International Journal of
Nanotechnology and Allied Sciences

Review Article 2026 | Volume 10 | Issue 1 | 25-41

Open Access

Article Information

Received: October 28, 2025

Accepted: March 15, 2026

Published: April 10, 2026

Authors' Contribution

FA conceived and designed the study; analysed the results; wrote and revised the paper.

How to cite

Afzal, F., 2026. Review on Modification in Tomato Genome by Genome Editing Tools. Int. J. Nanotechnol. Allied Sci., 10(1): 25-41.

***Correspondence**

Faiqa Afzal
Email: faiqaafzal50@gmail.com

Review on Modification in Tomato Genome by Genome Editing Tools

Faiqa Afzal*

University of Agriculture Faisalabad, Faisalabad, Pakistan.

Abstract:

Tomato (*Solanum lycopersicum*) is a globally important horticultural crop with significant nutritional, economic, and industrial value. However, its production is frequently challenged by biotic stresses such as bacterial wilt and viral infections, abiotic stresses including drought, salinity, and temperature fluctuations, and substantial post-harvest losses. Traditional breeding methods, while valuable, often lack precision and are time-consuming. This review highlights the transition from conventional breeding to advanced genetic technologies, focusing on genome editing tools such as zinc finger nucleases (ZFNs), transcription activator-like effector nucleases (TALENs), and particularly the CRISPR/Cas9 system. CRISPR/Cas9 has revolutionized tomato improvement by enabling precise, efficient, and inheritable genome modifications, enhancing traits such as fruit quality, shelf life, disease resistance, and stress tolerance. Additionally, modern approaches like RNA interference (RNAi), marker-assisted selection, and Agrobacterium-mediated transformation have contributed significantly to functional genomics and trait development. Post-harvest loss management strategies, including biological, chemical, and physical interventions, are also discussed. This review underscores the role of modern biotechnological tools in sustainable tomato production and offers insights into future directions for genetic improvement to meet the challenges of global food security and climate change.

Keywords: CRISPR/Cas9, TALENs, ZFN, Conventional methods, genome editing.

Scan QR code to visit this journal.

INTRODUCTION

Tomato (*Solanum lycopersicum*), formerly known as *Lycopersicum esculentum*, is one of the most widely cultivated and consumed vegetable crops globally. Belonging to the Solanaceae (nightshade) family, which includes around 3,000 species, tomato has 12 closely related species (Peralta and Spooner, 2005). It is a self-pollinated and day-neutral crop (Rick and Butler, 1956), valued for both fresh consumption and processing into products such as sauces, purees, and pastes. Globally, tomato ranks fourth among fresh-market vegetables after potato, lettuce, and onion, and second in commercial production after potato.

Pakistan ranks 35th among tomato-producing countries. Its significance as a model plant species is well established, with the International Solanaceae Genome Project (SOL) initiated in 2003 to sequence its genome (Roxana *et al.,* 2007). In 2020, global tomato production reached 41.52 million tons, and projections suggest an increase to 51.93 million tons by 2026 (Chandrasekaran *et al.,* 2021). Besides its economic value, the tomato is nutritionally rich, providing vitamin C, β-carotene, folate, potassium, flavonoids, and the antioxidant lycopene, making it a vital component of a healthy diet (Collins *et al.,* 2022).

The genomic size of tomato is 950 mb of DNA (Arumuganathan and Earle, 1991) that contains 12 chromosomes and about 35,000 genes. The tomato plant originated from Western South America and Central America (Andean origin). Evolution in tomato has occurred due to its mating system. Tomato was domesticated in Mexico (Jenkins, 1948) and diverged from *Solanum pimpinellifolium*. In early human history, people did not use tomatoes for consumption because they considered these plants harmful. With the passage of time, people started to use these plants for consumption due to their health benefits. Tomato is particularly amenable to genome editing due to its diploid nature, well-characterized genome, and economic relevance. By using the CRISPR/Cas system, mutations can be induced in tomato successfully and efficiently by *Agrobacterium*-mediated transformation. A lot of research is going on with tomatoes to study the flower and fruit development (Chandrasekaran *et al.,* 2021).

There are many production challenges that we have to face in tomato production, including losses due to biotic, abiotic, and post-harvest processes. Biotic challenges include bacterial wilt, leaf mold, early and late blight, bacterial spot, and tomato yellow leaf curl virus. Abiotic challenges include atmospheric temperature, humidity, pH of soil, salinity, water, and light. To overcome these production challenges, plant breeders employ a range of strategies, including conventional breeding, genetic engineering, and modern gene editing techniques. Traditional approaches such as hybridization, selection, somaclonal variation, marker-assisted selection, and hybrid development have long been used to improve tomato tolerance against biotic and abiotic stresses (Rezk *et al.,* 2021).

Research in functional genomics of plants and crop improvement has been revolutionized by the introduction of precise genome editing that provides targeted genome modification. Gene editing techniques include ZFNs, TALENs, and CRISPR, which have brought revolution in the plant research field. These genetic tools create site-specific double-strand breaks and provide modifications in the genome by either homologous recombination or non-homologous end-joining repair mechanism (Gaj *et al*., 2013). Double-strand breaks, in eukaryotes, are repaired by the non-homologous end-joining repair mechanism, which proves an amazing strategy for doing research in crop improvement (Ray and Langer, 2002).

ZFNs are proteins that are used for making cuts in targeted DNA. TALENs are also site-specific endonucleases that cut on targeted DNA. ZFNs and TALENs have been used for a long time in a number of organisms for modifications in the genome, but these are expensive and difficult to use (Gaj *et al.,* 2013). Early tools like zinc finger nucleases (ZFNs) and transcription activator-like effector nucleases (TALENs), although effective,

had limitations in cost and precision. This led to the rise of RNA-based approaches, including RNA interference (RNAi), which uses small non-coding RNAs to silence pathogen-responsive genes. Similarly, microRNAs (miRNAs) play a critical role in regulating gene expression, helping plants combat a wide range of pathogens. Another method, TILLING (Targeting Induced Local Lesions IN Genomes), has been used to introduce random mutations for breeding improved tomato varieties (Chandrasekaran *et al.,* 2021). However, the specificity and efficiency of gene targeting remain issues. Thus, researchers have continued to refine genome editing techniques to overcome these hurdles and achieve more precise genetic improvements.

Importance of Tomato

Tomato is scientifically known as *Solanum lycopersicum,* and it belongs to the Solanaceae family. Tomato has 12 chromosomes and is a diploid species. *S. lycopersicum* is an important and beneficial plant that is being used in the whole world. Tomato is a self-pollinated crop (Rick and Butler, 1956) and a day-neutral plant. Tomatoes are used for both fresh eating and cooking purposes. Tomatoes contribute to the vegetable production in the world (FAO 2016).

S. lycopersicum contains several healthy compounds, for example, carotenoids, vitamins (B, C) that play an important role in promoting human health and preventing diseases (Fraser and Bramley, 2004). Tomatoes contain 95% water and 4% carbohydrates. There is high consumption of tomato because it contains mineral salts like potassium and magnesium, Vitamins (B1, B2, B5, and C), and carotenoids like lycopene. In 2005, it was reported that consumption of tomatoes and their products is useful for giving protection against chronic diseases, cancer, and cardiovascular diseases due to the presence of lycopene (Blum, 2005). Moreover, tomatoes maintain blood pressure, protect against cancer, and decrease the risk of diabetes and heart disease.

Control of Post-harvest Losses

Control by non-chemical methods

a) Control by physical methods

Delaying tomato ripening can significantly reduce post-harvest losses. Controlled storage conditions—such as low temperature, pressure, ethylene concentration, oxygen levels, and specific humidity—help extend shelf life. Low-pressure storage prolongs fruit preservation by limiting oxygen availability required for respiration, thus preventing rotting (Stenvers and Stork, 1977). Similarly, low temperatures restrict respiration, increasing shelf life; optimal ranges vary by fruit stage: 15°C for green, 10°C for orange-green, and 8°C for red tomatoes, though temperatures below 10°C may cause chilling injuries (Hobson, 1981). Maintaining low CO_2 and O_2 levels further prevents fungal growth and inhibits enzymatic activity and pathogen development (Sams and Conway, 1987).

b) Control by pre-cooling

Pre-cooling means that fruits are being cooled before storage. This type of cooling prevents fruit from post-harvest losses, improves fruit quality, and delays ripening in fields (Shehla and Tariq, 2007). Moreover, all the metabolic activities of harvested fruits, like the activity of micro-organisms, ethylene production, and the rate of respiration, are decreased by using the pre-cooling method. The process of pre-cooling maintains the fruits' quality and enhances shelf life by decreasing the process of ripening (Becker and Fricke, 2002).

c) Control by the heating

Heat not only removes the fungus from the surface of fruit but also from under the surface. Fruit deterioration can be stopped by heating at 34-36°C for 2-3 days (Del Rio *et al.,* 1992). In heating methods, treatment with hot water is the most commonly used and cheapest method that increases the resistance against pathogens. Irradiation is also used for heating, in which both ionizing and non-ionizing irradiations are used to

increase the shelf life. During irradiations, micro-organisms are killed by the process of sterilization (Abdel-Kader *et al.,* 1968).

Heat from a microwave reduces the population of bacteria in food (Karabulut and Baykal, 2002). The microwave heat method has proved more effective in killing *Botrytis cinerea* and *Penicillium expansum* (Wang *et al.,* 2001). UV light is also a useful control method for post-harvest losses. Ripening is delayed by using UV with a low dose. UV has proved useful for decreasing the post-harvest losses up to 90% in many crops like tomato, strawberry, peach, potato, carrot, citrus, and onion (D'hallewin *et al.,* 2000). UV has to be used in a specific dose, otherwise it may harm the fruits, such as tissue decaying and blemishing of fruit skin (Ben-Yehoshua *et al.,* 1992).

Control by Chemical Methods

a) Control by potassium

Potassium control is a practical example of chemical regulation in plants. As a key macronutrient in NPK, potassium is essential for normal plant growth (Das, 1999) and regulates around 60 enzymes involved in metabolic activities, enhancing yield and reducing post-harvest losses (Mengel and Kirkby, 1987). Applying potassium to K-deficient soils improves lycopene concentration in tomatoes, enhancing fruit color and appearance (Trudel and Ozbun, 1971). Adequate K supply also promotes early maturation, minimizes post-harvest weight loss, and maintains fruit texture and color (Lester, 2005).

b) Control by calcium chloride treatment

Calcium chloride treatment is a well-established method to reduce post-harvest losses and extend the shelf life of fruits and vegetables (Senevirathna and Daundasekera, 2010). It influences both extracellular and intracellular processes, enhancing fruit firmness, delaying ripening and flowering, and maintaining physiological balance (Hong *et al.,* 1999). For instance, treating strawberries with 1% calcium chloride delays ripening and prevents fungal attack (Lara *et al.,* 2004), while in loquat, shelf life increases by 4–5 weeks (Akhtar *et al.,* 2010). In tomatoes, calcium chloride significantly delays ripening, reduces ethylene production, increases firmness, and improves shelf life by up to 92% (Senevirathna and Daundasekera, 2010).

Control by biological methods

Biological methods are safe and effective alternatives to chemical fungicides for controlling post-harvest losses in fruits and vegetables (El-Ghaouth *et al.,* 2003; Iqbal and Ashraf, 2019). They utilize beneficial microorganisms such as bacteria and yeasts to combat pathogens responsible for decay (Friedman *et al.,* 2000; Wisniewski *et al.,* 2001), showing significant success in various crops (Sugar and Basile, 2008; Hassanein *et al.,* 2018). Commercially available biocontrol products based on antagonistic microorganisms are widely used to prevent post-harvest losses (Castoria *et al.,* 2001; Iqbal and Ashraf, 2017) and can be combined with other treatments for enhanced efficiency (Spotts *et al.,* 2002).

Role of conventional breeding

Pure-line selection is a conventional breeding method in which two superior varieties of the same species are crossed, and the best-performing plants are selected. This process is repeated across different environments to assess stability and achieve uniform desirable traits. Once confirmed through trials, the selected line is multiplied for seed production and eventually released as a new variety. The main goal of this method is to develop homozygous inbred lines (Kaiser *et al.,* 2020).

Modern Genetic Approaches

The genetic approaches are time-saving, quick, and efficient. For example, genetic engineering, marker-assisted selection, and gene editing.

Genetic Engineering

Genetic engineering is carried out in crop plants in various ways, for example, micro-injection,

gene gun, electroporation, and *Agrobacterium-mediated* transformation. The *Agrobacterium-mediated* transformation method is the most common and widely used method throughout the world, and by using this technique, the first transgenic plant was developed. Engineered *Agrobacterium* introduces the Ti plasmid containing genes of interest into the plant genome by entering through any cut or wound and makes crown galls (Fatima *et al.,* 2018; Wang *et al.,* 2025).

In vitro techniques play an important role in crop improvement, for example, anther culture, somaclonal variation, somatic hybridization, and pollen culture. By using in-vitro techniques, genes are introduced across the species. Many plants can be regenerated from a single cell through in-vitro techniques, for example, tomato. In 1972, Sharp and his colleagues successfully cultivated pollen cells of tomato after isolation from nurse culture (Sharp *et al.,* 1972). Gresshoff and Doy got haploid plants from the callus of anther (Gresshoff and Doy, 1972). Production of haploid plants from either anther or pollen produces homozygous lines and also facilitates the analysis of new genes of hybrid plants in less time. This technique is more useful than the conventional breeding methods. But this procedure is not commonly used because it is more expensive and has a low frequency as compared to the conventional breeding method (Roxana *et al.,* 2007). Pomato is the first somatic hybrid that was result of tomato and potato in 1978 (Melchers *et al.,* 1978). This attempt proved that somatic hybridization can play a key role in the breeding of tomato.

Following the introduction of Pomato, significant advancements have been made in protoplast culture and in vitro regeneration, enabling the production of various hybrids and cybrids. However, somatic hybridization in tomato has been limited due to challenges in backcrossing hybrids with diploid tomatoes (Wolters *et al.,* 1993). In recent years, genetic engineering has largely replaced somatic hybridization in tomato improvement. Among in-vitro techniques, embryo culture has proven highly effective for tomato regeneration and overcoming incompatibility barriers in breeding programs (Roxana *et al.,* 2007).

In 1954, Norton and Boll successfully observed the regeneration of tomato callus in cell culture (Norton and Boll, 1954). The efficiency of in-vitro tomato propagation depends on several factors, including explant type and condition, growth regulator concentration, light exposure, and seedling age. Later, Pugliese et al. (1999) highlighted that light is an essential factor for tomato regeneration under in-vitro conditions, as no regeneration occurred in its absence. Similarly, Lercari and Bertram (2004) experimented with tomato hypocotyl segments under varying light conditions and found that only those cultured under white light showed successful regeneration, emphasizing the critical role of light quality in morphogenesis.

For more than three decades, genetically modified organisms (GMOs) have played a transformative role in crop improvement (Fatima *et al.,* 2018; Khan *et al.,* 2020). Horsch et al. (1985) and McCormick et al. (1986) were the first to report *Agrobacterium*-mediated transformation in tomato, marking a breakthrough in plant biotechnology. The Flavr-Savr tomato, developed using a polygalacturonase antisense construct through this transformation method, became the first commercialized GMO crop. This tomato exhibited a prolonged shelf life (Smith *et al.,* 1988) and reached the market in 1994. Table (1) highlights some reports of transformation in Tomato.

Marker Assisted Selection System

With the help of marker-assisted selection (MAS), the identification and selection of desired traits can be efficiently tracked even at the seedling stage (Peleman and Voort, 2003). Different types of markers, such as morphological, biochemical, cytological, and DNA-based markers, are used to monitor the expression of target genes in plants. Among these, molecular markers, which are DNA-based, have revolutionized plant breeding.

Common examples include RFLP (Restriction Fragment Length Polymorphism), AFLP (Amplified Fragment Length Polymorphism), SNP (Single Nucleotide Polymorphism), RAPD (Random Amplified Polymorphic DNA) and SSR (Simple Sequence Repeats), all of which are widely used to explore and exploit the genetic diversity of tomato and other crop plants (Carelli *et al.,* 2006; Zaynab *et al.,* 2017).

Isozymes (also known as allozymes) were the first molecular markers applied to tomato for studying the genetic variation between wild and cultivated species (Rick, 1973). Based on these markers, the first morphological linkage map of tomato was developed, which later led to the construction of a comprehensive genomic map using advanced DNA-based markers (Haanstra *et al.,* 1999). In addition, PCR-based markers such as CAPS (Cleaved Amplified Polymorphic Sequences) and SCAR (Sequence Characterized Amplified Regions) are extensively used in marker-assisted breeding programs to increase selection precision (Bai *et al.,* 2004).

Table 1. Successful reports of transformation in Tomato.

Crop	Gene introduction	Selective agent	Transformation method	Successive results	References
Tomato	nptII	GUS	Biolistics	Antibiotic resistance	(Van Eck *et al.,* 1995)
Tomato	Populus bsp A	GUS	Agrobacterium	Drought tolerance	(Roy *et al.,* 2006a,b)
Tomato	Ipt	Kanamycin	Agrobacterium	Delayed leaf senescence	(Luo *et al.,* 2005)
Tomato	Erwinia uredovora CrtB	Kanamycin	Agrobacterium	Carotenoids	(Fraser *et al.,* 2002)
Tomato	Arabidopsis NPR1	Kanamycin	Agrobacterium	Fungal and bacterial disease	(Lin *et al.,* 2004)

Modern Genome editing tools

New genomic techniques (NGTs) — particularly gene-editing tools like ZFNs, TALENs, and CRISPR/Cas — have emerged as powerful solutions to address these challenges by enabling precise and targeted genetic modifications. Tomatoes, as one of the world's most cultivated vegetable crops, are a key focus of these efforts. Gene-editing has significantly advanced tomato breeding, enabling improvements in stress tolerance, nutritional content, and fruit shelf life (Larriba *et al.,* 2024).

ZFNs

ZFN stands for zinc finger nuclease, which was the first genome editing tool. This molecular scissor creates the link between the DNA-binding domain of ZFPs (transcription factor zinc-finger proteins) and the nuclease domain of Fok1 restriction enzyme. The cleavage domain of Fok1 is present on ZFN. ZFN binds to its target and 3-6 fingers at the same time. These fingers are specially engineered for the recognition of the desired sequence, and they are flanked at the cleavage site. This molecular scissor creates double-strand breaks on a specific target sequence. This DSB was then repaired by the DNA repair mechanism. In 2016, scientists mutated the LIL4 gene in tomato with the help of ZFN. This mutation has delayed ripening in tomato (Hilioti *et al*., 2016).

TALENs

TALEN stands for transcription activator-like effector nucleases. It is also a molecular scissor like ZFNs. TALENs have two domains, just like ZFNs, which are the Fok1 cleavage domain and the DNA-targeting binding domain. Tandem repeats form the DNA-binding domain, and these repeats were discovered in *Xanthomonas*. TALENs can target any DNA sequences and have a high range of targets. Scientists can construct TALENs easily, and it has proved very reliable tool for genome editing. In 2014, scientists targeted the TaMLO gene in wheat

with the help of TALENs. As a result, powdery mildew resistance has developed in wheat (Wang *et al*., 2014). Moreover, scientists have targeted two genes in potato that are the ALS gene (Butler *et al*., 2016) and the endogenous constituent promoter gene (Forsyth *et al*., 2016) with the help of TALENs. This targeting resulted in the development of resistance against the herbicide. Brooks and his colleagues, in 2014, targeted the SlAGO7 gene in tomato, which resulted in the formation of iRNA (Brooks *et al.,* 2014). Similarly, another gene known as the PROCERA gene was targeted in 2014 by Lor, which caused enhancing the GA metabolism (Lor *et al.,* 2014).

CRISPR/Cas9

CRISPR stands for Clustered regularly interspaced short palindromic repeats. CRISPR/Cas, a natural DNA cutter, is a natural mechanism for defense in bacteria and archaea and provides an immunity system to them against any invading genetic elements (Mojica *et al.,* 2000). CRISPR is preferred over other gene editing techniques because it shows more benefits, such as cost, efficiency, targeting, specificity, and construction. CRISPR/Cas system has three types that are Type I, Type II, and Type III (Makarova *et al.,* 2011). Among these, Type II is widely used for targeting the DNA sequences. It originates from *Streptococcus pyogenes* and consists of three components that are Cas9 endonuclease, CRISPR RNA, and trans-activating tracrRNA (Gaj *et al.,* 2013).

Successful reports of CRISPR/Cas

CRISPR/Cas9 allows for the rapid introduction of domestication traits from wild relatives into cultivated varieties and vice versa. Its versatility is further augmented by online sgRNA design tools, multiplex editing capabilities, advanced cloning methods (such as Golden Gate, GoldenBraid, and BioBrick systems), and efficient transformation techniques, including Agrobacterium-mediated and DNA-free protoplast transformations (Ansori *et al.,* 2023). Newer innovations—like Cas9 variants (e.g., Cas12a, Cas9-NG), homologous recombination-based knock-ins using geminivirus replicons, and base/prime editing (e.g., Target-AID)—are expanding the potential of genome editing in tomato (Tiwari *et al.,* 2023).

With the help of the CRISPR/Cas9 system, a number of improvements and modifications have been developed in various plants and animals. After getting success in model plants with the help of CRISPR editing technology (*Arabidopsis thaliana* and *Nicotiana benthamiana*) in 2013 (Li *et al.,* 2013), people started working on *Oryza sativa* (Zhang *et al.,* 2014), *Solanum lycopersicum* (Brooks *et al*., 2014), maize (Liang *et al*., 2014), Populus (Fan *et al*., 2015), *Citrus sinensis* (Jia and Wang, 2014), *Sorghum bicolor* (Jiang *et al.,* 2013) and *Triticum aestivum* (Wang *et al.,* 2014).

Tomato is a dicot on which the CRISPR gene editing tool can be efficiently applied because a well-established transformation methodology exists. TALEN is also used to cause mutations in tomato, but CRISPR is most popular due to ease and specific targeting of DNA sequences. Moreover, it is reported that the chances of off-target effects are very low in plants by using the CRISPR system (Shan *et al.,* 2013; Zhang *et al.,* 2014; Sun *et al.,* 2015). In 2016, it was experimentally proved that the CRISPR/Cas system can induce heritable mutations in tomato plants (Changtian *et al*., 2016).

The UVR8 gene regulates the process of photomorphogenesis by regulating gene transcription (Jenkins, 2017). However, the function of UVR8 in the tomato plant is known because scientists don't have the mutant lines of SLUVR8. In 2020, scientists knocked out the SLUVR8 gene in tomato plants using the help of CRISPR gene editing approach and produced the sluvr8 mutant lines to observe its function at the early seedling stage. They compared the mutant line with the wild type in the presence of strong UV-B and observed that the mutant plant was wilted. By producing the mutant lines, scientists showed that SLUVR8 regulates the development of seedlings, tolerance, and acclimation to the stress of UV-B (Xiaorui *et al.,*

2020). Scientists have suppressed SlAP2a by RNAi repression and successful by getting early ripening of tomato fruit (Mi-Young *et al.,* 2010). By the suppression of this transcription factor, the production of ethylene increases, and it also alters the carotenoid pathway flux (modification in carotenoid accumulation).

In 2017, ripening in tomato was successfully delayed by silencing the histone deacetylase SlHDT3 (positive regulator for fruit ripening). As a result, the time period of ripening of fruit was delayed, and ultimately, the shelf life of tomato fruit increased. With the silencing of SlHDT3, several ripening-associated genes (RIN, E4, E8, LOXB, PG, and Pti4) and ethylene biosynthetic genes (ACS2, ACS4, ACO1, and ACO3) were also down-regulated in mutated lines (Guo *et al.,* 2017). It shows that the expression of a number of ripening-related genes can be suppressed by silencing SlHDT3 in tomato. The scientists increased the shelf life of tomatoes by knocking out the ALC gene, using the CRISPR/Cas9 system (Paran and van der Knaap, 2007).

In 2002, Li and Steffens introduced transgenic tomatoes that were showing disease resistance when these transgenic tomato infected by the *Pseudomonas syringae*, a bacterial pathogen (Li and Steffens, 2002). Scientists have developed resistance in tomato against multiple diseases by using systemic acquired resistance-related genes (Chan *et al.,* 2005). In 2004, scientists developed a transgenic tomato by the introduction of the Arabidopsis NPR1 gene. This transgenic tomato has resistance against the tomato mosaic virus. Moreover, this transgenic also shows resistance against bacterial wilt and Fusarium wilt (Lin *et al.,* 2004). In 2006, scientists developed a transgenic tomato that has resistance against the oomycete pathogen, *Phytophthora* (Sarowar *et al.,* 2006).

CRISPR/Cas9 has enabled precise editing of genes responsible for key domestication traits: *SP* (self-pruning) for plant habit, *FAS* (fasciated) for fruit size, *O (Ovate)* for shape, *MULT* (multiflora) for fruit number, *FW2.2* for weight, and *CYC-B* (lycopene beta-cyclase) for significantly increased lycopene levels. Other edited targets include genes for male fertility control (*Ms1035*, *GSTAA*) for hybrid seed production, as well as *J2* and pectin-degrading genes to improve mechanical harvesting and fruit firmness. Mutations in *GAD2/3* have led to up to 15× increases in GABA content (Nonaka *et al.,* 2017), while editing *INVINH1* and *VPE5* enhanced soluble sugars and total soluble solids (Wang *et al.,* 2021).

CRISPR/Cas9 technology was successfully employed to knock out *SlPMR4* in tomato (Santillán Martínez *et al.,* 2020). The generated mutants displayed enhanced resistance to PM, validating the approach and highlighting the utility of CRISPR-based mutagenesis in resistance breeding and functional genomics.

Tomato productivity is constrained by diseases (e.g., TYLCV, powdery mildew, and late blight) and environmental stresses. CRISPR/Cas9 has been used to knock out key susceptibility genes such as *Pelo* (TYLCV resistance) (Pramanik *et al.,* 2021), *SlMlo1* (powdery mildew), *DMR6-1* (broad-spectrum bacterial resistance) (Thomazella *et al.,* 2021), and *MYBS2* (late blight) (Liu *et al.,* 2021). For abiotic stress, editing genes like *CPK28* improved heat tolerance (Hu *et al.,* 2021), while alteration of *HKT1;2*, *RAD51/54*, *GRXS* gene family (Vu *et al.,* 2020), and *PR-1* conferred tolerance to salinity, dehydration, and temperature extremes.

Tomatoes are vulnerable to a wide array of biotic and abiotic stresses. CRISPR/Cas9 has been instrumental in engineering resistance against devastating diseases like TYLCV, through editing of the *Ty-5*, *Pelo*, and *Mlo1* genes (Pramanik *et al.,* 2021). Editing of *DMR6-1* has yielded broad-spectrum resistance to bacterial pathogens such as *Pseudomonas syringae*, *Xanthomonas spp.*, and *Phytophthora capsici* by enhancing salicylic acid (SA) accumulation. Similarly, resistance to late blight was achieved through targeted editing of *MYBS2*. Table (2) documents some successful reports of genome editing tools.

Table 2. Successful Reports of Genome Editing Tools.

Genome Editing Techniques	Crops	Genes to be targeted	Modifications	References
ZFN	*Brassica napus*	Beta-Ketoacyl-ACP synthase II	Enhanced C18 content	(Gupta *et al.,* 2012)
	Tomato	LIL4	Delayed ripening.	(Hilioti *et al.,* 2016)
TALEN	*Brassica oleracea*	FRIGIDA	Gene targeted to a specific site.	(Sun *et al.,* 2013)
	Tomato	PROCERA	Metabolism of GA.	(Lor *et al.,* 2014)
	Wheat	TaMLO	Resistance developed against powdery mildew.	(Wang *et al.,* 2014)
	Potato	Endogenous constituent promoter	Resistance developed against the herbicide.	(Forsyth *et al.,* 2016)
		ALS	Resistance developed against the herbicide.	(Butler *et al.,* 2016)
CRISPR	*Brassica napus*	FAD2	Oleic acid content has increased.	(Okuzaki *et al.,* 2018)
	Arabidopsis	dsDNA of the virus	Resistance developed against the beet severe curly top virus.	(Ji *et al.,* 2015)
		TFL1	Resistance against viral infection.	(Zhao *et al.,* 2016)
		NPTII	Resistance against Kanamycin.	(Schiml *et al.,* 2014)
	Tobacco	dsDNA of the virus	Resistance developed against the beet severe curly top virus.	(Ji *et al.,* 2015)
	Rice	CAO1	Enhanced production of chlorophyll b.	(Miao *et al.,* 2013)
	Banana	ORF region of the virus	Resistant to banana streak virus.	(Tripathi *et al.,* 2019)
	Cucumber	eIF4E	Resistant to cucumber vein yellowing virus.	(Chandrasekaran *et al.,* 2016)
	Grape	MLO7	Resistant to powdery mildew.	(Malnoy *et al.,* 2016)
	Cacao	NPR3	Resistant to Phytophthora tropicalis.	(Fister *et al.,* 2018)
	Papaya	alEPIC8	Resistant to Phytophthora palmivora.	(Gumtow *et al.,* 2018)
	Citrus	LOB1 promoter	Resistant to citrus canker.	(Peng *et al.,* 2017)
	Apple	DIPM1, 2, 4	Resistant to fire blight disease.	(Malnoy *et al.,* 2016)
	Watermelon	ALS	Resistant to herbicides.	(Tian *et al.,* 2018)
	Kiwifruit	CEN4, CEN	Enhance the development of flowers.	(Varkonyi-Gasic *et al.,* 2019)
	Tomato	DCL2	Resistant to biotic stresses, i.e., tomato mosaic virus.	(Wang *et al.,* 2018)
		CP	Resistant to tomato yellow leaf curl virus.	(Tashkandi *et al.,* 2018)
		DMR6	Resistant to downy mildew.	Thomazella *et al.,* 2016
		PMR4	Resistant to powdery mildew.	(Koseoglou, 2017)
		JAZ2	Resistant to bacterial speck disease.	(Ortigosa *et al.,* 2019)
		PL	Enhanced shelf life.	(Uluisik *et al.,* 2016)
		Solyc08g075770	Resistant to biotic stress.	(Prihatna *et al.,* 2019)
		BOP1, BOP2, BOP3	Development of early flowering.	(Xu *et al.,* 2016)

CONCLUSION

In plants, modifications and improvements are being carried out to overcome the losses of crops due to production challenges. These modern genetic tools are ZFNs, TALENs, and the CRISPR/Cas system. CRISPR is the most popular and efficiently used genome editing tool among all these genome editing technologies. Because the CRISPR/Cas system is the most efficient genome editing tool in targeting sequences, easy to carry out, and cheap.

Despite its success, CRISPR/Cas9 still faces challenges. Efficient sgRNA design, reliable Cas9 constructs, robust transformation systems (Agrobacterium, nanoparticle-mediated delivery), and protoplast-based approaches are critical for enhancing CRISPR efficiency. Transgene-free plants can be obtained through segregation, aiding compliance with biosafety regulations.

Public perception and regulatory frameworks will significantly influence the deployment of CRISPR-edited crops. USDA has approved genome-edited crops like mushrooms and corn. Conversely, the EU currently treats genome-edited plants under GMO regulations. Nevertheless, the release of virus-resistant tomatoes in the USA and public-friendly breeding strategies highlight the growing acceptance of CRISPR technology.

CONFLICT OF INTEREST

The author declares that there are no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

FUNDING

The author did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

REFERENCES

Arumuganathan, K., Earle, E.D., 1991. Estimation of nuclear DNA content of plants by flow cytometry. Plant Mol. Biol. Rep., 9: 229–241.

Abdel-Kader, M.M., Zaki, A.Y., Kamel, S.M., 1968. Fungi associated with tomato fruits and their control. Phytopathol. Mediterr., 7: 199–205.

Akhtar, A., Abbasi, N.A., Hussain, A., 2010. Effect of calcium chloride treatments on quality characteristics of loquat fruit during storage. Pak. J. Bot., 42(1): 181–188.

Ansori, A.N., Antonius, Y., Susilo, R.J., Hayaza, S., Kharisma, V.D., Parikesit, A.A., Zainul, R., Jakhmola, V., Saklani, T., Rebezov, M., Ullah, M.E., 2023. Application of CRISPR-Cas9 genome editing technology in various fields: A review. Narra. J., 3(2): e184.

Becker, P., Fricke, W., 2002. Water relations, growth, and cell wall extensibility in the upper and lower regions of the growing barley leaf. J. Experim. Bot., 53(379): 1495–1501.

Ben-Yehoshua, S., Rodov, V., Nafussi, B., Fuchs, Y., 1992. Control of postharvest decay in citrus fruit by curing. Plant Dis., 76(10): 958–961.

Bai, Y., Huang, C.C., van der Hulst, R., Meijer-Dekens, F., Bonnema, G., Lindhout, P., 2004. QTLs for tomato powdery mildew resistance (*Oidium lycopersici*) in Lycopersicon parviflorum G1.1601 co-localize with two qualitative resistance genes. Mol. Plant-Microbe Inter., 17(11): 1171–1179.

Blum, R.W., 2005. A Case for School Connectedness. Educational Leadership, 62: 16-20.

Brooks, C., Nekrasov, V., Lippman, Z. B., Van Eck, J., 2014. Efficient gene editing in tomato in the first generation using the CRISPR/Cas9 system. Plant Physiol., 166(3): 1292–1297.

Butler, N.M., Baltes, N.J., Voytas, D.F., Douches, D.S., 2016. Geminivirus-

mediated genome editing in potato (*Solanum tuberosum* L.) using sequence-specific nucleases. Front. Plant Sci., 7: 1045.

Carelli, B.P., Gerald, L.T., Grazziotin, F.G., Echeverrigaray, S., 2006. Genetic diversity among Brazilian cultivars and landraces of tomato *Lycopersicon esculentum* Mill. revealed by RAPD markers. Genet. Resour. Crop Evol., 53(2): 395-400.

Chan, Y.L., Wang, C.N., Yeh, K.W., Hwang, S.Y., Yeh, C.H., 2005. Generation of transgenic tomato with defensin gene and enhanced resistance to *Ralstonia solanacearum*. Plant Sci., 168(4): 707–714.

Castoria, R., De Curtis, F., Lima, G., Caputo, L., Pacifico, S., De Cicco, V., 2001. *Aureobasidium pullulans* (LS30) as a biocontrol agent of postharvest brown rot of peaches. Postharvest Biol. Technol., 22(1): 7–17.

Changtian, Y., Yanan, J., Xue, Z., Zhenying, D., Yali, L., 2016. Application of CRISPR/Cas9 genome editing technology in vegetable crops. J. Agric. Biotechnol., 24(11): 1841–1850.

Chandrasekaran, J., Brumin, M., Wolf, D., Leibman, D., Klap, C., Pearlsman, M., Sherman, A., Arazi, T., Gal-On, A., 2016. Development of broad virus resistance in non-transgenic cucumber using CRISPR/Cas9 technology. Mol. Plant Pathol., 17(7):1140-53.

Chandrasekaran, M., Boopathi, T., Paramasivan, M., 2021. A status-quo review on CRISPR-Cas9 gene editing applications in tomato. Int. J. Biol. Macromol., 190: 120–129.

Collins, E.J., Bowyer, C., Tsouza, A., Chopra, M., 2022. Tomatoes: An extensive review of the associated health impacts of tomatoes and factors that can affect their cultivation. Biol., 11(2): 239.

D'hallewin, G., Schirra, M., Manueddu, E., 2000. Treatments to control postharvest diseases of peaches and nectarines. Postharv. Biol. Technol., 18(1): 35–42.

Das, H., 1999. Food processing operations analysis. New Delhi, India: Asian Books Pvt. Ltd.

Del Rio, L.A., Pastori, G.M., Palma, J.M., Sandalio, L.M., Sevilla, F., Corpas, F.J., Jiménez, A., López-Huertas, E., Hernández, J.A., 1992. The activated oxygen role of peroxisomes in senescence. Plant Physiol. Biochem., 30: 123–130.

El-Ghaouth, A., Wilson, C.L., Wisniewski, M., 2003. Control of postharvest decay of apple fruit with Candida saitoana and induction of defense responses. Postharvest Biol. Technol., 29(1): 93–100.

Fan, D., Liu, T., Li, C., Jiao, B., Li, S., Hou, Y., Luo, K., 2015. Efficient CRISPR/Cas9-mediated targeted mutagenesis in Populus in the first generation. Scient. Rep.,. 5(1): 12217.

Fister, A.S., Landherr, L., Maximova, S.N., Guiltinan, M.J., 2018. Transient expression of CRISPR/Cas9 machinery targeting TcNPR3 enhances defense response in *Theobroma cacao*. Front. Plant Sci., 9: 268.

Friedman, M., Levin, C.E., Lee, S.U., 2000. Composition of tomatoes grown in Southeast Asia: Nutrient content and health implications. J. Agric. Food Chem., 48(11): 5995–6001.

Fatima, M., Zaynab, M., Sharif, Y., Abbas, S., Zaffar, M.H., Saleem, T., 2018. Recent Advances in Plant Biotechnology and Genetic Engineering: Application in Agriculture. Int. J. Mol. Microbiol., 1(2): 40-43.

Forsyth, A., Weeks, T., Richael, C., Duan, H., 2016. Transcription activator-like effector nucleases (TALEN)-mediated targeted DNA insertion in potato plants. Front. Plant Sci., 7: 1572.

Fraser, P.D., Truesdale, M.R., Bird, C.R., Schuch, W., Bramley, P.M., 2002. Carotenoid biosynthesis during tomato fruit development (evidence for tissue-specific gene expression). Plant Physiol., 127(2): 505–513.

Fraser, P.D., Bramley, P.M., 2004. The biosynthesis and nutritional uses of carotenoids. Progress. Lipid Res., 43: 228-265.

FAO, 2016. Food and Agriculture Organization of the United Nations (FAO). FAOSTAT Database.

Gupta, M., DeKelver, R.C., Palta, A., Clifford, C., Gopalan, S., Miller, J.C., Novak, S., Desloover, D., Gachotte, D., Connell, J., Flook, J., 2012. Transcriptional activation of *Brassica napus* β-ketoacyl-ACP synthase II with an engineered zinc finger protein transcription factor. Plant Biotechnol. J., 10(7): 783-91.

Gumtow, R., Wu, D., Uchida, J., Tian, M., 2018. A *Phytophthora palmivora* extracellular cystatin-like protease inhibitor targets papain to contribute to virulence on papaya. Mol. Plant-Microbe Interac., 31(3): 363-73.

Guo, Y., Jiang, L., Zhang, T., Ma, X., An, G., 2017. Genome-wide association study of rice root traits under drought stress using a high-throughput phenotyping system. BMC Genom., 18: 377.

Gaj, T., Gersbach, C.A., Barbas, C.F., 2013. ZFN, TALEN, and CRISPR/Cas-based methods for genome engineering. Trends Biotechnol., 31(7): 397–405.

Gresshoff, P.M., Doy, C.H., 1972. Development and differentiation of haploid *Solanum lycopersicum* (tomato). Planta, 107: 161–170.

Hilioti, Z., Ganopoulos, I., Ajith, S., Bossis, I., Tsaftaris, A., 2016. A novel arrangement of zinc finger nuclease system for in vivo targeted genome engineering: the tomato LEC1-LIKE4 gene case. Plant Cell Rep., 35(11): 2241-55.

Horsch, R.B., Fry, J.E., Hoffmann, N.L., Eichholtz, D., Rogers, S.G., Fraley, R.T., 1985. A simple and general method for transferring genes into plants. Science., 227(4691): 1229–1231.

Haanstra, J.P.W., Wye, C., Verbakel, H., Meijer-Dekens, F.R., van den Berg, P.M.M.M., Odinot, P., Zabel, P., 1999. Molecular markers linked to the root-knot nematode resistance gene Mi in tomato. Theor. Appl. Genet., 99: 801–810.

Hassanein, N.M., Shoala, T., Gouda, S.A., 2018. In vitro Studies on Biological Control of Drechslera species Causing Brown Spot Disease in Rice Plants. PSM Microbiol. 3(2): 43-54.

Hobson, G.E., 1981. The short-term storage of tomato fruit. Scient. Horticult., 14(1): 57–64.

Hong, J.H., Gross, K.C., Wang, C.Y., 1999. Biochemical changes and firmness loss in tomatoes stored at chilling and non-chilling temperatures. J. Am. Soc. Horticult. Sci., 124(2): 189–193.

Hu, Z., Li, J., Ding, S., 2021. The protein kinase CPK28 phosphorylates ascorbate peroxidase and enhances thermotolerance in tomato. Plant Physiol., 186(2): 1302–1317.

Iqbal, M.N., Ashraf, A., 2017. Antagonism in Rhizobacteria: Application for Biocontrol of Soil-borne Plant Pathogens. PSM Microbiol., 2(3): 78-79.

Iqbal, M.N, Ashraf, A., 2019. Trichoderma: a Potential Biocontrol Agent for Soilborne Fungal Pathogens. Int. J. Mol. Microbiol., 2(1): 22-24.

Jenkins, J.A., 1948. The origin of the cultivated tomato. Econ. Bot., 2(4): 379–392.

Jenkins, G.I., 2017. Photomorphogenic responses to ultraviolet-B light. Plant. Cell. Environ., 40(11): 2544–2557.

Ji, X., Zhang, H., Zhang, Y., Wang, Y., Gao, C., 2015. Establishing a CRISPR–Cas-like immune system conferring DNA virus resistance in plants. Nat. Plants., 1(10): 15144.

Jia, H., Wang, N., 2014. Targeted genome editing of sweet orange using Cas9/sgRNA. PloS one. 9(4): e93806.

Jiang, W., Zhou, H., Bi, H., Fromm, M., Yang, B., Weeks, D.P., 2013. Demonstration of CRISPR/Cas9/sgRNA-mediated targeted gene modification in Arabidopsis, tobacco,

sorghum and rice. Nucleic Acids Res., 41(20): e188.

Kaiser, N., Douches, D., Dhingra, A., Glenn, K.C., Herzig, P.R., Stowe, E.C., Swarup, S., 2020. The role of conventional plant breeding in ensuring safe levels of naturally occurring toxins in food crops. Trends Food Sci. Technol., 100: 51-66.

Khan, N., Hassan, G., Ahmad, N., Iqbal, T., Ahad, F., Hussain, I., Hussain, Q., 2020. Estimation of Heritability and Genetic Advance in F_2 Populations of Wheat. PSM Biol. Res., 5(2): 61-73.

Karabulut, O.A., Baykal, N., 2002. Evaluation of the use of antagonistic yeast and hot water treatment to control postharvest diseases of peaches. Postharv. Biol. Technol., 26(2): 181–186.

Koseoglou, E., 2017. CRISPR-Cas systems in plant genome editing: An overview of applications, challenges and future prospects. J. Agric. Sci. Technol., 19(1): 23–33.

Larriba, E., Yaroshko, O., Pérez-Pérez, J.M., 2024. Recent advances in tomato gene editing. Int. J. Mol. Sci., 25(5): 2606.

Liu, C., Zhang, Y., Tan, Y., et al. 2021. CRISPR/Cas9-mediated SlMYBS2 mutagenesis reduces tomato resistance to phytophthora infestans. Int. J. Mol. Sci., 22(21): 11423.

Lester, G.E., 2005. Organic versus conventionally grown produce: Quality differences, and guidelines for future research. HortSci., 40(4): 1096–1102.

Lara, I., García, P., Vendrell, M., 2004. Modifications in cell wall composition after cold storage of calcium-treated strawberry (*Fragaria* × *ananassa* Duch.) fruit. Postharvest Biol. Technol., 34(3): 331–339.

Li, L., Steffens, J.C., 2002. Overexpression of polyphenol oxidase in transgenic tomato plants results in enhanced bacterial disease resistance. Planta., 215: 239–247.

Liang, Z., Zhang, K., Chen, K., Gao, C., 2014. Targeted mutagenesis in Zea mays using TALENs and the CRISPR/Cas system. J. Genet. Genom., 41(2): 63-8.

Lin, T., Zhu, G., Zhang, J., Xu, X., Yu, Q., Zheng, Z., Huang, S., 2004. Comparative analyses of 142 genes in tomato and related species. The Plant Cell., 16: 619–634.

Li, J.F., Norville, J.E., Aach, J., McCormack, M., Zhang, D., Bush, J., Church, G.M., Sheen, J., 2013. Multiplex and homologous recombination–mediated genome editing in *Arabidopsis* and *Nicotiana benthamiana* using guide RNA and Cas9. Nat. Biotechnol., 31(8): 688-91.

Lercari, B., Bertram, L., 2004. Light quality and hormone effects on anthocyanin accumulation in tomato hypocotyls. Biologia Plantarum., 48(4): 537–540.

Lor, V.S., Starker, C.G., Voytas, D.F., Weiss, D., Olszewski, N.E., 2014. Targeted mutagenesis of the tomato PROCERA gene using transcription activator-like effector nucleases. Plant Physiol., 166(3): 1288-91.

Luo, Y., Ma, D., Xu, Q., 2005. Improvement of lycopene production in Escherichia coli by metabolic engineering. Appl. Microbiol. Biotechnol., 70(6): 769–775.

Miao, J., Guo, D., Zhang, J., Huang, Q., Qin, G., Zhang, X., Wan, J., Gu, H., Qu, L.J., 2013. Targeted mutagenesis in rice using CRISPR-Cas system. Cell Res., 23(10): 1233-6.

Mi-Young, K., Yong-Sun, L., Byung-Dong, K., Doil, C., 2010. Overexpression of a pepper basic pathogenesis-related protein 1 gene (CaPR-1) in tobacco plants enhances resistance against heavy metal and pathogen stresses. Plant Cell Rep., 29: 1025–1035.

Mojica, F.J.M., Díez-Villaseñor, C., Soria, E., Juez, G., 2000. Biological significance of a family of regularly spaced repeats in the genomes of Archaea, Bacteria and mitochondria. Mol. Microbiol. 36(1): 244–246.

Malnoy, M., Viola, R., Jung, M.H., Koo, O.J., Kim, S., Kim, J.S., Velasco, R., Nagamangala Kanchiswamy, C., 2016. DNA-free genetically edited grapevine and apple protoplast using CRISPR/Cas9 ribonucleoproteins. Front. Plant Sci., 7: 1904.

Makarova, K.S., Haft, D.H., Barrangou, R., et al. 2011. Evolution and classification of the CRISPR–Cas systems. Nat. Rev. Microbiol., 9(6): 467–477.

Mengel, K., Kirkby, E.A., 1987. Principles of plant nutrition (4th ed.). Bern, Switzerland: International Potash Institute.

McCormick, S., Niedermeyer, J., Fry, J., Barnason, A., Horsch, R., Fraley, R., 1986. Leaf disc transformation of cultivated tomato (*Lycopersicon esculentum*) using *Agrobacterium tumefaciens*. Plant Cell Rep., 5: 81–84.

Melchers, G., Mohri, Y., Watanabe, K., Burkart, W., Dietz, P., Harada, K., 1978. Somatic hybrid plants obtained by protoplast fusion. Planta., 139(2): 123–132.

Nonaka, S., Arai, C., Takayama, M., Matsukura, C., Ezura, H., 2017. Efficient increase of ɣ-aminobutyric acid (GABA) content in tomato fruits by targeted mutagenesis. Sci. Rep., 7: 7057.

Norton, J.D., Boll, W.H., 1954. Resistance of tomato varieties to fruit cracking. Proceed. Am. Soc. Hortic. Sci., 63: 341–346.

Okuzaki, A., Ogawa, T., Koizuka, C., Kaneko, K., Inaba, M., Imamura, J., Koizuka, N., 2018. CRISPR/Cas9-mediated genome editing of the fatty acid desaturase 2 gene in *Brassica napus*. Plant Physiol. Biochem., 131: 63-9.

Ortigosa, A., Gimenez-Ibanez, S., Leonhardt, N., Solano, R., 2019. Design of a bacterial speck resistant tomato by CRISPR/Cas9-mediated editing of SlJAZ2. Plant Biotechnol. J., 17(3): 665–673.

Pugliese, M., Gullino, M.L., Garibaldi, A., 1999. Effect of chemical and biological seed treatments on the control of soilborne pathogens of tomato. Acta Hortic., 506: 219–226.

Peng, A., Chen, S., Lei, T., Xu, L., He, Y., Wu, L., Yao, L., Zou, X., 2017. Engineering canker-resistant plants through CRISPR/Cas9-targeted editing of the susceptibility gene Cs LOB 1 promoter in citrus. Plant Biotechnol. J., 15(12): 1509-19.

Peralta, I.E., Spooner, D.M., 2005. Morphological characterization and relationships of wild tomatoes (Solanum L. section Lycopersicon). Monographs in Systematic Botany from the Missouri Botanical Garden, 104: 227–257.

Pramanik, D., Shelake, R.M., Park, J., Kim, M.J., Hwang, I., Park, Y., et al. 2021. CRISPR/Cas9-mediated generation of pathogen-resistant tomato against tomato yellow leaf curl virus and powdery mildew. Int. J. Mol. Sci., 22(4): 1878.

Paran, I., van der Knaap, E., 2007. Genetic and molecular regulation of fruit and plant domestication traits in tomato and pepper. J. Experim. Bot., 58(14): 3841–3852.

Peleman, J.D., van der Voort, J.R., 2003. Breeding by design. Trends in Plant Science., 8(7): 330–334.

Prihatna, C., Chen, H.J., Hsu, Y.T., 2019. CRISPR/Cas9-mediated knockout of polygalacturonase gene in tomato confers reduced fruit softening and longer shelf life. Int. J. Mol. Sci., 20(22): 5691.

Ray, A., Langer, M., 2002. Homologous recombination: ends as the means. Trends Plant Sci., 7: 435–440

Roxana, P., Cristina, M., Gabriela, C., 2007. The influence of storage conditions on tomato fruit quality. J. Agroaliment. Process. Technol., 13(2): 579–584.

Rezk, A., Abhary, M., Akhkha, A., 2021. Tomato (*Solanum lycopersicum* L.) breeding strategies for biotic and abiotic stresses. InAdvances in Plant Breeding Strategies: Vegetable Crops: Volume 9: Fruits and Young Shoots 2021 Aug 26 (pp. 363-405). Cham: Springer International Publishing.

Roy, S., Chakrabarti, S., Hohn, T., 2006a. A geminivirus promoter drives strong

transgene expression in plants. Plant Cell Rep., 25: 137–145.

Roy, S., Ghosh, R.K., Chakrabarti, S., 2006b. Development of transgenic tomato plants resistant to Tomato leaf curl virus using AV2 gene-specific hairpin RNA. Curr. Sci., 91(6): 749–754.

Rick, C.M., Butler, L., 1956. Cytogenetics of the tomato. Adv. Genet., 8: 267–382.

Rick, C.M., 1973. Potential genetic resources in tomato species: Clues from observations in native habitats. Euphytica, 22: 521–533.

Sun, Z., Li, N., Huang, G., Xu, J., Pan, Y., Wang, Z., Tang, Q., Song, M., Wang, X., 2013. Site-S pecific Gene Targeting Using Transcription Activator-L ike Effector (TALE)-B ased Nuclease in *Brassica oleracea*. J. Integr. Plant Biol., 55(11): 1092-103.

Sun, Y., Zhang, X., Wu, C., He, Y., Ma, Y., Hou, H., Guo, X., Du, W., Zhao, Y., Xia, L. 2015. Engineering herbicide-resistant rice plants through CRISPR/Cas9-mediated homologous recombination of acetolactate synthase. Mol. Plant., 9(4): 628–631.

Shan, Q., Wang, Y., Li, J., Zhang, Y., Chen, K., Liang, Z., Zhang, K., Liu, J., Xi, J.J., Qiu, J.L., Gao, C., 2013. Targeted genome modification of crop plants using a CRISPR-Cas system. Nat. Biotechnol., 31(8): 686–688.

Senevirathna, J.D.M., Daundasekera, W.A.M., 2010. Effect of storage conditions on the shelf life of tomato (Lycopersicon esculentum Mill.) in different maturity stages. Trop. Agric. Res. Extens., 13(2): 45–50.

Sugar, D., Basile, S.R., 2008. Integrated postharvest decay control in pear fruit: Influence of controlled atmosphere, delayed cooling and sanitizing drench. Postharvest Biol. Technol., 49(3): 404–408.

Sharp, J.L., Porrit, S.W., Lidster, P.D., 1972. Hot water treatment to control postharvest decay of tomatoes. Can. J. Plant Sci., 52(1): 83–86.

Spotts, R.A., Cervantes, L.A., Mielke, E.A., 2002. Variability in postharvest decay among apple cultivars. Plant Dis., 86(5): 525–530.

Smith, C. J. S., Watson, C. F., Bird, C. R., Ray, J., Schuch, W., Grierson, D., 1988. Expression of a truncated tomato polygalacturonase gene inhibits expression of the endogenous gene in transgenic plants. Mol. Gen. Genet., 211(2): 210–215.

Shehla, N., Tariq, M., 2007. Effect of pre-cooling treatment on postharvest losses and quality of fruits. Pak. J. Agric. Sci., 44(3): 512–516.

Stenvers, N., Stork, W., 1977. The influence of low pressure storage on respiration and decay of fruits. Acta Horticult., 61: 77–84.

Sams, C.E., Conway, W.S., 1987. Physiological changes in harvested apple fruit treated with calcium chloride. HortSci., 22(5): 861–863.

Santillán Martínez, M.I., Bracuto, V., Koseoglou, E., Appiano, M., Jacobsen, E., Visser, R.G.F., Wolters, A.-M.A., Bai, Y., 2020. CRISPR/Cas9-targeted mutagenesis of the tomato susceptibility gene PMR4 for resistance against powdery mildew. BMC Plant Biol., 20: Article 284.

Sarowar, S., Kim, Y.J., Kim, E.N., Kim, K.D., Hwang, B.K., Islam, R., Shin, J.S., 2006. Overexpression of lipid transfer protein (LTP) genes enhances resistance to plant pathogens and LTP functions in long-distance systemic signaling in tobacco. Plant Cell. Rep., 25: 566–572.

Schiml, S., Fauser, F., Puchta, H., 2014. The CRISPR/C as system can be used as nuclease for in planta gene targeting and as paired nickases for directed mutagenesis in Arabidopsis resulting in heritable progeny. Plant J., 80(6): 1139-50.

Tashkandi, M., Ali, Z., Aljedaani, F., Shami, A., Mahfouz, M.M., 2018. Engineering resistance against Tomato yellow leaf curl virus via the CRISPR/Cas9 system in tomato. Plant Sign. Behav., 13(10): e1525996.

Tian, S., Jiang, L., Cui, X., Zhang, J., Guo, S., Li, M., Zhang, H., Ren, Y., Gong, G., Zong, M., Liu, F., 2018. Engineering herbicide-resistant watermelon variety through CRISPR/Cas9-mediated base-editing. Plant Cell Rep., 37(9): 1353-6.

Tiwari, J.K., Singh, A.K., Behera, T.K., 2023. CRISPR/Cas genome editing in tomato improvement: Advances and applications. Front. Plant Sci., 14: 1121209.

Thomazella, D.P.T., Brail, Q., Dahlbeck, D., Staskawicz, B., 2016. CRISPR–Cas9 mediated mutagenesis of a DMR6 ortholog in tomato confers broad-spectrum disease resistance. BioRxiv, 064824.

Thomazella, D., Seong, K., Mackelprang, R., et al. 2021. Loss of function of a DMR6 ortholog in tomato confers broad-spectrum disease resistance. Procd Natl. Acad. Sci. U.S.A. 118(27): e2026152118.

Tripathi, J.N., Ntui, V.O., Ron, M., Muiruri, S.K., Britt, A., Tripathi, L., 2019. CRISPR/Cas9 editing of endogenous banana streak virus in the B genome of Musa spp. overcomes a major challenge in banana breeding. Commun. Biol., 2(1): 46.

Trudel, M.J., Ozbun, J.L., 1971. Influence of carbohydrate concentration and temperature on translocation of ^{14}C-labeled photosynthate in tomato fruits. Plant Physiol., 47(4): 509–514.

Uluisik, S., Chapman, N.H., Smith, R., Poole, M., Adams, G., Gillis, R.B., Seymour, G.B., 2016. Genetic improvement of tomato by targeted control of fruit softening. Nat. Biotechnol., 34(9): 950–952.

Vu, T.V., Sivankalyani, V., Kim, E.J., Doan, D., Tran, M.T., Kim, J., 2020. Highly efficient homology-directed repair using CRISPR/Cpf1-geminiviral replicon in tomato. Plant Biotechnol. J., 18(10): 2133–2143.

Van Eck, J., Kirk, D.D., Walmsley, A.M., 1995. Tomato (*Lycopersicon esculentum*) as a model plant for molecular farming. Methods Mol. Biol., 44: 459–473.

Varkonyi-Gasic, E., Wang, T., Voogd, C., Jeon, S., Drummond, R.S., Gleave, A.P., Allan, A.C., 2019. Mutagenesis of kiwifruit CENTRORADIALIS-like genes transforms a climbing woody perennial with long juvenility and axillary flowering into a compact plant with rapid terminal flowering. Plant Biotechnol. J., 17(5):869-80.

Wang, C.Y., Chen, C.T., Wang, S.Y., 2001. Changes in flavonoid content of broccoli during postharvest storage and cooking. Food Chem., 74(3): 395–400.

Wang, X., Wang, Y., Huang, H., Chen, B., Chen, X., Hu, J., Chang, T., Lin, R.J., Yee, J.K., 2014. Precise gene modification mediated by TALEN and single-stranded oligodeoxynucleotides in human cells. PloS one. 9(4): e93575.

Wang, Z., Hardcastle, T.J., Pastor, A.C., Yip, W.H., Tang, S., Baulcombe, D.C., 2018. A novel DCL2-dependent miRNA pathway in tomato affects susceptibility to RNA viruses. Genes. Develop., 32(17-18): 1155-60.

Wang, B., Li, N., Huang, S., Hu, J., Wang, Q., Tang, Y., et al. 2021. Enhanced soluble sugar content in tomato fruit using CRISPR/Cas9-mediated SlINVINH1 and SlVPE5 gene editing. Peer J., 9: e12478.

Wang, P., Si, H., Li, C., Xu, Z., Guo, H., Jin, S., Cheng, H., 2025. Plant genetic transformation: achievements, current status and future prospects. Plant Biotechnol. J., 23(6): 2034-58.

Wisniewski, M.E., Wilson, C.L., Biles, C.L., 2001. Response of apple fruit to postharvest heat treatment: Effect on fungal decay and expression of heat shock proteins. Postharvest Biol. Technol., 22(3): 249–256.

Wolters, A.-M.A., Trindade, L.M., Sousa, M., Roest, S., Jacobsen, E., Schilperoort, R.A., 1993. Regeneration of *Solanum lycopersicum* L. cv. moneymaker from protoplasts. Plant Cell. Rep., 12: 113–117.

Xiaorui, W., Mengyuan, L., Shaoling, Z., and Qingmei, G., 2020. The roles of plant

cuticle in plant–pathogen interactions. Front. Plant Sci., 11: 591823.

Xu, R., Li, H., Qin, R., Wang, L., Li, L., 2016. Gene targeting using the *Agrobacterium tumefaciens*-mediated CRISPR-Cas system in rice. Rice., 9: 21.

Zaynab, M., Kanwal, S., Hussain, I., Qasim, M., Noman, A., Iqbal, U., Ali, G.M., Bahadar, K., Jamil, A., Sughra, K., Rehman, N., Buriro, M., Abbas, S., Ali, M., Alvi, A.H., Anwar, M., Khan, M.I., Tayyab, M., 2017. Rice Chitinase Gene Expression in Genetically Engineered Potato Confers Resistance against *Fusarium solani* and *Rhizictonia solani*. PSM Microbiol., 2(3): 63-73.

Zhang, H., Zhang, J., Wei, P., Zhang, B., Gou, F., Feng, Z., Mao, Y., Yang, L., Zhang, H., Xu, N., Zhu, J.K., 2014. The CRISPR/Cas9 system produces specific and homozygous targeted gene editing in rice in one generation. Plant Biotechnol. J., 12(6): 797–807.

Zhao, Y., Zhang, C., Liu, W., Gao, W., Liu, C., Song, G., Li, W.X., Mao, L., Chen, B., Xu, Y., Li, X., 2016. An alternative strategy for targeted gene replacement in plants using a dual-sgRNA/Cas9 design. Scient. Rep., 6(1): 23890.