



## Molecular Regulation of Fruit Development and Ripening in Tomato: Recent Advances and Future Perspectives

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Tomato (*Solanum lycopersicum* L.) is an economically important vegetable crop and a widely used model for understanding fleshy-fruit development and ripening. Fruit development involves coordinated changes in cell division, cell expansion, pigmentation, texture, flavour, nutritional composition and hormone signalling. At the molecular level, these processes are controlled by complex interactions among ethylene, auxin, abscisic acid, gibberellins and other regulatory signals, together with transcription factors, epigenetic mechanisms and metabolic pathways. Genes involved in ethylene biosynthesis, cell-wall modification, carotenoid accumulation and flavour formation play major roles during ripening. Recent advances in genomics, transcriptomics, metabolomics, epigenomics and CRISPR/Cas genome editing have provided new opportunities to understand and manipulate these processes. This article highlights major molecular mechanisms controlling tomato fruit development and ripening, recent biotechnological advances and future opportunities for developing tomato cultivars with improved quality, nutritional value, shelf life and climate resilience.

**Keywords:** Tomato, Fruit development, Fruit ripening, Ethylene, Molecular regulation

### Introduction

Tomato is one of the world's most widely cultivated vegetable crops and is valued for its nutritional, culinary and economic importance. Its fruits provide lycopene,  $\beta$ -carotene, vitamin C, phenolic compounds and other health-promoting metabolites. Tomato is also a major model system for studying fleshy-fruit development because its developmental stages and ripening-associated molecular changes are comparatively well characterized. Fruit development is a highly coordinated biological process beginning with flowering and fertilization and progressing through fruit set, cell division, cell expansion, maturation and ripening. These stages are controlled by genetic networks that interact with environmental factors and plant hormones. Modern molecular research has revealed that tomato ripening is not controlled by a single pathway. Instead, transcription factors, hormone signalling, epigenetic regulation and metabolic networks act together to determine colour, firmness, aroma, flavour and nutritional quality.

### From Fruit Set to Ripening: A Coordinated Developmental Process

Following successful pollination and fertilization, the tomato ovary undergoes rapid changes that establish the developing fruit. Early fruit growth is mainly associated with cell division,

followed by substantial cell expansion that determines final fruit size. Hormones such as auxin and gibberellins have important roles in fruit initiation and growth. As development progresses, the fruit transitions from the mature-green stage towards ripening. During this transition, chlorophyll degradation, carotenoid accumulation, softening, flavour development and changes in volatile compounds occur simultaneously. These processes are coordinated through large-scale changes in gene expression and metabolism.

**Table 1. Major molecular regulators involved in tomato fruit development and ripening**

| Molecular component | Major role                               | Important fruit trait |
|---------------------|------------------------------------------|-----------------------|
| Ethylene            | Initiation and coordination of ripening  | Ripening and colour   |
| Auxin               | Fruit set and early development          | Fruit growth          |
| ABA                 | Ripening regulation and stress responses | Maturation            |
| RIN                 | Master transcriptional regulation        | Ripening              |
| NOR                 | Ripening-associated gene regulation      | Maturation            |
| CNR                 | Transcriptional regulation               | Ripening              |
| FUL1/FUL2           | Regulation of ripening networks          | Fruit development     |
| PSY1                | Carotenoid biosynthesis                  | Red colour            |
| Polygalacturonase   | Cell-wall degradation                    | Softening             |
| Expansins           | Cell-wall loosening                      | Texture               |

### Ethylene: A Central Signal for Tomato Ripening

Ethylene is one of the most important hormones regulating climacteric fruit ripening in tomato. Its biosynthesis involves the conversion of S-adenosyl methionine to 1-aminocyclopropane-1-carboxylic acid (ACC), followed by conversion of ACC to ethylene by ACC oxidase. The expression and activity of ACC synthase and ACC oxidase increase during ripening, resulting in enhanced ethylene production. Ethylene subsequently activates downstream signalling pathways that regulate pigmentation, softening, aroma formation and other ripening-associated processes. However, tomato ripening is not simply an ethylene-dependent process. Ethylene interacts with other hormonal and transcriptional pathways, making the regulation of ripening a complex network rather than a single linear pathway.

### Master Transcription Factors Orchestrating Ripening

Several transcription factors act as important regulators of tomato fruit ripening. RIN (RIPENING INHIBITOR), NOR (NON-RIPENING), CNR (COLORLESS NON-RIPENING) and FUL1/FUL2 are among the best-known regulators associated with ripening progression. These transcription factors influence genes involved in ethylene production, cell-wall modification, carotenoid biosynthesis and other metabolic processes. Additional regulators such as AP2a, TAGL1 and NAC-domain proteins contribute to the formation of the ripening regulatory network. Rather than working independently, these transcription factors form interconnected regulatory circuits. Understanding their interactions provides opportunities to modify individual fruit traits without disrupting overall plant productivity.

### Hormonal Crosstalk During Fruit Development

Although ethylene receives considerable attention, several other hormones participate in tomato fruit development and ripening. Auxin has a major role in fruit set and early growth, while gibberellins influence cell expansion and developmental progression. Absciscic acid is increasingly recognized as an important regulator of ripening-related responses. The balance among these hormones changes throughout fruit development. Hormonal crosstalk can influence ethylene biosynthesis, transcription-factor activity and metabolic pathways. Consequently, manipulating one hormone pathway may produce effects on several developmental processes. A better understanding of hormonal interactions could support the development of strategies for improving fruit size, uniform ripening, firmness and nutritional quality.

## Molecular Control of Fruit Colour and Carotenoids

The colour transformation from green to red is one of the most visible characteristics of tomato ripening. During this transition, chlorophyll is degraded while carotenoids, particularly lycopene and  $\beta$ -carotene, accumulate in chromoplasts. Genes associated with carotenoid biosynthesis and chromoplast development become highly active during ripening. Phytoene synthase, phytoene desaturase,  $\zeta$ -carotene desaturase and lycopene  $\beta$ -cyclase are among the important components of the carotenoid pathway. Lycopene accumulation not only determines the characteristic red colour of ripe tomato but also contributes to its nutritional value. Molecular understanding of this pathway has therefore become important for breeding tomatoes with enhanced nutritional quality.

## Cell-Wall Modification and Fruit Softening

Fruit softening is another major molecular event during tomato ripening. The process involves modification of the cell wall and middle lamella, resulting in changes in fruit firmness and texture. Enzymes such as polygalacturonase, pectin methylesterase, expansins and pectate lyases contribute to cell-wall modification. Several transcriptional and hormonal signals regulate the expression of these enzymes. Excessive softening, however, reduces transportability and shelf life, creating an important challenge for commercial tomato production. Modern breeding aims to achieve a balance between desirable eating quality and sufficient firmness. Targeted modification of individual cell-wall genes offers opportunities to delay softening while maintaining other desirable ripening characteristics.

## Epigenetic Regulation and Ripening

Recent research has demonstrated that tomato ripening is also influenced by epigenetic mechanisms. DNA methylation, histone modifications and chromatin organization can affect the expression of ripening-related genes. Changes in DNA methylation patterns occur during fruit development and ripening, contributing to the activation or repression of specific genes. Epigenetic regulation may therefore help explain how developmental signals are translated into coordinated changes in gene expression. This area is particularly promising because epigenetic mechanisms may provide additional targets for improving fruit quality without necessarily changing the protein-coding sequence of important genes.

## Omics Technologies and Genome Editing

The development of transcriptomics, proteomics, metabolomics and epigenomics has transformed understanding of tomato fruit biology. These approaches allow researchers to examine thousands of genes, proteins and metabolites simultaneously and identify regulatory networks associated with important fruit traits. CRISPR/Cas genome editing has further expanded the possibilities for tomato improvement. Researchers can precisely modify genes associated with ripening, plant architecture, nutritional quality, stress tolerance and shelf life. Combining multi-omics information with genome editing can accelerate the identification and validation of candidate genes. This integrated strategy represents an important direction for next-generation tomato breeding.

## Environmental Regulation of Molecular Ripening

Tomato fruit development and ripening are strongly influenced by environmental conditions. Temperature, water availability, light intensity and nutrient supply can alter hormone metabolism, gene expression and fruit metabolite accumulation. High temperatures, for example, can interfere with normal pigmentation and reduce lycopene accumulation. Water stress may influence fruit growth and biochemical composition, while changing temperatures can affect the timing and uniformity of ripening. Understanding the interaction between genotype, environment and molecular regulation is therefore essential for developing tomatoes capable of maintaining fruit quality under changing climatic conditions.

## Future Perspectives for Precision Tomato Improvement

Future tomato improvement will increasingly integrate molecular genetics, high-throughput phenotyping, artificial intelligence and precision breeding. Identification of regulatory genes and their interactions can allow breeders to target specific traits such as delayed softening, enhanced nutritional quality, uniform ripening and climate resilience. Gene editing provides an opportunity to make precise modifications while retaining desirable characteristics of elite cultivars. However, edited lines must be evaluated carefully for agronomic performance, fruit quality, stability and regulatory requirements. The combination of conventional breeding with genomic selection, multi-omics and genome editing could shorten breeding cycles and facilitate development of tomato cultivars suited to diverse production environments.

## Conclusion

Tomato fruit development and ripening are controlled by an intricate molecular network involving hormones, transcription factors, metabolic pathways and epigenetic mechanisms. Ethylene acts as a central regulator, but its effects are integrated with auxin, gibberellins, abscisic acid and other signalling pathways. Recent advances in genomics, transcriptomics, metabolomics and genome editing have substantially improved our understanding of these processes. Future research should focus on translating molecular discoveries into practical breeding strategies for improving fruit quality, nutritional value, shelf life and environmental adaptability. An integrated approach combining molecular biology, omics technologies, precision breeding and advanced phenotyping will be crucial for developing the next generation of high-quality and climate-resilient tomato cultivars.

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