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BIOTECHNOLOGICAL APPROACHES IN FRUIT SCIENCE: A REVIEW

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ABSTRACT

Fruit crops contribute to human nutrition, dietary diversity, agricultural income and rural livelihoods and are an important part of the world's food systems. However, conventional crop improvement faces many challenges in fruit crops due to their long juvenile phase, high heterozygosity, complex reproductive biology, and long breeding cycles. Thus, biotechnological methods have emerged as effective tools for genetic improvement, rapid propagation and conservation of valuable fruit genetic resources. *In vitro* technologies like micropropagation, somatic embryogenesis and cryopreservation enable the mass production of genetically uniform and disease-free planting material and long-term preservation of elite germplasm. The application of molecular markers, marker-assisted selection, quantitative trait locus analysis and genomics has led to increased identification and selection of genes and genomic regions associated with yield, fruit quality and stress tolerance. Progress in transcriptomics, proteomics and metabolomics has further improved the understanding of the molecular and biochemical processes underlying fruit development, ripening, nutritional quality and responses to environmental obstacles. Genetic engineering and genome-editing technologies especially the CRISPR/Cas systems can be used to precisely modify fruit quality, ripening, disease resistance, abiotic stress tolerance and shelf life. Despite these advances, genotype-dependent regeneration, transformation efficiency, off-target effects, biosafety issues, regulatory complexity, market acceptance and commercialisation are salient barriers. The combination of tissue culture, molecular breeding, multi-omics and precise genome editing is expected to be beneficial to the future fruit improvement efforts. Therefore, biotechnology has a great potential to develop fruit cultivars of high quality, durable, productive and to solve new problems in sustainable fruit farming.

Key words: Fruit crops; Biotechnology; Tissue culture; Molecular breeding; Omics; Genetic engineering; CRISPR/Cas; Fruit quality; Stress tolerance

Introduction

Fruit crops are of prime importance in global horticulture for their contributions to human nutrition,

dietary diversity, farm income and the agricultural economy. The growing awareness of the relationship between diet and human health has led to a growing

demand for fruits with improved nutritional and functional properties (Sabbadini *et al.*, 2021). The growing threats to fruit production such as climate unpredictability, new pests and diseases, water scarcity, salt and postharvest losses are demanding the development of superior cultivars with higher resilience, productivity and quality. Traditional breeding for genetic improvement of fruit crops often is much slower and more complicated than for many annual crops. Most fruit trees have in common a long juvenile phase, high heterozygosity, polyploidy or complex reproductive behaviour, self-incompatibility, seedless ness and high linkage drag. These characteristics make it difficult to fix desirable trait combinations and increase the time needed to develop and evaluate breeding populations. Since many fruit crops are perennial, evaluation of important horticultural and fruit-quality traits may require several years. Consequently, traditional breeding might not be able to react fast enough to novel production and quality problems (Dalla Costa *et al.*, 2017; Savadi *et al.*, 2021). As a result, biotechnology now plays a significant role in fruit research, enhancing rather than displacing traditional breeding. Rapid multiplication of elite genotypes, the creation of genetically homogeneous planting material, and the establishment of regeneration systems necessary for genetic transformation and genome editing are all made possible by *In vitro* methods including micropropagation, organogenesis, and somatic embryogenesis. Additionally, tissue culture has helped in cryobiological research and germplasm conservation, especially in clonally propagated and genetically complex fruit crops like apples (Teixeira da Silva *et al.*, 2019). These methods offer a crucial basis for both sophisticated molecular improvement and commercial propagation. Fruit breeding has been significantly boosted by the introduction of molecular markers, which allow DNA-based germplasm characterisation, cultivar identification, genetic diversity evaluation, and desirable allele selection. Marker-assisted methods can lessen reliance on phenotypic assessment and make it easier to choose characteristics that are challenging, costly, or time-consuming to evaluate directly (Ahmad *et al.*, 2021). Fruit improvement has thus entered an era of genomics and post-genomics study thanks to the availability of reference genomes and high-throughput sequencing. Fruit development, ripening, nutritional quality, and responses to biotic and abiotic stresses are all better understood thanks to the complementary information that transcriptomics, proteomics, and metabolomics provide on gene expression, protein abundance, and metabolite composition (Li *et al.*, 2019; Singh & Pradhan, 2020). More recently, focused fruit improvement has been made possible by novel breeding methods and genetic

engineering. While genome-editing technologies, especially CRISPR/Cas systems, enable targeted change of particular genomic sequences, genetic transformation allows the introduction or modification of genes linked to significant agronomic and quality factors. Enhancement of disease resistance, stress tolerance, plant architecture, fruit quality, nutritional composition, ripening, and shelf life are among the applications in fruit crops (Penna & Jain, 2023; Ma *et al.*, 2023). For perennial fruit crops, genome editing holds great promise since it may be able to produce precise genetic modifications without the enormous backcrossing needed in traditional breeding. The efficiency of transformation and regeneration, genotype dependence, editing specificity, biosafety, regulatory requirements, and consumer acceptability, however, continue to be significant factors (Alvarez *et al.*, 2021; Dalla Costa *et al.*, 2017). Fruit science was mostly phenotype-driven, but biotechnology has gradually changed it into an integrated system that incorporates tissue culture, molecular markers, genomics, multi-omics, genetic engineering, and precision genome editing. Fruit cultivars that combine high productivity with excellent nutritional and sensory quality, resistance to biotic and abiotic stressors, and enhanced postharvest performance can be developed more quickly thanks to these technologies. Therefore, the current study looks at the main biotechnology methods employed in fruit research, their uses in crop development and quality enhancement, their present constraints, and new prospects for precision-oriented and sustainable fruit production.

Cellular and *In vitro* Biotechnology for Fruit Crop Enhancement

Modern fruit crop enhancement now heavily relies on *In vitro* and cellular biotechnology, which allows for quick multiplication, regeneration, pathogen removal, and the preservation of priceless genetic resources. Additionally, these methods offer crucial platforms for genome editing and genetic transformation, linking traditional propagation with cutting-edge precision-breeding techniques across a variety of fruit crops (Penna & Jain, 2023; Teixeira da Silva *et al.*, 2019).

Micropropagation and Production of Disease-Free Planting Material

Because they enable the quick replication of superior genotypes under aseptic and regulated circumstances, *In vitro* culture and micropropagation have grown to be significant elements of contemporary fruit biotechnology. Micropropagation can produce a high number of genetically homogeneous plants in a comparatively short amount of time, in contrast to conventional propagation, which may be slow or constrained by the availability of

suitable propagules. Fruit crops including bananas, strawberries, grapes, apples, and citrus that are clonally propagated benefit greatly from this (Lal *et al.*, 2023; Erol *et al.*, 2023). Regeneration effectiveness is significantly influenced by genotype, explant type, basal media, and plant-growth regulators. The process typically entails culture setup, shoot multiplication, rooting and subsequent acclimatisation (Teixeira da Silva *et al.*, 2019). The creation of disease-free, healthy planting material is one of micropropagation's main uses. Meristem and shoot-tip cultures are being used in conjunction with thermotherapy, chemotherapy, micrografting, and cryotherapy to eradicate viruses because they can lower systemic pathogen burdens. In apple, pear, and other pome fruits, where virus- and viroid-free material is crucial for sustainable production and safe germplasm movement, such integrated techniques are especially significant (Bettoni *et al.*, 2024). Similar *In vitro* approaches are being developed for *Prunus* species, but traditional meristem-based virus eradication may be limited because of low regeneration capacity and heat sensitivity (Szabó *et al.*, 2024). The potential of micropropagation for quick multiplication, disease control, and the creation of consistent planting material is further demonstrated by recent advancements in papaya and banana. (Rajan *et al.*, 2025; Kumar *et al.*, 2024).

Somatic Embryogenesis, Organogenesis and Regeneration

In fruit crop development programs that need effective regeneration systems, somatic embryogenesis and organogenesis offer alternate routes for regenerating entire plants from somatic tissues. While organogenesis creates branches or roots either directly or indirectly through callus, somatic embryogenesis uses somatic cells to construct bipolar embryo-like structures. In addition to offering crucial regeneration platforms for genetic transformation and genome-editing technologies, both pathways can facilitate large-scale propagation (Penna & Jain, 2023). Fruit species and genotypes differ significantly in these processes' effectiveness. Since many genotypes of citrus have great embryogenic potential, somatic embryogenesis is helpful for regeneration, transformation, somatic hybridisation, and other biotechnological applications, making citrus one of the most investigated groups. Mango nucellar tissues have been used to create embryogenic cultures, however genotype dependence, phenolic exudation, tissue browning, and anomalies during embryo germination continue to be significant constraints (Krishna & Singh, 2007). While recent research in grapevine has focused on the integration of somatic embryogenesis with

transformation and breeding programs, guava and grapevine have both benefited from somatic embryogenesis for propagation, germplasm conservation, and genetic improvement (Chandra *et al.*, 2010; Carra *et al.*, 2024). Another effective example of how adventitious shoot proliferation, indirect organogenesis, somatic embryogenesis, and bioreactor-based multiplication have broadened the application of *In vitro* biotechnology is strawberries (Mukherjee & Gantait, 2024).

Germplasm Conservation and Cryopreservation

Protecting the genetic diversity of fruit crops, especially those that are vegetatively propagated, highly heterozygous, or challenging to maintain as seed, is becoming more and more dependent on *In vitro* conservation and cryopreservation. By slowing plant growth through regulated temperature, light, medium composition, and osmotic conditions, slow-growth storage can increase the time between subcultures while minimising labour requirements and contamination hazards (Benelli *et al.*, 2022). These methods offer an intermediate conservation strategy between long-term cryogenic storage and active field collections. Because shoot tips, latent buds, or embryogenic tissues can be preserved in liquid nitrogen with little metabolic activity, cryopreservation provides more secure long-term conservation. Numerous economically significant fruit trees have been treated with vitrification, encapsulation-dehydration, encapsulation-vitrification, and droplet-vitrification techniques (Benelli *et al.*, 2013). For vegetatively propagated crops like *Vitis*, *Malus*, *Pyrus*, *Prunus*, *Actinidia*, and others, cryo-banking is especially important because field collections are susceptible to environmental stressors, pests, diseases, and unintentional losses. Shoot-tip cryopreservation in grapevines can promote both cryotherapy-mediated virus eradication and long-term conservation (Bettoni *et al.*, 2021). Cryo-plates, cryo-mesh systems, and integrated cryobiological techniques are also highlighted as prospective tools for enhancing survival and genetic stability during storage in recent evaluations of tropical and subtropical fruit crops. Thus, a thorough *In vitro* framework for fruit crop propagation, conservation, and genetic improvement is provided by the combination of micropropagation, regeneration, slow-growth storage, and cryopreservation.

Molecular, Genomic and Omics-Based Approaches in Fruit Science

Fruit crop improvement has shifted from primarily phenotype-based selection to accurate genome-assisted breeding due to rapid advancements in molecular biology and high-throughput sequencing. The identification of genetic variation, genes, regulatory networks, and

Table 1: Major biotechnological approaches and their applications in fruit crop improvement.

Biotechnological approach	Major applications	Representative fruit crops	Principal outcomes
Micropropagation	Rapid clonal multiplication, disease-free planting material	Banana, apple, citrus, grape, strawberry	Uniform and healthy planting material
Somatic embryogenesis	Regeneration, mass propagation, transformation	Citrus, mango, grape, banana	Efficient plant regeneration
Cryopreservation	Long-term germplasm conservation	Apple, grape, citrus, strawberry	Conservation of valuable genetic resources
Molecular markers	Diversity analysis, cultivar identification, parent selection	Mango, grape, apple, citrus	Precise characterization and selection
MAS/QTL/GWAS	Selection of desirable alleles and trait mapping	Apple, peach, grape, citrus	Accelerated breeding
Genomics & genomic selection	Gene discovery and prediction of breeding value	Apple, grape, banana, citrus	Genome-assisted crop improvement
Transcriptomics	Gene-expression and pathway analysis	Mango, strawberry, grape	Identification of regulatory genes
Metabolomics	Analysis of nutritional and flavour-related metabolites	Grape, strawberry, mango	Identification of quality-associated metabolites
Genetic transformation	Introduction of specific traits	Papaya, apple, banana	Disease resistance and quality improvement
CRISPR/Cas genome editing	Targeted gene modification	Apple, grape, citrus, strawberry	Precise improvement of quality and stress traits
Source: (Penna & Jain, 2023)			

metabolites linked to economically significant traits is made possible by molecular markers, genome-wide analysis, and multi-omics technologies. Their combination offers significant chances to speed up selection and comprehend the intricate biological mechanisms that underlie fruit quality, production, and environmental adaptation (Peace, 2017; Migicovsky & Myles, 2017).

Molecular Markers and Marker-Assisted Selection

Identifying DNA polymorphisms are provided by molecular markers, which can be utilised to describe genetic variation and establish connections between phenotypic features and genomic areas. A number of marker systems have been widely used in fruit crops, such as single nucleotide polymorphisms (SNPs), random amplified polymorphic DNA (RAPD), amplified fragment length polymorphism (AFLP), and simple sequence repeats (SSR). Because they didn't require a lot of preexisting sequence information, RAPD and AFLP were very helpful in the early stages of molecular characterisation. Due to their repeatability, codominant inheritance, multi-allelic character, and utility in cultivar fingerprinting, genetic diversity research, and linkage mapping, SSR markers eventually gained significance (Varshney *et al.*, 2005). Due of their abundance in plant genomes and compatibility with high-throughput genotyping techniques, SNPs have recently gained significant value. (Mammadov *et al.*, 2012). Using

markers associated with genes or quantitative feature loci, marker-assisted selection (MAS) selects attractive individuals without solely depending on phenotypic assessment. This method is particularly useful for perennial fruit crops, where enormous plant sizes and lengthy juvenile periods make traditional selection costly and time-consuming. In apple, peach, grapevine, and several other fruit species, selection for disease resistance, fruit-quality attributes, and other horticultural qualities has been aided by molecular markers (Ru *et al.*, 2015; De Mori *et al.*, 2023). Therefore, marker-assisted breeding can increase the efficiency of selection, but it becomes less efficient for highly polygenic traits that are controlled by multiple loci with relatively tiny individual effects.

Genomics, QTL Mapping, GWAS and Genomic Selection

The genomic resources available for fruit crops have significantly increased thanks to whole-genome sequencing and next-generation sequencing. The systematic study of genome structure, gene families, allelic variation, and potential genes governing significant horticultural traits is made possible by reference genome assemblies. In crops including apple, peach, strawberry, and grapevine, high-quality genomes have been especially helpful in moving from individual molecular markers to genome-wide breeding techniques (Jung *et al.*, 2019; Daccord *et al.*, 2017). Genomic areas linked to variance

in complex characteristics are identified by quantitative trait locus (QTL) mapping. The genetic architecture of fruit size, firmness, colour, sugar and acid composition, harvest date, and resistance to significant diseases has been better understood in fruit crops thanks to QTL analysis. By taking advantage of past recombination and genetic variation among larger germplasm populations, genome-wide association studies (GWAS) supplement traditional QTL mapping. Dense SNP datasets have improved GWAS resolution and made it easier to identify candidate genes and loci linked to economically significant traits (Myles *et al.*, 2011). Instead of choosing just a small number of important loci, genomic selection (GS) simultaneously employs genome-wide marker information to forecast genomic breeding values, which is an additional step. Because of this characteristic, GS is especially helpful for complicated quantitative features that are regulated by a large number of small-effect genes. Genomic prediction has shown promise for fruit quality and breeding efficiency parameters in apples (Kumar *et al.*, 2012a). Thus, in long-lived fruit crops, combining QTL mapping, GWAS, and genomic selection can increase selection precision and possibly reduce breeding cycles (Muranty *et al.*, 2015).

Transcriptomics, Proteomics and Metabolomics

Functional information that goes beyond the DNA sequence is provided by omics technologies. Genome-wide analysis of gene-expression patterns across developmental stages, tissues, and environmental factors is made possible by transcriptomics, especially RNA sequencing. Regulatory genes and networks governing flowering, fruit development, pigmentation, ripening, softening, scent generation, and responses to biotic and abiotic stimuli have been found in fruit crops through transcriptome investigations (Gapper *et al.*, 2014). By detecting alterations in protein quantity, modification, and function, proteomics offers supplementary information. Proteomic analysis can identify post-transcriptional and post-translational regulation that cannot be sufficiently anticipated from transcriptome data alone since transcript quantity does not always correlate directly to protein abundance. Deeper understanding of the physiological changes that take place throughout fruit development and ripening has thus been made possible by integrated transcriptome and proteomic research (Yu *et al.*, 2022). Because sugars, organic acids, pigments, volatile compounds, phenolics, and other metabolites directly determine nutritional and sensory characteristics, metabolomics—which focuses on thorough characterisation of small molecules—represents a particularly useful approach for fruit-quality research.

According to (Shiratake and Suzuki, 2016) and (Zhang *et al.*, 2020), metabolomic profiling can discover chemicals linked to flavour, colour, nutritional value, and stress reactions, as well as show biochemical changes during development and ripening. Changes in metabolites can also be connected to the expression of potential biosynthetic and regulatory genes through the integration of transcriptomics and metabolomics (Osorio *et al.*, 2011). Fruit biology can be understood at the systems level by the integration of molecular markers, genomes, transcriptomics, proteomics, and metabolomics. By linking genetic variation with proteins, metabolites, gene expression, and final phenotypes, multi-omics techniques can enhance molecular breeding and candidate-gene identification. Precision breeding for improved fruit quality, productivity, stress tolerance, and response to shifting production conditions is anticipated to be strengthened by such integrated approaches.

Genetic Engineering and Genome Editing for Trait Improvement

Fruit crops where conventional breeding is limited by protracted juvenile periods, high heterozygosity, polyploidy, sterility, and limited genetic variation can now be improved thanks to genetic engineering and genome editing. While genome editing allows targeted modifications within endogenous genes while possibly maintaining the genetic background of elite crops, genetic transformation allows the insertion or modification of specific genes. Fruit crops have benefited from these technologies in terms of disease resistance, fruit quality, ripening, shelf life, nutritional composition, and stress tolerance (Song *et al.*, 2019; Lobato-Gómez *et al.*, 2021).

Genetic Transformation and Transgenic Approaches

One of the most crucial methods for stable genetic transformation of woody fruit crops is still transformation mediated by *Agrobacterium tumefaciens*. The technique selects and regenerates transformed plants after introducing a chosen gene construct into plant cells using *Agrobacterium*'s innate capacity to transport DNA. Apple, grape, citrus, kiwifruit, plum, and a number of other fruit crops have all had successful transformation systems established; however, genotype, explant type, regeneration capability, and culture conditions continue to have a significant impact on transformation efficiency (Song *et al.*, 2019). Because it can change certain traits while maintaining the desired horticultural qualities of established cultivars, direct transformation of elite cultivars is especially beneficial. One of the main goals of fruit genetic engineering has been disease and insect resistance. One of the most effective examples is papaya: transgenic papaya resistant to papaya ringspot virus

Table 2: Target traits, biotechnological strategies and potential applications in fruit crops.

Target trait	Biotechnological strategy	Biological target/process	Expected application
Disease resistance	MAS, genomics, transgenics, CRISPR/Cas	Resistance and susceptibility genes	Reduced disease losses
Drought tolerance	Transcriptomics, genomics, genome editing	Stress-responsive pathways	Improved performance under water deficit
Salinity tolerance	Omics, molecular breeding, gene editing	Ion transport and osmotic regulation	Enhanced salinity tolerance
Fruit ripening	Transcriptomics, genetic engineering, CRISPR	Ethylene and ripening-associated pathways	Controlled ripening
Shelf life	Molecular breeding, genome editing	Cell-wall degradation and softening pathways	Reduced postharvest deterioration
Nutritional quality	Metabolomics, genomics, metabolic engineering	Vitamins, carotenoids, phenolics	Enhanced nutritional value
Fruit colour	Transcriptomics, metabolomics, gene editing	Anthocyanin/carotenoid pathways	Improved colour and market appeal
Flavour and aroma	Metabolomics, transcriptomics	Volatile and secondary-metabolite pathways	Improved sensory quality
Yield/productivity	QTL mapping, MAS, genomic selection	Growth and yield-associated loci	Increased and stable productivity
Stress resilience	Multi-omics and precision breeding	Multiple stress-response pathways	Climate-resilient fruit cultivars
Source: (Sabbadini <i>et al.</i> , 2021); (Campa <i>et al.</i> , 2023); (Kumar <i>et al.</i> , 2012b)			

(PRSV) was created using pathogen-derived resistance and then commercialised, proving the usefulness of genetic engineering for shielding a fruit crop from a deadly viral disease (Fitch *et al.*, 1992). Through the production of defense-related or resistance-associated genes, transgenic methods for apple resistance to fire blight and apple scab have been studied. Similarly, citrus genetic engineering has been thoroughly investigated for resistance to Huanglongbing, citrus canker, and other diseases (Boscariol *et al.*, 2006; Orbovi  & Grosser, 2015). Additionally, transgenic methods have been used to alter fruit ripening and quality. Postharvest life may be extended by modifying ethylene production, cell-wall metabolism, and associated processes to postpone ripening and minimise softness. One example of how genetic engineering can address commercially significant quality attributes is the creation of a non-browning apple by suppressing polyphenol oxidase activity (Waltz, 2015). Additionally, enhanced firmness, nutritional composition, colour, and tolerance to environmental challenges have been studied in transgenic tomatoes, strawberries, and other fruit crops. However, the commercialisation of transgenic fruit crops may be impacted by legal requirements, public acceptance, intellectual property issues, and the presence of foreign DNA (Lobato-G mez *et al.*, 2021).

CRISPR/Cas-Mediated Genome Editing

An improved method of genetic improvement has

been made possible by the invention of CRISPR/Cas systems. A guide RNA guides the Cas9 nuclease to a complementary genomic sequence next to a suitable protospacer adjacent motif (PAM) in the traditional CRISPR/Cas9 system. Cellular processes then repair Cas9-mediated DNA cleavage, often producing tiny insertions or deletions that can interfere with target genes. CRISPR/Cas9 is particularly appealing for complex fruit genomes due to its relative simplicity, programmability, and adaptability to multiple targets as compared to previous genome-editing systems (Zhou *et al.*, 2020). In a number of fruit crops, targeted editing has already yielded significant proof-of-concept outcomes. Citrus plants with significantly increased resistance to citrus canker were produced by deleting the susceptibility gene CsLOB1, illustrating how altering host susceptibility pathways can offer an alternative to traditional resistance breeding (Jia *et al.*, 2017). Although variations in editing effectiveness and plant phenotypes highlighted the significance of precise target selection and regeneration methods, CRISPR/Cas9-mediated editing of VvMLO3 in grapevine yielded lines with increased resistance to powdery mildew (Wan *et al.*, 2020). Disruption of MdDIPM4, a susceptibility factor involved in fire-blight infection, decreased disease susceptibility in apples and showed that combining genome editing with systems intended to eliminate the editing construct is feasible (Pompili *et al.*, 2020). Multiple genes or genomic locations can be

addressed at once with multiplex genome editing. This may enable the simultaneous adjustment of disease resistance, plant architecture, or quality attributes and is especially useful for fruit qualities regulated by gene families or several pathways. The banana is a significant example because, although CRISPR/Cas9 systems have been established for trait stacking and disease resistance, conventional breeding is challenging due to its polyploid and clonally propagated nature (Tripathi *et al.*, 2020). Kiwifruit has also been shown to benefit from genome editing, which offers chances for functional characterisation and focused enhancement of genes influencing development and agronomic performance (Wang *et al.*, 2018). The precision of genome engineering has been significantly increased by the introduction of base editing and other next-generation editing tools. Base editors provide a method for replicating beneficial naturally occurring alleles or fixing particular nucleotide variants by introducing precise nucleotide replacements without inducing typical double-strand DNA breaks. Prime editing and related methods are being studied as new strategies for improving horticulture crops because they offer more flexibility for specific sequence changes (Mishra *et al.*, 2020; Zong *et al.*, 2017). For perennial fruit crops, where precise alteration of a single gene may result in a desired phenotype without prolonged breeding, these technologies may be especially beneficial.

Applications in Fruit Quality, Ripening and Stress Resistance

Considering that various fruit quality variables are regulated by distinct biochemical or developmental mechanisms, fruit quality is one of the most promising fields for genome editing. Targeted editing has the potential to increase shelf life; in strawberries, CRISPR/Cas9-mediated deletion of the polygalacturonase gene *FaPG1* produced significantly harder fruits and slower postharvest softening (López-Casado *et al.*, 2023). Genes related to sugar accumulation, acidity, pigmentation, volatile generation, cell-wall metabolism, and the manufacture of nutritious compounds can all be altered using similar techniques. By altering genes related to stress signalling, ion transport, antioxidant defence, and water-use regulation, genome editing may enhance drought, salinity, and temperature tolerance in addition to disease resistance. Another new focus is improving nutrition; gene editing is being investigated to change anthocyanin, carotenoid, and other metabolic pathways that promote health. The promise of precision breeding for biofortification is demonstrated in bananas, where editing of carotenoid-pathway genes has been studied to boost provitamin-A-related chemicals (Tripathi *et al.*, 2024).

Applications, Challenges and Future Perspectives

Improvement of Nutritional, Nutraceutical and Sensory Quality:

Nutritional and sensory enhancement: Vitamins, carotenoids, phenolic compounds, sugars, organic acids, pigments, volatile compounds, flavour, and scent are only a few of the nutritional, biochemical, and sensory aspects that affect fruit quality. Many of these characteristics have been enhanced via conventional selection, but biotechnology offers chances for more accurate control of the underlying metabolic pathways. Targeted nutritional enhancement is now possible because to the identification of candidate genes linked to the accumulation of vitamins, carotenoids, phenolics, and other bioactive chemicals made possible by molecular characterisation and novel breeding strategies (Sabbadini *et al.*, 2021). Because it offers a clear picture of biochemical composition and may be combined with genomic data to find genes governing sensory and nutritional characteristics, metabolomics is very useful (Xue *et al.*, 2025). Strawberry serves as an example of how omics and biotechnology can be combined to increase quality. Genetic and environmental variables interact to determine its colour, flavour, aroma, firmness, and nutritional composition. To better understand these characteristics, combined genomic, transcriptomic, proteomic, and metabolomic investigations are being used more frequently (Wang *et al.*, 2025). Similar techniques can be used to enhance the antioxidant capacity, pigment accumulation, flavour, and scent of grape, apple, citrus, and other fruit crops. These methods are especially important because breeding only for yield can occasionally lead to unfavourable alterations in sensory quality. Thus, simultaneous selection for productivity and consumer-preferred quality traits can be supported by integrating metabolomic data with genome-wide techniques.

Biotic/Abiotic Stress Management and Postharvest Quality:

Stress resilience and postharvest improvement: During production and storage, fruit crops are subjected to a variety of stresses, including heat, chilling, salinity, drought, insects, and diseases. Genes related to plant defence, stress signalling, ion homeostasis, and antioxidant metabolism can be altered using molecular breeding and genome editing. CRISPR/Cas technologies have already been studied for enhancing drought and salinity tolerance in horticultural crops as well as resistance against bacterial, fungal, and viral diseases (Sardar, 2023). These methods could make production systems more resilient and less reliant on chemical inputs. Because fruits continue to be metabolically active after harvest and are vulnerable

to softening, physiological problems, and microbial deterioration, postharvest losses provide a significant challenge. Biotechnology can contribute to shelf-life extension by alteration of ethylene biosynthesis and signalling, cell-wall breakdown, oxidative stress responses and pathogen resistance. According to recent assessments, ripening rate, fruit hardness, browning, and other postharvest properties can be influenced by genetic engineering, RNA-based techniques, and genome editing (Sharma *et al.*, 2025). In order to find biomarkers and potential routes for better postharvest management, multi-omics techniques also offer information on the molecular alterations linked to senescence, chilling injury, decay, and storage treatments (Belay & Caleb, 2022).

Technical, Biosafety and Regulatory Challenges:

Translation and commercialisation barriers: Despite significant advancements, biological, technical, and regulatory issues continue to limit the practical implementation of biotechnology in fruit crops. Numerous woody and perennial fruit species show poor regeneration ability, low transformation efficiency, and considerable genotype dependence in tissue culture. When genome editing is coupled with tissue culture, these restrictions become very significant because the modified cells must then regenerate into whole, fertile plants while maintaining the intended genotype. Stable inheritance, unwanted mutations, and editing specificity must all be carefully considered when modifying a genome. In many fruit crops, it is still challenging to deliver editing reagents and recover modified plants, despite the increased precision of more recent CRISPR systems. Depending on the type of genetic change, regulatory frameworks may differentiate between genome-edited plants and traditional transgenic plants. Thus, the commercial adoption of fruit cultivars produced from biotechnology can be influenced by public opinion, biosafety evaluation, intellectual property concerns, and consumer acceptance (Gouthu *et al.*, 2022). Responsible deployment will require clear communication of scientific evidence and transparent risk assessment.

Future Directions: Precision Breeding and Integrated Biotechnology:

According to individual technologies to systems of integrated breeding: Fruit biotechnology's next stage will probably involve integration as opposed to the discrete application of separate technologies. Fruit and vegetable breeding programs are increasingly using genomic selection, which may forecast breeding values for complex traits using genome-wide marker information (Lee *et al.*, 2024). Selection for characteristics including yield, fruit size, quality, and stress tolerance may be accelerated by

combining genomic selection with high-throughput phenotyping. Another potent framework is created by combining multi-omics with CRISPR-based functional validation. Candidate genes found by transcriptomics, metabolomics, or genomics can be verified experimentally and then altered via genome editing. Because they can prevent the stable introduction of foreign DNA, emerging DNA-free editing techniques utilising ribonucleoprotein complexes are especially promising; recent research in red raspberry shows both the potential of this approach and the ongoing need to improve protoplast regeneration (Creeth *et al.*, 2026). The breadth of alterations that can be made to fruit crops may be further expanded by advanced CRISPR platforms, such as base editing and other precision-editing systems (Uranga *et al.*, 2024). Additionally, it is anticipated that machine learning and artificial intelligence would grow in significance. Large genomic, phenotypic, and metabolomic information can be analysed by these methods, which can also find intricate correlations and enhance the prediction of breeding values and quality attributes. High-throughput phenotyping, genomic selection, and AI-assisted breeding may increase the effectiveness of selection while cutting down on cultivar development time and expense (Bhat *et al.*, 2023). A data-driven framework for creating fruit cultivars with enhanced nutrition, sensory quality, production, stress resilience, and postharvest performance may eventually be established through the integration of AI, multi-omics, tissue culture, genomic selection, and precise genome editing. Precision fruit breeding will be especially crucial for attaining sustainable production in the face of shifting consumer and climate conditions.

Conclusion

In offering cutting-edge instruments for quick propagation, germplasm conservation, genetic characterisation, and focused crop development, biotechnology has significantly changed fruit science. While molecular markers, genomics, and omics techniques have enhanced the comprehension and selection of genes and pathways linked to complex fruit traits, *In vitro* technologies like micropropagation, somatic embryogenesis, and cryopreservation have strengthened the production of high-quality planting material and conservation of valuable genetic resources. Opportunities to precisely improve disease resistance, stress tolerance, fruit quality, nutritional composition, ripening, and shelf life have increased thanks to genetic engineering and genome-editing technologies, especially CRISPR/Cas systems. However, as successful fruit development depends on the combination of genetic resources, phenotypic selection, and molecular technologies,

biotechnology should be viewed as a supplementary strategy rather than a replacement for traditional breeding. Future developments will depend more and more on integrating tissue culture with improved genome editing, multi-omics, genomic selection, high-throughput phenotyping, and artificial intelligence. Enhancing transformation and regeneration efficiency, reducing unwanted genetic modifications, creating science-based regulatory frameworks, and boosting customer confidence should all receive special focus. In the end, the creation of fruit cultivars that are prolific, nutritionally superior, climate-resilient, and sustainable enough to fulfil future agricultural and nutritional demands can be accelerated by an integrated and precision-oriented biotechnology framework.

References

- Ahmad, R., Anjum M.A., Naz S. and Balal R.M. (2021). Applications of molecular markers in fruit crops for breeding programs—A review. *Phyton-International Journal of Experimental Botany*, **90**(1), 17–34. <https://doi.org/10.32604/phyton.2020.011680>
- Alvarez, D., Cerda-Bennasser P., Stowe E.C., Ramirez-Torres F., Capell T., Dhingra A. and Christou P. (2021). Fruit crops in the era of genome editing: Closing the regulatory gap. *Plant Cell Reports*, **40**(6), 915–930. <https://doi.org/10.1007/s00299-021-02664-x>
- Belay, Z.A. and Caleb O.J. (2022). Role of integrated omics in unravelling fruit stress and defence responses during postharvest: A review. *Food Chemistry: Molecular Sciences*, **5**, 100118. <https://doi.org/10.1016/j.fochms.2022.100118>
- Benelli, C., De Carlo A. and Engelmann F. (2013). Recent advances in the cryopreservation of shoot-derived germplasm of economically important fruit trees of Actinidia, Diospyros, Malus, Olea, Prunus, Pyrus and Vitis. *Biotechnology Advances*, **31**(2), 175–185. <https://doi.org/10.1016/j.biotechadv.2012.09.004>
- Benelli, C., Tarraf W., Izgu T. and De Carlo A. (2022). *In vitro* conservation through slow growth storage technique of fruit species: An overview of the last 10 years. *Plants*, **11**(23), 3188. <https://doi.org/10.3390/plants11233188>
- Bettoni, J.C., Markovic Z., Bi W., Volk G.M., Matsumoto T. and Wang Q.C. (2021). Grapevine shoot tip cryopreservation and cryotherapy: Secure storage of disease-free plants. *Plants*, **10**(10), 2190. <https://doi.org/10.3390/plants10102190>
- Bettoni, J.C., Wang M.R., Li J.W., Fan X., Fazio G., Hurtado-Gonzales O.P., Volk G.M. and Wang Q.C. (2024). Application of biotechniques for *In vitro* virus and viroid elimination in pome fruit crops. *Phytopathology*, **114**(5), 930–954. <https://doi.org/10.1094/PHYTO-07-23-0232-KC>
- Bhat, J.A., Feng X., Mir Z.A., Raina A. and Siddique K.H.M. (2023). Recent advances in artificial intelligence, mechanistic models, and speed breeding offer exciting opportunities for precise and accelerated genomics-assisted breeding. *Physiologia Plantarum*, **175**(4), e13969. <https://doi.org/10.1111/ppl.13969>
- Boscariol, R.L., Monteiro M., Takahashi E.K., Chabregas S.M., Vieira M.L.C., Pereira L.F.P. and Cristofani-Yaly M. (2006). Susceptibility to citrus canker is reduced by a transgene overexpressing the AtNPR1 gene in citrus. *European Journal of Plant Pathology*, **114**, 131–140.
- Campa, M., Miranda S., Licciardello C., Lashbrooke J.G., Dalla Costa L., Guan Q., Spök A. and Malnoy M. (2023). Application of new breeding techniques in fruit trees. *Plant Physiology*, **194**(3), 1304–1322. <https://doi.org/10.1093/plphys/kiad374>
- Carra, A., Wijerathna-Yapa A., Pathirana R. and Carimi F. (2024). Development and Applications of Somatic Embryogenesis in Grapevine (*Vitis* spp.). *Plants*, **13**(22), 3131. <https://doi.org/10.3390/plants13223131>
- Chandra, R., Kamle M. and Bajpai A. (2010). Guava. In H. P. Singh, V. A. Parthasarthy and N. Babu (Eds.), *Advances in horticultural biotechnology: Vol. 1. Regeneration systems—Perennial fruit crop plants and spices* (103–120). Westville Publishers.
- Creeth, R., Thompson A. and Kevei Z. (2026). Low hanging fruit: Harvesting the potential of DNA-free genome editing in red raspberry (*Rubus idaeus*). *Plant Cell, Tissue and Organ Culture*, **164**, 98. <https://doi.org/10.1007/s11240-026-03409-y>
- Daccord, N., Celton J.M., Linsmith G., Becker C., Choise N., Schijlen E. & others (2017). High-quality de novo assembly of the apple genome and methylome dynamics of early fruit development. *Nature Genetics*, **49**, 1099–1106. <https://doi.org/10.1038/ng.3886>
- Dalla Costa, L., Malnoy M. and Gribaudo I. (2017). Breeding next generation tree fruits: Technical and legal challenges. *Horticulture Research*, **4**, 17067. <https://doi.org/10.1038/hortres.2017.67>
- De Mori, G., Cipriani G. and Testolin R. (2023). Marker-assisted selection in breeding for fruit trait improvement: A review. *International Journal of Molecular Sciences*, **24**(10), 8984. <https://doi.org/10.3390/ijms24108984>
- Erol, M.H., Dönmez D., Biçen B., Simsek Ö. and Kaçar Y.A. (2023). Modern approaches to *In vitro* clonal banana production: Next-generation tissue culture systems. *Horticulturae*, **9**(10), 1154. <https://doi.org/10.3390/horticulturae9101154>
- Fitch, M.M.M., Manshardt R.M., Gonsalves D., Slightom J.L. and Sanford J.C. (1992). Virus resistant papaya plants derived from tissues bombarded with the coat protein gene of papaya ringspot virus. *Bio/Technology*, **10**, 1466–1472. <https://doi.org/10.1038/nbt1192-1466>
- Gapper, N.E., Giovannoni J.J. and Watkins C.B. (2014). Understanding development and ripening of fruit crops in an ‘omics’ era. *Horticulture Research*, **1**, 14034. <https://doi.org/10.1038/hortres.2014.34>
- Gouthu, S., Mandelli C., Eubanks B.A. and Deluc L.G. (2022). Transgene-free genome editing and RNAi ectopic

- application in fruit trees: Potential and limitations. *Frontiers in Plant Science*, **13**, 979742. <https://doi.org/10.3389/fpls.2022.979742>
- Jia, H., Zhang Y., Orbovic V., Xu J., White F.F., Jones J.B. and Wang N. (2017). Genome editing of the disease susceptibility gene CsLOB1 in citrus confers resistance to citrus canker. *Plant Biotechnology Journal*, **15**(7), 817–823. <https://doi.org/10.1111/pbi.12677>
- Jung, S., Lee T., Cheng C.H., Buble K., Zheng P. and Yu J. *et al.* (2019). 15 years of GDR: New data and functionality in the Genome Database for Rosaceae. *Nucleic Acids Research*, **47**(D1), D1137–D1145. <https://doi.org/10.1093/nar/gky1000>
- Krishna, H. and Singh S.K. (2007). Biotechnological advances in mango (*Mangifera indica* L.) and their future implication in crop improvement: A review. *Biotechnology Advances*, **25**(3), 223–243. <https://doi.org/10.1016/j.biotechadv.2007.01.001>
- Kumar, D., Chakradhar P., Ranganna G., Vimal V.K., Raj R., Anusha C., Patra S. and Nagaraju V. (2024). Tissue Culture in Banana Cultivation: A Review of its Impact on Disease Management, Yield Improvement, and Sustainable Production. *Journal of Advances in Biology & Biotechnology*, **27**(9), 628–644. <https://doi.org/10.9734/jabb/2024/v27i91336>
- Kumar, S., Bink M.C.A.M., Volz R.K., Bus V.G.M. and Chagné D. (2012a). Towards genomic selection in apple (*Malus × domestica* Borkh.) breeding programmes: Prospects, challenges and strategies. *Tree Genetics & Genomes*, **8**(1), 1–14. <https://doi.org/10.1007/s11295-011-0425-z>
- Kumar, S., Chagné D., Bink M.C.A.M., Volz R.K., Whitworth C. and Carlisle C. (2012b). Genomic selection for fruit quality traits in apple (*Malus × domestica* Borkh.). *PLoS ONE*, **7**(5), e36674. <https://doi.org/10.1371/journal.pone.0036674>
- Lal, M., Jamwal M., Sood Y., Bakshi P., Sharma N., Sharma S. and Kumar S. (2023). Micropropagation of fruit crops: A review. *Plant Science Today*, **10**(1), 108–117. <https://doi.org/10.14719/pst.1891>
- Lee, A.M.J., Foong M.Y.M., Song B.K. and Chew F.T. (2024). Genomic selection for crop improvement in fruits and vegetables: A systematic scoping review. *Molecular Breeding*, **44**, 60. <https://doi.org/10.1007/s11032-024-01497-2>
- Li, T., Wang Y.H., Liu J.X., Feng K., Xu Z.S. and Xiong A.S. (2019). Advances in genomic, transcriptomic, proteomic, and metabolomic approaches to study biotic stress in fruit crops. *Critical Reviews in Biotechnology*, **39**(5), 680–692. <https://doi.org/10.1080/07388551.2019.1608153>
- Lobato-Gómez, M., Hewitt S., Capell T., Christou P., Dhingra A. and Girón-Calva P.S. (2021). Transgenic and genome-edited fruits: Background, constraints, benefits, and commercial opportunities. *Horticulture Research*, **8**, 166. <https://doi.org/10.1038/s41438-021-00601-3>
- López-Casado, G., Sánchez-Raya C., Ric-Varas P.D., Paniagua C., Blanco-Portales R., Muñoz-Blanco J., Pose S., Matas A.J. and Mercado J.A. (2023). CRISPR/Cas9 editing of the polygalacturonase FaPG1 gene improves strawberry fruit firmness. *Horticulture Research*, **10**(3), uhad011. <https://doi.org/10.1093/hr/uhad011>
- Ma, Z., Ma L. and Zhou J. (2023). Applications of CRISPR/Cas genome editing in economically important fruit crops: Recent advances and future directions. *Molecular Horticulture*, **3**, 1. <https://doi.org/10.1186/s43897-023-00049-0>
- Mammadov, J., Aggarwal R., Buyyarapu R. and Kumpatla S. (2012). SNP markers and their impact on plant breeding. *International Journal of Plant Genomics*, **2012**, 728398. <https://doi.org/10.1155/2012/728398>
- Migicovsky, Z. and Myles S. (2017). Exploiting wild relatives for genomics-assisted breeding of perennial crops. *Frontiers in Plant Science*, **8**, 460. <https://doi.org/10.3389/fpls.2017.00460>
- Mishra, R., Joshi R.K. and Zhao K. (2020). Base editing in crops: Current advances, limitations and future implications. *Plant Biotechnology Journal*, **18**(1), 20–31. <https://doi.org/10.1111/pbi.13225>
- Mukherjee, E. and Gantait S. (2024). Strawberry biotechnology: A review on progress over past 10 years. *Scientia Horticulturae*, **338**, 113618. <https://doi.org/10.1016/j.scienta.2024.113618>
- Muranty, H., Troggio M., Sadok I.B., Rifaï M.A., Auwerkerken A., Banchi E. and others (2015). Accuracy and responses of genomic selection on key traits in apple breeding. *Horticulture Research*, **2**, 15060. <https://doi.org/10.1038/hortres.2015.60>
- Myles, S., Boyko A.R., Owens C.L., Brown P.J., Grassi F., Aradhya M.K. and others (2011). Genetic structure and domestication history of the grape. *Proceedings of the National Academy of Sciences*, **108**(9), 3530–3535. <https://doi.org/10.1073/pnas.1009363108>
- Orbovic, V. and Grosser J.W. (2015). Citrus genetic engineering for disease resistance: Past, present and future. *Genes*, **6**(4), 1171–1190. <https://doi.org/10.3390/genes6041171>
- Osorio, S., Alba R., Damasceno C.M.B., Lopez-Casado G., Lohse M., Zanol M.I. and others (2011). Systems biology of tomato fruit development: Combined transcript, protein, and metabolite analysis of tomato transcription factor (nor, rin) and ethylene receptor (Nr) mutants reveals novel regulatory interactions. *Plant Physiology*, **157**(1), 405–425. <https://doi.org/10.1104/pp.111.175463>
- Peace, C.P. (2017). DNA-informed breeding of rosaceous crops: Promises, progress and prospects. *Horticulture Research*, **4**, 17006. <https://doi.org/10.1038/hortres.2017.6>
- Penna, S. and Jain S.M. (2023). Fruit crop improvement with genome editing, *In vitro* and transgenic approaches. *Horticulturae*, **9**(1), 58. <https://doi.org/10.3390/horticulturae9010058>
- Pompili, V., Dalla Costa L., Piazza S., Pindo M. and Malnoy M. (2020). Reduced fire blight susceptibility in apple cultivars using a high-efficiency CRISPR/Cas9-FLP/FRT-based gene editing system. *Plant Biotechnology Journal*, **18**(3), 845–858. <https://doi.org/10.1111/pbi.13253>

- Rajan, P., Kang J.H., Natraj P., Lim C.K., Kim H.B. and Kim S.C. (2025). Advances, challenges, and future prospects of *In vitro* propagation in papaya (*Carica papaya* L.). *Plant Cell, Tissue and Organ Culture*, **161**, 36. <https://doi.org/10.1007/s11240-025-03051-0>
- Ru, S., Main D., Evans K. and Peace C. (2015). Current applications, challenges, and perspectives of marker-assisted seedling selection in Rosaceae tree fruit breeding. *Tree Genetics & Genomes*, **11**, 8. <https://doi.org/10.1007/s11295-015-0834-5>
- Sabbadini, S., Capocasa F., Battino M., Mazzoni L. and Mezzetti B. (2021). Improved nutritional quality in fruit tree species through traditional and biotechnological approaches. *Trends in Food Science & Technology*, **117**, 125–138. <https://doi.org/10.1016/j.tifs.2021.01.083>
- Sardar, A. (2023). Genetic amelioration of fruit and vegetable crops to increase biotic and abiotic stress resistance through CRISPR genome editing. *Frontiers in Plant Science*, **14**, 1260102. <https://doi.org/10.3389/fpls.2023.1260102>
- Savadi, S., Mangalassery S. and Sandesh M.S. (2021). Advances in genomics and genome editing for breeding next generation of fruit and nut crops. *Genomics*, **113**(6), 3718–3734. <https://doi.org/10.1016/j.ygeno.2021.09.001>
- Sharma, R., Yadav A., Lata C., Verma A., Singh D., Rajput L.S., Joshi R., Samota M.K., Kumar S., Kumar K., Ram A., Kumar N. and Arunachalam A. (2025). Role of biotechnology for shelf-life extension and quality improvement of perishable fruits and vegetables: A comprehensive review. *Food Science and Biotechnology*, **34**(15), 3487–3506. <https://doi.org/10.1007/s10068-025-01858-3>
- Shiratake, K. and Suzuki M. (2016). Omics studies of citrus, grape and Rosaceae fruit trees. *Breeding Science*, **66**(1), 122–138. <https://doi.org/10.1270/jsbbs.66.122>
- Singh, S.K. and Pradhan S. (2020). Transcriptomics in fruit crops: Present status and future prospects. *Indian Journal of Horticulture*, **77**(4), 563–581. <https://doi.org/10.5958/0974-0112.2020.00083.3>
- Song, G., Prieto H. and Orbovic V. (2019). Agrobacterium-mediated transformation of tree fruit crops: Methods, progress, and challenges. *Frontiers in Plant Science*, **10**, 226. <https://doi.org/10.3389/fpls.2019.00226>
- Szabó, L.K., Desiderio F., Kirilla Z., Hegedűs A., Várallyay É. and Preininger É. (2024). A mini-review on *In vitro* methods for virus elimination from *Prunus* sp. fruit trees. *Plant Cell, Tissue and Organ Culture*, **156**, 42. <https://doi.org/10.1007/s11240-023-02670-9>
- Teixeira da Silva, J.A., Gulyás A., Magyar-Tábori K., Wang M.R., Wang Q.C. and Dobránszki J. (2019). *In vitro* tissue culture of apple and other *Malus* species: Recent advances and applications. *Planta*, **249**(4), 975–1006. <https://doi.org/10.1007/s00425-019-03100-x>
- Tripathi, L., Ntui V.O. and Tripathi J.N. (2020). CRISPR/Cas9-based genome editing of banana for disease resistance. *Current Opinion in Plant Biology*, **56**, 118–126. <https://doi.org/10.1016/j.pbi.2020.05.003>
- Tripathi, L., Ntui V.O. and Tripathi J.N. (2024). Application of CRISPR/Cas-based gene-editing for developing better banana. *Frontiers in Bioengineering and Biotechnology*, **12**, 1395772. <https://doi.org/10.3389/fbioe.2024.1395772>
- Uranga, M., Martín-Hernández A.M., De Storme N. and Pasin F. (2024). CRISPR–Cas systems and applications for crop bioengineering. *Frontiers in Bioengineering and Biotechnology*, **12**, 1483857. <https://doi.org/10.3389/fbioe.2024.1483857>
- Varshney, R.K., Graner A. and Sorrells M.E. (2005). Genic microsatellite markers in plants: Features and applications. *Trends in Biotechnology*, **23**(1), 48–55. <https://doi.org/10.1016/j.tibtech.2004.11.005>
- Waltz, E. (2015). Nonbrowning GM apple cleared for market. *Nature Biotechnology*, **33**, 326–327. <https://doi.org/10.1038/nbt0415-326c>
- Wan, D.Y., Guo Y., Cheng Y., Hu Y., Xiao S., Wang Y. and Wen Y.Q. (2020). CRISPR/Cas9-mediated mutagenesis of VvMLO3 results in enhanced resistance to powdery mildew in grapevine (*Vitis vinifera*). *Horticulture Research*, **7**, 116. <https://doi.org/10.1038/s41438-020-0339-8>
- Wang, Z., Wang S., Li D., Zhang Q., Li L., Zhong C., Liu Y. and Huang H. (2018). Optimized paired-sgRNA/Cas9 cloning and expression cassette triggers high-efficiency multiplex genome editing in kiwifruit. *Plant Biotechnology Journal*, **16**(8), 1424–1433. <https://doi.org/10.1111/pbi.12884>
- Wang, Z.Y., Shen A.Q., Ge Y.X., Zhou C.L., Qiao Y.S., Xiong A.S. and Wang G.L. (2025). Regulation of fruit quality formation in strawberry: From omics to biotechnology. *Peer. J.*, **13**, e19497. <https://doi.org/10.7717/peerj.19497>
- Xue, H., Liu Z., Liu W., Huang G., Wang X., Du M., Li C., Xu X., Li J., Yang X., Xiao H., Peng Y. and Zhou Y. (2025). The genomic design of fruit metabolomes. *Plant Communications*, **6**(10), 101484. <https://doi.org/10.1016/j.xplc.2025.101484>
- Yu, Y., Guo S., Ren Y., Zhang J., Li M., Tian S., Wang J., Sun H., Zuo Y., Chen Y., Gong G., Zhang H. and Xu Y. (2022). Quantitative transcriptomic and proteomic analysis of fruit development and ripening in watermelon (*Citrullus lanatus*). *Frontiers in Plant Science*, **13**, 818392. <https://doi.org/10.3389/fpls.2022.818392>
- Zhang, C. and Hao Y.J. (2020). Advances in genomic, transcriptomic, and metabolomic analyses of fruit quality in fruit crops. *Horticultural Plant Journal*, **6**(6), 361–371. <https://doi.org/10.1016/j.hpj.2020.11.001>
- Zhou, J., Li D., Wang G., Wang F., Kunjal M., Joldersma D. and Liu Z. (2020). Application and future perspective of CRISPR/Cas9 genome editing in fruit crops. *Journal of Integrative Plant Biology*, **62**(3), 269–286. <https://doi.org/10.1111/jipb.12793>
- Zong, Y., Wang Y., Li C., Zhang R., Chen K., Ran Y., Qiu J.L., Wang D. and Gao C. (2017). Precise base editing in rice, wheat and maize with a Cas9-cytidine deaminase fusion. *Nature Biotechnology*, **35**, 438–440. <https://doi.org/10.1038/nbt.3811>