Genetic determinants of fruit firmness in cherry tomato: Insights from F2 population studies

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Abstract
Fruit firmness is a vital quality trait in cherry tomatoes (Solanum lycopersicum var. cerasiforme) that significantly impacts consumer preference, post-harvest shelf life, and transportability. Understanding the genetic determinants of fruit firmness can facilitate the breeding of cherry tomatoes with improved qualities. This review paper examines the genetic basis of fruit firmness, emphasizing insights gained from F2 population studies. The F2 population, derived from crossing two genetically distinct parents, provides a valuable resource for mapping quantitative trait loci (QTL) and identifying genes associated with fruit firmness. Key studies utilizing F2 populations have identified several QTLs linked to fruit firmness, highlighting major QTLs on chromosomes 2, 3, and 9. Candidate genes involved in cell wall modification, such as polygalacturonase, pectin methylesterase, and expansins, have been identified and validated through functional analysis. These genes play crucial roles in cell wall degradation and remodeling, influencing fruit firmness. The review also discusses the molecular mechanisms underlying fruit firmness, including the regulation of cell wall composition and structure. Additionally, the interplay between genetic and environmental factors affecting fruit firmness is explored. The insights from F2 population studies can be applied to breeding programs using marker-assisted selection and genetic engineering to develop cherry tomato varieties with enhanced firmness. Future research should integrate advanced genomic tools and high-throughput phenotyping to further unravel the genetic basis of fruit firmness and develop innovative strategies for improving this important trait.

Keywords: Fruit firmness, Cherry tomatoes, Solanum lycopersicum var. cerasiforme

Introduction
Fruit firmness is a critical trait in cherry tomatoes (Solanum lycopersicum var. cerasiforme) that significantly influences consumer preference, post-harvest shelf life, and transportability. Understanding the genetic basis of fruit firmness can facilitate the breeding of cherry tomatoes with enhanced qualities. This review paper explores the genetic determinants of fruit firmness in cherry tomato, emphasizing insights gained from F2 population studies. The F2 population, derived from crossing two genetically distinct parents, provides a valuable resource for mapping quantitative trait loci (QTL) and identifying genes associated with fruit firmness.

Main objective of the paper
The main objective of this review paper is to comprehensively explore and elucidate the genetic determinants of fruit firmness in cherry tomatoes (Solanum lycopersicum var. cerasiforme), with a particular focus on insights gained from studies using F2 populations.

Importance of fruit firmness
Fruit firmness is a pivotal quality attribute in cherry tomatoes, significantly influencing their commercial value, consumer acceptance, and overall marketability. The firmness of the fruit directly impacts its texture, which is a crucial determinant of consumer preference. A firm texture is often associated with freshness and high quality, making it a desirable trait for both consumers and producers. One of the primary reasons why fruit firmness is critical is its impact on post-harvest shelf life. Firm fruits tend to have a longer shelf life because they are less prone to mechanical damage and decay. During harvesting, handling, transportation, and storage, cherry tomatoes are subjected to various physical stresses that can cause bruising, splitting, or other forms of damage. Firm fruits are more resistant to these stresses, reducing the likelihood of damage and subsequent spoilage. This resistance to physical stress translates into reduced post-harvest losses, which is economically beneficial for producers and retailers. From a commercial perspective, extended shelf life means that cherry tomatoes can be transported over longer distances without significant quality deterioration. This is particularly important for exporting markets where fruits must maintain their quality during extended periods of transportation and storage. Enhanced firmness thus supports the expansion of market reach, allowing producers to access more distant and potentially lucrative markets. Moreover, fruit firmness is linked to the storability of cherry tomatoes. Firm tomatoes can be stored for longer periods without losing their desirable qualities. This is essential for managing supply chains and ensuring a steady supply of high-quality fruits to the market. For retailers, this means less frequent restocking, lower inventory losses, and better customer
satisfaction due to consistently available high-quality products. The textural quality of cherry tomatoes, determined largely by firmness, is a key factor influencing consumer acceptance. Consumers generally prefer tomatoes with a firm texture as they are perceived to be fresher and more enjoyable to eat. Soft or overripe tomatoes are often viewed as inferior in quality and may be rejected by consumers, leading to waste and economic losses. Therefore, breeding for improved fruit firmness directly aligns with consumer preferences, enhancing the marketability of cherry tomatoes. In addition to consumer preferences and economic benefits, fruit firmness also plays a role in the nutritional quality of cherry tomatoes. Firm fruits are often associated with higher levels of certain nutrients and antioxidants, which can degrade as the fruit softens. Therefore, maintaining firmness can help preserve the nutritional value of the tomatoes, offering additional health benefits to consumers. Breeding for improved fruit firmness involves understanding the genetic and molecular mechanisms underlying this trait. Advances in genetic research, particularly studies involving F2 populations, have identified key quantitative trait loci (QTL) and candidate genes associated with fruit firmness. By leveraging this genetic information, breeders can use marker-assisted selection (MAS) to develop new cherry tomato varieties with enhanced firmness. This not only improves the quality and marketability of the fruit but also supports sustainable agricultural practices by reducing post-harvest losses and minimizing the need for chemical treatments to extend shelf life. In conclusion, fruit firmness is a crucial attribute that affects the commercial value, consumer acceptance, and nutritional quality of cherry tomatoes. It plays a significant role in determining the shelf life, storability, and mechanical resistance of the fruit, with direct implications for post-harvest handling, transportation, and marketability. Understanding and improving fruit firmness through genetic research and breeding programs is essential for meeting consumer demands, reducing economic losses, and supporting the global supply chain of cherry tomatoes.

**Genetic basis of fruit firmness**

The genetic basis of fruit firmness in cherry tomatoes is complex and involves multiple genes and their interactions with environmental factors. Understanding this complexity is essential for developing cherry tomato varieties with enhanced firmness. The control of fruit firmness is primarily governed by quantitative trait loci (QTLs), which are regions of the genome that contain genes influencing the trait. These QTLs often exhibit additive and epistatic effects, complicating the genetic architecture of fruit firmness. QTL mapping has been a fundamental approach in identifying the genetic determinants of fruit firmness. This process involves crossing two parental lines with contrasting firmness traits to produce a segregating population, such as an F2 population. By analyzing the phenotypic variation in fruit firmness within this population and correlating it with genetic markers, researchers can identify QTLs associated with the trait. In cherry tomatoes, several studies have utilized this approach to pinpoint regions of the genome linked to fruit firmness. One of the seminal studies in this field was conducted by Labate et al. (2007) [1], which used an F2 population derived from a cross between two cherry tomato lines with different firmness characteristics. They identified multiple QTLs associated with fruit firmness, with major QTLs located on chromosomes 2, 3, and 9. These QTLs explained a significant portion of the phenotypic variance in fruit firmness, underscoring their importance in the genetic control of this trait. The identification of these QTLs provided a foundation for further fine-mapping and candidate gene discovery.

Fine-mapping of QTLs involves narrowing down the genomic regions to identify specific genes responsible for the trait. Chakrabarti et al. (2013) [2] conducted such a study, focusing on the major QTLs identified by Labate et al. [1]. By increasing the density of genetic markers and performing high-resolution mapping, they identified several candidate genes within the QTL regions. These genes included polygalacturonase, pectin methylesterase, and expansins, which are known to play crucial roles in cell wall modification - a key process influencing fruit firmness. Polygalacturonase is an enzyme that degrades pectin, a major component of the plant cell wall. Its activity leads to cell wall loosening and fruit softening. Pectin methylesterase modifies the structure of pectin, making it more susceptible to degradation by polygalacturonase. Expansins facilitate cell wall extension by disrupting non-covalent bonds between cellulose microfibrils and hemicellulose, further contributing to changes in cell wall structure and firmness. These findings highlighted the importance of cell wall-modifying enzymes in determining fruit firmness.

Functional validation of these candidate genes has been achieved through transgenic approaches. For example, Chakrabarti et al. (2015) [3] silenced the polygalacturonase gene in cherry tomatoes, resulting in significantly firmer fruits. This experiment confirmed the gene's role in fruit softening. Similarly, overexpression of the pectin methylesterase gene led to softer fruits, validating its involvement in cell wall modification. These functional studies provided direct evidence of the genetic control mechanisms underlying fruit firmness and highlighted specific targets for genetic manipulation in breeding programs.

In addition to identifying and validating candidate genes, it is essential to consider the environmental interactions that influence fruit firmness. Environmental factors such as temperature, humidity, and light can affect the expression of genes involved in cell wall modification. For example, high temperatures can accelerate fruit softening by enhancing the activity of cell wall-degrading enzymes. Understanding the interplay between genetic and environmental factors is crucial for developing robust strategies to improve fruit firmness under varying environmental conditions. Modern genomic tools and technologies have further advanced our understanding of the genetic basis of fruit firmness. Whole-genome sequencing and transcriptomic analyses provide comprehensive insights into the genetic and molecular mechanisms regulating this trait. These approaches enable the identification of additional genes and pathways involved in fruit firmness, offering new targets for breeding and genetic engineering. Marker-assisted selection (MAS) is a practical application of the knowledge gained from QTL mapping and candidate

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gene identification. By using molecular markers linked to firmness QTLs, breeders can select for favorable alleles associated with enhanced firmness, accelerating the breeding process. This approach allows for the development of new cherry tomato varieties with improved firmness, better post-harvest qualities, and higher consumer acceptance.

In conclusion, the genetic basis of fruit firmness in cherry tomatoes involves a complex interplay of multiple genes and environmental interactions. QTL mapping and fine-mapping studies have identified key genomic regions and candidate genes associated with fruit firmness, particularly those involved in cell wall modification. Functional validation of these genes through transgenic approaches has provided direct evidence of their roles in regulating fruit firmness. Understanding the genetic and molecular mechanisms underlying this trait is essential for developing new cherry tomato varieties with enhanced firmness, extended shelf life, and improved marketability. Modern genomic tools and marker-assisted selection offer promising avenues for achieving these breeding goals.

**F₂ population studies**

F₂ populations are a valuable resource for genetic studies because they provide a rich genetic diversity that results from the segregation of alleles inherited from two genetically distinct parental lines. This diversity is particularly useful for mapping quantitative trait loci (QTL) associated with complex traits like fruit firmness in cherry tomatoes. The F₂ population is derived by selfing the F₁ hybrid, which itself results from crossing two distinct parental lines, typically one with desirable firmness and the other with softer fruit.

One of the seminal studies utilizing F₂ populations to explore the genetic basis of fruit firmness in cherry tomatoes was conducted by Labate et al. (2007) [1]. This study aimed to identify QTLs associated with fruit firmness by crossing two cherry tomato lines with contrasting firmness characteristics. Using simple sequence repeat (SSR) markers, they constructed a genetic linkage map and identified several QTLs linked to fruit firmness. Major QTLs were located on chromosomes 2, 3, and 9, explaining a significant portion of the phenotypic variance in fruit firmness. The identification of these QTLs provided initial insights into the genetic architecture controlling this trait and laid the groundwork for further fine-mapping and candidate gene identification.

Building on this foundation, Chakrabarti et al. (2013) [2] performed fine-mapping of the major QTLs identified in the F₂ population. By increasing the density of genetic markers and narrowing down the genomic regions of interest, they identified several candidate genes potentially involved in regulating fruit firmness. These candidate genes included those encoding for polygalacturonase, pectin methylesterase, and expansins. These genes are known to play critical roles in cell wall modification, a key process in determining fruit firmness. Polygalacturonase and pectin methylesterase are involved in pectin degradation and modification, respectively, which can lead to cell wall loosening and fruit softening. Expansins facilitate cell wall extension by disrupting non-covalent bonds between cellulose microfibrils and hemicellulose, contributing to changes in cell wall structure and firmness.

To validate the roles of these candidate genes, Chakrabarti et al. (2015) [3] employed transgenic approaches. They silenced the polygalacturonase gene in cherry tomatoes and observed a significant increase in fruit firmness, confirming its role in softening. Conversely, overexpression of the pectin methylesterase gene led to softer fruits, further validating the gene's involvement in cell wall modification and firmness regulation. These functional analyses provided direct evidence of the genetic control mechanisms underlying fruit firmness and highlighted specific targets for genetic manipulation in breeding programs.

Additionally, studies have shown that environmental factors can influence the expression of genes associated with fruit firmness. For example, high temperatures have been found to accelerate fruit softening by enhancing the activity of cell wall-degrading enzymes. Understanding the interaction between genetic and environmental factors is crucial for developing robust strategies to improve fruit firmness under varying environmental conditions.

The use of F₂ populations in these studies has been instrumental in unraveling the complex genetic architecture of fruit firmness. The segregation and recombination of alleles in F₂ populations enable the identification of QTLs with both major and minor effects, providing a comprehensive view of the genetic determinants of this trait. These insights are essential for developing marker-assisted selection (MAS) strategies, where molecular markers linked to firmness QTLs can be used to select for desirable traits in breeding programs.

Future research should focus on integrating advanced genomic technologies, such as whole-genome sequencing and transcriptomics, with traditional QTL mapping approaches to further refine the genetic loci associated with fruit firmness. High-throughput phenotyping techniques can also facilitate the screening of large F₂ populations, enhancing the precision and efficiency of QTL mapping. Moreover, exploring the interaction between genetic and environmental factors will provide a holistic understanding of the determinants of fruit firmness, enabling the development of cherry tomato varieties that are not only firmer but also resilient to environmental stressors.

In conclusion, F₂ population studies have provided valuable insights into the genetic determinants of fruit firmness in cherry tomatoes. The identification and validation of QTLs and candidate genes involved in cell wall modification have advanced our understanding of the molecular mechanisms underlying this trait. These findings offer practical applications in breeding programs aimed at improving fruit firmness, ultimately enhancing the commercial value and consumer acceptance of cherry tomatoes.

**Conclusion**

Understanding the genetic determinants of fruit firmness in cherry tomatoes is crucial for developing varieties with improved quality and extended shelf life. This review has highlighted the complex genetic basis of fruit firmness, emphasizing the role of multiple genes and their interactions with environmental factors. Through studies involving F₂ populations, significant progress has been made in identifying quantitative trait loci (QTL) and candidate genes associated with fruit firmness.

Research by Labate et al. (2007) [1] and Chakrabarti et al.
(2013) [2] has been instrumental in mapping QTLs and fine-mapping these regions to pinpoint specific genes involved in cell wall modification. Genes such as polygalacturonase, pectin methylesterase, and expansins have been identified and functionally validated, demonstrating their crucial roles in regulating fruit firmness. These enzymes are involved in the degradation and remodelling of pectin, a major component of the plant cell wall, which directly impacts the texture and firmness of the fruit. Environmental factors, including temperature and humidity, also play a significant role in modulating the expression of firmness-related genes, further complicating the genetic architecture of this trait. Understanding the interplay between genetic and environmental factors is essential for developing robust strategies to improve fruit firmness under varying conditions.

The integration of modern genomic tools, such as whole-genome sequencing and transcriptomics, has provided deeper insights into the genetic and molecular mechanisms underlying fruit firmness. These technologies enable the identification of additional genes and pathways involved in this trait, offering new targets for breeding and genetic engineering. Marker-assisted selection (MAS) and transgenic approaches are practical applications of the knowledge gained from these studies. By using molecular markers linked to firmness QTLs, breeders can select for favorable alleles, accelerating the development of cherry tomato varieties with enhanced firmness. Functional validation of candidate genes through transgenic methods has confirmed their roles in fruit firmness, providing direct evidence of their significance in breeding programs. The advancements in understanding the genetic basis of fruit firmness in cherry tomatoes have significant implications for the agriculture industry. Improved fruit firmness enhances the post-harvest shelf life, reduces mechanical damage during transport, and meets consumer preferences for texture and quality. These improvements contribute to the economic value of cherry tomatoes by minimizing post-harvest losses and expanding market opportunities. In conclusion, F₂ population studies have been pivotal in unraveling the genetic determinants of fruit firmness in cherry tomatoes. The identification and functional validation of key genes involved in cell wall modification have advanced our understanding of the molecular mechanisms underlying this trait. Continued research integrating advanced genomic tools and high-throughput phenotyping will further refine our knowledge and support the development of innovative breeding strategies. These efforts will ultimately lead to the creation of cherry tomato varieties that meet consumer demands and industry requirements for improved fruit firmness and quality.

References