

## Breeding tomato (*Solanum lycopersicum*) for processing quality: integrated perspectives

Jagesh Kumar Tiwari\*, Jayshree Singh, Manish K. Singh and Nagendra Rai

ICAR-Indian Institute of Vegetable Research, Varanasi 221 305, Uttar Pradesh, India

### ABSTRACT

Tomato (*Solanum lycopersicum* L.) is a globally important vegetable crop with significant relevance in both fresh consumption and processing industries. Despite India being one of the largest producers, the proportion of tomatoes utilized for processing remains negligible, highlighting the need for targeted breeding strategies. Processing tomatoes require a unique combination of morphological, biochemical, and molecular traits such as high total soluble solids (TSS), deep red colour, high lycopene content, optimal acidity, firmness, thick pericarp, and suitability for mechanical harvesting. This review comprehensively examines key traits influencing processing quality, including fruit morphology, plant architecture, biochemical composition, and physiological attributes such as ripening behavior and stress tolerance. The genetic basis of these traits is discussed with emphasis on major genes and quantitative trait loci (QTLs) controlling sugar accumulation, acidity, colour, firmness, and viscosity. Advances in molecular breeding approaches, including marker-assisted selection (MAS), genome-wide association studies (GWAS), and CRISPR/Cas9-based genome editing, have accelerated the development of superior processing cultivars. Integration of wild germplasm, genomic tools, and multi-environment testing is essential to overcome challenges such as yield quality trade-offs and climate stress. The review underscores the importance of a multidisciplinary approach to develop high-yielding, stress-resilient, and industry-oriented tomato cultivars, thereby strengthening the processing sector and enhancing farmers' profitability.

**Key words:** Biochemical, Breeding, Genomics, Processing, Tomato

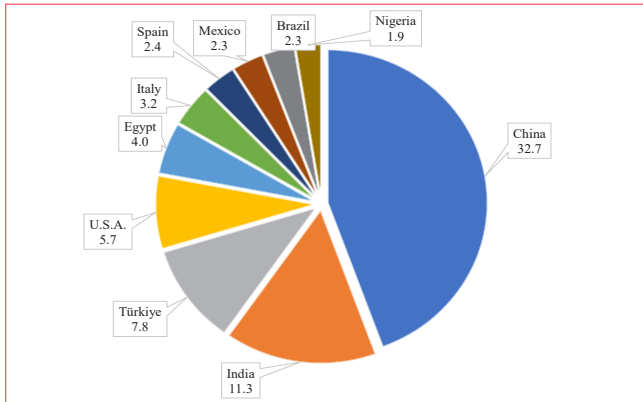
Tomato (*Solanum lycopersicum* L.) is one of the most significant vegetable crops, globally utilized extensively for both fresh consumption and a wide array of processed products, including juice, ketchup, paste, and purees (NAAS, 2022). Often described as “protective food” (Kumar *et al.*, 2013; Somappa *et al.*, 2013), it holds immense agricultural and economic significance (Vats *et al.*, 2020) which is matched by its nutritional value, offering high levels of vitamins, minerals and bioactive compounds such as carotenoids, polyphenols and most notably lycopene, which is known for its anti-cancerous effects (Canene-Adams *et al.*, 2005; Omoni and Aluko, 2005; Kun *et al.*, 2006). Besides carotenoids, tomato is rich in natural antioxidants (Davies and Hobson, 1981) that inhibit the oxidation of lipids and other molecules by preventing oxidative chain reactions (Velioglu *et al.*, 1998). Tomato is one of the most cultivated vegetables in the world, with a global production of 188.49 million tonnes from 5.12 million ha area at the productivity rate of 36.80 t/ha (FAOSTAT, 2024). The leading producer is China, followed by India, which produced around 21.32 million tonnes, contributing 11.3% of global tomato production (FAO STAT, 2024) (Fig. 1).

Around 40-46 million tonnes (20-25 %) of global tomatoes are processed into value-added products, whereas India processes very low, i.e. < 1% of its total

production (NAAS, 2022; Tiwari *et al.*, 2022). This high demand for processing tomatoes, which is driven by industrial standards to maximize product recovery and manufacturing efficiency, highlights a fundamental genetic and phenotypic dichotomy between fresh-market and processing tomato cultivars (Chattopadhyay *et al.*, 2013). While fresh-market breeding predominantly emphasizes visual aesthetics, uniform ripening, and prolonged shelf-life, processing tomatoes are bred for a set of morphological and physiochemical characteristics that are less important in table varieties, in order to maximize product recovery and manufacturing efficiency (Stommel *et al.*, 2005).

The tomato processing industry relies on cultivars with specific quality attributes that ensure high extraction efficiency, desirable sensory properties and superior stability during manufacturing of puree, paste, ketchup, juice and canned products. Key processing-related traits include high total soluble solids (TSS) (> 5.5 °Brix), deep red colour (a/b, Hunter colour value: > 1.95), lycopene content (> 8.5 mg/100 g), balanced titratable acidity (< 0.4 %), low pH (< 4.40), fruit firmness/ texture (> 4 N), thick pericarp thickness (> 0.4 cm), high viscosity/ consistency (7-14 Botswick, cm/30 sec), determinate, oval shape, small locule (2-3), pulp (65-75%), low seed content, small core, no radial and concentric cracking, elongated, smooth surface/free from wrinkles and

\*Corresponding author: jageshtiwari@gmail.com



**Fig. 1.** Top ten tomato-producing countries (% share) (FAO STAT, 2024)

high alcohol-insoluble solids so on (Tiwari *et al.*, 2026) (Table 1).

**Table 1:** Processing criteria of tomato

| Processing trait   | Standard values desired by processors |
|--------------------|---------------------------------------|
| TSS                | >5.5°Brix                             |
| Colour value       | >1.95                                 |
| Acidity            | 0.3-0.4%                              |
| Titrate acidity    | 6-8 mmol/L                            |
| pH                 | < 4.30                                |
| Texture/firmness   | >8.00                                 |
| Lycopene           | >12 mg/100g FW                        |
| Viscosity          | 12-14 Bostwick cm/30 sec              |
| Vitamin C          | >25 mg/100g                           |
| Pericarp thickness | >0.4cm                                |
| Fruit weight       | >80g                                  |
| Juice yield        | >70%                                  |
| No. of locules     | 2-4                                   |
| Sugar : acid ratio | 15:1                                  |
| Yield              | >75-80 t/ha                           |
| Fruit colour       | Deep red                              |
| Fruit maturity     | Concentrated fruit maturity           |
| Vine storability   | Prolonged                             |
| Pedicel            | Jointless                             |
| Fruit shoulder     | Uniform green                         |

Source: Tiwari *et al.* (2026)

Tomato breeding for processing required integration of traits/genes, *viz.* determinate/ self-pruning (*sp*), concentrated fruit maturity (*cfm*), jointless (*j-2*), uniform ripening (*u*), single flower truss (*SFT*), sucrose accumulator (for high TSS) (*sucr*), old gold crimson (*og*<sup>e</sup>), intense pigment (deep red) (*Ip*), and high pigment-2 (high lycopene) (*hp-2*) so on. In addition under the changing climate scenario, resistance to biotic stresses like diseases (tomato leaf curl virus, late blight, early blight, bacterial leaf spot and root knot nematode) and pest (white fly) resistance, and abiotic stresses (heat, drought and salinity) are also important.

The processing tomato varieties tend to have the determinate growth habit that is regulated by the self-pruning gene (*SP*), making it possible to obtain plants with synchronized maturity and firmness to harvest them in one pass using the machinery (Rothan *et al.*, 2019) and must have firm, blocky or oval fruits, with a thick pericarp to withstand the mechanical stress of bulk transportation and industrial handling without compromising tissue integrity (Chattopadhyay *et al.*, 2013; Rothan *et al.*, 2019). In terms of biochemical traits, the economic viability of tomato processing is heavily reliant on high Total Soluble Solids (TSS), above 5.0° Brix because it drastically decreases the thermal energy and time required to concentrate paste (Kumar *et al.*, 2019) and processors prefer high titratable acidity and a low pH (<4.4) to ensure microbial food safety and flavour balance, as well as elevated lycopene concentrations (> 10 mg/100 g fresh weight) that impart the deep-red pigmentation required for high-quality commercial products (Chattopadhyay *et al.*, 2013).

Even with these defined parameters, developing elite processing cultivars is subject to many agronomic bottlenecks, such as negative genetic correlation between high yield and high metabolite concentration, known as the yield-quality trade-off (Gur and Zamir, 2004), and increasingly adverse effects of climate change that manifest as extreme drought, rising temperatures, and soil salinity that threaten reproductive physiology and biochemical stability of crop (Alsamir *et al.*, 2021). Mild stress conditions may improve certain quality traits, including total soluble solids and secondary metabolites, due to concentration effects; however, severe stress significantly reduces plant growth and overall yield (Rigano *et al.*, 2016). Therefore, improvement programmes should combine conventional breeding with modern approaches such as marker-assisted selection (MAS), quantitative trait loci (QTL) mapping and CRISPR/Cas-based genome editing to develop cultivars that are both stress tolerant and capable of maintaining high yield and processing quality (Rothan *et al.*, 2019; Wang *et al.*, 2019).

To address these challenges, tomato improvement requires a combination of classical breeding and modern genomic tools. The recent progress in marker-assisted selection coupled with modern genomics tools and emerging CRISPR/Cas-based genome editing has enabled targeted genetic improvement of tomato. Strengthening the use of wild relatives (*S. pennellii*, *S. pimpinellifolium* and *S. habrochaites*) for trait introgression, integrating multi-environment testing, and deploying genomic selection can accelerate breeding gains. Moreover, genome-wide association studies (GWAS) using diverse panels have identified

novel alleles/QTLs in tomato breeding. Overall, the convergence of conventional breeding and modern genomics is reshaping the landscape of processing tomato improvement. The identification of robust QTLs, trait-specific candidate genes and predictive genomic markers would form the foundation for developing next-generation processing tomato cultivars with better fruit quality and fitting to industrial standards. For future advancement, India requires stronger public–private partnerships, dedicated processing tomato breeding programmes tailored to regional agro-industrial needs, and enhanced farmer–industry linkage through efficient value chains. These innovations will be pivotal to develop resilient, high-quality processing tomato varieties that can support sustainable growth of India's processing sector and improve farm profitability.

### Morphological traits affecting processing quality

Breeding for processing tomato quality has historically relied on phenotypic selection and introgression of favourable alleles from adapted cultivars and wild relatives such as *S. pennellii*, *S. pimpinellifolium* and *S. habrochaites*. Wild donors have been particularly valuable for enhancing TSS, acidity, firmness and stress tolerance. However, many processing traits exhibit polygenic inheritance with strong genotype  $\times$  environment interactions, making them difficult to improve solely through conventional selection. The advent of molecular markers, linkage mapping and introgression line (IL) populations revolutionized the identification of quantitative trait loci (QTLs) controlling fruit quality. Landmark discoveries such as the Brix9-2-5 QTL and its candidate gene *LIN5*, major-effect loci like *ogc*, and ripening regulators including *rin*, *nor* and *alc* provided breeders with molecular targets for improving fruit solids, colour and firmness.

The integration of genomic resources has further accelerated processing tomato improvement. High-density SNP arrays, genotyping-by-sequencing (GBS) and whole-genome resequencing have enabled fine-mapping of QTLs for sugars, acids, lycopene content, pectin metabolism and viscosity. Genome-wide association studies (GWAS) using diverse panels have identified novel alleles for fruit quality, while meta-QTL and haplotype analyses have refined large-effect loci into narrow, breeder-friendly intervals. Candidate genes located within these regions, such as those involved in carbohydrate metabolism (invertases, sucrose synthases), carotenoid biosynthesis (PSY1, ZISO, CRTISO, CYC-B), and cell-wall remodeling (polygalacturonase, pectin methylesterase, expansins), now guide marker-assisted and genomic selection

strategies. Overall, the convergence of classical breeding, quantitative genetics and modern genomics is reshaping the landscape of processing tomato improvement. The identification of robust QTLs, trait-specific candidate genes and predictive genomic markers now forms the foundation for developing next-generation processing tomato cultivars with greater quality, consistency and industrial performance.

The morphological architecture of tomato plant and its fruit play a critical role in determining its suitability for processing applications (Bai and Lindhout, 2007; Ortega-Salazar *et al.*, 2025). Accordingly, processing tomatoes are bred for specific structural and anatomical traits such as, firm texture, high total soluble solids, uniform ripening, and a compact plant habit to enhance industrial efficiency and facilitate mechanical harvesting (Lin *et al.*, 2014; Kyriacou and Roupael, 2018). Although these traits are heritable, their phenotypic expression is also influenced by environmental conditions. Growth habit, stem strength, and fruit uniformity are important traits for breeding programs, and studies have demonstrated strong positive correlations between morphology and soluble solids, viscosity, and recovery percentage.

### Fruit size, shape and locular cavity

The physical attributes including fruit shape and internal anatomy have been found to play a significant role in determining processing effectiveness in tomatoes (Rodríguez *et al.*, 2021). For instance, processing industries tend to use pear-, oval-, oblong-, blocky- or Roma-shaped varieties than round varieties, partly owing to their low locule number (2–4) to enhance paste concentration efficiency with reduced energy input (Chattopadhyay *et al.*, 2013). The differences in internal anatomy between various tomato varieties are related to their varying numbers of locules and pericarp ratios. Major QTLs controlling fruit shape and locule number include *lc* and *fas* (Lin *et al.*, 2014). The locule cavity size impacts on fruit composition by contributing to acidity while the pericarp is responsible for fruit sugar content and aroma production. A small locule cavity, therefore, means that the pericarp ratio will be high, thus increasing TSS concentration and minimizing dehydration during processing (Chattopadhyay *et al.*, 2013).

The shape of fruit is primarily governed by genetic determinants, where genes like *OVATE* and *SUN* have an important function in the determination of elongated fruits (Causse *et al.*, 2002). Fruit size is, on the other hand, affected by both genetic and environmental factors, as well as agricultural techniques used. The development of pericarp first takes place by means of cell division (10–25

days after anthesis) and subsequently by cell expansion (Ho, 1996; Bertin *et al.*, 2003; Bertin and Génard, 2018).

### Pericarp thickness

A thick pericarp (more than 0.50 cm) is one of the important considerations in the processing of tomatoes (Chattopadhyay *et al.*, 2013). The increased resistance against mechanical damage by having a thick pericarp reduces loss of fruits during transportation and other processing activities. Thick pericarp has also been noted to be positively correlated with recovery percentage and can be used as a selective trait in the breeding programme (Kumar *et al.*, 2019). Pericarp development helps to ensure fruit development, mainly determining its size (Ho, 1996). Features such as anatomical characteristics, especially the thickness of the pericarp, affect texture and firmness of fruits (Aurand *et al.*, 2012). In the earlier stages of fruit development, cells of the inner and radial pericarp act as storage organs for starch, reaching their maximum level at 10-25 days after anthesis and are later broken down to soluble sugars (Schaffer and Petreikov, 1997). Cell expansion in later stages depends on water movement by the xylem and phloem systems and is dependent on sugar metabolism and turgor pressure.

### Fruit firmness and mechanical handling resilience

A high level of firmness is required for tomatoes used for processing (Nie *et al.*, 2024). Such a feature affects not only consumer preferences but also the storage and transportation processes (Causse *et al.*, 2010; Seymour *et al.*, 2013). The fruits that have firmness can survive mechanical harvesting, handling and transportation without sustaining damages. The lack of firmness leads to cell disintegration, accelerated respiration, the development of ethylene, and susceptibility to infections (Held *et al.*, 2015). During ripening, the decrease in the level of firmness is caused mostly by the degradation of the cell wall material, especially the degradation of pectins of the middle lamella by enzymes like polygalacturonase (PG) and pectate lyases (PL) (Quinet *et al.*, 2019). Tissue thickness, cell size and turgor pressure affect the firmness of the fruits in the development process. Additionally, genetic traits have their impact on this trait, since such QTLs as (*fir5.1*) located on chromosome 5 affect firmness, making it more pronounced in processing tomatoes than fresh tomatoes (Lin *et al.*, 2014). Thus, breeding programs should include increasing the firmness and thickening of tomato walls to prevent softening (Nie *et al.*, 2024).

### Plant architecture: determinate growth and jointless pedicels

The combination of a determinate compact habit, concentrated maturity, and jointless pedicels is the

necessary requirement for mechanical once-over harvesting that reduces labor and provides a stable supply chain to the processing units (Tiwari *et al.*, 2022). The plant architecture of tomato crops is thus equally as vital as its fruit attributes in industrial cultivation practices. In contrast to fresh market tomatoes, which usually have an indeterminate or semi-determinate growth pattern, processed tomato varieties usually display determinate growth. The reason behind this is that the growth pattern is regulated by the self-pruning gene which restricts the vegetative growth and produces a bushy plant with enough leaf surface to shade the fruits from burning (Rothan *et al.*, 2019). Importantly, this highly managed growth habit directs the plant's metabolic energy predominantly toward reproductive development, thereby promoting concentrated fruit maturity (CFM), a physiological phenomenon in which most fruits ripen simultaneously on the vine (Rothan *et al.*, 2019). Processing varieties must also have a jointless pedicel, a trait in which the fruit readily separates from the vine without the stem or calyx remaining attached to the fruit, to fully take advantage of CFM (Tiwari *et al.*, 2022). Breeding targets for processing tomato are given in Table 2.

**Promising lines for processing quality:** The ICAR-IIVR, Varanasi, has developed tomato genotypes (hybrids/OP) with high TSS such as VRTH-24-58 (5.95 °Brix), VRTH-24-41 (5.93 °Brix), VRTH-24-56 (5.91 °Brix), VRTPH-24-18 (5.75 °Brix), VRTPH-24-5 (5.71 °Brix) and VRTH-24-19 (5.63 °Brix). Among advance hybrids, VRTH-16-4 (recently released as Kashi Shreshth) (4.5 °Brix) is found suitable for dual purpose i.e. both fresh and processing purpose. A few promising OP lines possessing high TSS are EC-620456 (5.93 °Brix), EC-62032 (5.73 °Brix), (5.73 °Brix), VRT-67 (5.70 °Brix), AVTO-2101 (5.60 °Brix), EC-715384 (5.60 °Brix) and VRT-06 (5.26 °Brix). Besides, there are many more lines in pipeline under evaluation stage (Fig. 2).

### Biochemical traits for processing

The biochemical make-up of tomato fruit is a major determinant of its adaptability to processing because it influences the nutritional quality, palatability, and efficiency of processing (Bertin and Génard, 2018; Amr and Raie, 2022). In contrast to fresh-market varieties which are graded according to visual attributes and texture, those grown for processing are selected by certain physicochemical factors. Factors such as total soluble solids, colour, pH, and texture are crucial because they affect the yield, processing efficiency, and quality of products such as paste, puree, ketchup, and juice (Amr and Raie, 2022).

**Table 2:** Breeding targets for processing tomato

| Trait category                       | Specific trait              | Target value                             | Breeding objective                                       | Rationale for processing industry              |
|--------------------------------------|-----------------------------|------------------------------------------|----------------------------------------------------------|------------------------------------------------|
| Fruit physical traits                | Plant growth habit          | Determinate, compact                     | Improve uniform ripening and mechanical harvesting       | Allows synchronized harvest and reduces labour |
|                                      | Fruit shape                 | Oval/ roma/ pear-shaped                  | Standardize fruit size for processing                    | Reduces sorting loss; suits pulping equipment  |
|                                      | Fruit firmness              | High firmness ( $\geq 5-6$ N)            | Delay softening                                          | Essential for transport and peeling            |
|                                      | Pericarp thickness          | $\geq 5-7$ mm                            | Increase pulp yield                                      | Higher recovery for paste/ puree               |
|                                      | Placenta & locule number    | 2–3 locules, thick walls                 | Reduce seediness                                         | Improves puree smoothness                      |
|                                      | Seed content                | Low                                      | Minimize seed residues                                   | Ensures high-quality pastes and sauces         |
|                                      | Fruit cracking resistance   | High                                     | Prevent pre-harvest losses                               | Maintains transport quality                    |
| Colour and pigment                   | Lycopene content            | 80–20 mg/ kg FW                          | Enhance colour intensity                                 | Deep red colour desired by industry            |
|                                      | Beta-carotene               | Moderate                                 | Balanced nutritional quality                             | Influences colour hue and health benefits      |
|                                      | Uniform ripening gene (u/u) | Stable uniform red colour                | Avoid blotchy ripening                                   | Improves grading and consumer appeal           |
| Physico-chemical traits              | Total soluble solids (TSS)  | 6–8 °Brix (fresh fruit)                  | Reduce evaporation time                                  | High solids = lower processing cost            |
|                                      | Titratable acidity          | 0.30–0.50% citric acid                   | Balanced flavour                                         | Ideal for sauces and ketchup                   |
|                                      | pH                          | < 4.4                                    | Microbial safety                                         | Avoids need for acidification                  |
|                                      | Sugar–acid ratio            | 15:1 (high reducing sugars)              | Improve flavour                                          | Consumer preference                            |
|                                      | Viscosity (pulp)            | High viscosity; low Bostwick (4–6 cm)    | Increase thickness                                       | Required for paste/ketchup                     |
| Industrial / processing traits       | Pulp percentage             | $\geq 65-75\%$                           | Maximize processed yield                                 | Critical in paste factories                    |
|                                      | Colour a*/b* ratio          | > 2.0                                    | Stable bright red colour                                 | Used for premium paste and ketchup             |
|                                      | Consistency (Bostwick)      | Paste: 4–6 cm; Ketchup: 7–10 cm          | Improve product texture (Lower = thicker, premium grade) | Standard industry measurement                  |
|                                      | Peelability                 | Easy peel (hot/cold)                     | Reduce processing loss                                   | Essential for canned/whole tomatoes            |
|                                      | Concentration ability       | High                                     | Efficient evaporation                                    | Saves energy cost                              |
|                                      | Dry matter                  | $\geq 6-8\%$                             | Higher TSS and viscosity                                 | Key for pulp/paste industries                  |
|                                      | Yield potential             | $\geq 50-70$ t/ha                        | Ensure economic returns                                  | Needed for industrial supply                   |
| Agronomic and stress traits          | Heat tolerance              | High                                     | Maintain quality under stress                            | Processing zones often face high temp          |
|                                      | Disease resistance          | ToLCV, BW, EB, PM, CMV                   | Stable fruit quality                                     | Avoids yield fluctuations                      |
|                                      | Shelf life                  | 48–72 hours post-harvest                 | Allow transport to processing plants                     | Especially important in India                  |
| Genetic traits and molecular targets | High-Brix genes/ QTL        | Brix9-2-5, Lin5, Sugar-enhancing alleles | Increase °Brix naturally                                 | Reduces energy cost in factories               |
|                                      | Colour QTL/ genes           | RIN, nor, hp-1, ogc                      | Enhanced lycopene & uniform red                          | Used in colour-intensive products              |
|                                      | Firmness genes              | PG, Expansin, ACO, ACS mutants           | Improve shelf-life & firmness                            | Essential for mechanical harvesting            |
|                                      | Viscosity QTL               | fw2.4, pectate lyase regions             | Improve paste viscosity                                  | Key trait for ketchup                          |
|                                      | Disease-resistance genes    | Ty series, Mi-1, Pto, I2, Ve, Ph3        | Durable resistance                                       | Lower pesticide residues in processed foods    |

**Total soluble solids (TSS):** The most important economic parameter in tomato processing is total soluble solids (TSS), which is composed of approximately 65–75% sugars (primarily fructose and glucose), 8–15% organic acids, and smaller fractions of amino acids, pectins, minerals, and phenols (Portugal *et al.*, 2015). The processing industry requires at least 5.0–5.5 °Brix for industrial use (Tiwari *et al.*, 2023). The higher the TSS content, the more efficient the

process is due to high recovery of the product and less energy/time spent on concentration. Higher °Brix values also improve processing efficiency by reducing water evaporation during paste production, resulting in increased industrial yield and profitability. In other words, an increase of 1% in TSS content leads to high recovery of the processed product and less need for raw materials by 25% to produce 28% tomato sauce (Portugal *et al.*, 2015).



**Fig. 2:** Tomato genotypes with special horticultural traits

**Acidity (pH and titratable acidity):** The acidity of tomatoes is essential not only from the point of view of the consumer qualities of the vegetable but also from the perspective of its shelf-life safety. The food industry needs to use varieties with inherent acidity below 4.4 (Tiwari *et al.*, 2026). Generally, tomatoes are classified as high-acid fruits; however, keeping acidity lower than 4.45 is a must from an industrial point of view in order to minimize the activity of spoilage microorganisms, namely, *Bacillus coagulans*, and thus the intensity of heat treatment required in canning (Chattopadhyay *et al.*, 2013). Titratable Acidity (TA): Titratable acidity (TA) plays an important role in the process of food manufacture since higher titratable acidity enables the adjustment of thermal treatment period in the process of sterilization that provides energy saving (Vieira *et al.*, 2020). The most important attributes determining consumer acceptance of the foodstuff include its sweetness, sourness, and tartness, which mainly depend on the sugar/acid ratio. Although citric acid remains the dominating acid in terms of TA contribution, malic and glutamic acids should also be mentioned. On the contrary, over maturity results in the decreasing of total TA whereas glutamic acid increases ten times (Anthon *et al.*, 2011).

**Lycopene content:** The carotenoid responsible for the red colour of tomatoes is called lycopene, and this 40 carbon atom isoprenoid is known to have 11 double

bonds and be a very effective antioxidant (Alda *et al.*, 2009; Arballo *et al.*, 2021). It makes tomatoes look red and provides their strong health properties by reducing the likelihood of suffering from cardiovascular disease or prostate cancer (Vats *et al.*, 2020). From the point of view of processing, lycopene level in tomatoes remains unchanged and can even increase under such conditions. Carotenoids accumulate while processing takes place; for instance, the number of carotenoids rises from 6.74 mg/100 g in fresh tomato juice up to 34.31 mg/100 g of tomato paste (Kamil *et al.*, 2011). From the point of view of industrial use, a desirable amount of lycopene would be between 10–14 mg/100 g of fresh tomatoes, along with a high colour value (a/b ratio above 2.0) to achieve a proper red colour (Chattopadhyay *et al.*, 2013). Heat processing converts lycopene to its cis form and enhances its bioavailability relative to raw tomatoes.

**Sugars and organic acids:** The taste of tomato products is dependent upon the ratio of soluble sugars to organic acids. An ideal sugar-to-acid ratio should be about 15:1, as it ensures the product is neither too sour nor too sweet. In domesticating tomatoes, the process of breeding has centered on ensuring an appropriate malate and citrate ratio (Chattopadhyay *et al.*, 2013; Sadashiva *et al.*, 2022). Glucose and fructose sugars, along with organic acids such as citric acid and malic acid, contribute to the taste profile, including sweetness and sourness (Beckles, 2012). Also, glutamic acid content has been known to

increase by ten times in concentration as tomatoes ripen, interacting with 5'-AMP to provide the umami taste (Oruna Concha *et al.*, 2007; Anthon *et al.*, 2011).

**Pectin and cell wall components:** Viscosity and textural properties of tomato products such as tomato paste and ketchup rely heavily on the structural stability of their cell walls, which consist mainly of pectic polysaccharides, hemicellulose, and cellulose (Steele *et al.*, 1997; Barrett *et al.*, 1998). As tomato fruits mature, the enzymes PG and PME degrade pectic compounds, causing cell separation and the fruits' softening (van Dijk *et al.*, 2006; Wang *et al.*, 2018). Temperature during processing can affect the function of these enzymes. When the hot break technique ( $\geq 85^\circ\text{C}$ ) is employed, both PG and PME get deactivated instantly, yielding a highly viscous product. On the other hand, when using the cold break technique ( $\sim 60^\circ\text{C}$ ), PG and PME retain some enzymatic activity, generating a product that is less viscous but more flavoursome (Sánchez *et al.*, 2002). Ideally, when tomato products are being made, a natural juice viscosity level of 12–14 Bostwick cm/30 sec is recommended (Sadashiva *et al.*, 2022).

**Volatile compounds:** Aroma and flavour attributes of tomato products are attributed primarily to volatile organic compounds (VOCs), which make up only small concentrations but still are significant in sensory evaluation (Goff and Klee, 2006). In spite of the fact that over 400 different VOCs are found in tomatoes, only 30 VOCs occur at concentrations high enough to be able to influence taste (Baldwin *et al.*, 2000; Distefano *et al.*, 2022). These VOCs can be synthesized through metabolic processes associated with amino acids, lipids, phenolics, and carotenoids. The key volatiles hexanal, cis-3-hexenal, linalool, and apocarotenoids work together with sugars and organic acids to create the typical taste of tomatoes (Klee and Tieman, 2013; 2018). The aroma is due to the interaction of all these volatiles and other dissolved components, forming the sensory profile of tomato-based foods (Tieman *et al.*, 2012).

### Physiological traits

Tomato plant physiology is crucial for assessing growth potential, adaptability, and fruit quality. With regard to processed tomatoes, physiological efficiency with respect to ripening performance, cell stability, carbon allocation, and stress tolerance greatly affects yield and recovery rates (Nie *et al.*, 2024).

### Fruit ripening behavior

*Uniform ripening (Concentrated Fruit Maturity) (CFM):* Concentrated ripeness (uniform ripening) is one of the desirable characteristics in processing tomatoes.

Being climacteric fruits, the respiration rate increases when tomato fruits ripen. The even colouration in tomato fruits is essential for both marketability and processing purposes (Nunes, 2009; Yahia and Brecht, 2012). Tomato fruits need to uniformly turn from orange to deep red colour without the presence of any green shoulders or patches. In actual situations, fruits that have matured to the green stage are exposed to ethylene treatment to encourage uniform ripening (Kandasamy, 2022). For processing types, tomato fruits are chosen because of their uniform maturity to ensure that most fruits attain their required colour and soluble solids content at the same time, which makes harvesting easier.

*Ethylene regulation:* Ethylene ( $\text{C}_2\text{H}_4$ ) is another important phytohormone that plays an essential role in tomato development, ripening, and senescence. Therefore, its regulation is necessary during postharvest treatment. Variations in ethylene levels can impact the shelf-life of fruits, since storage conditions such as heat above  $38^\circ\text{C}$  and cold temperatures could limit its production. Molecules such as 1-methylcyclopropene (1-MCP) help to control fruit ripening through the binding of ethylene receptors, thus lowering the activity of enzymes, including ACC synthase and ACC oxidase (Khan and Singh, 2009). On a molecular basis, ripening is associated with higher levels of expression of genes responsible for the biosynthesis of ethylene, for example, the Le-ACO1 gene, leading to the degradation of chlorophyll and activating genes encoding carotenoids biosynthesis, such as *Psy1*, causing lycopene accumulation (Yin *et al.*, 2010; Li *et al.*, 2018, 2020).

### Shelf-life and textural integrity

*Delayed softening:* Being rigid and increasing shelf-life after harvest is important in minimizing mechanical injury that occurs during transportation since fruit softening is a consequence of degradation of cell wall constituents such as pectin and hemicellulose through enzymatic activities (Wann, 1996). Enzymes responsible for this include PG (polygalacturonase), pectinases,  $\beta$ -galactosidases and expansins. Several options can be considered to help slow down fruit softening and improve their qualities. One is genetic engineering where, for instance, PL gene is silenced, which leads to increased rigidity without changing other qualities such as yield, colour and soluble solid contents (Ulusik *et al.*, 2016). Alternatively, there are physiological and postharvest methods such as precooling, application of 1-MCP (1-methylcyclopropene), ultrasonic treatment or thermosonication.

*Resistance to physiological disorders:* Prevention of early decay in tomatoes demands genetic and physiological regulation. Genetically induced mutations

like *rin* (ripening inhibitor), *nor* (non-ripening) and *alc* (alcobaca) have been extensively used in tomato breeding programs to inhibit softening and prolong shelf life due to additive and epistatic interactions (Rothan *et al.*, 2019; Wang *et al.*, 2020). Like most fruits, tomatoes also suffer from chilling sensitivity. It occurs when fruits are exposed to temperatures lower than 12–13 °C, causing poor colour distribution, development of surface pitting, seed darkening and off-flavour formation in tomatoes (Biswas *et al.*, 2016). Chilling resistance can be induced in tomato fruits by heat preconditioning before storage by dipping tomatoes into hot water at 42 °C or hot air, thus increasing the level of antioxidants (Yahia *et al.*, 2007).

### Photosynthate partitioning and source-sink dynamics

**Source-sink relationship:** Dry matter and soluble solid contents in tomatoes are controlled by source-sink interactions in which the assimilates generated in mature leaves (sources) are transferred to immature fruits (sinks). In development, the fruit serves as an important sink for carbohydrates for respiratory and energetic purposes (Saltveit, 2019). Post-harvesting, the availability of nutrients ceases, and the fruit relies solely on internal stores. As the stores are progressively consumed due to respiration, the fruit ages and deteriorates (Nunes, 2009). For tomatoes, the sugar content is governed by assimilate transport, accounting for almost 80% of the sugars derived from mature leaves (Khapte *et al.*, 2019). This determines the total amount of soluble solids. In addition to that, gluconeogenesis plays a role during fruit ripening by stimulating the expression of the phosphoenolpyruvate carboxykinase (PEPCK) gene, increasing sugars and organic acids (Yin *et al.*, 2010).

Fresh tomatoes have 5–7.5% dry weight content. Most of the dry matter consists of sugars, specifically fructose, glucose, and sucrose, which impart sweetness (Hou *et al.*, 2020). The maximum content of starch is attained during the mature green stage and then becomes transformed into simple sugars as the fruits continue to ripe (Zhu *et al.*, 2022). The composition of sugar within the fruit may differ depending on the parts of the fruit as well, with more simple sugars present in seeds than locular tissues and less amount of organic acids, thus impacting its taste. Environmental factors such as heat may impact assimilate translocation to fruits hence decreasing their weight and soluble solids content (Plaut *et al.*, 2004).

### Stress tolerance and quality stability

**Heat, drought, and disease tolerance:** Tomatoes grown using open-field techniques suffer from different types of environmental stresses. Current strategies

including CRISPR/Cas9 have demonstrated their effectiveness in enhancing stress tolerance (Ahmad *et al.*, 2018). Heat stress (temperatures exceeding 32 °C) is highly detrimental, as it impacts pollen viability, pollen tube growth, and stigma functionality, thereby causing flower abortion and yield loss (Peet *et al.*, 1998; Alsamir *et al.*, 2021). Besides, it also negatively impacts the photosynthetic process by limiting the function of enzymes such as Rubisco activase and decreasing lycopene synthesis (Wahid *et al.*, 2007).

At a genetic level, *BZR1* gene expression responds to elevated temperatures via the Feronia (FER) pathway, whereas *CBF1* gene is responsible for defending tomato against cold stress through electrolyte leakage prevention (Yin *et al.*, 2018; Yun *et al.*, 2022). On the other hand, under drought stress, *MAPK3* gene assists in maintaining the integrity of the cell membrane and stress resistance (Huang *et al.*, 2023). Physiologically, water management techniques such as regulated deficit irrigation (RDI) and partial root-zone drying (PRD) minimize vegetative growth and promote assimilate partitioning, eventually enhancing total soluble solids without significant yield penalties (Khapte *et al.*, 2019). Genetics can also be used to enhance resistance to disease. For instance, altering the *JAZ2* gene will lead to resistance to bacterial speck resulting from infection by *Pseudomonas syringae* (Ortigosa *et al.*, 2019). Modifying genes that increase susceptibility to pathogens like *DMR6*, *PMR4* and *Mlo1* may also confer resistance to diseases caused by fungi. Resistance to viruses may be conferred by targeting viral sequences and plant defences, including *DCL2* that confers resistance to tomato yellow leaf curl virus and other RNA viruses (Tashkandi *et al.*, 2018; Zhang *et al.*, 2024).

**Important for stable processing quality:** To sustain stability in the process of tomato production, there is a need for good management of the biotic stress factors as well as pre- and post-harvest factors. The occurrence of quality losses such as early softening and decay results in considerable financial losses (Thole *et al.*, 2020). Some of the organisms that cause post-harvest losses include *Erwinia*, *Alternaria*, *Botrytis*, and *Aspergillus* (Youssef *et al.*, 2022). Through genetic methods involving control of ethylene formation, extending shelf-life, and improving disease resistance, losses during storage and transportation can be reduced (Shipman *et al.*, 2021). Genes like *Ve1* for *Verticillium* wilt and *Bs2* for bacterial spots also play an important role in maintaining good health and consistency of produce (Chaudhary *et al.*, 2019). The quality of the fruit's processing depends on its metabolism as well. Abiotic stress in moderate quantities like salinity and heat leads to an increase in the amount

of sugar, amino acids, and antioxidants like ascorbate, carotenoids, and flavonoids, thus improving the quality of the fruit and making it more nutritious without significantly reducing the yield (Massaretto *et al.*, 2018; Egea *et al.*, 2022). Gene expression regulation related to shelf life and stress tolerance improves the quality of the products and their availability for processing (Cappetta *et al.*, 2021).

### Molecular and genomic aspects

Progress made in classical genetics and novel genomic approaches has significantly enhanced breeding programs in tomato. The presence of a reference genome of approximately 900 Mb size with 34,700 protein-coding genes makes tomato an attractive model plant for the study of processes of fruit development and tolerance to abiotic stresses (Tomato Genome Consortium, 2012). Innovative methods of functional genomics, transcriptomics, and gene editing provide the possibility of thorough analysis of processing quality-related traits (Ranjan *et al.*, 2012). Processing traits and genes for tomato breeding are summarised below in Table 3. Besides other traits are thick pericarp, fruit firmness, small locule, small core, no radial and concentric cracking, elongated, smooth surface/ free from wrinkles, high viscosity (consistency), high alcohol-insoluble solids, high yield, resistance to diseases like tomato leaf curl virus (ToLCV), bacterial wilt, early blight and late blight.

**Table 3:** Processing traits and genes for tomato breeding

| Trait                              | Gene                  |
|------------------------------------|-----------------------|
| Determinate/ self-pruning          | <i>sp</i>             |
| Concentrated fruit maturity        | <i>cfm</i>            |
| Jointless                          | <i>j-2</i>            |
| Uniform ripening                   | <i>u</i>              |
| Single flower truss                | <i>SFT</i>            |
| Sucrose accumulator (for high TSS) | <i>sucr</i>           |
| Old gold crimson                   | <i>og<sup>c</sup></i> |
| Intense pigment (deep red)         | <i>Ip</i>             |
| High pigment-2 (high lycopene)     | <i>hp-2</i>           |

### Key genes in tomato processing traits

**RIN (Ripening-inhibitor):** The RIPENING INHIBITOR (RIN) gene encodes a MADS-box transcription factor that acts as a key regulator of climacteric fruit ripening (Vrebalov *et al.*, 2002). It modulates the expression of genes associated with ethylene biosynthesis, carotenoid accumulation, and cell wall modification (Martel *et al.*, 2011; Li *et al.*, 2018). The classical *rin* mutation (LeMADS-RIN) delays ripening and extends shelf life in F<sub>1</sub> hybrids, leading to reduced lycopene accumulation, impaired softening, and downregulation of ripening-associated genes; the

absence of a climacteric ethylene peak primarily reflects transcriptional repression of key ethylene biosynthetic genes (Kitagawa *et al.*, 2005). Recent CRISPR/Cas9 studies further show that RIN is not essential for ripening initiation but is required for its proper progression, particularly for inducing the system-2 ethylene burst necessary for full colour and flavour development (Li *et al.*, 2020). Furthermore, RIN has been implicated in preventing excessive fruit softening (Ito *et al.*, 2020), and its activity is enhanced through interaction with the SnRK1 kinase, which promotes the expression of ripening-associated genes (Yu *et al.*, 2018). These findings indicate that RIN plays an important role in coordinating hormonal, transcriptional and metabolic processes involved in climacteric fruit ripening.

**PG and PL (Cell Wall Softening):** Firmness of fruits and thickness of pastes mainly depend on how much pectin breaks down. This breakdown relies on enzymes like polygalacturonase (PG) and pectate lyase (PL). Blocking PL activity increases fruit firmness and helps keep cell walls intact, without harming other important qualities like total soluble solids and colour (Ulusik *et al.*, 2016). Processing methods affect enzyme activity. For example, high-pressure and heat treatments can deactivate key enzymes, but they each have different levels of resistance. Polygalacturonase can be deactivated even at moderate temperatures. In contrast, pectin methylesterase is more resistant, so it requires a carefully adjusted approach using these methods (Crelie *et al.*, 2001). Additionally, different types of PG respond differently to temperature and high-pressure treatments, while pectin methylesterase remains stable (Rodrigo *et al.*, 2006). Processing methods can also improve product quality by reducing off-flavours through enzyme inactivation, such as lipoxygenase and PG, while maintaining texture (Shook *et al.*, 2001). At the molecular level, silencing certain genes, like SIPL and SIPL16, can manage cell wall metabolism to improve firmness and extend shelf life (Yang *et al.*, 2017, 2021; Ren *et al.*, 2023).

### Genome editing and Marker-Assisted Selection (MAS)

Marker-assisted selection (MAS) has advanced the development of processing tomato cultivars through increased efficiency in the breeding of complex traits while reducing the need for extensive phenotyping and linkage drag (Foolad and Panthee, 2012). A few genes/QTLs associated with processing traits in tomato are outlined in Table 4. In parallel, CRISPR/Cas9- based genome editing has emerged as a powerful tool for precise trait improvement. For instance knockout of *SLINVINH1* and *SLVPE5* using CRISPR/Cas9 resulted

**Table 4:** Genes/QTLs associated with processing traits in tomato

| Trait                                           | Gene / QTL                                                        | Chr    | Marker / position                    | Function                                                      |
|-------------------------------------------------|-------------------------------------------------------------------|--------|--------------------------------------|---------------------------------------------------------------|
| <b>TSS (°Brix)</b>                              |                                                                   |        |                                      |                                                               |
| TSS                                             | <i>Lin5</i> (cell wall invertase) ( <i>Brix9-2-5</i> )            | 9      | SSRs, SNPs near 9:4–6 Mb             | Sucrose hydrolysis (Suc → Glc + Fru); major TSS regulator     |
| TSS                                             | <i>Solyc09g010080</i> ( <i>Lin5</i> )                             | 9      | SNPs                                 | Sugar metabolism                                              |
| Glucose–fructose ratio                          | <i>gfa</i>                                                        | 9      | Linked with <i>Lin5</i>              | Sugar partitioning (Fru↑)                                     |
| TSS                                             | <i>TSS1.1</i> (QTL)                                               | 1      | 1:20–55 Mb                           | Minor sugar modifier                                          |
| TSS                                             | <i>TSS9.1</i> (QTL)                                               | 9      | 9:3–7 Mb ( <i>Lin5</i> region)       | Major TSS QTL                                                 |
| Fruit sweetness                                 | <i>SUT1</i> ( <i>Solyc03g007150</i> )                             | 3      | SNP linked to SUT1                   | Sucrose transporter from phloem to fruit                      |
| TSS                                             | <i>SUT2</i> ( <i>SUC2</i> family)                                 | 9      | Near 9:60–65 Mb                      | Long-distance sucrose unloading                               |
| Sugar accumulation                              | <i>TIV</i> ( <i>Tomato Invertase-Vacuum</i> )                     | 6      | 6:30–40 Mb                           | Cell wall/ vacuolar invertase activity                        |
| Soluble sugars                                  | <i>TST1</i> / <i>TST2</i> ( <i>Tonoplast sugar transporters</i> ) | 4 / 11 | SNP regions 4:5–8 Mb, 11:45–48 Mb    | Vacuolar sugar loading                                        |
| TSS                                             | <i>FUL1</i> / <i>FUL2</i> ( <i>Fruit ripening regulators</i> )    | 6 / 11 | QTL peaks linked to <i>FUL1-FUL2</i> | Regulate cell expansion and sugar influx                      |
| TSS                                             | <i>fw2.2-associated sugar QTL</i>                                 | 2      | 2:45–60 Mb                           | Small fruit → higher concentration                            |
| Fruit quality index                             | <i>GAD2</i> ( $\gamma$ -aminobutyrate decarboxylase)              | 10     | SNP in 10:4–7 Mb                     | Alters carbon flux → sugars                                   |
| TSS                                             | <i>Hexokinase</i> ( <i>H XK1</i> )                                | 2      | QTL co-localized                     | Sugar sensing and metabolism                                  |
| Sugar content                                   | <i>Sucrose phosphate synthase</i> ( <i>SPS</i> )                  | 8      | 8:2–4 Mb                             | Controls sucrose synthesis                                    |
| Sugar retention                                 | <i>Alba1</i> ( <i>cuticle thickness</i> )                         | 11     | 11:50–52 Mb                          | Lower water loss → ↑ TSS                                      |
| <b>Acidity / titratable acidity (TA) and pH</b> |                                                                   |        |                                      |                                                               |
| TA (malate)                                     | <i>ALMT9</i> ( <i>Aluminum-activated malate transporter</i> )     | 4      | SNP near gene <i>Solyc04g005080</i>  | Vacuolar malate uptake → ↑ acidity                            |
| TA (malate)                                     | <i>NAD-ME</i> ( <i>Solyc06g072910</i> )                           | 6      | SNP region                           | Malate decarboxylation and metabolism                         |
| TA                                              | <i>TA2.1</i> (QTL)                                                | 2      | SSR/SNP cluster                      | Organic acid biosynthesis regulation                          |
| Fruit pH                                        | <i>PH3</i> ( <i>proton homeostasis gene</i> )                     | 3      | SNP associated                       | Regulates H <sup>+</sup> pumping and apoplastic acidification |
| TA (citrate)                                    | <i>Solyc03g083130</i> ( <i>CS – Citrate synthase</i> )            | 3      | Linked SNP in 3:63–67 Mb             | Citrate accumulation at early ripening                        |
| TA (citrate)                                    | <i>ACO1</i> ( <i>Aconitase</i> )                                  | 12     | QTL-linked SNP                       | Converts citrate → isocitrate; ↓ TA                           |
| TA (total acids)                                | <i>mdh</i> ( <i>Malate dehydrogenase</i> )                        | 10     | SNP/QTL co-localized                 | Malate ↔ OAA equilibrium                                      |
| Acidity and flavour                             | <i>V-ATPase subunit A/B</i>                                       | 11 / 9 | Candidate SNP peaks                  | Vacuolar acidification, fruit sourness perception             |
| Fruit pH / TA                                   | <i>SLNR</i> ( <i>Nitrate reductase regulatory</i> )               | 6      | Linked in 6:40–55 Mb                 | Nitrate assimilation influences acid flux                     |
| Organic acids                                   | <i>GA2ox1</i>                                                     | 2      | SNP in TA2 QTL                       | Hormonal effects → fruit size vs. acid dilution               |
| <b>Fruit firmness</b>                           |                                                                   |        |                                      |                                                               |
| Firmness                                        | <i>PG2A</i> ( <i>Polygalacturonase</i> )                          | 10     | TfmA, PG-linked SNPs                 | Pectin degradation; major softening enzyme                    |
| Firmness                                        | <i>PL</i> ( <i>Pectate lyase</i> ; <i>Solyc08g062490</i> )        | 8      | SNP associated                       | Pectate cleavage → reduced firmness                           |
| Firmness                                        | <i>CEL2</i> ( <i>Cellulase</i> )                                  | 9      | SNP near gene                        | Cell wall breakdown; softening rate                           |
| Firmness                                        | <i>Firm3.1</i> (QTL)                                              | 3      | Major QTL peak                       | Texture regulation                                            |
| Firmness / storage shelf-life                   | <i>RIN</i> ( <i>Ripening-Inhibitor</i> )                          | 5      | 5:3–5 Mb, SNPs & Indels              | Master ripening transcription factor; delays softening        |
| Firmness / delayed softening                    | <i>NOR</i> ( <i>Non-ripening</i> )                                | 10     | Linked SNPs & Indels                 | Ethylene regulation of ripening and texture                   |
| Firmness                                        | <i>EXP1</i> ( <i>Expansin 1</i> )                                 | 2      | 2:45–48 Mb QTL                       | Cell wall loosening, early softening                          |
| Firmness                                        | <i>PME1</i> ( <i>Pectin Methylesterase</i> )                      | 1      | SNP cluster                          | Pectin modification → firmness retention                      |
| Cuticle-linked firmness                         | <i>CD2</i> ( <i>Cutin Deficient 2</i> )                           | 11     | 11:50–53 Mb                          | Cuticle structure → reduces water loss                        |
| Fruit firmness and shelf-life                   | <i>LCY-E</i> (via cell wall-associated pathways)                  | 11     | SNP/QTL linked                       | Lycopene metabolism → correlates with firmness QTL            |
| Firmness                                        | <i>FIR2</i> (QTL)                                                 | 4      | 4:20–30 Mb                           | Texture stability                                             |

| Trait                                                                    | Gene / QTL                                                            | Chr    | Marker / position                         | Function                                                                           |
|--------------------------------------------------------------------------|-----------------------------------------------------------------------|--------|-------------------------------------------|------------------------------------------------------------------------------------|
| Mechanical firmness                                                      | JOINTLESS2-associated QTL                                             | 12     | 12:42–46 Mb                               | Reduces abscission-related softening                                               |
| <b>Colour (lycopene, <math>\beta</math>-carotene, colour uniformity)</b> |                                                                       |        |                                           |                                                                                    |
| Lycopene (red pigment)                                                   | <i>Psy1</i> ( <i>Phytoene synthase</i> )<br>( <i>Solyc03g031860</i> ) | 3      | SNPs / functional alleles                 | Rate-limiting carotenoid biosynthesis step                                         |
| $\beta$ -carotene (orange fruit)                                         | <i>Beta</i> ( <i>B</i> ) ( <i>Solyc06g074240</i> )                    | 6      | SNP markers                               | Converts lycopene $\rightarrow$ $\beta$ -carotene (orange pigmentation)            |
| Colour uniformity                                                        | <i>t</i> ( <i>uniform ripening</i> )<br>( <i>Solyc10g086180</i> )     | 10     | SNP near Golden2-like gene                | Chloroplast development in immature fruit; uneven ripening if recessive            |
| Red colour formation                                                     | <i>r</i> / <i>r</i> <sup>2</sup>                                      | 3      | Linked with <i>Psy1</i> region            | Loss-of-function reduces red pigmentation                                          |
| Lycopene                                                                 | <i>LYC1.1</i> (QTL)                                                   | 1      | SNP cluster                               | Minor lycopene contributor                                                         |
| Carotenoid stability                                                     | <i>CRTR-B1</i> ( $\beta$ -carotene hydroxylase)                       | 6      | SNP close to B locus                      | Converts $\beta$ -carotene $\rightarrow$ zeaxanthin; modulates $\beta$ -carotene   |
| Lycopene accumulation                                                    | <i>ZISO</i> ( <i>Z-isomerase</i> )                                    | 2      | SNP around 2:40–45 Mb                     | Enhances cis-carotenoid accumulation $\rightarrow$ $\uparrow$ lycopene             |
| Carotenoid sequestration                                                 | <i>CHRC</i> ( <i>Chromoplast protein</i> )                            | 1      | Co-localized QTL SNPs                     | Maintains lycopene crystals for red colour intensity                               |
| Ripening and colour                                                      | <i>RIN</i> ( <i>Ripening-Inhibitor</i> )                              | 5      | SNP / Indel                               | Ripening TF increase lycopene; mutants cause pale fruit                            |
| Ethylene-linked colour                                                   | <i>NOR</i> ( <i>Non-ripening</i> )                                    | 10     | Marker-linked region                      | Controls carotenoid onset; non-ripening mutants: green-yellow fruit                |
| High-pigment phenotype                                                   | <i>hp-1</i> / <i>hp-2</i> ( <i>DDB1</i> / <i>DET1</i> )               | 7 / 1  | SNPs widely used in breeding              | $\uparrow$ Chloroplasts $\rightarrow$ $\uparrow$ lycopene, vitamin C, firmness     |
| External / internal colour                                               | <i>BIC1</i> / <i>BIC2</i> ( <i>BLUE-LIGHT INHIBITOR genes</i> )       | 3 / 11 | SNP/Indel                                 | Carotenoid precursor regulation by light response                                  |
| <b>Viscosity and processing recovery</b>                                 |                                                                       |        |                                           |                                                                                    |
| Viscosity / pectin strength                                              | <i>PE1</i> ( <i>Pectinesterase</i> / <i>PME</i> )                     | 1      | SNP linked                                | Pectin de-esterification $\rightarrow$ $\uparrow$ cell wall rigidity and viscosity |
| Viscosity / cell wall integrity                                          | <i>XTH</i> ( <i>Xyloglucan endotransglycosylase</i> )                 | 3      | SNP near candidate locus                  | Xyloglucan modification $\rightarrow$ pulp consistency                             |
| Major viscosity QTL                                                      | <i>QTL-Visc9.1</i>                                                    | 9      | RFLP / SNP cluster                        | Controls pulp thickness and serum viscosity                                        |
| Serum viscosity                                                          | <i>QTL-Visc5.2</i>                                                    | 5      | SNP region                                | Water/juice separation regulation                                                  |
| Pulp thickness and yield                                                 | <i>fw11.3-associated QTL</i>                                          | 11     | 11:48–52 Mb                               | Thick pericarp $\rightarrow$ $\uparrow$ viscosity                                  |
| Processing consistency                                                   | <i>VGT</i> QTL (viscosity and firmness related)                       | 2      | SNP peaks co-localized with firmness loci | Coordinated control of pectin retention                                            |
| Pectin biosynthesis                                                      | <i>GAUT</i> family<br>( <i>Galacturonosyltransferases</i> )           | 4      | New GWAS SNP hits                         | Homogalacturonan synthesis $\rightarrow$ improves viscosity                        |
| <b>Fruit size</b>                                                        |                                                                       |        |                                           |                                                                                    |
| Fruit size (major QTL)                                                   | <i>fw2.2</i>                                                          | 2      | SNP interval 2:44–46 Mb                   | Regulates carpel cell division; negative growth regulator                          |
| Fruit size                                                               | <i>fw3.2</i> ( <i>Cytochrome P450 family</i> )                        | 3      | QTL region 3:60–70 Mb                     | Regulates pericarp cell proliferation                                              |
| Locule number                                                            | <i>lc</i> ( <i>locule number</i> )                                    | 2      | Near WUSCHEL response element             | Controls carpel primordia $\rightarrow$ $\uparrow$ locules                         |
| Fruit size and locule number                                             | <i>fas</i> ( <i>fasciated</i> ) ( <i>YABBY</i> transcription factor)  | 11     | SNP near <i>Solyc11g071840</i>            | Floral meristem development; increases locules $\rightarrow$ large fruit           |
| Fruit weight and shape                                                   | <i>fw11.3</i>                                                         | 11     | QTL peak                                  | Pericarp thickening and weight gain                                                |
| Fruit weight / introgressed trait                                        | <i>SUN</i>                                                            | 7      | 7:60–65 Mb                                | Horizontal elongation; increased weight                                            |
| Shape and size                                                           | <i>OVATE</i>                                                          | 2      | 2:25–28 Mb                                | Controls pear/elongated shapes; weight effects                                     |
| Locule number                                                            | <i>QTL-loc5.1</i>                                                     | 5      | QTL region                                | Minor contributor to locule variation                                              |
| Fruit size                                                               | <i>CSR</i> / <i>QTL-FW9.1</i>                                         | 9      | SNP cluster                               | Cell expansion in pericarp                                                         |
| Pericarp development                                                     | <i>SLKLUH</i> ( <i>CYP78A5</i> )                                      | 1      | SL4.0 SNP hits                            | Organ size expansion $\rightarrow$ $\uparrow$ fruit weight                         |
| <b>Ascorbic acid (vitamin C)</b>                                         |                                                                       |        |                                           |                                                                                    |
| Ascorbic acid biosynthesis                                               | <i>GME</i> ( <i>GDP-mannose epimerase</i> )                           | 9      | SNP linked to <i>Solyc09g008900</i>       | GDP-mannose $\rightarrow$ L-galactose pathway precursor                            |

| Trait                                          | Gene / QTL                                          | Chr       | Marker / position             | Function                                                      |
|------------------------------------------------|-----------------------------------------------------|-----------|-------------------------------|---------------------------------------------------------------|
| Ascorbic acid biosynthesis (final step)        | <i>GLDH (L-galactono-1,4-lactone dehydrogenase)</i> | 9         | SNP region                    | Catalyzes final step of AsA biosynthesis in mitochondria      |
| Ascorbic acid QTL                              | <i>QTL-AsA8.1</i>                                   | 8         | SNP cluster                   | Variation in total AsA concentration                          |
| Recycling of AsA                               | <i>MDHAR (Monodehydroascorbate reductase)</i>       | 6         | Putative SNP peak             | Regenerates AsA from oxidized form → ↑ antioxidant content    |
| Ascorbate–glutathione cycle                    | <i>APX (Ascorbate peroxidase)</i>                   | 4         | Candidate SNP                 | Detoxifies ROS; maintains reduced AsA pool                    |
| High-pigment antioxidant boost                 | <i>hp-1/hp-2 (DET1/DDB1)</i>                        | 1/7       | Indels/SNPs                   | ↑ Chloroplast development → ↑ AsA + lycopene                  |
| Stress-linked Vit-C QTL                        | <i>QTL-AsA3.2</i>                                   | 3         | QTL-linked markers            | UV and stress-induced AsA accumulation                        |
| Minor AsA contributor                          | <i>PMI (Phosphomannose isomerase)</i>               | 5         | GWAS SNP hits                 | Regulates hexose flux into AsA pathway                        |
| <b>Jointless trait (mechanical harvesting)</b> |                                                     |           |                               |                                                               |
| Jointless pedicel                              | <i>J (Soly11g010570)</i>                            | 11        | SNP, CAPS markers (11:0–2 Mb) | MADS-box gene controlling abscission zone formation           |
| Improved jointless                             | <i>j-2 (Jointless-2) (Soly12g038510)</i>            | 12        | SNP markers                   | Jointless phenotype without deleterious inflorescence defects |
| Jointless QTL Complex                          | <i>J-comp/ej2</i>                                   | 11 and 12 | Linked QTL blocks             | Epistasis between J and ej2 stabilizes jointless trait        |

in the accumulation of more sugars, including glucose, fructose, and total soluble solids (TSS) in tomato fruits, and a double knockout had a synergistic effect with higher sugar accumulation than single gene knockouts, which may be a potential strategy to increase fruit sweetness and processing quality (Wang *et al.*, 2021).

Furthermore, CRISPR/Cas9 has been used to increase the fruit's lycopene content by stimulating its biosynthesis and repressing conversion to other forms of carotenoid, thereby improving the nutritional properties of the fruit (Li *et al.*, 2018). Studies conducted on transcriptomics have shown that genes related to the activity of pectinases, such as pectate lyase (PL) and pectin methyl esterase (PME), play an important role in fruit development due to cell wall remodelling processes (Wen *et al.*, 2025). The MAS technique is useful in early screening for various desirable traits like better fruit colour, increased levels of lycopene and resistance to root-knot nematodes (Kumar *et al.*, 2023). Moreover, techniques like genome resequencing, pan-genomics, SNP genotyping, GWAS and GS have also helped in identifying significant genes and markers, making the process more efficient (Tiwari *et al.*, 2022). In summary, the CRISPR/Cas9-mediated targeted genome editing of genes related to soluble sugar accumulation or carotenoid metabolism is a highly effective strategy for enhancing sweetness and lycopene content in fruit, with stable, heritable effects over multiple generations (Li *et al.*, 2018; Wang *et al.*, 2021).

## CONCLUSION

The improvement in tomato for processing quality requires a holistic integration of morphological, biochemical, physiological, and molecular traits.

Processing efficiency and product quality are largely governed by attributes such as high TSS, balanced acidity, enhanced lycopene content, firm texture, and desirable fruit architecture, all of which are controlled by complex genetic mechanisms and influenced by environmental factors. Traditional breeding approaches, although valuable, are insufficient to address the polygenic nature of these traits and the challenges posed by climate variability and yield quality trade-offs. Recent advancements in genomics, including QTL mapping, GWAS, marker-assisted selection, and CRISPR/Cas9-mediated genome editing, have provided precise tools for targeted improvement of processing traits. Identification of key genes such as *RIN*, *LIN5*, *hp-2*, and those involved in cell wall metabolism and sugar transport has enabled more efficient breeding strategies. Furthermore, utilization of wild relatives and genomic selection approaches offers opportunities to broaden the genetic base and enhance stress tolerance. For countries like India, strengthening dedicated processing tomato breeding programs, fostering public–private partnerships, and improving value chain linkages are critical for expanding the processing industry. Future breeding efforts should focus on developing high-yielding, climate-resilient cultivars with superior processing quality tailored to industrial requirements. The convergence of conventional and modern breeding approaches will be pivotal in achieving sustainable growth and global competitiveness in the tomato processing sector.

## ACKNOWLEDGMENTS

Research was supported by the Indian Council of Agricultural Research, Department of Agricultural

Research and Education, Government of India. We thank the Competent Authority of ICAR-IIVR, Varanasi, for support.

## REFERENCES

- Ahmad S, Wei X, Sheng Z, Hu P and Tang S. 2018. CRISPR/Cas9 for development of disease resistance in plants: Recent progress, limitations and future prospects. *Briefings in Functional Genomics* **19**: 26–39.
- Alda LM, Gogoasă I, Bordean DM, Gergen I, Alda S, Moldovan C and Niță L. 2009. Lycopene content of tomatoes and tomato products. *Journal of Agroalimentary Processes and Technologies* **15**: 540–42.
- Alsamir M, Mahmood T, Trethowan R and Ahmad N. 2021. An overview of heat stress in tomato (*Solanum lycopersicum* L.). *Saudi Journal of Biological Sciences* **28**: 1654–1663.
- Amr A and Raie W. 2022. Tomato components and quality parameters: A review. *Jordan Journal of Agricultural Sciences* **18**: 199–220.
- Anthon GE, LeStrange M and Barrett D M. 2011. Changes in pH, acids, sugars, and other quality parameters during extended vine holding of ripe processing tomatoes. *Journal of the Science of Food and Agriculture* **91**: 1175–81.
- Arballo J, Amengual J and Erdman JW Jr. 2021. Lycopene: A critical review of digestion, absorption, metabolism, and excretion. *Antioxidants* **10**: 342.
- Aurand LW, Woods AE and Wells MR. 2012. Food Composition and Analysis, Springer.
- Bachmann J and Earles R. 2000. Postharvest handling of fruits and vegetables. ATTRA, Fayetteville, NC, USA.
- Bai Y and Lindhout P. 2007. Domestication and breeding of tomatoes: What have we gained and what can we gain in the future. *Annals of Botany* **100**: 1085–94.
- Baldwin EA, Scott JW, Shewmaker CK, Schuch W. 2000. Flavor trivia and tomato aroma: Biochemistry and possible mechanisms for control of important aroma components. *HortScience* **35**: 1013–22.
- Barrett DM, Garcia E, Wayne JE. 1998. Textural modification of processing tomatoes. *Critical Reviews in Food Science and Nutrition* **38**: 173–58.
- Beckles D M. 2012. Factors affecting the postharvest soluble solids and sugar content of tomato (*Solanum lycopersicum* L.) fruit. *Postharvest Biology and Technology* **63**: 129–40.
- Bertin N and Génard M. 2018. Tomato quality as influenced by preharvest factors. *Scientia Horticulturae* **233**: 264–76.
- Bertin N, Borel C, Brunel B, Cheniclet C, Causse M. 2003. Do genetic make-up and growth manipulation affect tomato fruit size by cell number, or cell size and DNA endoreduplication? *Annals of Botany* **92**: 415–424.
- Biswas P, East AR, Hewett EW, Heyes JA. 2016. Chilling injury in tomato fruit. In J. Janick (Ed.), *Horticultural Reviews* (Vol. 44, pp. 229–278). John Wiley & Sons, Inc.
- Canene-Adams K, Campbell JK, Zaripheh S, Jeffery EH, Erdman JW Jr. 2005. The tomato as a functional food. *Journal of Nutrition* **135**: 1226–30.
- Cappetta E, Andolfo G, Guadagno A, Di Matteo A, Barone A, Frusciante L, Ercolano MR. 2021. Tomato genomic prediction for good performance under high temperature and identification of loci involved in thermotolerance response. *Horticulture Research* **8**: 212.
- Causse M, Saliba-Colombani V, Lecomte L, Duffé P, Rousselle P, Buret M. 2002. QTL analysis of fruit quality in fresh market tomato: A few chromosome regions control the variation of sensory and instrumental traits. *Journal of Experimental Botany* **53**: 2089–98.
- Chattopadhyay A, Chakraborty I V I and Siddique W. 2013. Characterization of determinate tomato hybrids: search for better processing qualities. *Journal of Food Processing and Technology* **4**: 222.
- Chaudhary J, Alisha A, Bhatt V, Chandanshive S, Kumar N, Mir Z *et al.* 2019. Mutation breeding in tomato: Advances, applicability and challenges. *Plants* **8**: 128.
- Crelier S, Robert M C, Claude J, Juillerat M A. 2001. Thermal and high-pressure inactivation of pectin methylesterase, polygalacturonase and peroxidase in tomato juice. *Journal of Food Science* **66**: 521–26.
- Distefano M, Mauro R P, Page D, Giuffrida F, Bertin N and Leonardi C. 2022. Aroma volatiles in tomato fruits: The role of genetic, preharvest and postharvest factors. *Agronomy* **12**: 376.
- Egea I, Estrada Y, Flores F B and Bolarín M C. 2022. Improving production and fruit quality of tomato under abiotic stress: Genes for the future of tomato breeding for a sustainable agriculture. *Environmental and Experimental Botany* **204**: 105086.
- FAOSTAT. 2024. FAOSTAT (<https://www.fao.org/faostat/en/#home>). Accessed on 15.03.2026
- Foolad M R and Panthee D R. 2012. Marker-assisted selection in tomato breeding. *Critical Reviews in Plant Sciences* **31**: 93–123.
- Goff S A and Klee H J. 2006. Plant volatile compounds: Sensory cues for health and nutritional value? *Science* **311**: 815–19.
- Gur A and Zamir D. 2004. Unused natural variation can lift yield barriers in plant breeding. *PLoS Biology* **2(10)**: e245.
- Held M T, Anthon G E and Barrett D M. 2015. The effects of bruising and temperature on enzyme activity and textural qualities of tomato juice. *Journal of the Science of Food and Agriculture* **95**: 1598–604.
- Ho L C. 1996. The mechanism of assimilate partitioning and carbohydrate compartmentation in fruit in relation to

- the quality and yield of tomato. *Journal of Experimental Botany* **47**(Special Issue): 1239–43.
- Hou X, Zhang W, Du T, Kang S and Davies W J. 2020. Responses of water accumulation and solute metabolism in tomato fruit to water scarcity and implications for main fruit quality variables. *Journal of Experimental Botany* **71**: 1249–64.
- Huang X, Wei J M, Feng W Z, Luo Q, Tan G F and Li Y Z. 2023. Interaction between *SLMAPK3* and *SLASR4* regulates drought resistance in tomato (*Solanum lycopersicum* L.). *Molecular Breeding* **43**: 73.
- Ito Y, Nishizawa-Yokoi A, Endo M, Mikami M, Shima Y, Nakamura N *et al.* 2020. Re-evaluation of the rin mutation and the role of RIN in tomato fruit ripening. *Nature Plants* **6**: 553–57.
- Kamil M M, Mohamed G F and Shaheen M S. 2011. Fourier transformer infrared spectroscopy for quality assurance of tomato products. *Journal of American Science* **7**: 559–72.
- Kandasamy P. 2022. Respiration rate of fruits and vegetables for modified atmosphere packaging: A mathematical approach. *Journal of Postharvest Technology* **10**: 88–102.
- Khan A S and Singh Z. 2009. 1-MCP application suppresses ethylene biosynthesis and retards fruit softening during cold storage of ‘Tegan Blue’ Japanese plum. *Plant Science* **176**: 539–44.
- Khapte P S, Kumar P, Burman U, Kumar P. 2019. Deficit irrigation in tomato: Agronomical and physio-biochemical implications. *Scientia Horticulturae* **248**: 256–64.
- Kitagawa M, Ito H, Shiina T, Nakamura N, Inakuma T, Kasumi T, Ishiguro Y, Yabe K and Ito Y. 2005. Characterization of tomato fruit ripening in the rin mutant and its application to breeding. *Journal of the Japanese Society for Horticultural Science* **74**: 302–308.
- Klee H J and Tieman D M. 2013. Genetic challenges of flavor improvement in tomato. *Trends in Genetics* **29**: 257–62.
- Klee H J and Tieman D M. 2018. The genetics of fruit flavour preferences. *Nature Reviews Genetics* **19**: 347–56.
- Kumar A, Lakshmi V, Sangam S, Goswami T N, Kumar M, Akhtar S and Chattopadhyay T. 2023. Marker assisted early generation identification of root knot disease-resistant, orange-fruited tomato segregants with multiple desirable alleles. *Physiology and Molecular Biology of Plants* **29**: 1179–92.
- Kumar R, Srivastava K, Kumar V, Saroj S K, Sharma S K and Singh R K. 2019. Heterosis analysis in tomato (*Solanum lycopersicum* L.) for lycopene, TSS, titrable acidity and ascorbic acid. *Electronic Journal of Plant Breeding* **10**: 1547–53.
- Kumar R, Srivastava K, Singh R K and Kumar V. 2013. Heterosis for quality attributes in tomato (*Lycopersicon esculentum* Mill.). *Vegetos* **26**: 101–106.
- Kun Y, Lule U S and Xiao-Lin D. 2006. Lycopene: Its properties and relationship to human health. *Food Reviews International* **22**: 309–33.
- Kyriacou M C and Roupael Y. 2018. Towards a new definition of quality for fresh fruits and vegetables. *Scientia Horticulturae* **234**: 463–69.
- Li S, Xu H, Ju Z, Cao D, Zhu H, Fu D, Grierson D and Qin G. 2018. The RIN transcription factor regulates multiple aspects of fruit ripening through direct transcriptional control. *The Plant Journal* **94**: 450–65.
- Li S, Zhu B, Pirrello J, Xu C, Zhang B, Bouzayen M, Chen K and Grierson D. 2020. Roles of RIN and ethylene in tomato fruit ripening and ripening-associated traits. *New Phytologist* **226**: 460–75.
- Li X, Wang Y, Chen S, Tian H, Fu D, Zhu B, Luo Y and Zhu H. 2018. Lycopene is enriched in tomato fruit by CRISPR/Cas9-mediated multiplex genome editing. *Frontiers in Plant Science* **9**: 559.
- Lin T, Zhu G, Zhang J, Xu X, Yu Q, Zheng Z, Zhang Z, Lun Y, Li S, Wang X *et al.* 2014. Genomic analyses provide insights into the history of tomato breeding. *Nature Genetics* **46**: 1220–26.
- Martel C, Vrebalov J, Tafelmeyer P, and Giovannoni J J. 2011. The tomato MADS-box transcription factor RIPENING INHIBITOR interacts with promoters involved in numerous ripening processes. *Plant Physiology* **157**: 1568–79.
- Massaretto I L, Albaladejo I, Purgatto E, Flores F B, Plasencia F, Egea-Fernández J M, Bolarin M C and Egea I. 2018. Recovering tomato landraces to simultaneously improve fruit yield and nutritional quality against salt stress. *Frontiers in Plant Science* **9**: 1778.
- NAAS. 2022. Need for breeding tomatoes suitable for processing. Strategy No. 16, National Academy of Agricultural Sciences, New Delhi, pp 20.
- Nie H, Yang X, Zheng S and Hou L. 2024. Gene-based developments in improving quality of tomato: focus on firmness, shelf life, and pre- and post-harvest stress adaptations. *Horticulturae* **10**: 641.
- Nunes M C. 2009. *Color atlas of postharvest quality of fruits and vegetables*. John Wiley & Sons.
- Omoni A O and Aluko R E. 2005. The anticarcinogenic and anti-atherogenic effects of lycopene: A review. *Trends in Food Science & Technology* **16**: 344–50.
- Ortega-Salazar I, Ozminkowski R H Jr, Adaskaveg J A, Sbodio A O and Blanco-Ulate B. 2025. Genetic basis of fruit quality traits in processing tomatoes. *Journal of Agriculture and Food Research* **22**: 102096.
- Ortigosa A, Gimenez-Ibanez S, Leonhardt N and Solano R. 2019. Design of a bacterial speck resistant tomato by CRISPR/Cas9-mediated editing of *SlJAZ2*. *Plant Biotechnology Journal* **17**: 665–73.

- Oruna-Concha M J, Methven L, Blumenthal H, Young C and Mottram D S. 2007. Differences in glutamic acid and 5'-ribonucleotide contents between flesh and pulp of tomatoes and the relationship with umami taste. *Journal of Agricultural and Food Chemistry* **55**: 5776–80.
- Peet M M, Sato S and Gardner R G. 1998. Comparing heat stress effects on male-fertile and male-sterile tomatoes. *Plant, Cell and Environment* **21**: 225–31.
- Plaut Z, Butow B J, Blumenthal C S and Wrigley C W. 2004. Transport of dry matter into developing wheat kernels and its contribution to grain yield under post-anthesis water deficit and elevated temperature. *Field Crops Research* **86**: 185–98.
- Portugal J, Rego F C, Moreira I, Vidal R A. 2015. Quality of processing tomato fruits in competition with *Solanum americanum*. *Planta Daninha* **33**: 689–97.
- Quinet M, Angosto T, Yuste-Lisbona F J, Blanchard-Gros R, Bigot S, Martinez J P and Lutts S. 2019. Tomato fruit development and metabolism. *Frontiers in Plant Science* **10**: 1554.
- Ranjan A, Ichihashi Y and Sinha N R. 2012. The tomato genome: Implications for plant breeding, genomics and evolution. *Genome Biology* **13**: 167.
- Ren Y, Wang Y, He Y, Ding Y, Zhang H and Liu H. 2023. Functional characterization of *SlPL16* in regulating fruit softening and cell wall metabolism in tomato. *Postharvest Biology and Technology* **196**: 112159.
- Rigano M M, Arena C, Di Matteo A, Sellitto S, Frusciante L and Barone A. 2016. Eco-physiological response to water stress of drought-tolerant and drought-sensitive tomato genotypes. *Plant Biosystems* **150**: 682–91.
- Rodrigo D, Cortés C, Clynen E, Schoofs L, Van Loey A and Hendrickx M. 2006. Thermal and high-pressure stability of purified polygalacturonase and pectinmethylesterase from four different tomato processing varieties. *Food Research International* **39**: 440–48.
- Rothan C, Diouf I and Causse M. 2019. Trait discovery and editing in tomato. *The Plant Journal* **97**: 73–90.
- Sadashiva A, Oberoi H S, Singh T H, Prasanna H C, Madhavi Reddy K, Krishna Reddy M and Ravishankar K V. 2022. Breeding tomatoes suitable for processing with triple disease resistance to tomato leaf curl disease, bacterial wilt, and early blight. *Journal of Horticultural Sciences* **17**: 1386.
- Saltveit M E. 2019. Respiratory metabolism. In E. M. Yahia (Ed.), *Postharvest physiology and biochemistry of fruits and vegetables* Woodhead Publishing, pp. 73–91
- Sánchez M C, Valencia C, Gallegos C, Ciruelos A and Latorre A. 2002. Influence of processing on the rheological properties of tomato paste. *Journal of the Science of Food and Agriculture* **82**: 990–97.
- Schaffer A A and Petreikov M. 1997. Sucrose-to-starch metabolism in tomato fruit undergoing transient starch accumulation. *Plant Physiology* **113**: 739–46.
- Seymour G B, Østergaard L, Chapman N H, Knapp S and Martin C. 2013. Fruit development and ripening. *Annual Review of Plant Biology* **64**: 219–41.
- Shipman E N, Yu J, Zhou J, Alborno K and Beckles D M. 2021. Can gene editing reduce postharvest waste and loss of fruit, vegetables, and ornamentals? *Horticulture Research*, **8**: 1.
- Shook C M, Shellhammer T H and Schwartz S J. 2001. Polygalacturonase, pectinesterase, and lipoxygenase activities in high-pressure processed tomato juice. *Journal of Agricultural and Food Chemistry* **49**: 664–68.
- Somappa J, Srivastava K, Sarma B K, Pal C and Kumar R. 2013. Studies on growth conditions of the tomato Alternaria leaf spot causing *Alternaria solani* L. *The Bioscan* **8**: 101–104.
- Steele N M, McCann M C and Roberts K. 1997. Pectin modification in cell walls of ripening tomatoes occurs in distinct domains. *Plant Physiology* **114**: 373–81.
- Stommel J R, Abbott J A, Saftner R A and Camp M J. 2005. Sensory and objective quality attributes of beta-carotene and lycopene-rich tomato fruit. *Journal of the American Society for Horticultural Science* **130**: 244–51.
- Tashkandi M, Ali Z, Aljedaani F, Shami A and Mahfouz M M. 2018. Engineering resistance against tomato yellow leaf curl virus via the CRISPR/Cas9 system in tomato. *Plant Signaling & Behavior* **13**: e1525996.
- Thole V, Vain P, Yang R Y, Almeida Barros da Silva J, Enfissi E M A et al. 2020. Analysis of tomato post-harvest properties: Fruit color, shelf life, and fungal susceptibility. *Current Protocols in Plant Biology* **5**: e20108.
- Tieman D, Bliss P, McIntyre L M, Blandon-Ubeda A, Bies D. et al. 2012. The chemical interactions underlying tomato flavor preferences. *Current Biology*, **22**: 1035–39.
- Tiwari J K, Rai N, Hussain Z, Reddy Y S, Gowda M T, Prasanna H C and Kumar R. 2026. Tomato Hybrid Development Technology. Technical Bulletin No. 122, ICAR-Indian Institute of Vegetable Research, Varanasi.
- Tiwari J K, Rai, N, Singh M K, Mishra L K, Mishra G and Behera T K. 2023. Characterization of tomato lines for yield components, processing traits, and disease resistance based on phenotype and molecular markers. *Vegetable Science* **50**: 302–309.
- Tiwari J K, Yerasu S R, Rai N, Singh D P, Singh A K, Karkute S G, Singh P M and Behera T K. 2022. Progress in marker-assisted selection to genomics-assisted breeding in tomato. *Critical Reviews in Plant Sciences* **41**: 321–50.
- Tomato Genome Consortium. 2012. The tomato genome sequence provides insights into fleshy fruit evolution. *Nature* **485**: 635–41.
- Uluşık S, Chapman N H, Smith R, Poole M, Adams G, Gillis R B, Besong T M et al. 2016. Genetic improvement of tomato by targeted control of fruit softening. *Nature Biotechnology* **34**: 950–52.

- van Dijk C, Boeriu C G, Stolle-Smits T and Tijskens L M M. 2006. The firmness of stored tomatoes (cv. Tradiro). 2. Kinetic and Near Infrared models to describe pectin-degrading enzymes and firmness loss. *Journal of Food Engineering* **77**: 585–93.
- Vats S, Bansal R, Rana N, Kumawat S, Bhatt V, Jadhav P, Kale V, Sathe A, Sonah H, Jugdaohsingh R, Sharma T R and Deshmukh R. 2022. Unexplored nutritive potential of tomato to combat global malnutrition. *Critical Reviews in Food Science and Nutrition*, **62**: 1003–34.
- Velioglu Y S, Mazza G, Gao L and Oomah B D. 1998. Antioxidant activity and total phenolics in selected fruits, vegetables, and grain products. *Journal of Agricultural and Food Chemistry* **46**: 4113–17.
- Vieira D A P, Caliari M, Souza E R B and Soares Júnior M S. 2020. Methods for pigments extraction and determination of color in tomato for processing cultivars. *Food Science and Technology* **40**: 11–17.
- Vrebalov J, Ruezinsky D, Padmanabhan V, White R, Medrano D, Drake R, Schuch W and Giovannoni J. 2002. A MADS-box gene necessary for fruit ripening at the tomato ripening-inhibitor (rin) locus. *Science* **296**: 343–46.
- Wahid A, Gelani S, Ashraf M and Foolad M R. 2007. Heat tolerance in plants: an overview. *Environmental and Experimental Botany* **61**: 199–223.
- Wang B, Li N, Huang S, Hu J, Wang Q, Tang Y, Yang T, Asmutola P, Wang J and Yu Q. 2021. Enhanced soluble sugar content in tomato fruit using CRISPR/Cas9-mediated *SLINVINH1* and *SIVPE5* gene editing. *PeerJ* **9**: e12478.
- Wang D, Samsulrizal N H, Yan C, Allcock N S, Craigon J, Blanco-Ulate B. *et al.* 2019. Characterization of CRISPR mutants targeting genes modulating pectin degradation in ripening tomato. *Plant Physiology* **179**: 544–57.
- Wang D, Yeats T H, Ullisik S, Rose J K C and Seymour G B. 2018. Fruit softening: revisiting the role of pectin. *Trends in Plant Science* **23**: 302–10.
- Wang R, Lammers M, Tikunov Y, Bovy A G, Angenent G C and de Maagd R A. 2020. The *rin*, *nor* and *Cnr* spontaneous mutations inhibit tomato fruit ripening in additive and epistatic manners. *Plant Science* **294**: 110436.
- Wann E V. 1996. Physical characteristics of mature green and ripe tomato fruit tissue of normal and firm genotypes. *Journal of the American Society for Horticultural Science* **121**: 380–83.
- Wen J, Li Q, Tao X, Zhou R, Yan C and Zhong Q. 2025. Integrated analysis of transcriptomes and pectinase gene families reveals a novel pathway mediating tomato fruit malformation. *International Journal of Molecular Sciences* **26**: 10739.
- Yahia E M and Brecht J K. 2012. Tomatoes. In R. Debbie, F. Graham, & O. John (Eds.), *Crop post-harvest: Science and technology: Perishables* (pp. 5-17). Blackwell Publishing Ltd.
- Yahia E M, Soto-Zamora G, Brecht J K and Gardea A. 2007. Postharvest hot air treatment effects on the antioxidant system in stored mature-green tomatoes. *Postharvest Biology and Technology* **44**: 107–15.
- Yang L, Huang W, Xiong F, Xian Z, Su D, Ren M and Li Z. 2017. Silencing of *SIPL*, a pectate lyase gene, enhances fruit firmness and shelf life in tomato. *Plant Physiology and Biochemistry* **117**: 111–19.
- Yang L, Xian Z, Li Z and Huang W. 2021. Oligogalacturonides delay tomato fruit softening by regulating cell wall metabolism and hormone signaling pathways. *Postharvest Biology and Technology* **178**: 111561.
- Yin Y G, Kobayashi Y, Sanuki A, Kondo S, Fukuda N, Ezura H, Sugaya S, and Matsukura C. 2010. Salinity induces carbohydrate accumulation and sugar-regulated starch biosynthetic genes in tomato (*Solanum lycopersicum* L. cv. 'Micro-Tom') fruits in an ABA- and osmotic stress-independent manner. *Journal of Experimental Botany* **61**: 563–74.
- Yin Y, Qin K, Song X, Zhang Q, Zhou Y, Xia X, Yu J. 2018. BZR1 transcription factor regulates heat stress tolerance through FERONIA receptor-like kinase-mediated reactive oxygen species signalling in tomato. *Plant and Cell Physiology* **59**: 2239–54.
- Youssef K, Ippolito A and Roberto S R. 2022. Editorial: Post-harvest diseases of fruit and vegetable: Methods and mechanisms of action. *Frontiers in Microbiology* **13**: 900060.
- Yu S M, Lo S F and Ho T H D. 2018. Source–sink communication: Regulated by SnRK1-mediated signaling pathways. *Trends in Plant Science* **23**: 1026–37.
- Yun S D, Kim M H, Oh S A, Soh M S and Park S K. 2022. Overexpression of C-repeat binding factor 1 (*CBF1*) gene enhances heat stress tolerance in *Arabidopsis*. *Journal of Plant Biology* **65**: 253–60.
- Zhang Y, Tian X, Xu H, Zhan B, Zhou C, Li S and Zhang Z. 2024. Knockout of *SLDCL2b* attenuates the resistance of tomato to potato spindle tuber viroid infection. *Molecular Plant Pathology* **25**: e13441.
- Zhu F, Wen W, Cheng Y *et al.* 2022. The metabolic changes that affect fruit quality during tomato fruit ripening. *Molecular Horticulture* **2**: 2.