



Advancements in biotechnology for enhancing fruit quality and nutritional value: A review

Muhammad Muhammad^{1,*}, Imran Hussain¹ and Summar Abbas Naqvi²

1, College of Horticulture, Hebei Agricultural University, Baoding, 071001, China

2, Institute of Horticultural Science, University of Agriculture Faisalabad, 38040, Pakistan

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*Corresponding author:

College of Horticulture, Hebei Agricultural University, Baoding, 071001, China.

Email: muhammadagric@gmail.com

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ABSTRACT

Purpose: Fruit species are essential for nutritional and health security, rich in micronutrients, antioxidants, and bioactive compounds. Recognized as functional foods, they meet current and future dietary requirements. Traditional breeding techniques have successfully enhanced various traits, including quality, aroma, antioxidant content, yield, and nutritional value. However, challenges such as climate change and the need for enhanced stress resistance require innovative solutions. **Findings:** Biotechnology has significantly expanded the potential for the large-scale propagation of elite clones through advancements in tissue culture, mutagenesis, and genetic transformation. Cutting-edge tools, such as CRISPR-Cas9, RNA interference (RNAi), genome-wide association studies (GWAS), and smart sensors, have revolutionised the development of novel germplasms with enhanced agronomic and nutritional traits. These technologies enable precise genetic modifications in the fruit species, boosting nutritional quality and stress tolerance. Metabolic pathway engineering allows for targeted manipulation of biochemical pathways to increase bioactive compounds, such as antioxidants and vitamins. Additionally, these innovations enhance resilience to environmental stressors such as drought, salinity, and temperature extremes, ensuring stable yields. **Limitations:** Despite significant progress, fully harnessing the potential of biotechnological tools to improve fruit quality and nutrition remains a work in progress. Challenges, such as limited genetic resources, regulatory barriers, high costs, and variable consumer acceptance, continue to limit their widespread application. **Directions for future research:** Creation of novel fruit products through biotechnology underscores the potential for trait-based enhancements, thereby opening new avenues for the development of genetically superior fruit cultivars. This review highlights the extensive applications of biotechnological approaches for improving fruit quality and nutritional value, and addressing the dynamic challenges in fruit crop enhancement.

INTRODUCTION

Fruit, a distinctive organ found in angiosperms, plays a crucial role in providing humans with dietary fibre, vitamins, and essential nutrients, as well as in global food security (Ahmed et al., 2024; Farooq et al., 2020; Li et al., 2020). According to projections, the global population is expected to attain a staggering 10 billion by 2050, presenting a formidable predicament for agriculturists and breeders to effectively address the escalating need for sustenance (Hou & Wan, 2021). However, complex genetic and environmental factors frequently affect fruit quality attributes such as colour, flavour, and nutritional value. Although traditional breeding techniques have proven effective in improving fruit harvest, they are often accompanied by the loss of genetic diversity and fitness, and the management of complex characteristics remains a challenging task (Lee et al., 2024; Meyer et al., 2013; Saini et al., 2020). However, traditional plant breeding has struggled to enhance fruit production because of several constraints. These include a lengthy juvenile period that can extend breeding programs across multiple generations of scientists. In addition, challenges arise from the erosion of natural genetic variability, unplanned transfer of undesirable genes along with desirable traits, and reproductive barriers that hinder the transfer of beneficial alleles from diverse genetic resources (Rai et al., 2014).

Some fruit crops have also been subjected to tissue culture-based technologies for crop improvement, such as somatic hybridization (Dambier et al., 2022; Liu et al., 2024), in vitro selection (Rai et al., 2014; Zhong et al., 2022), haploid and double haploid production (Jin et al., 2022), and encapsulation technology. Therefore, novel biotechnological innovations are essential to meet the growing consumer demand. In recent years, several biotechnological approaches have emerged as potential tools for understanding and modifying the features of fruit crops. Biotechnology has significantly broadened the horizons and potential of conventional approaches to crop improvement, crop protection, crop quality improvement, and enhancement of various horticultural traits (Campa et al., 2024). It has opened up amazing opportunities for fruit production by facilitating the development of new genotypes for breeding purposes, ensuring the availability of healthy and disease-free planting materials, and elevating fruit quality. Moreover, biotechnology plays a vital role in extending the shelf life of fruits and providing access to biopesticides, biofertilizers, and other beneficial products (Mihrete et al., 2024). Biotechnology facilitates the enhancement of fruit crops with vital vitamins and minerals, thereby addressing the challenges of malnutrition. Additionally, improved storage technologies stemming from biotechnological advancements contribute to minimizing postharvest losses and ensuring enhanced food security (Abdallah et al., 2025). In addition, advancements in biotechnology have enabled the integration of specifically desired traits via genetic enhancement using techniques such as genetic engineering, CRISPR-Cas9, genome editing, RNA interference, and marker-assisted selection, thereby revolutionising the landscape of fruit production and nutritional quality. These advancements contribute to a longer shelf life and enrich the nutritional composition of fruits, thereby promoting greater health benefits for consumers (Gouthu et al., 2022; Irfan et al., 2023; Penna & Jain, 2023). Genetic engineering has facilitated the development of transgenic fruit crops with improved pest resistance and nutritional value (Sushmitha et al., 2024). This approach enables isolation and incorporation of specific genes of interest in horticultural crops. The process involves ligating the target gene with a suitable vector to construct a recombinant DNA molecule, which is then introduced into the plant genome to improve traits, such as flavour, texture, and appearance (Adaskaveg et al., 2023; Brummell et al., 2022). This approach has shown promise in minimizing post-harvest losses by enhancing shelf life, delaying fruit softening, and improving resistance to post-harvest pathogens in crops such as tomato and capsicum

(Kumari et al., 2022; Wang et al., 2019). Notably, transgenic technology has been identified as a rapidly expanding field in agriculture (James, 2016; Keul et al., 2022). Ninama et al. (2024) showed that altering genes linked to the ripening process results in fruits and vegetables that remain fresh for longer durations, thus improving their transport and storage potential. This technology has enabled precise and targeted changes in the genetic material of organisms, leading to important progress in fruit crop improvement (Pal et al., 2024).

Zinc fingers are protein domains that have been extensively studied in molecular biology research. TALENs and CRISPR-Cas9 have emerged as powerful tools for gene transcription research, particularly in developing fruits with high nutrient content (Kim et al., 2017; Puchta et al., 2022). CRISPR-Cas9 a cutting-edge gene-editing technology, is used to modify specific traits, offering precise and efficient modifications to achieve desirable characteristics in fruit crops (Bhattacharyya et al., 2022; Biswas et al., 2022; Mitra et al., 2022; Nidhi et al., 2021; Sirohi et al., 2022). This has not only led to enhanced consumer satisfaction but also has significant implications for public health, as it allows consumers access to fruits with improved health benefits. A study demonstrated that CRISPR-Cas9 technology enables the modification of genes responsible for the size, taste, and ripening process of fruits. By targeting specific genes associated with aroma, sugar levels, and texture, it is possible to develop mango varieties with enhanced flavors and longer shelf lives (Antwi-Boasiako et al., 2024). Furthermore, the use of molecular markers in molecular breeding accelerates the breeding process, allowing for the rapid detection of favorable traits (Singh et al., 2024). However, a new concept has now emerged in agriculture: Horticulture 4.0. This concept encompasses various operational or developing technologies such as robotics, nanotechnology, synthetic proteins, cellular agriculture, AI, blockchain, and machine learning, which may have pervasive effects on future agriculture and food systems, offering major transformative potential (Klerkx & Rose, 2020). The integration of modern technologies has the potential to boost fruit quality, optimize resource utilization, and enhance the livelihoods of smallholder farmers. Nevertheless, the successful introduction and adoption of these technologies depends on various socioeconomic and institutional factors. Precision agriculture, a contemporary farming practice, involves the use of GPS and remote sensing by farmers to optimize resource application, minimize waste, and increase crop yields (Tolesa & Gejea, 2024). Additionally, automation and robotics can streamline horticultural machinery, enhancing efficiency and reducing labor costs. Furthermore, big data and AI can offer valuable insights for more informed decision-making in farming practices (Rathi et al., 2024). As illustrated in Figure 1, biotechnology plays a vital role in modern plant breeding by overcoming species gene transfer barriers, eliminating unreliable traits, and shortening breeding cycles, ultimately contributing to the improvement in fruit quality. This review provides an overview of recent advances in biotechnology aimed at enhancing fruit quality and nutritional value, and offers insights into the transformative impact of these technologies on fruit production and consumption. Furthermore, we discuss the future challenges and opportunities associated with the introduction of desirable alleles and refining fruit traits.

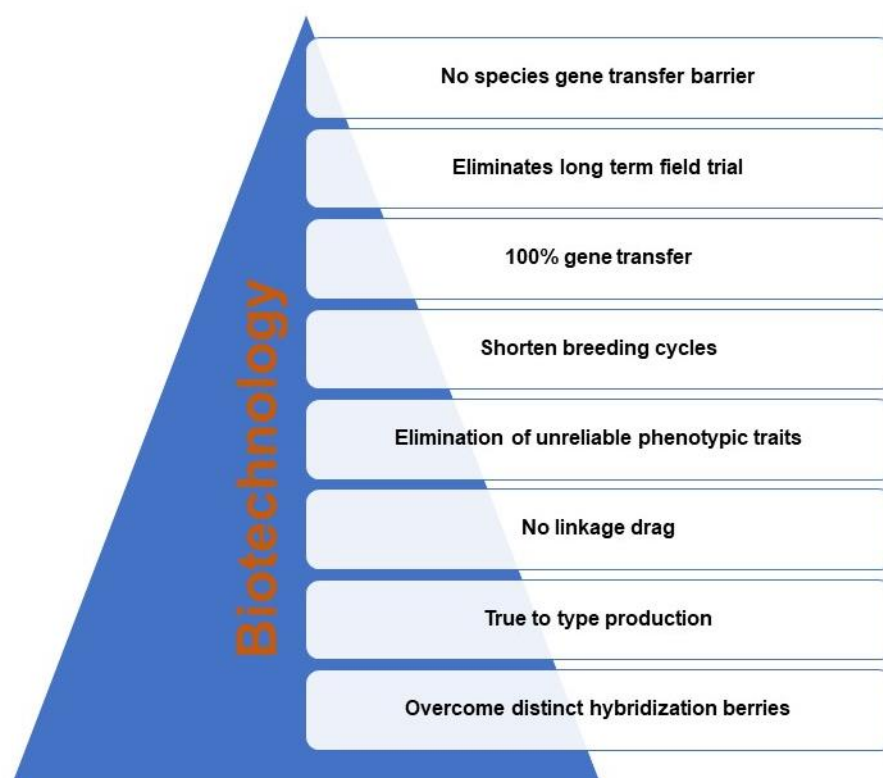


Fig. 1. Depicts the necessity of biotechnology in crop improvement, highlighting its role in addressing the limitations of traditional breeding methods.

Biotechnological strategies for enhancing fruit quality traits

Although conventional breeding methods have been employed to reduce pre- and postharvest losses, their use is restricted because they are time-consuming and labour-intensive. To augment the conventional breeding of fruit crops, a variety of biotechnological approaches, such as genetic transformation and transgenics, antisense technology, RNA interference, and genome editing, have been employed (Fig. 2). Biotechnological approaches play a key role in enhancing fruit quality and nutritional status (Bashir et al., 2023).

Transgenic overexpression method

Biotechnological tools have revolutionised molecular insights into fruit quality and plant traits. By manipulating genes from different sources and inserting them into plants, desirable traits can be imparted to improve crops (Mathiazhagan et al. 2021). This method has been particularly effective in developing fruit crops and preventing post-harvest yield losses (Irfan et al., 2023). The potential of biotechnology to further advance agricultural practices is an immense and exciting area for future research and development. The study showed that banana (*Musa acuminata*) has great economic significance in tropical regions, with commercial production spanning over 130 countries (Sau et al., 2023). However, the industry faces a significant threat from the Sigatoka leaf spot disease, which is caused by the fungus *Mycosphaerella fijiensis*. In response to this challenge, Vishnevetsky et al. (2018) have undertaken the expression of the *Trichoderma harzianum* endochitinase (ThEn-42) gene, in conjunction with the stilbene synthase gene from grape and a superoxide dismutase gene Cu,Zn-SOD from tomato, to develop transgenic banana plants. This innovative approach holds promise for addressing the impact of disease on banana production. These transgenic

banana plants displayed improved resistance to this disease under field conditions without compromising fruit quality, yield, or the Gray Mold *Botrytis cinerea*, a major fruit pathogen (Paul et al., 2017). Another study showed that the expression of *PbSPMS* in Xiusu pears improves plant resistance to both drought and salt stress (Jiang et al., 2020). Moreover, the study revealed that overexpression of the *SlORH5* gene alone effectively boosted carotenoid accumulation in tomatoes, achieving levels similar to those seen with the co-overexpression of key regulatory enzymes (SIDXS, SIPSY) (Zhang et al., 2024). Notably, transgenic lines expressing *SIBHY* produced valuable carotenoid derivatives, such as zeaxanthin and violaxanthin, along with increased sugar content and antioxidant capacity. These findings underscore a promising multi-gene stacking strategy for developing biofortified tomatoes with enhanced nutritional profiles using phytoene synthase (PSY) and iron (Brookes et al., 2020; Zhang et al., 2024). However, overexpression of kiwifruit *AeMDHAR3* negatively regulates ascorbic acid (AaA) accumulation by enhancing *MDHAR* and *APX* activities, suggesting a feedback regulatory mechanism for (AsA) content in kiwifruit (Jia et al., 2023). Moreover, with the rise of genomic tools and sequencing technologies, functional genomics has advanced significantly in fruit crops, enabling insights into traits, such as fruit quality. MYB transcription factors have been linked to the regulation of pigments and flavours, and their overexpression, such as *MYB10* in apples, has shown potential to enhance flavonoid content and improve health benefits (Allan et al., 2018; Canani et al., 2015; Espley et al., 2014). Another study showed that overexpression of *PcMYB44* enhanced the resistance of pear calli to *Botryosphaeria dothidea* by promoting lignin biosynthesis through the *PcmiR397*-*PcLACs* module and activating genes in the JA/SA/ET pathways. These findings indicated that *PcMYB44* is a crucial regulator of host resistance and provides valuable genetic resources for breeding, ultimately improving fruit quality (Lv et al., 2025). In addition to these examples using transgenic technology, several other transgenic fruit crops have also been developed, as listed in Table 1.

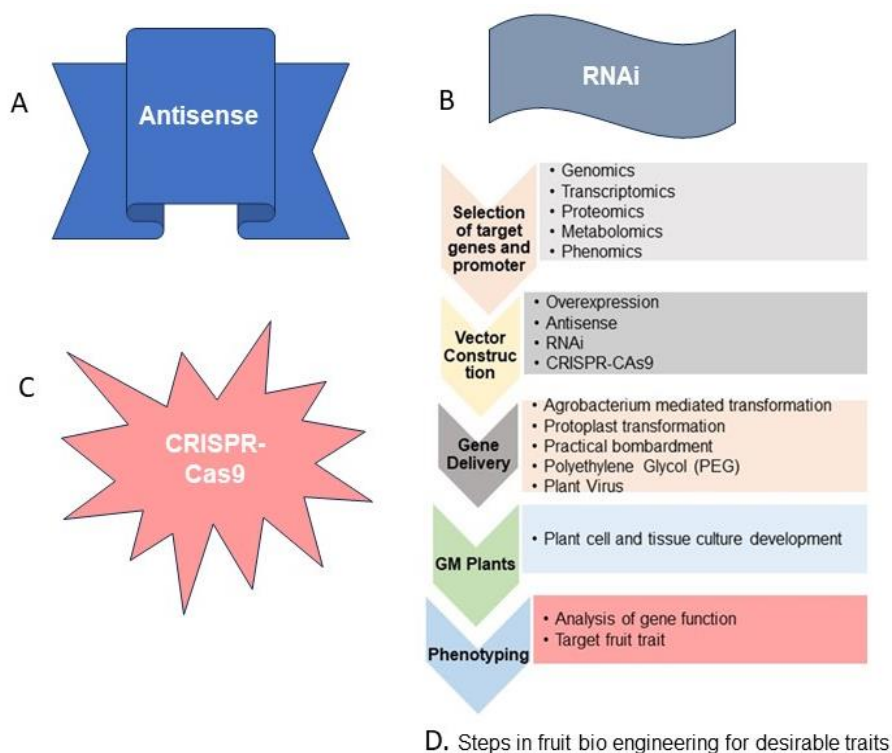


Fig. 2. Pictorial representation shows key stages in the development of genetically and genomically engineered fruit crops utilizing the above-mentioned technologies.

Table 1. Overview of biotechnological strategies employed to improve quality traits in fruit crops.

Fruits	Genes	Approaches	Application method	Functions	References
Citrus	<i>CsMYB1-CwINV6</i>	Transient overexpression	<i>Agrobacterium</i> -mediated gene transfer	Promotes soluble sugar distribution	(Khan et al., 2025)
	<i>CsPALs</i>	Transient overexpression	<i>Agrobacterium</i> -mediated gene transfer	Improved enzymatic activities and sugar content	(Wei et al., 2024)
	<i>CsGH3.1, CsGH3.1L</i>	Overexpression	<i>Agrobacterium</i> -mediated gene transfer	Resistance to <i>Xanthomonas citri</i>	(Zou et al., 2019)
	<i>CsLOB1</i>	CRISPR-Cas9	<i>Agrobacterium</i> -mediated gene transfer	Resistance against citrus canker	(Hao et al., 2016)
Pear	<i>PpZIP44</i>	Transient overexpression and RNAi	<i>Agrobacterium</i> -mediated gene transfer	Improved Flavor, texture, nutrition overall fruit quality	(Wang et al., 2023)
	<i>CAMTA2</i>	Overexpression	<i>Agrobacterium</i> -mediated gene transfer	Improved shelf life of pear fruit by inhabiting fruit ripening	(Song et al., 2024)
	<i>PbFRK1</i>	Overexpression	<i>Agrobacterium</i> -mediated gene transfer	Reregulated sugar metabolism	(Zhao et al., 2024)
Sweet Cheery	<i>IbCBF3</i>	Overexpression	<i>Agrobacterium</i> -mediated gene transfer	Improved cold and drought stress tolerance	(Irfan et al., 2023)
Mango	<i>MiRZFP34</i>	Overexpression	Floral dip method in <i>Arabidopsis thaliana</i>	Promoted early flowering and stress tolerance	(Lu et al., 2023)
Sweet orange	<i>MTSE1</i>	Virus Induced gene silencing	<i>Agrobacterium</i> -mediated gene transfer	Increased resistance to <i>Xanthomonas citri</i>	(Rodriguez et al., 2017)
	<i>CsPALs</i>	Transient overexpression	<i>Agrobacterium</i> -mediated gene transfer	Upregulated shikimate pathways and enzyme activities	(Wei et al., 2024)
Grapefruit	<i>CsLOB1</i>	CRISPR-Cas9	<i>Agrobacterium</i> -mediated gene transfer	Effective against <i>Xanthomonas citri</i>	(Gapper et al., 2014)
	<i>VvCslD5</i>	Overexpression	<i>Agrobacterium</i> -mediated gene transfer	Improved fruit firmness	(Hu et al., 2025)
Pomegranate	<i>PgUGT84A23 and PgUGT84A24</i>	CRISPR-Cas9	<i>Agrobacterium</i> -mediated gene transfer	Help in gallic acid accumulation to enhanced flavonoids contents	(Chauhan et al., 2025)
Papaya	<i>CP</i>	RNAi	Particle-bombardment transformation	Resistance against Hainan papaya ring spot virus (PRSV)	(Jia et al., 2017)
	<i>ACO1, ACO2</i>	RNAi	<i>Agrobacterium</i> -	Enhanced fruit shelf	(Kowsalya et al.,

			mediated gene transfer	life	(2024)
	<i>FveARF2-RNAi</i>	RNAi and overexpression	<i>Agrobacterium</i> -mediated gene transfer	Improved shelf life and ripening	(Yi et al., 2022)
Banana	<i>MaMADS1, MaMADS2</i>	Antisense and RNAi interference	<i>Agrobacterium</i> -mediated gene transfer	Improve fruit quality and shelf life	(Elitzur et al., 2016; Hermawaty et al., 2024)
	<i>MaACO1</i>	CRISPR-Cas9	<i>Agrobacterium</i> -mediated gene transfer	Extended fruit shelf-life period of up to 40 days	(Hu et al., 2022)
	<i>Hrap</i> and <i>Pflp10</i>	Transgenic	<i>Agrobacterium</i> -mediated gene transfer	Effective against BXW	(Jin et al., 2017)
	<i>PDS</i>	CRISPR-Cas9	<i>Agrobacterium</i> -mediated gene transfer	Improved carotenoids biosynthesis	(Naim et al., 2018)
Tomato	<i>MYB12, SGR1</i>	CRISPR-Cas9	<i>Agrobacterium</i> - mediated gene transfer	Enhanced fruit color	(Yang et al., 2023)
	<i>CLV3</i>	CRISPR-Cas9	<i>Agrobacterium</i> - mediated gene transfer	Improved fruit size, resulting in enhanced tomato yield	(Sethi et al., 2024)
	<i>CsCCD1</i>	CRISPR-Cas9	<i>Agrobacterium</i> - mediated gene transfer	Increased carotenoid contents	(Dai et al., 2025)
	<i>LCY-E, LCY-B1 and LCY-B2</i>	CRISPR-Cas9	<i>Agrobacterium</i> - mediated gene transfer	Improved lycopene content in fruit	(Li et al., 2018)
	<i>RIN</i>	CRISPR-Cas9	<i>Agrobacterium</i> - mediated gene transfer	Inhibit ethylene biosynthesis and delayed fruit senescence process	(Jung et al., 2018)
	<i>SIORRM4</i>	CRISPR-Cas9	<i>Agrobacterium</i> - mediated gene transfer	Delayed fruit ripening	(Yang et al., 2017)
Watermelon	<i>PDS</i>	CRISPR-Cas9	<i>Agrobacterium</i> - mediated gene transfer	Carotenoid biosynthesis	(Wang et al., 2019d)
Kiwifruit	<i>CEN</i>	CRISPR-Cas9	<i>Agrobacterium</i> - mediated gene transfer	Fruit development	(Varkonyi-Gasic et al. 2019)
Apple	<i>MdPGT1</i>	CRISPR-Cas9	<i>Agrobacterium</i> - mediated gene transfer	Improved plant growth and fruit size	(Miranda et al., 2023)
	<i>MdPL5</i>	Transient Overexpression	<i>Agrobacterium</i> - mediated gene transfer	Enhanced fruit firmness	(Su et al., 2024)
	<i>MdWRKY126</i>	Overexpression	<i>Agrobacterium</i> -mediated gene transfer	Upregulated sucrose phosphate synthase (SPS) activity	(Zhang et al., 2024b)

Antisense and RNAi technology

Gene silencing methods such as antisense and RNAi technologies have demonstrated significant effectiveness in enhancing the structure and characteristics of fruit crops. Antisense RNA technology is gaining momentum in agricultural research, in which complementary RNA molecules hybridise with mRNA to inhibit protein production (Malakondaiah et al., 2024). These biotechnological approaches allow for precise gene regulation, leading to improved traits such as shelf life, nutritional content, and reduced undesirable compounds. This technique, which includes RNA interference (RNAi) and long non-coding RNA (lncRNA), has been employed by crop breeders to develop new varieties by controlling the expression of specific genes (Sindhura et al., 2024). A notable example is the successful development of bananas with delayed ripening and extended shelf life, achieved by targeting two key MADS box genes, *MaMADS1* and *MaMADS2*, which are crucial in banana ripening (Tilahun et al., 2021). Similarly, Antisense RNA technology has been utilized to increase the nutritional value of crops by inhibiting genes responsible for undesirable traits. For instance, the *FLAVR SAVR* tomato was engineered to slow ripening, enhancing shelf life (Sinha et al., 2023). In tomatoes, antisense RNA targeting polygalacturonase (PG) has been shown to affect fruit texture and firmness during ripening (Wong, 2018). Li et al. (2022) investigated the enhancement of vitamin D₃ content through the knockout of *Sl7-DR2*. Post-harvest losses pose a threat to global food security, underscoring the need for crops with longer shelf lives and consistent nutritional qualities. Genetic engineering, particularly RNA interference (RNAi), offers a promising solution for controlling postharvest damage by delaying ripening, reducing browning, and enhancing disease resistance. RNAi techniques, such as SIGS, enable the application of gene silencing across diverse crop species, improving both yield quality and shelf life (Kaur et al., 2024; Singh et al., 2025). However, this technology involves the use of short double-stranded RNA (dsRNAs), small interfering RNA (siRNAs), or hairpin RNA (hpRNAs) to induce post-transcriptional gene silencing. This approach has shown promise in reducing postharvest losses by extending shelf life, preventing softening, and enhancing resistance to pathogens in crops such as tomatoes, strawberries, and bananas (Meena, 2024; Nie et al., 2024; Zhou et al., 2023). This genetic modification represents a significant milestone in agricultural biotechnology, offering the potential to improve crop quality and sustainability (Zhou et al., 2020). Pinkglow, a genetically modified pineapple (*Ananas comosus*) with altered fruit colour, delayed ripening, and senescence, was recently introduced to the US market by Del Monte. This pineapple accumulates pink flesh because of the expression of the tangerine (*Citrus reticulata*) phytoene synthase gene, which is essential for fruit carotenoid biosynthesis, and the suppression of endogenous lycopene- β and ϵ -cyclase genes (β -LYC and ϵ -LYC, respectively) through RNAi. The product has received FDA approval prior to commercialisation (Alvarez et al., 2021; Bashir et al., 2023; Firoozbady et al., 2015). Research has shown that dsRNA is transcribed in grapes (*Vitis vinifera*) and citrus crops under tissue culture conditions by administering the solution through root zone drenching or trunk injection. The aim of this study was to target the arginine kinase process of two psyllids against a brown plant hopper (Hunter et al. 2012; Saberi et al. 2023). Citrus canker disease, caused by *Xanthomonas citri* subsp. remains a major threat to citrus production, affecting both yield and fruit quality, with current control methods posing environmental risks. Recent studies demonstrated that antisense oligonucleotides (ASOs) targeting *CsLOB1* can significantly reduce disease symptoms and protect fruit quality, offering a promising, non-transgenic strategy for sustainable disease management (Lima et al., 2024). RNAi has successfully increased carotenoid and flavonoid levels in tomatoes by suppressing the *DET1* gene, demonstrating its potential for enhancing health-promoting compounds (Davuluri et al., 2005). In papaya, RNAi targeting ethylene

biosynthesis genes significantly delayed ripening, extending shelf life from 4 to 20 days (Sekeli, 2013). Both RNAi and antisense technologies can address various agricultural challenges, including resistance to biotic and abiotic stresses, and the removal of allergens. However, there are concerns regarding biosafety and potential off-target effects, necessitating thorough risk assessments for genetically modified crops (Rajam, 2021; Saurabh et al., 2014). While both technologies offer momentous improvements in fruit quality and nutrition, the ongoing estimation of their safety and environmental impact remains crucial for their widespread adoption in agriculture (Penna and Shri, 2023). Consequently, safety concerns regarding the use of genetically engineered products have arisen. Additionally, Antisense oligonucleotides (ASOs) have progressed from functional genomics tools to precision crop pest management strategies with chemical modifications to improve their stability and specificity. ASOs selectively target pest genes, offer an alternative to conventional pesticides, and enhance crop yield and quality. The potential for sustainable agriculture depends on further advancements in stability, delivery, and environmental safety (Patil et al., 2024).

Genome editing techniques for fruit crop improvement

Genome editing has swiftly become a transformative tool for precise genetic modification in plants, allowing for the targeted enhancement of key fruit traits (Zhang et al., 2021). Initially, site-directed nucleases (SDNs) like mega-nucleases (MegaNs), zinc finger nucleases (ZFNs), and transcription activator-like effector nucleases (TALENs) have been employed in the genetic engineering of fruit crops (Mishra et al., 2023; Mamrutha et al., 2024). However, recent advancements in the CRISPR-Cas9 system have revolutionised fruit crop improvement owing to its precision, cost-effectiveness, and ease of reprogramming (Guo et al., 2023; Zhou et al., 2023). CRISPR-Cas9 facilitates targeted alterations, such as gene insertion, deletion, or replacement, through sequence-specific recombination, making the process more efficient and reproducible (Shi et al., 2024). This system has been successfully applied to various fruits, including tomato (*Solanum lycopersicum*), apple (*Malus domestica*), pear (*Pyrus pyrifolia*), banana (*Musa acuminata*), and sweet cherry (*Prunus avium*), leading to delayed fruit senescence, enhanced productivity, improved fruit quality, and an extended shelf life (Fiol et al., 2022; Ming et al., 2022; Ntui et al., 2020; Zhou et al., 2023). Genetically encoded delivery methods, such as *Agrobacterium*-mediated transformation and biolistic particle delivery, have facilitated the effective implementation of CRISPR tools in plant cells (Kumari et al., 2022). Furthermore, these innovations contribute to sustainable agriculture by enhancing both the field performance and the postharvest quality of fruit crops (Zhu et al., 2020). For instance, in citrus plants, the bacterium *Xanthomonas citri* subsp. *citri* causes citrus canker, leading to severe symptoms in the stem, leaf, and fruit and significant economic losses at both the pre- and post-harvest stages (Ali et al., 2023). To address this issue, the susceptibility gene (*CsLOB1*), a key transcription factor responsible for disease expression, was eliminated using the CRISPR-Cas9 approach (Martins et al., 2020; Zou et al., 2021). Moreover, CRISPR-Cas9-mediated silencing of *CsWRKY22* enhances resistance to citrus canker by inhibiting cell hypertrophy and *CsLOB1* expression, identifying *CsWRKY22* as a key regulator of disease susceptibility and contributing to the improved post-harvest control of fruit cell size (Long et al., 2021). Similarly, CRISPR-Cas9-based mutants (*DLOB9* and *DLOB10*) with enhanced resistance to *Xanthomonas citri* were developed in Duncan grapefruit (*Citrus paradisi*) by targeting *CsLOB1* (Jia et al., 2017). Additionally, modulating the expression of genes, such as *OVATE*, *SUN*, *SIWUS*, and *SIICLV3*, can regulate tomato fruit shape, size, and locule number, with mutations in *CLV3* and *WUS* enhancing fruit size (Yuste-Lisbona et al., 2020; Zsogon et al., 2018). Furthermore, pale blue flower torenia varieties and pale purplish-pink flowered petunia varieties were created by interrupting F3H with CRISPR-Cas9 (Yu et al., 2021).

CRISPR-Cas9 technology has significant potential for extending the shelf life of tomatoes and bananas by targeting genes such as *Nr*, *alc*, *rin*, and *Cnr*, although mutations can affect colour, flavour, and nutrition (Wang et al., 2019d). Research has demonstrated that mutations in the *alc* gene and knockout of *SIPL* or *MA-ACO1* can enhance fruit firmness, delay softening, and improve storage without compromising organoleptic and nutritional qualities (Liu et al., 2022). Similarly, Tripathi et al. (2019) employed CRISPR-Cas9-mediated targeted mutagenesis to confer resistance to the banana streak virus strain *Obino l'Ewai* (BSOLV) in bananas. This editing technique also reduced softening, water loss, and damage to *B. ytestiscinerea*, without affecting other fruit quality traits. However, CRISPR-Cas9-mediated knockout of *FaPG1* in strawberry plants significantly increased fruit firmness, with firmness rising from 33% to 70%, and improved post-harvest shelf life (Lopez-Casado et al., 2023). For instance, Yang et al. (2017) developed *SIORRM4* mutants in tomatoes that resulted in delayed fruit ripening. Similarly, Li et al. (2018a) reported that targeted mutations in the *lncRNA1459* locus using CRISPR-Cas9 suppressed the ripening process Yang et al. (2023). Utilised CRISPR-Cas9-mediated knockout of *PSY1*, *MYB12*, and *SGR1* to create tomato lines with diverse fruit colours, offering a more efficient and time-saving breeding approach. Multiplex editing of genes related to carotenoid metabolism in tomatoes leads to a significant increase in lycopene content, demonstrating the potential to enhance nutrient levels through genetic manipulation (Sethi et al., 2024). Carotenoids, especially lycopene, support plant development and human health by reducing oxidative damage and disease risk; CRISPR-Cas9-mediated editing of genes like *LCY-B*, *SGR1*, and *PSY1* in tomatoes has significantly enhanced or altered lycopene accumulation during fruit ripening (Shahrour et al., 2020). CRISPR-Cas9-mediated editing of *SIGAD2*, *SIGAD3*, and key metabolic genes significantly increases GABA accumulation in tomatoes, enhancing its health benefits while affecting fruit traits (Li et al., 2018; Nonaka et al., 2017). Within this framework, CRISPR-Cas9 has shown its capability to alter the specific characteristics of fruits. For example, editing *MdMKK9* using this method resulted in a beneficial increase in anthocyanin levels, which resulted in the typical red color of apples (Sun et al., 2022). These findings highlight the potential of gene editing to manipulate bioactive compounds in fruits for nutritional enhancement. This method produces transgene-free plants with altered color phenotypes while maintaining key agronomic traits, demonstrating its potential for enhancing multigene-controlled traits in horticultural crops. Additionally, the APOBEC-Cas9 fusion-induced deletion system (AFIDs) represents an innovative approach to genome editing, particularly to enhance fruit quality and nutrition (Pacesa et al., 2024). This system leverages the precision of CRISPR-Cas9 technology to induce targeted deletions, potentially improving traits such as size, color, and nutritional value in fruit crops (Jin et al., 2020). The application of AFIDs in fruit quality and nutrition is promising, as it allows for the precise modification of the genes responsible for these traits, thereby enhancing the overall quality and nutritional profile of fruits. CRISPR-Cas9 technology, including AFIDs, can be used to improve fruit traits such as size, colour, and nutritional value by precisely editing genes that control these characteristics (Pimentel & Fortes, 2020). For instance, the targeted deletion of specific genes in grapes has been shown to potentially alter fruit skin colour, which is a key quality trait in many fruit crops (Nakajima et al., 2023). AFIDs have the potential to enhance the nutritional content of fruits by targeting genes involved in the biosynthesis of beneficial compounds. CRISPR-Cas9-mediated deletions have been used to explore the role of *FvMYB46* in flavonoid biosynthesis, which is crucial for both fruit quality and nutritional value in strawberries (Rai et al., 2024). This technology also shows promise for improving the resilience of fruits to biotic and abiotic stressors, thereby indirectly supporting nutritional quality by reducing postharvest losses (Shipman et al., 2021; Wan et al., 2021). Although AFIDs offer significant potential for

enhancing fruit quality and nutrition, challenges such as regulatory barriers, insights into gene function, and long-term safety considerations must be addressed to facilitate their effective agricultural application.

Utilizing omics and bioinformatics in fruit biotechnology

In recent years, the use of various bioinformatics and omics techniques, including genomics, metabolomics, transcriptomics, proteomics, ionomics, and phenomics, has propelled significant advancements in fruit biotechnology (Dhiman et al., 2025; Ijaz et al., 2024). These methodologies have been pivotal for enhancing fruits and vegetables, addressing quality concerns, and elucidating product deterioration. Multi-omics approaches aid breeding by identifying stress-resilient genotypes with desirable fruit traits (Roychowdhury et al., 2023). Transcriptomics reveals gene expression dynamics associated with fruit ripening and senescence, while genomics identifies key genes that regulate traits such as texture, flavour, and colour. Proteomics complements this by profiling proteins involved in postharvest metabolic processes (Mathiazhagan et al., 2021; Sang et al., 2022). Studies have demonstrated that omics methods can be employed to select slower ripening lines, modify ethylene responses, and reduce softening rates, thereby extending postharvest life and maintaining quality (Gapper et al., 2014; Habibi et al., 2024). In the past, the genomes of numerous fruits, including cassava (Wang et al., 2014), citrus (Teh et al., 2017), pomegranate (Luo et al., 2020), and lychee (Hu et al., 2022), have been sequenced using advancements in genomic sequencing technologies. Gu et al. (2024) developed a metabolite-gene association database, revealing that DNA methylation regulates carotenoid biosynthesis and ABA accumulation during pear flesh development. Inhibiting DNA methylation increased xanthophyll and β -carotene levels and identified *PbZFPI* as a key transcription factor that promotes ABA biosynthesis, suggesting that methylation delays ripening. Additionally, while cold storage extends the shelf life of fruits, it often results in chilling injuries, such as superficial scalds in apples and pears, or internal disorders in peaches and nectarines, influenced by genetics and storage conditions (Rodrigues et al., 2024). Multi-omics approaches have uncovered key pathways and regulatory mechanisms underlying these injuries, enabling targeted interventions such as 1-MCP and controlled atmosphere, which demonstrate cultivar-specific effectiveness in Granny Smith and Ladina apples (Vittani et al., 2023). Recent studies have also underscored the role of ethylene metabolism in heat stress adaptation, highlighting the need for tailored postharvest strategies to enhance fruit resilience and quality under changing climates (Nguyen et al., 2023). The sequencing of fruit crop genomes not only provides insights into their molecular evolution and genetics but also offers opportunities for developing molecular tools and breeding to improve fruit quality traits. Furthermore, the emergence of computational tools such as artificial intelligence and machine learning has facilitated the prediction of gene sequences and functional relationships between plant metabolic pathways and biological processes, particularly in rapidly accumulating but poorly annotated genomes, including those of tropical crops. Omics technologies and bioinformatics have revolutionised horticultural crop improvement by decoding complex genomes, identifying key genes, and developing genome-wide DNA markers. These advances, along with genetic engineering, have enabled the enhancement of fruit and vegetable quality traits, such as shelf life, aroma, and nutritional value, directly benefiting consumer health and agricultural productivity (Bashir et al., 2023; Fatima et al., 2023). These advancements hold great promise in the future of fruit biotechnology.

Novel smart technologies are accelerating horticultural plant breeding

Smart horticulture, utilizing technologies like AI, big data, and Internet of Things (IoT), is key to enhancing yield, resource efficiency, and productivity amid challenges like climate change and labour shortages. Integrating these technologies into breeding, cultivation, transportation, and sales will help the horticulture industry transition to a smart, automated system within the next 30 years (Zhang et al., 2023). Breeding new cultivars is crucial for improving the yield and quality of fruit crops. There are four main stages of breeding patterns. The first stage, known as artificial selection (breeding 1.0), involves breeding new cultivars with higher nutritional value based on direct observation, but it is a random and inefficient process (Moose & Mumm, 2008). The second stage, experimental design breeding (breeding 2.0), has become more popular with the rapid development of genetics and has achieved success in crops like citrus and grapes. Classical breeding in this stage produces new cultivars with improved agronomic features, but the breeding cycle length is a significant high (Ahmar et al., 2020). The third stage, molecular breeding (breeding 3.0), is emerged in the 1980s with genetic engineering and modern molecular biology, leading to the development of transgenic crops with good agronomic characteristics and high disease resistance (Qaim, 2020). The fourth stage, smart breeding (breeding 4.0), has developed in the 21st century with the advancement of computational biology and synthetic biology, driving breeding technology toward intelligence through biological and information sciences are shown in Fig 3. Smart breeding, based on important identified genes, integrates multi-omics, new-generation biotechnology, and novel information technology (i.e., AI and big data). First, the number of important genes identified using genetics i.e., through map-based cloning, quantitative trait locus (QTL) and genome-wide association analysis (GWAS) and transgenics methods are the basis for applying smart breeding. However, with further research, it is increasingly believed that the plant phenotype is determined by the genotype, environmental type I, and genotype \times environment interaction. Multi-level phytomics data (i.e., multi-omics data) includes genomics, metabolomics, phenomics, proteomics, and transcriptomics. However, seedling transplantation is the primary method for growing horticultural plants, but the quality of seedlings produced by individual farmers often fails to meet production standards. Large-scale intensive seedling nursing has emerged as a practical solution to enhance efficiency, reduce labor, and ensure the production of high-quality seedlings with strong root systems for rapid establishment after transplantation (Tay et al., 2024). Protected cultivation, utilizing controlled environments like greenhouses, ensures stable yields and quality, but requires significant labor input and environmental regulation (Liu et al., 2022). The rapid advancement of AI and machine learning has led to the development of smart monitoring systems that enable precise control over environmental and growth factors, predict pest outbreaks, and optimize plant growth dynamics (Lastochkina et al., 2022; Weiss et al., 2025). These systems, which integrate phenotypic, environmental, and stress data, facilitate smart decision-making and improve crop quality and production efficiency in both protected and open-field cultivation. These approaches assist in the analysis of complex biological changes and regulatory processes systematically, helping in the discovery of key genes and regulatory elements efficiently, which is beneficial to plant breeding (Yang et al., 2021). However, exploring and integrating this knowledge is challenging, as multivariate data are usually characterized by high dimensionality, redundancy, and noise.

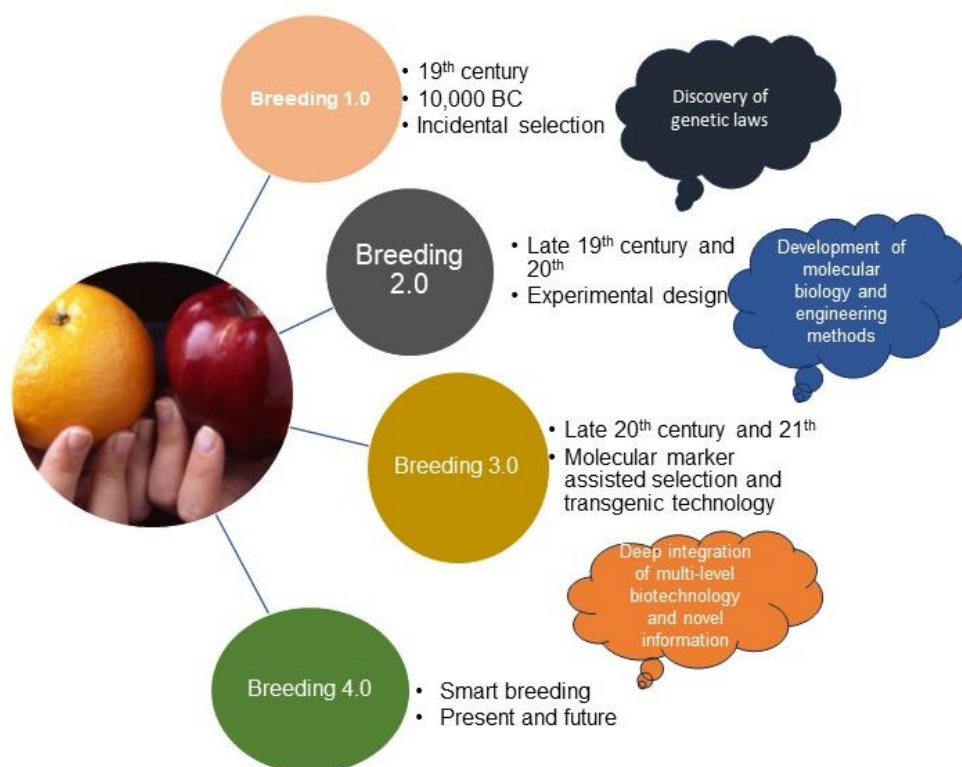


Fig. 3. Evolution of the breeding patterns of horticultural crops.

Future prospects

Continued improvements in biotechnological tools and other smart agricultural methods are expected to further improve the quality and nutritional value of fruits. The addition of artificial intelligence, machine learning, and other computational tools will enable the calculation of gene sequences and functional associations, leading to more specific genetic and genomic engineering in fruit crops. Furthermore, the progress in CRISPR-edited fruit crops holds great potential for sustainable agriculture, promoting both economically growing countries and food security. In general, the current progress in biotechnological approaches offers exciting potential for fruit quality improvement and nutritional value. Similarly, smart horticulture is still in its early stages, with most research focusing on common crops, such as citrus, grapes, and tomatoes, while other plants, such as flowers and tea, remain underexplored. Current studies primarily focus on crop-specific factors, with limited attention given to broader aspects, such as weed detection, soil health, and environmental impacts, making the development of a systematic approach challenging. Future research should integrate knowledge from industry, academia, and scientific research, leveraging emerging technologies like AI, big data, and biotechnology to enhance crop quality, yield, and sustainability.

CONCLUSION

This review primarily focuses on the application of cutting-edge biotechnological tools for genetic and genome engineering in fruit crops, aiming to reduce production losses and enhance nutritional value. By integrating breeding techniques, biotechnology, omics, and computational biology, we can develop innovative approaches for the sustainable cultivation of fruit crops. These strategies lead to improved fruit yields and enhanced postharvest

stability, ensuring the preservation of nutritional attributes. The advantages of CRISPR technology over traditional methods are evident, positioning it as a promising avenue for future research. By developing CRISPR-edited fruit crops, we can create sustainable solutions to minimize losses, ultimately benefiting economically developing countries and contributing to food security for the rapidly growing global population. However, a better and advanced understanding in the physiological mechanisms leading to fruit quality are paving the way for more sustainable and resilient agricultural systems and a better control of the postharvest ripening. By harnessing innovative technologies and interdisciplinary approaches, we can address current and future challenges in fruit production, ensuring the world-wide availability and accessibility of high-quality products. A more knowledge-based and science-driven postharvest will also contribute to promoting fruit security by minimizing fruit wastage while enhancing fruit quality. This is an exciting time for the agricultural industry and academia, with the promise that close-future discoveries will enhance our ability to feed a growing population while protecting natural resources.

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Conflict of interest

The authors have no conflict of interest to report.

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