



Review

Gene-Based Developments in Improving Quality of Tomato: Focus on Firmness, Shelf Life, and Pre- and Post-Harvest Stress Adaptations

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Abstract: Tomato (*Solanum lycopersicum*) is a widely consumed vegetable crop with significant economic and nutritional importance. This review paper discusses the recent advancements in gene-based approaches to enhance the quality of tomatoes, particularly focusing on firmness, shelf life, and adaptations to pre- and post-harvest stresses. Utilizing genetic engineering techniques, such as Clustered Regularly Interspaced Short Palindromic Repeats/CRISPR-associated proteins 9 (CRISPR/Cas9) and Transcription Activator-like Effector Nucleases (TALENs), researchers have made remarkable progress in developing tomatoes with improved traits that address key challenges faced during cultivation, storage, and transportation. We further highlighted the potential of genetic modifications in enhancing tomato firmness, thereby reducing post-harvest losses and improving consumer satisfaction. Furthermore, strategies to extend tomato shelf life through genetic interventions are discussed, emphasizing the importance of maintaining quality and freshness for sustainable food supply chains. Furthermore, the review delves into the ways in which gene-based adaptations can bolster tomatoes against environmental stresses, pests, and diseases, thereby enhancing crop resilience and ensuring stable yields. Emphasizing these crucial facets, this review highlights the essential contribution of genetic advancements in transforming tomato production, elevating quality standards, and promoting the sustainability of tomato cultivation practices.

Keywords: tomato; genetic engineering; CRISPR/Cas9; firmness; shelf life; pre- and post-harvest stress



Citation: Nie, H.; Yang, X.; Zheng, S.; Hou, L. Gene-Based Developments in Improving Quality of Tomato: Focus on Firmness, Shelf Life, and Pre- and Post-Harvest Stress Adaptations. *Horticulturae* **2024**, *10*, 641. <https://doi.org/10.3390/horticulturae10060641>

Academic Editors: Xuewu Duan, Xiaochun Ding and Guoxiang Jiang

Received: 12 April 2024

Revised: 27 May 2024

Accepted: 12 June 2024

Published: 14 June 2024



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1. Introduction

Tomatoes, scientifically known as *Solanum lycopersicum*, hold significant importance as a vegetable crop globally, with a substantial production value exceeding USD 55 billion [1]. Common issues like squashed and softened fruits incur significant costs in transportation and storage. To address this, the ripening inhibitor (RIN) mutation has been utilized in tomato hybrids to yield firm fruits with extended shelf life and better transportability. However, these genetically modified fruits often lack taste and color development speed [2]. Therefore, the focus of modern tomato breeding lies in enhancing fruit firmness without compromising other desirable qualities. Fruit firmness is a multifaceted trait influenced by various physical properties such as cell wall structure, cellular turgor, and cuticle characteristics. The process of fruit softening involves the breakdown and degradation of the cell wall, driven by the upregulation of genes encoding enzymes responsible for cell wall degradation [3,4]. The thickness of the cuticle, a protective layer on the fruit surface, increases gradually to maintain structural integrity during fruit growth. Changes in cuticle composition and structure play a vital role in determining fruit firmness. The cuticle is primarily composed of cutin and cuticular wax, and decreasing their levels results in a thinner cuticle, impacting fruit water retention, shelf life, and firmness [5,6]. Understanding the intricate mechanisms governing fruit firmness is crucial for effectively manipulating this trait in breeding programs.

Tomato fruit firmness is primarily influenced by various factors, with alterations in pectin composition in the primary cell walls being the most significant determinant [7]. Throughout the ripening process, pectin undergoes restructuring, breakdown, and dissolution via a sequence of enzymatic reactions, leading to diminished cell wall integrity and subsequent softening of the tissue. While specific pectin-modifying enzymes associated with fruit softening have been extensively studied over the years, further research is necessary to explore their collaborative actions during fruit development and post-harvest storage [8,9]. Therefore, future investigations into the interplay between key cell wall-modifying enzymes and their impact on pectin composition could enhance our comprehension of fruit-softening mechanisms, enabling the development of effective breeding and management strategies to prolong tomato fruit shelf life and reduce decay.

Shelf life, another critical quality attribute of tomatoes, is influenced by multiple factors, including fruit-ripening dynamics, susceptibility to pathogens, and physiological disorders. Post-harvest losses due to premature softening, decay, and senescence pose significant challenges to the tomato industry and necessitate sustainable solutions to extend shelf life and minimize food waste [10]. Gene-based interventions targeting key ripening regulators, such as ethylene biosynthesis and perception genes, have shown promising results in delaying fruit senescence and enhancing shelf life characteristics [11]. Advances in gene-editing technologies, such as Clustered Regularly Interspaced Short Palindromic Repeats/CRISPR-associated proteins 9 (CRISPR/Cas9) and TALENs, have revolutionized the field of plant biotechnology by enabling precise and heritable modifications of the tomato genome [12]. These tools offer unprecedented opportunities for targeted gene editing to improve tomato quality traits, including firmness and shelf life, with a high degree of precision and efficiency [13]. By harnessing the potential of gene-editing technologies, researchers can overcome the limitations of traditional breeding methods and accelerate the development of elite tomato cultivars with enhanced quality attributes and market competitiveness.

This review will explore the current state of gene-based developments in improving tomato quality, with a particular emphasis on firmness, shelf life, and the application of cutting-edge gene-editing technologies. By highlighting the recent research findings, technological innovations, and prospects, this review aims to contribute to the ongoing dialogue surrounding genetic enhancement strategies for sustainable and resilient tomato production systems. Ultimately, the integration of gene-based approaches in tomato breeding programs holds great promise for meeting the evolving demands of the global tomato industry and ensuring the availability of high-quality tomatoes for consumers worldwide.

2. Enhancement of Firmness

When considering the post-harvest stability of horticulture crops, the attribute of texture holds significant importance. Multiple enzymes including polygalacturonase (PG), pectin methylesterase (PME), endo-b-(1,4)-glucanase (EG), β -galactosidase (β -gal), and expansion (EXP), as well as N-glycoprotein-modifying enzymes like α -mannosidase (α -Man) and β -D-N-acetylhexosaminidase (β -Hex), play crucial roles in determining the degree of firmness and softening processes in various plants [14,15]. Several studies have highlighted the suppression of key gene expressions in strawberries and tomatoes. For example, while the suppression of the *PG* gene in tomatoes did not significantly impact fruit softening, it did influence the firmness of strawberries with higher Brix levels to some extent [13,16]. On the other hand, the silencing of the pectate lyase (*PL*) gene, a cell wall-related protein, through approaches like antisense RNA (asRNA) effectively enhanced fruit firmness without altering its physical (size and color) and biochemical (total soluble solids, metabolites, etc.) characteristics [17]. This manipulation ultimately affected the sensory attributes of tomatoes. Furthermore, the application of CRISPR/Cas9 editing on the *PL* gene led to mutants that exhibited improved fruit firmness while preserving the fruit's color, aroma, and flavor in tomatoes [18]. These findings underscore the intricate molecular

mechanisms underlying texture maintenance in horticulture crops and the potential for targeted gene modifications to enhance post-harvest quality.

3. Improving Tomato Quality

The significance of tomato fruit in promoting human health is underscored by its widespread high consumption per person globally. Consequently, there is a growing emphasis on identifying tomato varieties that possess elevated levels of primary and secondary metabolites in their fruits [19]. Traditionally, agricultural practices are aimed at increasing fruit yield, but in recent years, a surge in interest in enhancing fruit quality has been observed, particularly by boosting the quantity and composition of primary and secondary metabolites [20]. A relatively new approach improves fruit quality by subjecting crop plants to controlled environmental stress conditions. This method suggests that abiotic stress could enhance the quality of tomato fruit by prompting higher levels of sugars, amino acids, and organic acids, thereby positively influencing its flavor and water content [21]. Moreover, plants grown under stress may elevate their levels of antioxidants from both non-enzymatic and enzymatic systems [22]. The concept that environmental stress can impact the content and composition of metabolites in tomato fruit is grounded in the knowledge that many of these compounds are well-known antioxidants. The environmental stress triggers secondary oxidative stress that plants need to combat, highlighting the various environmental stressors that crops face in the Mediterranean region, such as drought, heat, salinity, and excessive light exposure, along with the alterations in plant metabolism in response to these abiotic stresses [23,24]. From an agricultural perspective, the goal is to enhance fruit quality without compromising production, a feat that may be achievable by applying moderate stress levels. Among the proposed strategies to boost tomato fruit quality, the controlled application of salt stress in greenhouses has emerged as an innovative approach [20,25]. Therefore, introducing controlled abiotic stress during tomato plant cultivation, without jeopardizing their yield, could be a promising tactic to significantly enhance the levels of various metabolites in their fruits, particularly those with antioxidant properties and recognized as beneficial for human health, such as ascorbate, carotenoids, tocopherols, flavonoids, and other phenolic compounds [26].

4. Upgrading of Nutritional and Flavor Values

Horticultural crops are rich in essential nutrients such as vitamins, minerals, dietary fibers, and antioxidants, all of which contribute to their flavor and quality [27]. Various factors, including genetic makeup, growing conditions, harvesting methods, and post-harvest practices, play a significant role in determining the taste, aroma, and nutritional value of these crops [28]. If not handled properly, these perishable crops can lose their desirable qualities and become inedible due to factors like off flavors that develop from the time of harvesting to consumption. Plant breeding stands at a critical juncture where the fusion of classical breeding methods with cutting-edge biotechnological tools like CRISPR/Cas9 heralds a new era of crop improvement. By contextualizing the intricate interplay between traditional breeding approaches and modern genetic manipulation techniques, researchers can harness the full potential of these tools to address pressing agricultural challenges. This paradigm shift not only underscores the importance of maintaining genetic diversity but also emphasizes the need to navigate regulatory landscapes and societal acceptance to ensure the sustainable advancement of agriculture [29]. Moreover, as we delve deeper into the realm of biotechnological innovation, it is imperative to scrutinize the food security implications of these advancements. Striking a delicate balance between technological progress and equitable access to resources, researchers must navigate geopolitical complexities and ethical considerations to safeguard global food security [30]. The real-world applications of CRISPR/Cas9 technology in horticultural crop improvement offer tangible examples of how these tools can revolutionize agricultural practices. From enhancing disease resistance in tomatoes to improving crop yields, these success stories underscore the transformative potential of precision genome editing in shaping the future of sustainable agriculture.

Therefore, the strategic integration of advanced methodologies like CRISPR/Cas9 genome editing with traditional breeding approaches is essential to cultivate horticultural crops that exhibit peak flavor profiles and nutritional richness throughout the entire production and consumption.

However, navigating the realm of agricultural innovation presents a myriad of challenges and costs across various fronts, from genetic composition to post-harvest procedures. The intricate process of manipulating genetic makeup, such as employing genome-editing techniques like CRISPR/Cas9, demands substantial investments in research, technology, and regulatory compliance [13]. Ensuring the compatibility of altered genetic traits with diverse cultivation environments requires meticulous planning and resource allocation to optimize crop performance while mitigating potential environmental risks. Additionally, implementing advanced harvesting methods and post-harvest practices to preserve the quality and freshness of produce incurs expenses related to equipment, training, and infrastructure. Balancing these expenses against the potential benefits of enhanced crop resilience, yield stability, and nutritional quality poses a significant financial challenge for stakeholders along the agricultural value chain [31]. Despite these hurdles, strategic investments and collaborative efforts are essential to overcome these challenges and unlock the full potential of gene-based advancements in agriculture. Recent studies have explored the use of gene-editing technologies like ZFN and CRISPR/Cas9 to modify specific genes in crops like tomatoes and potatoes to enhance their metabolic contents, such as organic acids, sugars, pigments, and antioxidants [32,33]. For instance, disrupting the *NF-Y* transcription factor gene in tomatoes resulted in mutants with altered metabolic profiles compared to wild types, highlighting the role of this gene in regulating key biosynthetic pathways [34]. Similarly, targeting genes involved in starch production in potato cultivars led to mutations affecting starch composition and quality, demonstrating the potential of gene editing to improve crop characteristics [35]. Furthermore, CRISPR/Cas9 editing has been successfully applied to modify genes responsible for nutrient accumulation in crops like grapes, apples, and tomatoes, resulting in increased levels of beneficial compounds like vitamin C and γ -aminobutyric acid (GABA) [36,37]. These advancements in gene-editing technology offer promising opportunities to enhance the nutritional quality and flavor of horticultural crops, paving the way for the development of improved crop varieties with enhanced health benefits and sensory attributes. Following the application of advanced biotechnological tools in plant improvement, it is imperative to conduct thorough field evaluations and implement meticulous selection techniques to complement and validate the outcomes of these technologies. While tools like CRISPR/Cas9 offer precision and speed in genetic manipulation, the dynamic and multifaceted environments of field settings provide a crucial real-world testing ground for assessing plant performance under varying conditions [38]. Field evaluations enable researchers to observe how genetically modified plants interact with their surroundings, respond to biotic and abiotic stresses, and express desired traits in complex ecosystems. Moreover, the judicious application of selection techniques after biotechnological interventions allows for the identification and propagation of superior genotypes that exhibit optimal performance characteristics. By integrating field evaluations and selection methodologies into the post-biotechnological workflow, researchers can ensure the practical applicability, resilience, and sustainability of genetically improved plant varieties, ultimately advancing the development of robust and high-performing crops for agricultural systems worldwide [39]. Figure 1 shows the use of these genetic technologies with its outcomes in tomato quality and other characteristics.

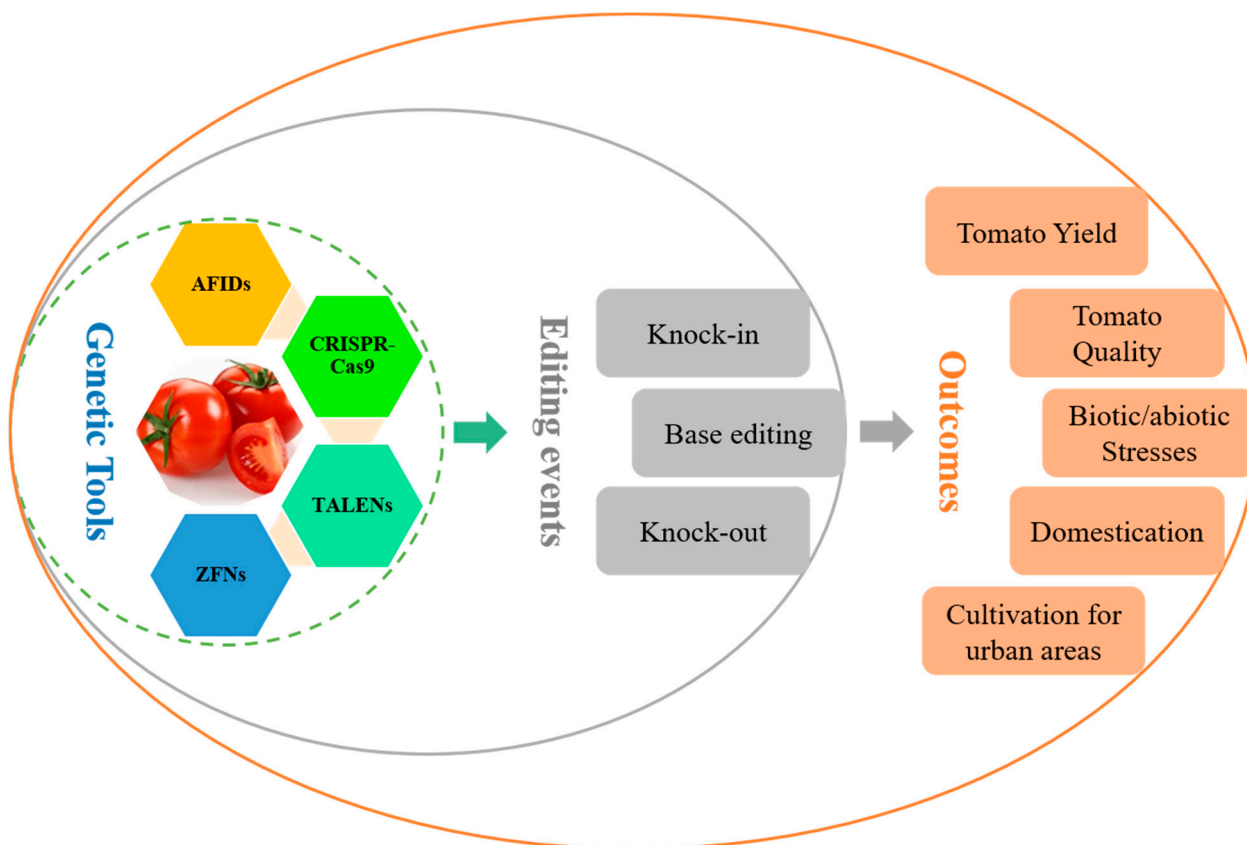


Figure 1. The recent developments in tomatoes as a result of genetic engineering technology. AFIDs: APOBEC-Cas9 fusion-induced deletion systems; CRISPR/Cas9: Clustered Regularly Interspaced Short Palindromic Repeats-associated Protein9; TALENs: Transcription Activator-like Effector Nucleases; and ZFNs: Zinc Finger Nucleases.

5. Developments in Fruit Ripening

During the ripening process of fleshy fruits, a series of physiological, biochemical, and structural changes occur as the fruit matures, ultimately attracting more seed spreaders. Once the fruit reaches its optimal edible stage, it begins to deteriorate gradually, leading to a reduction in fruit quality [40,41]. As a result, the regulation of fruit ripening has become a key focus for many scientists.

The ripening inhibitor gene (*RIN*), which belongs to the *MADS-box* gene family, plays a crucial role in the ripening of tomato fruits [42]. Mutations in the *RIN* gene have been found to inhibit fruit ripening. *RIN* is considered the primary regulatory gene in tomato fruit maturation, responsible for activating various physiological processes associated with ripening, such as color, texture, and flavor development [43]. Using the CRISPR/Cas9 system, researchers have been able to knock out the *RIN* gene in tomatoes, resulting in the analysis of *RIN* mutants. The *RIN* knockout mutation does not impact the initiation of ripening but does lead to a moderate red coloration, indicating that the *RIN* gene is not essential for ripening initiation [44].

The deletion of a DNA fragment between the *RIN* gene and the adjacent gene *MACRO-CALYX* (MC) in the *RIN* mutant can result in ripening failure. This deletion leads to the fusion of transcription factors *MADS-RIN* and *MADS-MC*, forming a fusion protein known as *RIN-MC*. The *RIN-MC* fusion protein encodes a novel transcription factor that regulates downstream gene expression, inhibiting fruit ripening and exerting a negative regulatory effect [45–47].

Researchers have utilized the *RIN* mutation in tomato breeding to develop improved hybrids, although this can negatively impact the flavor of the tomatoes. *RIN*-deficient fruits obtained through CRISPR/Cas9 technology have been shown to reduce ethylene

production, affecting the synthesis of volatile compounds and carotenoids [43,48]. The reduced ethylene production in RIN-deficient fruits is due to the inability to induce ethylene production in the autocatalytic system-2. These fruits also lack certain volatiles, carotenoids, and related transcripts. Additionally, it has been suggested that the fruit-ripening process involves the participation of ERFs, RIN, and ethylene. Ethylene plays a role in initiating the maturation of green fruit and influencing the expression of RIN and other factors, completing the ripening process of fruits [49,50].

6. Progress in Improving the Bioactive Components

Numerous studies have focused on enhancing the accumulation of bioactive substances in fresh fruits, such as lycopene, carotenoid, anthocyanin, and gamma-aminobutyric acid (GABA), which have anti-inflammatory, anti-cancer, anti-oxidative, and other beneficial physiological activities [51]. Carotenoids, mainly C40 terpenoids, play a protective role against ROS-mediated disorders and eye-related issues, affecting plant growth and development while improving the oxidative stability of poultry products [52]. Lycopene, a red pigment abundant in ripening fruits, has been linked to reducing the risk of various tumors and cardiovascular diseases [53]. Studies have shown that gene-editing techniques like CRISPR/Cas9 can be used to manipulate genes involved in lycopene biosynthesis, resulting in increased lycopene content in fruits [18]. Similarly, gene editing has been employed to target essential enzymes like lycopene desaturase (PDS) in bananas, resulting in mutants with altered carotenoid contents [54]. GABA, known for its neuro-suppressant effects, can be increased in fruits by manipulating genes involved in its biosynthesis pathway. Studies have shown that gene-editing techniques can enhance GABA accumulation in fruits, affecting fruit size and yield [55]. Furthermore, gene editing has been utilized to target genes involved in GABA metabolism, resulting in enhanced GABA content in tomatoes. These advancements in gene editing offer promising opportunities to manipulate fruit composition for improved health benefits [56,57].

7. Improving the Quality and Quantity

As a key trait in crop breeding, tomato yield is influenced by factors such as fruit-setting rate, flowering speed, and final fruit cell number and size, with genetic studies pinpointing specific yield-associated genes [58]. Through CRISPR/Cas9-induced mutations in genes like *CLV3*, compound inflorescence (*S*), and self-pruning (*SP*), researchers have observed increased floral organs or fruit size, resulting in enhanced tomato yield [59]. This highlights the potential of CRISPR/Cas9-driven mutagenesis of gene promoters as a precise method for plant breeding, especially in altering quantitative traits for crop enhancement. With consumers increasingly demanding higher fruit quality, genome editing has been leveraged to enhance tomato fruit quality [60]. Fruit quality encompasses various attributes like color, size, shape, nutrients, sweetness, acidity, aroma, and shelf life. While red tomatoes are standard, there is a market demand for tomatoes of different colors [61]. Pink tomatoes, particularly popular in Asia, have been successfully created by targeting the *MYB12* gene using CRISPR/Cas9, altering flavonoid biosynthesis in red tomatoes to produce pink varieties [62]. Similarly, gene editing has been employed to generate orange and yellow tomatoes by disrupting genes in the carotenoid biosynthesis pathway. Purple tomatoes rich in anthocyanins, like the “Sun Black” line, have also been developed to meet consumer preferences [37]. Moreover, genome editing has been instrumental in enhancing the nutritional content of tomatoes. Multiplex editing of genes related to carotenoid metabolism in tomatoes has led to a significant increase in lycopene content, demonstrating the potential for improving nutrient levels through genetic manipulation [59]. Similarly, modifications in genes associated with carotenoid accumulation have resulted in elevated levels of carotenoids, lycopene, and β -carotene in tomatoes. Furthermore, targeting genes involved in GABA metabolism has shown promising results, significantly increasing GABA content in tomato fruit. These advancements underscore the potential of genome editing to enhance plant nutrients by modulating synthesis and metabolic pathways effectively.

Table 1 shows the genetic editing in specific genes for improving the quality and yield of tomatoes.

Table 1. The important genes identified through genetic engineering tools used in improving the quality of tomatoes.

Gene	Phenotypic Property	Genetics Editing Tool	Reference
<i>PL</i>	Firmness	CRISPR/Cas9	[63]
<i>SIMAPK3</i>	Alleviate biotic/abiotic stress	CRISPR/Cas9	[64]
<i>L1L4</i>	Increase size and stress resistance	ZFN	[65]
<i>ALC</i>	Shelf life	CRISPR/Cas9	[66]
<i>RIN</i>	Fruit ripening	CRISPR/Cas9	[67]
<i>SBP-CNR</i> and <i>NAC-NOR</i>	Fruit ripening	CRISPR/Cas9	[68]
<i>SBE1</i> and <i>INV2</i>	Amylopectin, osmosis	CRISPR/Cas9	[69]
<i>StGBSS</i>	Amylase synthesis	CRISPR/Cas9	[70]
<i>SBE1</i> , <i>SBE2</i>	Starch regulator	CRISPR/Cas9	[71]
<i>CaMBD</i>	GABA regulator	CRISPR/Cas9	[72]
<i>MYB12</i>	Colorization	CRISPR/Cas9	[73]
<i>CLV3</i> , <i>S</i> or <i>SP</i>	Tomato yield	CRISPR/Cas9 (Cis-regulatory mutations)	[74]
<i>PSY1</i>	Colorization		[75]
<i>SLANT1</i>	Colorization	CRISPR/Cas9, (targeted insertion of the strong promoter)	[76]
<i>FW2.2</i> , <i>FAS</i> , <i>MULT</i> and <i>CycB</i>	Fruit size and number	CRISPR/Cas9	[77]
<i>SP</i> , <i>SP5G</i> and <i>SIER</i>	Firmness	CRISPR/Cas9	[78]
<i>ENO</i>	Fruit size	CRISPR/Cas9	[79]
<i>GABA-TP1</i> , <i>TP2</i> , <i>TP3</i> , <i>SSADH</i> , <i>CAT9</i>	GABA content	CRISPR/Cas9	[80]
<i>SLGAD2</i> , 3	GABA content	CRISPR/Cas9	[81]
<i>SGR1</i> , <i>LCY-E</i> , <i>LCY-B1</i> , <i>B2</i> , <i>Blc</i>	Lycopene synthesis	CRISPR/Cas9	[82]
<i>AP2a</i> , <i>FUL1</i> , <i>FUL2</i>	Fruit ripening	CRISPR/Cas9	[83]
<i>SLORRM4</i>	Fruit ripening	CRISPR/Cas9	[84]
<i>SIDML2</i>	Fruit ripening	CRISPR/Cas9	[85]
<i>SIAGL6</i>	Parthenocarpic fruit	CRISPR/Cas9	[86]
<i>PG2a</i> , <i>TBG4</i>	Fruit firmness	CRISPR/Cas9	[83]
<i>GGP1</i>	Ascorbic acid	CRISPR/Cas9	[87]
<i>ARF7</i>	Parthenocarpic fruit	CRISPR/Cas9	[88]
<i>ALMT9</i>	Regulate malate content	CRISPR/Cas9	[89]
<i>MAPK20</i>	Regulate sugar content	CRISPR/Cas9	[90]

8. Updates on Genetic Engineering Technology Used in the Development of Tomato

Genome-editing technology has been recognized as a rapid breeding method for crops, with ongoing studies focusing on its development and application across various crops. In the realm of tomato breeding, there has been significant research dedicated to exploring the potential of genome-editing technology. In this context, the utilization of CRISPR/Cas9 technology has been instrumental in creating a tomato variety enriched with high levels of γ -aminobutyric acid (GABA), a beneficial component for human health [91]. Notably, in 2021, Japan became the first country to introduce this engineered tomato to the market, marking a milestone as the world's inaugural instance of societal implementation of CRISPR-edited crops [72]. This overview outlines the current landscape of genome-editing research aimed at enhancing fruit quality, improving tolerance to environmental stresses, and fortifying resistance to pests and diseases as crucial breeding objectives in tomato cultivation. Furthermore, it delves into the challenges encountered and proposes potential solutions for establishing genome-editing technology as a swift breeding tool for tomatoes.

8.1. Prime Editing Technology

While genome editing has transformed basic research and precision breeding in plants, most existing systems lack the ability to achieve precise genome editing through targeted

substitutions, insertions, and deletions [56]. CRISPR/Cas9-mediated HDR has been a primary method for precise genome editing in plants, but challenges persist due to the low efficiency of HDR production and DNA template delivery in plants [92]. Prime editing, a groundbreaking advancement in precise genome editing initially developed in human cells, has swiftly been adopted in plant research by various global teams. The prime editing technique combines a modified Cas9 (H840A) enzyme with a reverse transcriptase enzyme called Moloney murine leukemia virus reverse transcriptase (M-MLV-RT) and an engineered guide RNA known as prime editing guide RNA (pegRNA). Peg RNA comprises a specific sight-targeting sgRNA, a reverse transcription (RT) template for desired edits, and a primer-binding site (PBS) for facilitating hybridization with the nicked DNA strand [93]. Prime editing is capable of generating all 12 types of base substitutions, surpassing the capabilities of DNA base editors, and can induce predefined multiple base insertions, deletions, and/or substitutions. Various prime editing technologies have been applied in multiple plant species, often involving the optimization of codons, promoters, or additional components like nuclear localization signals [94]. Notably, prime editing in plants has shown no off-target effects, although these systems may exhibit varying or relatively low editing efficiency in plants. Factors such as the length of PBS or the RT template in pegRNA and the positioning of the nicking sgRNA play a crucial role in the editing efficiency of prime editing systems in rice with increased pegRNA expression, leading to significantly higher prime editing efficiency in maize [95,96]. Overall, prime editing technology offers a promising avenue for advancing genetic improvements in tomatoes, leading to the development of new and improved varieties of tomatoes that benefit both farmers and consumers alike. By harnessing the precision and efficiency of this cutting-edge technology, the future of tomato breeding looks brighter than ever.

8.2. Mitochondria-Based Editing Technology (*mitoTALENs*)

Mitochondria-based editing technology, known as *mitoTALENs* (Transcription Activator-like Effector Nucleases), is a cutting-edge genetic engineering tool that allows precise modifications to be made to the mitochondrial DNA within cells. Mitochondria are organelles responsible for the production of energy in cells and have their separate genome, distinct from nuclear DNA [97]. *mitoTALENs* work by using a customizable DNA-binding domain derived from Transcription Activator-like Effectors (TALEs) to target specific sequences within the mitochondrial genome. This domain is fused to a nuclease enzyme that can then introduce double-strand breaks at the targeted location. The cell's natural DNA repair mechanisms are then utilized to either insert, delete, or replace specific sequences in the mtDNA, allowing for the precise editing of mitochondrial genes.

While the stable alteration of plant mitochondrial genomes remains a challenge, recent studies have achieved stable and heritable targeted modifications of mitochondrial genes in rice, rapeseed, and *Arabidopsis* by employing nuclear transformation and *mitoTALENs* [98]. These *mitoTALENs* consist of a TALEN nuclease coupled with a mitochondria localization signal. For instance, the mitochondrial gene *atp6-1*, responsible for encoding an ATP synthase subunit, also exists in the nuclear genome. Editing of *atp6-1* using *mitoTALENs* led to mutations solely in its mitochondrial counterpart, showcasing the specificity of *mitoTALEN*-mediated mitochondrial genome editing [99]. To enhance the efficiency of *mitoTALEN* technology in plants, researchers compared three different promoters (CaMV35S, Ubiquitin1, and RPS5A) and other types of TALENs such as compact and conventional TALENs. The RPS5A promoter and conventional TALENs were identified as the most effective combination [100]. Plant mitochondrial genomes contain around 60 genes along with abundant non-coding DNA. The use of *mitoTALENs* will shed further light on the role of mitochondrial genomes in plant cellular processes. Additionally, the successful engineering of plastid genomes has proven beneficial in enhancing various economic and agronomic traits in different plant species [99]. Therefore, there is great anticipation for the potential application of *mitoTALEN*-mediated mitochondrial genome editing in improving tomato quality.

8.3. Zinc Finger Nucleases (ZFN)

Zinc Finger Nucleases (ZFNs) are a type of genetic tool that has been used in tomato research to bring about precise changes in the DNA of the plant. ZFNs work by targeting specific DNA sequences and inducing double-strand breaks at those locations. These breaks can then be repaired by the plant's cellular repair mechanisms, leading to targeted genetic modifications. In the context of tomatoes, ZFNs have been utilized to enhance various desirable traits in the fruit [101,102]. For example, they have been employed to improve flavor profiles, increase nutritional value, extend shelf life, enhance resistance to pests and diseases, and optimize yield. By precisely editing the genetic code of tomatoes using ZFN technology, researchers and breeders have been able to create plants with improved characteristics that meet consumer preferences and agricultural needs [103]. Apart from other gene-editing systems like TALENs and CRISPR-Cas9, ZFN can also be utilized in tomato research. ZFNs were introduced into tomatoes using electroporation-based transient transformation. By electroporating a mix of germinating seeds and plasmid DNA containing ZFNs targeting the *LIL4* locus, researchers achieved over 65% mutagenesis efficiency. Mutation in the *LIL4* gene led to various developmental changes in tomatoes, including differences in leaf complexity, angle, and floral organ identity, as well as alterations in fruit characteristics like size, shape, and locule number [65]. This method of transient ZFN transformation via electroporation plays a significant role in improving tomato quality. By harnessing the power of this tool, scientists can expedite the development of tomato varieties with enhanced traits, ultimately benefiting both the agricultural industry and consumers. The use of ZFNs in tomato research creates exciting possibilities for further innovation in crop improvement and sustainable food production.

8.4. APOBEC-Cas9 Fusion-Induced Deletion Systems (AFIDs)

The commonly used genome-editing system CRISPR/Cas9 often leads to the creation of frequent small insertions and deletions (indels), which are unlikely to disrupt the small functional regulatory elements and domains within the genomic DNA [104,105]. Wang et al., 2020, suggests that in order to address this limitation, it is necessary to generate larger deletions using genome-editing techniques. In comparison to other methods of genome editing for generating large deletions, AFIDs, particularly AFID-3, offer significant advantages in generating predictable deletions. AFID-3 incorporates additional elements such as uracil DNA-glucosidase and apurinic or apyrimidinic site lyase from *Escherichia coli*, resulting in approximately one-third of the deletions produced by AFID-3 being predictable [106]. This AFID system allows for the accurate and predictable deletion of multiple nucleotides in plant genomes, facilitating the study of small functional regulatory elements and domains in genomic DNA [107]. Furthermore, there is growing evidence indicating the potential targets for improving crops include small functional regulatory elements and domains in genomic DNA, like upstream open reading frames (uORFs) and other cis-regulatory elements. Certain transcription factors exhibit diverse physiological functions by selectively binding to different cis-regulatory elements. Consequently, AFIDs have the potential to accelerate precise plant breeding by finely regulating the expression of target genes, primarily at the transcriptional and translational levels [104,106]. This setup represents an exciting new frontier in genome-editing technology. However, continued research and developmental efforts are needed to further refine this tool, improve its specificity and efficiency, and unlock its potential for advancing genetic research in tomatoes and other horticultural crops.

8.5. Possible Risks of the Genetic Technologies

Genetic technologies such as CRISPR/Cas9, mitoTALENs, ZFN, and AFIDs offer promising avenues for crop improvement, but they also come with inherent risks that must be carefully considered. One significant concern is off-target effects, where these tools may unintentionally modify genes other than the intended target, potentially leading to unforeseen consequences. Additionally, the potential for unintended genetic mutations

or disruptions in non-targeted regions of the genome poses a risk to the overall genetic integrity of the organism. Studies have highlighted the importance of thorough target sequence selection and rigorous validation processes to minimize off-target effects [108]. Future research should prioritize the development of improved tools and methodologies for enhancing the precision and specificity of gene-editing techniques, thereby mitigating these risks and ensuring the safe and effective application of these technologies in agriculture.

The global adoption of genetically modified (GM) food has prompted the establishment of diverse biosafety regulations tailored to each country's economic and political landscape. While some nations like the European Union have detailed directives like 2001/18/EL for GM biosafety, others such as the US and Canada regulate GMOs through agencies like the Canadian Food Inspection Agency (CFIA). In India, guidelines from Rules 1989 and recent initiatives by the Ministry of Environment Forest and Climate Change aim to assess environmental risks of GM products and genetically modified organisms GMOs [39]. Latin American countries like Brazil and Argentina lead in GM crop cultivation, while others like Peru and Venezuela enforce strict regulations against GM products. African nations are grappling with the balance between food security and concerns over GMO safety and environmental impacts. South Africa stands out as a pioneer in enacting regulatory frameworks for GM crops. China and Korea have also implemented stringent regulations for GM product safety evaluations and commercialization processes [109]. To ensure effective biosafety regulations worldwide, collaborative efforts among government bodies, NGOs, and private sectors are crucial for harmonizing standards and promoting public awareness.

8.6. Ethical Considerations in Genetic Technology

The use of genetic technologies in agriculture raises various ethical considerations that warrant careful deliberation. One key ethical concern is the potential for unintended environmental impacts resulting from the release of genetically modified organisms into ecosystems. Ensuring transparency in research, regulatory oversight, and comprehensive risk assessments are essential to address these concerns and safeguard biodiversity [109]. Moreover, ethical issues related to ownership and control of genetic resources, as well as equitable access to technology and benefits, must be carefully navigated to promote social justice and inclusivity in agricultural innovation. Instances of improper ethics in genetic technology have been documented, including cases of inadequate informed consent, lack of transparency, and conflicts of interest in research. To uphold ethical standards, researchers and stakeholders should adhere to established ethical guidelines, engage in open dialogue with diverse stakeholders, and prioritize the ethical implications of their work throughout the research and development process [39,108]. By addressing these ethical considerations and risks associated with genetic technologies, researchers can foster responsible innovation and contribute to the sustainable and ethical advancement of agriculture.

9. Genetic Tool Applied to Alleviate Pre- and Post-Harvest Challenges

Pre- and post-harvest challenges present a significant obstacle in affecting the quality and yield of tomatoes. These challenges include susceptibility to pests, diseases, and environmental stressors, as well as issues related to storage, transportation, and shelf life [42]. Genetic engineering tools like CRISPR-Cas9 offer promising solutions to alleviate these challenges. By precisely modifying the genes of crops, scientists can enhance traits such as pest resistance, disease tolerance, and post-harvest longevity [92]. For instance, through genetic engineering, tomatoes can be developed to have high firmness, improved resistance to common diseases, and prolonged shelf life. These genetic modifications not only improve the overall resilience of crops but also contribute to reducing pre- and post-harvest losses and ensuring a more sustainable and reliable food supply for communities worldwide [110]. The potential of genetic engineering to address pre- and post-harvest challenges highlights its importance in modern tomato farming and underscores its role in enhancing food security and agricultural sustainability. Figure 2 below shows various

challenges in the pre- and post-harvest of tomatoes including biotic and abiotic stresses and their adaptations through genetic engineering.

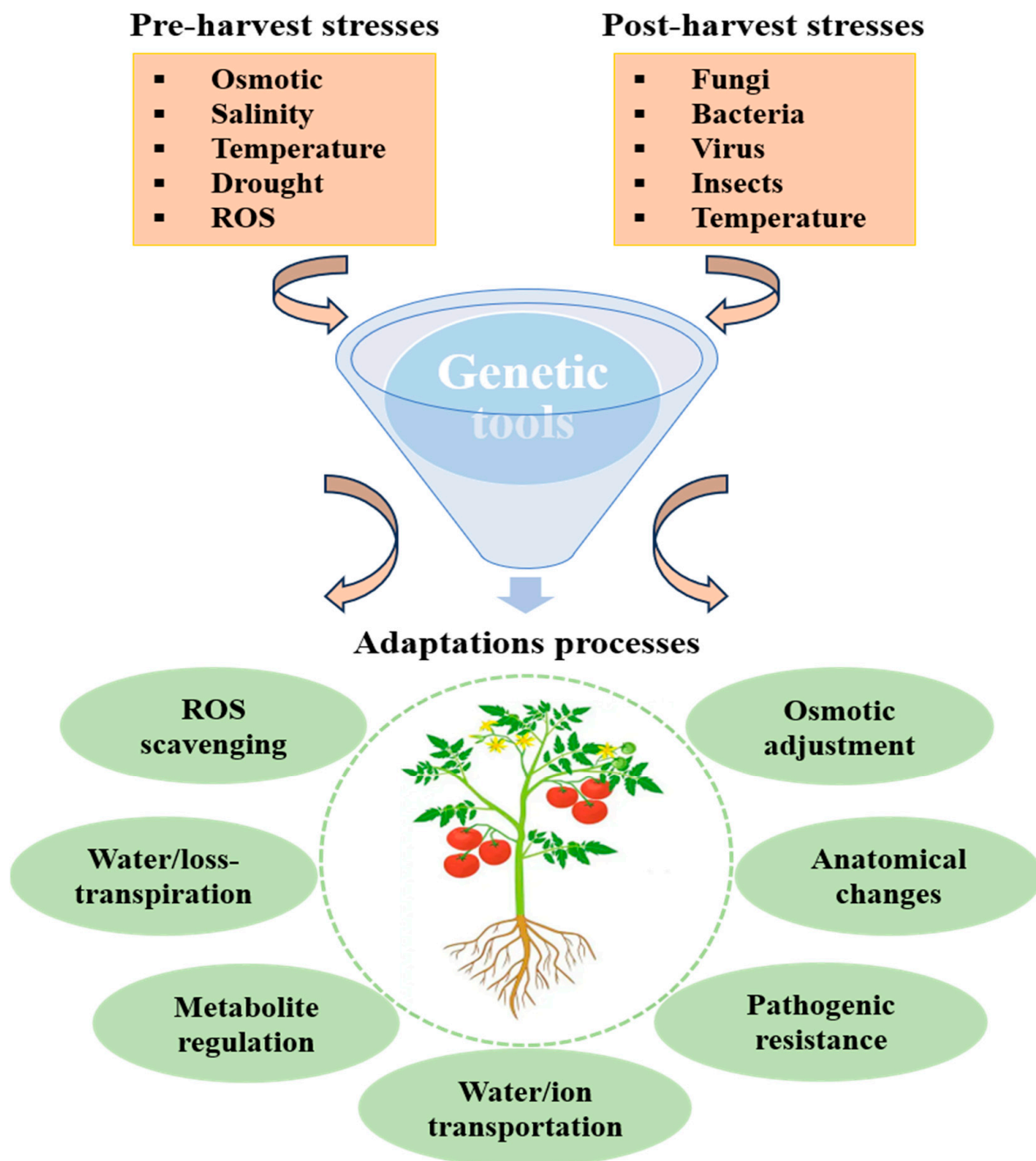


Figure 2. The adoption of tomatoes in various pre- and post-harvest conditions as a result of genetic developments.

9.1. Alleviating Biotic Stress

Biotic stresses, such as viruses, bacteria, fungi, and insects, pose threats to plants by causing damage. The advancement of CRISPR/Cas9 technology has enabled the development of disease-resistant plants since its successful application for creating stable transgenic lines in 2013 [111]. CRISPR/Cas9 has been effectively utilized to combat viral, fungal, and bacterial infections that lead to significant losses in tomato crops. In the case of viruses,

two main strategies have been employed. One approach involves designing specific guide RNAs (sgRNAs) to directly target the virus genome through sequence complementation, while the other focuses on modifying tomato genes that confer antiviral properties [112]. For instance, Tashkandi et al. engineered tomato plants resistant to the tomato yellow leaf curl virus using the CRISPR/Cas9 system to target specific regions of the virus genome. The resulting transgenic tomatoes exhibited reduced viral DNA accumulation compared to wild-type plants, showcasing the potential of CRISPR/Cas9 for developing durable virus-resistant plants [113]. Furthermore, CRISPR/Cas9 technology has been used to knock out key genes involved in antiviral pathways, such as the Tomato Dicer-like 2 (*DCL2*) gene, which when mutated, showed susceptibility to various RNA viruses [114].

Fungi, responsible for diseases like mildew, smut, rust, and rot, can also cause significant crop losses. By targeting genes like Downy mildew resistant 6 (*DMR6*) and mildew resistant locus O 1 (*Mlo1*) in tomatoes using CRISPR/Cas9, researchers have successfully generated mutants that exhibit resistance to pathogens without adverse effects [115]. Additionally, genes like Powdery mildew resistance 4 (*PMR4*) and mitogen-activated protein kinase 3 (*MAPK3*) have been identified as conferring resistance against specific fungal pathogens [116]. Plant pathogenic bacteria, such as *Pseudomonas syringae*, pose challenges due to asymptomatic infections and limited control options. By utilizing genetic resistance mechanisms, such as modifying the Jasmonate-zim domain protein 2 (*JAZ2*) gene in tomatoes, researchers have developed plants that show resistance to bacterial speck disease caused by *P. syringae*. This demonstrates the potential of CRISPR/Cas9 technology for enhancing fruit crop protection against bacterial pathogens in agricultural settings [117].

9.2. Controlling Abiotic Stresses

Environmental stresses like drought, flooding, heat, and cold, particularly in the context of climate change, present significant challenges to species, especially crops. While traditional breeding methods have boosted crop productivity, the escalating food demand necessitates new strategies to enhance crop production, with CRISPR/Cas9 technology emerging as a promising solution [118,119]. One specific gene, Brassinazole resistant 1 (*BZR1*), plays a crucial role in regulating plant response to brassinosteroids (BR) and is involved in various developmental processes mediated by BR [120]. In tomato plants, *BZR1* also helps in responding to high temperatures by influencing the *Feronia* (*FER*) genes, as demonstrated in both CRISPR-modified *bzr1* lines and *BZR1*-overexpressing plants. Since tomatoes are sensitive to cold temperatures, the quality of their fruits can be compromised by chilling stress [121]. A recent study discovered that C-repeat binding factor 1 (*CBF1*) plays a protective role against cold damage, as tomato plants with a CRISPR-induced *cbf1* mutation exhibited more severe chilling symptoms with increased electrolyte leakage compared to wild-type plants [122]. Additionally, *MAPK3*, which contributes to resistance against gray mold disease, also aids in tomato plants' response to drought stress by safeguarding cell membranes from oxidative harm [123] as shown in Table 2 below.

Table 2. Various genes identified in tomatoes involved in biotic and abiotic stress conditions.

Stress-Related	Genes	Phenotypic Traits	References
Biotic stress	<i>DCL2</i>	Vulnerability to tobacco mosaic virus, tomato mosaic virus, and potato virus.	[124]
	<i>MLO1</i>	Protection from powdery mildews.	[125]
	<i>CP</i> and <i>Rep</i> of virus	Protection from tomato yellow leaf curl virus	[113]
	<i>PMR4</i>	Protection from powdery mildews	[126]
	<i>DMR6</i>	Protection from powdery mildews	[127]

Table 2. Cont.

Stress-Related	Genes	Phenotypic Traits	References
	<i>Solyc08g075077</i>	Vulnerability to fusarium wilt disease	[128]
	<i>MAPK3</i>	Related to gray mold disease	[64]
	<i>JAZ2</i>	Protection against bacterial speck disease	[129]
	<i>SRLK5</i>	Resilience against <i>fusarium</i> wilt	[130]
	<i>Ve1</i>	Tolerance to <i>verticillium</i> wilt disease	[131]
	<i>SIMYB49</i>	Ability to withstand the fungal pathogen <i>phytophthora infestans</i>	[132]
	<i>ech42</i>	Resistance to fungal pathogen <i>Alternaria alternata</i>	[133]
	<i>Bs2</i>	Tolerance to bacterial spot disease	[134]
	<i>PPo, Pto, Prf</i>	Tolerance to bacterial pathogen, <i>Pseudomonas syringae</i> pv. tomato	[135]
Abiotic stress	<i>BZR1</i>	Reduced tolerance to heat stress	[121]
	<i>CBF1</i>	Reduced tolerance to cold stress	[136]
	<i>MAPK3</i>	Reduced tolerance to drought stress	[137]
	<i>BADH1</i>	Convert betaine aldehyde to glycine betaine	[138]
	<i>cAPX</i>	Minimize cellular damage by scavenging super oxides	[139]
	<i>NHX1</i>	Overexpressed NHX1 vacuolar Na ⁺ /H ⁺ antiporter	[140]
	<i>CaKR1</i>	Elevated expression of antioxidant enzyme that eliminate antioxidants	[141]
	<i>Ectoine (ectA, ectB, ectC)</i>	Enhances peroxidase activity and decreases MDA contents by the accumulation of ectoine	[142]
	<i>AtSIS0S2</i>	Regulates the Na ⁺ /H ⁺ and endosomal vacuolar K ⁺ , Na ⁺ /H ⁺ , mainly responsible for Na ⁺ extrusion out of the roots, loading of Na ⁺ into xylem, and the compartmentalization of Na ⁺ , and K ⁺	[143]
	<i>ToOsmotin</i>	When overexpressed, leads to the accumulation of solutes and protects the native protein's structure	[144]
	<i>TaNHX2</i>	Regulates the Na ⁺ , pH, and K ⁺ homeostasis	[145]
	<i>coda</i>	Enhances the NaCl-induced expression of genes encoding the K ⁺ transporter, Na ⁺ /H ⁺ antiporter, and H ⁺ -ATPase	[146]
	<i>HAL5</i>	Regulate and maintain the homeostasis of Na ⁺ and K ⁺ , and SIHKT1, SIHKT2, and SIHKT5	[147]
	<i>MdSOS2L1</i>	Interact with MdCBL1, MdCBL4 and MdCBL10 proteins to increase tolerance	[148]

9.3. Improving Post-Harvest Shelf Life

Extending the shelf life of fleshy fruits, vegetables, and ornamentals is crucial with significant implications for market viability. However, achieving prolonged shelf life poses a major challenge in breeding and genetic modification programs [103]. While cold storage has traditionally been used to preserve these crops, it is often too costly for small-scale growers. Therefore, there is an urgent need to develop cost-effective strategies for enhancing the shelf life of crops. Ethylene, a plant hormone responsible for ripening, plays a key role in the maturation of fruits and vegetables, making its regulation essential for maximizing shelf life [149]. When left unchecked, natural ripening processes lead to senescence, highlighting the importance of developing management strategies to delay ripening during transportation and storage and minimize post-harvest losses [150]. The progression of horticultural produce from ripening to senescence stages results in decreased quality, leading to consumer rejection and subsequent losses [103]. Therefore, it is crucial to control the expression of genes related to shelf life to preserve taste, aroma, and overall quality. Recent advancements in genome-editing technologies have shown promise in enhancing the quality and post-harvest characteristics of horticultural crops. Among these crops, tomatoes have been extensively studied due to their status as a model climacteric crop, making them ideal for genetic engineering research thanks to the wealth of molecular information available regarding shelf life processes [151,152].

9.4. Post-Harvest Pathogen Resistance

Post-harvest infections pose a significant threat to fruits, vegetables, and ornamentals, starting from the ripening and harvesting stages all the way to their transportation from

the field to processing units and storage facilities [153]. Various abiotic factors like temperature, relative humidity, and oxygen levels play a crucial role in making horticultural crops more susceptible to pathogenic attacks during storage [19]. The culprits behind post-harvest losses are primarily fungi, bacteria, yeast, and molds. Among these, bacterial and fungal rot are particularly destructive, causing extensive damage to perishables and canned goods. Bacterial soft rots are commonly caused by species like *Erwinia*, *Pseudomonas*, *Bacillus*, *Lactobacillus*, and *Xanthomonas* [154], while fungal infections, leading to rot in fruits and vegetables, are more prevalent during post-harvest processes [155]. Notable fungal pathogens responsible for post-harvest losses include *Alternaria*, *Aspergillus*, *Botrytis*, *Colletotrichum*, and many others. Factors such as fruit acidity also influence susceptibility to pathogen attacks, with more acidic fruits being prone to fungal attacks and those with a pH above 4.5 being vulnerable to bacterial pathogens [156]. To manage post-harvest diseases, various strategies such as the use of pesticides, proper handling during harvest, ventilated and temperature-controlled transport, cold storage, and pre-and post-harvest treatments with chemicals or UV-C are commonly employed [157]. Genetic engineering has also been instrumental in enhancing disease resistance in horticultural crops by incorporating genes like Cry genes, protease inhibitors, PR proteins, and others [56]. The advancement of gene-editing technologies offers new opportunities for developing crop varieties with improved responses to post-harvest storage challenges.

10. Conclusions

The review highlights the significant progress made in utilizing gene-based developments, particularly CRISPR/Cas9 technology, to enhance the quality of tomatoes by focusing on firmness, shelf life, and related characteristics. Researchers have successfully demonstrated the potential of gene-editing technologies in improving the resilience of crops against biotic and abiotic stresses, ultimately benefiting both producers and consumers. These advancements hold promise for addressing food security challenges and meeting the increasing demands for high-quality produce.

Looking ahead, further research in gene-based developments for improving tomato quality should continue to explore novel gene-editing technologies, such as CRISPR/Cas9, to target specific genes associated with firmness, shelf life, and other desirable traits. Collaborative efforts between scientists, policymakers, and agricultural stakeholders are essential to ensure the responsible application of these technologies and to address regulatory and ethical considerations. Additionally, efforts should be made to enhance public awareness and acceptance of genetically modified crops, emphasizing the benefits they offer in terms of sustainability, food security, and nutritional value. Furthermore, in the realm of tomato cultivation, addressing challenges related to aroma development and fruit setting presents promising avenues for future research endeavors. The enhancement of tomato aroma profiles is a critical aspect that can significantly influence consumer preferences and market value. Investigating the underlying genetic and biochemical mechanisms that govern aroma compound biosynthesis pathways could offer insights into strategies for improving and preserving desirable aroma characteristics in tomato varieties. Moreover, focusing on optimizing fruit-setting processes, including the regulation of hormonal signaling pathways and environmental factors affecting pollination and fertilization, could lead to advancements in enhancing fruit yield and quality. Additionally, exploring the intricacies of cell wall formation and composition to promote the development of a robust cell wall structure could be a compelling subject for analysis. Understanding the molecular mechanisms involved in cell wall synthesis, modification, and degradation may provide valuable knowledge for enhancing tomato fruit firmness and shelf life. By delving into these research directions, researchers can contribute to the sustainable improvement in tomato production and quality.

Funding: This work is supported by the Shanxi province basic research plan (202203021221162) and the Shanxi province key R&D plan (202102140601013).

Conflicts of Interest: The authors declare no conflict of interest.

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