases (bacterial, fungal and viruses), insect pests, abiotic stresses (heat, drought, frost and salinity) and climate change which severely impact tomato production all over the world (Liedl *et al*., 2013). There are various factors that affect plant growth and reduce crop yield. Hence, tomato improvement and varietal development is one of the major activities to address these issues by applying modern genomics tools. Hence, in this review we highlight on the advancement in the breeding and genomics of tomatoes.

Tomato Genetic Resources

Origin and spread

Tomato is one of the major vegetable crops under the family Solanaceae, which includes more than 3000 species (Causse *et al*., 2016). In Lycopersicon clade of Solanum section, 13 closely related tomato species exist including one cultivated type *S. lycopersicum*, and 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*) (Table 2). Tomato originated in the Andean regions of South America including Peru, Bolivia, Ecuador, Colombia, and Chile, and exact location of tomato domestication was described in both Mexico and Andean regions. The cultivated tomato represents nearly 5% of total genetic diversity in all tomato species. Tomato was first introduced by Spanish in 1523 in Europe from where it spread to Italy in 1544, England in 1597, and Philippines and Malaysia in 1650, and in 18th century it spread to North America from Europe (Liedl *et al*., 2013).

Genebank repository

Tomato is well represented in the world genebank collection with about 36,431 accessions (https://www.genesys-pgr.org). Among them, the maximum collections are found in the institute based in the United States of America (15,992) followed by World Vegetable Centre (WVC), Taiwan holds the largest collection (8497) among the single institute, Ukraine (2,178), Czech Republic (1,391), Bulgaria (1,365), Netherlands (1,337) and Australia (1276). Among various species, the predominant species are *S. lycopersicum* (28,435), *Lycopersicon esculentum* (5,319), *S. pimpinellifolium* (971), *S. peruvianum* (470), *S. habrochaites* (362), *S. chilense* (160), *S. pennellii* (132), *S. cheesmaniae* (71) so on. The collection includes advanced/improved cultivar (10,808), traditional cultivar/landrace (2,680), wild (1,942), breeding/research material (702), breeders' line (584), genetic stock (569), hybrid (234), mutant (186), inbred line (79) and many others/not-specified. Type of germplasm storage includes seed collection (14,516), long-term seed collection (6,670), medium-term seed collection (3,678), short-term seed collection (99), and not specified (14,465). Tomato is the most widely distributed crop after

Table 2: Cultivated and wild species of tomato

Species	*Distribution*
Section: Lycopersicon 'Lycopersicon group'	
Solanum lycopersicum	Globally cultivated tomato
Solanum cheesmaniae	Galápagos Islands
Solanum galapagense	Galápagos Islands
Solanum pimpinellifolium	South-western Ecuador to northern Chile
Section: Lycopersicon 'Eriopersicon group'	
Solanum chilense	Coastal Chile and southern Peru
Solanum peruvianum	Central Peru to northern Chile
Solanum corneliomulleri	Southern Peru (Lima southwards)
Solanum habrochaites	Andean Ecuador and Peru
Solanum huaylasense	Río Santa river drainage, north-central Peru
Section: Lycopersicon 'Arcanum group'	
Solanum arcanum	Northern Peru
Solanum chmielewskii	Southern Peru and northern Bolivia
Solanum neorickii	Southern Ecuador to southern Peru
Section: Lycopersicon 'Neolycopersicon group'	
Solanum pennellii	Northern Peru to northern Chile
Section: Juglandifolia	
Solanum ochranthum	Andean Colombia, Ecuador and Peru
Solanum juglandifolium	Andean Colombia, Ecuador and Peru
Section: Lycopersicoides	
Solanum lycopersicoides	Southern Peru and northern Chile
Solanum sitiens	Northern Chile

Source: Modified from Liedl *et al.* (2013) and Causse *et al.* (2016)

pepper by the WVC. Wild relatives of tomatoes are good sources of biotic and abiotic stress resistance/tolerance genes and virtually most significant resistance genes to tomato diseases were selected from wild species only. A major focus at WVC is on the introgression of disease-resistance genes to late blight, bacterial wilt, leaf curl (begomovirus) and heat-stress tolerance. The lines developed by WVC have been utilized to develop varieties across the world (https://www.genesys-pgr.org).

Conventional Breeding

Breeding efforts

Tomato breeding was started nearly a century back in the 1930s with a great diversity in terms of plant phenotype and fruit size, shape, color and taste. Tomato breeding became more specialized by 1950s to develop varieties for fresh market and processing purposes. Until 1980s, most tomato breeding programs rely upon phenotypic selection, which suffered limitations like phenotype screening environments, need of large space and large population, genotype × environment interactions, and reduced trait response with low heritability and linkage drag. In some cases, the phenotypic selection procedure is not able to characterize full genetic information of germplasm or breeding lines (Tanksley and McCouch, 1997). Therefore, with the advent of molecular markers technology, there has been a voluminous increase in interest in genetic maps and polymerase chain reaction (PCR) based molecular markers discovery for tomato breeding, especially disease-pest resistance.

Breeding objectives and methodology

Tomato breeding mainly aims on increasing yield and biotic and abiotic stress resistance, fruit quality for both fresh market and processing categories (Tiwari *et al*. 2022b). First, yield increase is the major objective of any breeding program through heterosis breeding (Kumar *et al*. 2021). Hybrid development is the preferred method for high yield, fruit uniformity and varietal protection. Second, resistance to diseases and insect pests is another breeding objective. Third, tolerance to abiotic stresses such as heat, drought, salinity and chilling injury is an additional target under climate change scenario, and to achieve it, mutation breeding play a key role. Finally, improving fruit quality is very important for both fresh and processed tomatoes (Liedl *et al*., 2013).

Usually fresh market tomato is consumed in raw, but processing type is usually processed for peeling and used for making juice, sauce and various other canned products. Breeding objectives are entirely different for fresh and processing types with a common objective of high yield per unit area, and resistance to disease, insect-pest and abiotic stress, adaptation to climate change and plant type for warm/temperate regions, and greenhouse/open field conditions, and harvest stage. Processing varieties possess certain processing characteristics such as high total soluble solid (TSS, 4–8°brix), high viscosity, high acidity (> 0.4%), high dry extract, low pH value (< 4.5), uniform red color, smooth surface, free from wrinkle, small core, firm flesh, uniform ripening, and quality traits like color, consistency, and flavor (Fentik, 2017). Indeterminate plants are suitable for protected cultivation in a greenhouse or polyhouse. Tomato is one of the most popular greenhouse crops. On the other hand, fresh market varieties have fruits with longer shelf life, shape, color, flavor, sweetness and juiciness. The physical traits like fruit size, shape and color, and internal chemical constituents like TSS, acidity, taste/flavor and sensory factors are very important in tomato breeding (Table 3).

The most common breeding method of tomatoes is hybridization followed by pedigree selection. Back-cross breeding is used to transfer desirable traits from donor to recipient parents. In some cases, a pedigree method in combination with a single seed descent method has been preferred a useful approach. The pedigree method is the most reliable breeding method for tomato varietal development. The pedigree method includes selected crosses followed

Table 3: Breeding objectives of tomato for fresh market and processing purposes

Parameters	*Tomato breeding objectives*	
	Fresh market tomatoes	*Processing tomatoes*
Use	Consumed raw/fresh & cooked vegetables	Peeled for making juice, soup, sauce, ketchup & other canned products
Yield	High	High
Biotic/abiotic resistance	Resistant	Resistant
Plant type	Indeterminate growth habit for glasshouse	Determinate and compact growth habit
Fruit traits	Fruit size, shape and color Sweeteness Juiciness Firmness Locule size and number Uniformity Appearance Longer shelf-life Taste & flavour	High yield Thick pericarp Firm flesh Small locule area Determinate growth Concentrated flowering Uniform fruit set Uniform ripening Uniform red color One-time fruit set and ripening Mechanical harvesting Jointless pedicel (easy to detach) Intense red color No cracking Elongated shape Smooth surface Free from wrinkle Small core High viscosity High dry extract High alcohol-insoluble solids
Special processing traits	NA	Total soluble solid (TSS): > 5.5°Brix Acidity: < 0.4% pH: < 4.4 Pericarp thickness: > 0.5 cm Vitamin C: > 25 mg/100 g Lycopene: > 8.5 mg/100 g Fruit weight: > 80 g No. of locules: 2-4

Source: Modified from Liedl *et al.* (2013), Causse *et al.* (2016), Fentik (2017)

by successive generation advancement based on visual single-plant selection. Individual plants in early generation are selected and further, each generation is advanced under natural field conditions. The pedigree method is faster than mass selection for varietal development in tomatoes. Hybrid development is also most common breeding method in tomatoes. A wide range of mutants have been exploited for trait discovery in tomatoes and further deployed in breeding.

Tomato breeding for therapeutic/nutraceutical formulations

Tomato with biologically active nutraceuticals may play an important role in the human diet. It has been explored recently as a sustainable alternative for the control and prevention of many diseases. They have received considerable attention in diet because are safe, efficacious, and have potential nutritional value as well as therapeutic effects. Among natural dietary supplements, tomatoes, being low in calories are enriched with phyto-nutraceuticals such as lycopene, carotenoids, lutein, zea-xanthine, vitamins, minerals, antioxidants and phytochemicals play vital role in disease prevention/reduction disease risk factors through antioxidant activities. Tomatoes are a rich source of the carotenoids beta-carotene and lycopene, the flavonoid naringenin, the triterpene lupeol, as well as melatonin, all of which have been found to have anti-cancer activities. Tomatoes have been shown to have antioxidant, anti-inflammatory, antimutagenic, and cardioprotective properties.GABA (gamma amino butyric acid) is the first successful case for plant-based therapeutics for the treatment lifestyle diseases like blood pressure. Glycoalkaloids have a strong inhibitory effect on cancer cell growth, which is thought to be driven by mechanisms that cause the cell to die through apoptosis. For the present study, researchers reviewed studies that looked at the anticancer properties of solanine, chaconine, solasonine, solamargine, and tomatine, which are found in the nightshade family including tomatoes and potatoes (Winkiel *et al*., 2022).

Therefore these important substances, important in human nutrition must be clearly identified and should be intend to breed cultivars with improved nutritional/ therapeutic attributes through conventional and molecular breeding approaches

Marker-Assisted Selection

Tomato was the first crop in which molecular markers were applied in mapping and marker-assisted selection (MAS) breeding (Tanksley and Rick, 1980). In 1980, isozyme marker acid phosphatase (*Aps-11*) was used in MAS for nematode resistance breeding resistance (Tanksley, 1983). Before that most breeding programs rely upon phenotypic selection. With the advent of molecular markers, there has been a tremendous increase in interest for the use of molecular markers particularly PCR-based technology in tomato breeding (reviewed by Foolad and Panthee 2012; Tiwari *et al.* 2022a). MAS is applied for testing of genetic purity of accessions especially overseas materials and single nucleotide polymorphisms (SNPs) are increasing regularly, screening of lines with tightly linked markers with disease resistance or fruit quality. MAS is highly useful in marker-assisted backcrossing selection for disease resistance, fruit

color, carotenoid content (lycopene and *β*-carotene), fruit ripening genes (*Rin* and *Nr*), jointless pedicel (*j2*) and field storage (*Alcobaca* and *Longkeeper*) genes. To our knowledge, MAS is being deployed regularly in seed industry for selecting qualitative traits like disease resistance such as fusarium wilt (*I, I-2, I-3* and *I7*), late blight (*Ph-3* and may be *Ph-2*), verticillium wilt (race 1), bacterial spot (*Rx3* and *Rx4*), tomato spotted wilt virus (*Sw5*), tomato yellow leaf curl virus (*Ty1*, *Ty2*, *Ty3, ty5* and *Ty6*), and root-knot nematode (*Mi*). MAS for quantitative traits are deployed to some extent for a few traits like fruit flavour and total soluble solid; and quantitative disease resistance like bacterial wilt (*Bwr-6* and *Bwr-12*), bacterial canker and powdery mildew. Despite the various efforts on mapping and gene identification for abiotic stress tolerance, no marker is yet available for MAS for salt, drought, heat, cold stress tolerance.

SNP markers are emerging for precise breeding of tomato crop. Several reports are available on the use of molecular markers in tomato breeding. Although several markers are reported but not all are applied in breeding. Presently, SNP genotyping is increasingly used in high-throughput genotyping and identification of candidate gene-associated markers for MAS. Thus, SNP-based markers such as Cleaved Amplified Polymorphic Sequences (CAPS), Sequence Characterized Amplified Region (SCAR), InDel and Kompetitive allele-specific PCR (KASP) are being developed rapidly for MAS in tomato. Some markers are reported for disease resistance especially for introgression of genes, gene pyramiding and stacking of genes when breeding for multiple disease resistance. The most frequently used markers in tomato breeding are PCR-based markers such as SCAR and CAPS markers for major-disease resistance breeding (Prasanna *et al.* 2015a, b, Hanson *et al.* 2016 and Reddy *et al.* 2018).

The Tomato Genome and Pan-Genomes

Developments in next-generation sequencing coupled with advancements in bioinformatics over the last decade led to an ever-increasing number of sequenced species. Due to their economic importance and high nutrient content vegetable crops have become the major targets for genomic research resulting in whole genome sequencing of many vegetable crops and their wild relatives. It helps in understanding the complete genome of species and clarifies gene functions. Tomato is another crop of Solanaceous vegetable, other than potato, pepper and eggplant, whose complete genome is available. Tomato is a model vegetable crop to study fleshy fruit traits. The International Tomato Genome Sequencing Project was started in 2004 by a multi-national team of scientists from 14 countries including the United States, Korea, China, the United Kingdom, India, the Netherlands, France, Japan, Spain and Italy. Initially, project was based on BAC-by-BAC sequencing approach. But in 2009, a whole genome shotgun approach was applied which yielded high-quality genome assemblies data, and the International Tomato Annotation Group (ITAG) annotated the genome sequence data. Then by 2012, the high-quality tomato genome sequence assembly SL2.40 and the ITAG2.3 annotations of the common processing variety 'Heiz 1706' was published, and the tomato genome size of 900 Mb was deciphered applying Sanger and NGS technologies (Tomato Genome Consortium, 2012). Further, this group sequenced the genome of *Solanum pimpinellifolium* (739 Mb), a closest wild relative of common tomato that revealed only 0.6% nucleotide diversity between wild and cultivated species, and thus indicating the role of environmental adaptation to various stress conditions (Tomato Genome Consortium, 2012).

In 2014, genome sequence of a stress-tolerant wild tomato species *S. pennellii* was also deciphered and compared with the reference genome, which indicated the presence of stress-tolerant genes in the wild genome (Bolger *et al.*, 2014). They identified some *cis*-acting elements which play important roles in stress tolerance and flavour-associated compounds. Of late, *de novo* genome and transcriptome assembly for *S.sitiens* (accession LA1974) has been done. *S.sitiens* is a self-incompatible wild relative of tomato, well known for salt and droughtresistance traits. Hybrid assembly strategy involving Illumina short reads (~159 × coverage) and PacBio long reads (~ 44 × coverage) was followed to generate a total of ~262 Gbp of DNA sequence and a reference genome of 1245 Mbp (Molitor *et al.*, 2021).

Recently, an improved version of the tomato reference genome assembly (SL4.0) has been released using de novo from long reads of PacBio, and scaffolds with Hi-C contact maps. The new reference map removed 11 Mb of contig gaps from a previous assembly resulting in a total size of 782.6 Mb with 71.77% repeat content. The updated annotation of tomato genome ITAG4.0 reported a total of 34,075 protein-coding genes using RNA-seq, resistance gene enrichment sequencing (RenSeq), and other forms of expression data (Hosmani *et al.*, 2019). The functional descriptions are known for 29,532 genes with 4794 novel genes associated with disease resistance (Hosmani *et al.*, 2019). The latest tomato genome sequence is available at https://solgenomics.net.

As a single reference genome is not sufficient to represent the total diversity of a species, re-sequencing of different cultivars, landraces, and wild accessions in the form Pan – genome has evolved. The information in the pan-genome is dynamic as it changes with the re-sequencing of new genotypes. The present large-size tomato evolved from a small-fruited cherry tomato through artificial selection. For better understanding of evolution and domestication, and genes involved in tomato trait improvement, pan-genomes have been sequenced covering 725 cultivated and wild species. This shows the presence of 4873 novel genes involved in disease resistance, fruit weight and flavor compounds, which were absent from the reference tomato genome, and thus play key roles in the domestication and

breeding of tomatoes (Gao *et al*., 2019). Recently, 1000 tomato accessions have been sequenced with the long-read sequencing technology and uncovered 2,38,490 structural variations (SVs), which are important for trait improvement and the domestication process in tomatoes (Alonge *et al*., 2020). The discovery of the tomato genome sequence and pan-genomes of many wild species shows a path ahead in the identification of new genes/QTLs and trait-linked markers for marker-assisted breeding. This has accelerated tomato breeding using a genome sequencing approach.

Genome-based gene identification approaches in vegetable crops

Mapping of QTLs governing agronomically important traits in crops provides a vital tool for plant breeders for marker-assisted selection (MAS) as it helps in overcoming the need for phenotypic selection which is cumbersome, resource consuming and highly influenced by the environment. Conventionally, QTL mapping has been carried out by linkage mapping approach wherein a number of individuals in a segregating population derived from a bi-parental cross are genotyped with large number of genome-wide markers and phenotyped for the target traits. It is labor-intensive, time-consuming and expensive (Salvi and Tuberosa, 2005).

Bulked-segregant analysis (BSA) (Giovannoni *et al*., 1991; Michelmore *et al*., 1991) is a simple and cost-effective alternative to map genes affecting a trait of interest, by genotyping only a pair of bulked DNA samples from individuals with distinct/ extreme phenotypes along with the parents. For identifying QTLs, a strategy called as "selective DNA pooling" was proposed to reduce the cost of genotyping instead of genotyping a large number of individuals in QTL mapping (Darvasi and Soller, 1994).

Table 4: Some recent examples of QTL-seq for mapping genes in tomato

Trait (Candidate Gene)	*Mapping Population used*	*Reference*
Early flowering [*EF1* (*Solyc01g017060*)]	F2 mapping population	Ruangrak *et al.* (2018)
Internode length	F2 mapping population	Schrager-Lavelle *et al.*(2019)
Internode length	F2 mapping population	Sun *et al.* (2019)
Fruit weight and locule number	F2 mapping population	Illa-Berenguer *et al.* (2015)
Tomato Yellow Leaf Curl Virus Resistance Gene	F2 mapping population	Wang *et al.* (2018)
Leaf mold	F2 mapping population	Liu *et al.* (2019)
Blossom-end rot	F2 mapping population	Topcu *et al.* (2021)
Bacteral canker resistance	F2 mapping population	Abebe *et al.* (2022)

However, the saturation of markers and genotyping costs were still the limiting factors.

Taking advantage of high throughput sequencing and the power of BSA QTL seq was proposed by Takagi *et al.* 2013 in rice by whole genome resequencing of DNA bulks of extreme phenotypes. Since then, QTL-seq has been effectively deployed in delineating genomic regions and identifying candidate genes governing different traits in tomato (Table 4)

High-throughput SNP Genotyping

The genetic maps of tomatoes were developed by interspecific crossing between cultivated and wild species using polymorphic markers such as *S. pennellii* used for the construction of a high-density genetic map (Pillen *et al*., 1996). On the contrary, breeding populations were mostly developed by intraspecific crosses within the cultivars or between the cultivated and closely related species like *S. pimpinellifolium*. Hence, the availability of polymorphic markers between interspecific crosses, tight linkage between the gene/QTL of the trait of interest and marker, and cost-effectiveness are important considerations for breeding applications (Arens *et al*., 2010). New markers have such as SNPs become popular in breeding while detecting both major and minor variations have leveraged in tomatoes. SNPs markers have several advantages such as abundant in number and the possibility of high-throughput SNP genotyping (Martino *et al*., 2010). The Illumina-based SNP array is now available by the USDA SolCAP initiative (http://solcap.msu.edu). This SolCAP tomato SNP array consists of nearly 9200 markers on the chip and was developed based on diverse genetic materials (germplasm and breeding lines) for tomato researchers. Recently, genotyping-by-sequencing (GBS) technology has become a marker of choice and deployed in tomato breeding (Elshire *et al*., 2011; Poland *et al*., 2012).

Since limited genetic diversity is available the cultivated tomato, wild species are a rich source of genetic variation for both simple and complex traits. Recent genome sequencing of 360 accessions including tomato wild species *S. pimpinellifolium*, *S. lycopersicum* var. *cerasiforme* and *S. lycopersicum*, 186 domestication and 133 improvement sweeps covering 15% of the genome assembly were identified. From these sweeps, 18 QTLs were identified for fruit quality, fruit size and stress tolerance, indicating role of these QTLs in domesticated tomatoes (Ye *et al*., 2017; Zhang *et al*., 2018). After the genome sequencing of tomatoes and its wild species, tomato breeding has entered in the post-genomics era. Genome-based technologies have been applied to discover genes using the reference genome and other genomes of tomato species. The recent availability of the reference tomato genome (Tomato Genome Consortium, 2012) has strengthened the genetic mapping for various traits related to plant phenotype, root, leaf, fruit, disease-

pest resistance, abiotic stress etc (Celik *et al*., 2017, Xie *et al*., 2019; 100 Tomato Genome Sequencing Consortium, 2014). A combination of RNA-seq and QTL mapping approaches has been applied to map QTLs to identify candidate genes. Disease resistance genes and associated markers have been discovered using the RenSeq techniques in tomatoes through sequencing of NBS-LRR gene-enriched libraries (Andolfo *et al*., 2014). Thus, recent genomics approaches have greatly increased fine mapping to discover new genes/QTLs in tomatoes for breeding purposes.

Genome-Wide Association Studies (GWAS)

Identifying genomic regions associated with economically important traits in essential for genomics-assisted breeding. GWAS is one such approach to apply genome-wide markers via high-throughput SNP genotyping to identify significant association between phenotype and genomic variants and thus identify linked markers for MAS. Presently, GWAS is being applied using SNP array genotyping and/or genotyping by reduced representation sequencing technologies such as genotype by sequencing (GBS), restriction site-associated DNA sequencing (RAD-seq) and double digest RAD sequencing (ddRAD-seq). With the availability of genome sequence and pan-genomes of many wild species, GWAS is increasingly being employed to dissect the genetic basis of complex trait variations such as yield and yield contributing traits, fruit quality and biotic/abiotic stress tolerance/resistance for fresh market and processing tomatoes. A number of candidate loci have been identified in tomatoes such as flavour and nutrition-associated metabolites agronomic, fruit, quality and root traits, salinity tolerance, high temperature tolerance so on. Kim *et al*. (2021) identified QTL for eight fruit traits in cultivated tomatoes through a genome-wide association study based on 34,550 confident SNPs from the 51 K Axiom® tomato array. Yang *et al*. (2022) investigated a genome-wide association study of eigenvectors indicating genetic insights into selective breeding for tomato metabolites in 331 accessions. They identified two independent gene sets of fruit metabolites and 57 candidate genes related to polyphenol and polyamine biosynthesis.

Genomic Selection (GS)

GS has been widely used in livestock breeding including dairy cattle, pigs, sheep, beef cattle, and chickens (Xu *et al*., 2020). To date, several GS-based breeding strategies have been conceived in different crops like wheat, maize, rice, barley, soybean, tomato, etc. GS uses estimated genetic potential based on genome-wide genotype data for a breeding selection. This method is now widely accepted to improve genetically complex traits in many agriculturally important crops including tomatoes (Cappetta *et al*., 2020). It has been suggested that the selection on genetic values predicted from markers could substantially increase genetic gain (Meuwissen *et al*., 2001). Genome-wide markers have been used to predict the genomic estimated breeding value (GEBV) of a line or population more accurately using the models trained on training populations (Goddard and Hayes, 2007). Genomic selection was proposed as a way to capture minor genetic effects there by an approach for breeding complex traits. In this it was hypostasized that with the help of high-density markers, every locus associated with the character should be associated with at least one marker and with the help of individuals' genomic estimated breeding values (GEBVs) top-ranked lines can be selected. GEBV is a linear function of marker effects (Jonas and de Koning, 2013). For example, a training population (TP) was developed by crossing six diverse lines with bacterial wilt resistance and inbred lines were developed (Liabeuf *et al*., 2018). The population was genotyped with SolCAP SNP chip array and different GS models were performed to predict GEBV. Based on the cross-validation, study concluded that GS provides more accuracy in estimating GEBV of both inbred progeny and hybrids compared to phenotypic selection (Liabeuf *et al*., 2018). Likewise, GS for tomato fruit quality was estimated for fruit quality and study concluded that marker density, population size and structure affect the accuracy of GEBV (Duangjit *et al*., 2016). Yamamoto *et al*. (2016) predicted a simulation-based genomics-assisted breeding approach based on whole genome in tomatoes for yield and flavour-related traits. Further, the potential of GS was assessed for increasing total soluble solids and total fruit weight in tomatoes (Yamamoto *et al*., 2017) (Table 5).

Genome Editing

With the advent of a clustered regularly interspaced short palindromic repeat (CRISPR)-associated protein9 (CRISPR/Cas9) genome editing, a fast and efficient technology, high-precision breeding has become possible in tomato breeding

Table 5: Genomic selection studies in tomato

Traits	*TP size and type*	*No of markers*	*Statistical model*	*Reference*
Metabolic and quality traits	163 genotypes	5995 SNPs	RR-BLUP	Duangjit *et al.* (2016)
SSC, FW	96 F1	337 SNPs	GBLUP, Bayesian Lasso (BL), Wbsr, BayesC, RKHS, RF	Yamamoto *et al.* (2017)
Bacterial spot resistance	109 families combining resistance from four sources and directionally selected from a population of 1100	387 SNPs	BL and Ridge regression (RR)	Liabeuf *et al.* (2018)

(Chaudhuri *et al*., 2022). The advances in genomics allow the identification of genes and their functional characterization using CRISPR/Cas9. With the availability of sequences of genes of interest and technologies for precise editing, now it is possible to do tweaking of the genomic sequences to get the desired phenotype. Most of the genome editing experiments of horticultural crops were done in tomatoes where 18 different genes have been edited independently such as plant architecture and phenotypes (e.g. leaf, stem, flower, male sterility, fruit, parthenocarpy), fruit ripening, quality and nutrition (e.g., lycopene, carotenoid, GABA, TSS, anthocyanin, shelf-life), disease resistance (e.g. TYLCV, powdery mildew, late blight), abiotic stress tolerance (e.g. heat, drought, salinity), C-N metabolism, and herbicide resistance. The first CRISPR/Cas9-mediated genome editing in vegetable crops was reported in tomatoes in 2014, where ARGONAUTE7 (SlAGO7) gene involved in leaf development was targeted (Brooks *et al*. 2014). Later on, other genes such as the *Anthocyanin 1 (ANT1)* gene of anthocyanin biosynthetic pathways in tomatoes (Cermak *et al*., 2015), *Phytoene desaturase (SlPDS), Phytochrome interacting factor (SlPIF4)* (Pan *et al*., 2016) functioning in carotenoid biosynthesis were mutated by CRISPR/Cas9.

CRISPR/Cas9 work proves the successful introgression of *de novo* domestication of elite traits from wild relatives to the cultivated tomato and vice versa. Research innovations in CRISPR/Cas allow the use of online tools for single guide RNA design and multiplexing, cloning (e.g. Golden Gate cloning, GoldenBraid, and BioBrick technology), robust CRISPR/Cas constructs, efficient transformation protocols such as *Agrobacterium, and DNA-free protoplast method for* Cas9-gRNAs ribonucleoproteins (RNPs) complex, Cas9 variants like PAM-free Cas12a, and Cas9-NG/XNG-Cas9, homologous recombination (HR)-based gene knock-in (HKI) by geminivirus replicon, base/prime editing (Target-AID technology), and so on (reviewed by Tiwari *et al*., 2023).

Conclusion

The key traits of tomato breeding are disease-pest resistance, heat and drought stress tolerance, fruit quality, shelf-life traits, plant architecture and mechanical harvesting of processing tomatoes. Currently, it is tough to completely negate phenotypic selection, instead adopt both together i.e. phenotypic selection and genomics-aided breeding in tomatoes. Genome sequencing approaches have emerged as an improved technology to identify markers for genomics-assisted breeding. Moreover, the tomato pan-genomes of cultivated and wild species accessions allow the mining of more genes for targeted breeding. The pan-genomes open new opportunities for advanced genetic mapping and breeding of tomatoes. With much advancement in tomato crop genetics and multi-omics approaches and genome editing and genomic selection technologies have the potential to accelerate the precision breeding of tomatoes.

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सारांश

टमाटर मानव आहार की एक महत्वपूर्ण सब्जी है। पिछले कई दशकों में पारंपरिक प्रजनन विधियों के द्वारा टमाटर के विभिन्न किस्मों का विकास हुआ है। अब सिक्वेंसिंग प्रौद्योगिकियों में प्रगति के साथ प्रति सैंपल लागत कम होने से, उच्च-थ्रूपुट जीनोटाइपिंग प्लेटफॉर्म और जैव सूचना विज्ञान ने टमाटर के विकाश में क्रांति ला दी है। 2012 में टमाटर का जीनोम सीक्वेंस होने के बाद, हजारों टमाटर के प्रजातियों का सीक्वेंस किया गया और विभिन्न पहलुओं जैसे जनसंख्या संरचना, आनुवंशिक विविधता, उच्च घनत्व मानचित्र और संरचनात्मक वेरिएंट विश्लेषण पर अध्ययन किया गया। वर्तमान में जीनोमिक्स तकनिक का उद्देश्य है कि तेजी से प्रजनन विधि के द्वरा उच्च किस्मों का विकास किया जाये। जिसके लिए उच्च-थ्रूपुट जीनोटाइपिंग (एसएनपी या जीनोटाइपिंग-बाय-सीक्वेंसिंग) का उपयोग करके जीनोम वाइड एसोसिएशन स्टडीज (जीडब्ल्यूएएस) द्वारा क्यूटीएल/जीन और एसएनपी मार्करों की खोज करना आवश्यक है। इसके अलावा, जीनोम एडिटिंग और जीनोमिक चयन विधि से टमाटर में प्रजनन क्षमता और उच्च अनुवांशिक लाभ को बढ़ाना है।