The Original

MOLECULAR GENETICS OF ENZYMATIC BROWNING IN POST-HARVEST FRUITS: GENE EXPRESSION, REGULATORY NETWORKS, AND FUNCTIONAL GENOMICS

Dr Satish Kumar Sharma[1], **Dr. Shyam Singh**[*2], **Dr. Payal Devi Chandrakar**[3], **Dr. D. P. Saha**[4], **Ramnath**[5], **Dr. Birendra Prasad**[6], **Dr. Poonam**[7], **Dr Neeraj Kotwal**[8]

[1] Regional Horticulture Research Station, Sher-e-Kashmir University of Agricultural Sciences and Technology Jammu
[2] Associate Professor, Department of Plant Pathology, Indira Gandhi Krishi Vishwavidyalaya, Raipur, Chhattisgarh- 492012
[3]Assistant Professor, Entomology At Mahatma Gandhi Udyanikee evam Vanikee Vishwavidyalaya, Durg (C.G)
[4]Assoc. Prof.- cum- Sr. Scientist , Horticulture (Fruit Sc.), Dr Kalam Agricultural College, Kishanganj, Under Bihar Agricultural University, Sabour, Bhagalpur
[5]Department Agronomy, Indira Gandhi Agriculture Univesity, Raipur (C.G.)
[6]University Professor -cum-Chief Scientist, Department of Horticulture (Fruit , Bihar Agricultural University, Sabour, Bhagalpur, Bihar -813210, present posting, Dr. Kalam Agricultural College, Arrabari, Kishanganj, Bihar,. Picode- 855107
[7]Programme Assistant, KVK Jammu, SKUAST JAMMU
[8]Regional Horticulture Research Station, Sher e Kashmir University of Agricultural Sciences and Technology Jammu
*Corresponding Author: Email: ssingh.igkv2012@gmail.com

ABSTRACT

Enzymatic browning is a major post-harvest disorder that adversely affects the quality, shelf life, nutritional value, and marketability of fruits. The process is primarily driven by the oxidation of phenolic compounds catalyzed by oxidative enzymes, but recent studies indicate that browning is regulated by complex genetic, molecular, and physiological mechanisms. This review aims to synthesize current knowledge on the molecular genetics of enzymatic browning in post-harvest fruits, with particular emphasis on gene expression dynamics, regulatory networks, and functional genomics approaches involved in browning development and control. Relevant literature on post-harvest browning, transcriptomics, proteomics, metabolomics, epigenetics, gene regulation, and genome-editing technologies was critically analyzed to evaluate advances in understanding browning-associated molecular mechanisms across diverse fruit crops. Recent research has revealed that enzymatic browning is governed by intricate interactions among oxidative enzymes, phenolic metabolism, reactive oxygen species (ROS), hormonal signaling pathways, transcription factors, non-coding RNAs, and epigenetic modifications. Multi-omics technologies have enabled the identification of candidate genes, molecular markers, and regulatory pathways associated with browning susceptibility and post-harvest quality. Comparative studies across fruit species have demonstrated both conserved and species-specific molecular responses, while functional genomics tools, including RNA interference and CRISPR-based genome editing, have provided opportunities for validating key genes and improving browning resistance. Advances in molecular genetics and functional genomics have substantially improved understanding of enzymatic browning mechanisms. Integrating multi-omics, systems biology, and precision breeding approaches offers promising strategies for developing browning-resistant fruit cultivars, enhancing post-harvest quality, and reducing global post-harvest losses.

KEYWORDS: Enzymatic browning; Post-harvest fruits; Gene expression; Functional genomics; Multi-omics integration.

1. INTRODUCTION

Post harvest losses are a significant problem in global fruit and vegetable value chains as it impacts food security, marketability and consumer acceptance. Enzymatic browning is among the several post-harvest physiological disorder that is one of the most important economically since it quickly reduces visual acceptability, nutritional value and shelf life of the product. It is a problem in fresh-cut and minimally processed commodities where cellular components are exposed to oxidative reactions due to tissue disruption in the processing. The phenomenon has been reported on a variety of fruit crops and it is influenced by physiological and biochemical characteristics of the species (Martínez-González et al., 2017). More recently, there has been a growing focus on elucidating the molecular mechanisms involved in the development of browning, particularly in economically valuable fruit crops like apples, where enzymatic browning is a major concern for both consumer preference and industrial processing (Sultan et al., 2025).

The socio-economic impact of post harvest browning has implications throughout the agricultural supply chain, leading to lower market value, greater waste production and significant monetary losses to the producers, distributors and retailers. Browning is often accompanied by undesirable changes in texture, flavor, aroma and nutritional composition. The same has been observed in vegetable crops where post harvest physiological activities keep on going after harvest and can lead to loss of quality if poorly managed. Therefore, it is necessary to understand these physiological changes in order to develop effective preservation methods and enhance the post-harvest management systems (Yang et al., 2025).

Enzymatic browning is a complex biological phenomenon which is the oxidation of phenolic compounds mainly by polyphenol oxidase (PPO) and other oxidative enzymes. The result is a series of quinones, which in turn polymerise to form brown pigments which are deposited in the tissues of the plant. The browning process, however, is not just a biochemical response, but a complex process comprising metabolic rewiring, membrane disruption, oxidative stress and coordinated gene regulation, as recently shown. The complexity of the molecular processes involved in post-harvest browning of pomegranate fruit has been revealed by investigations involving various metabolic pathways (Qi et al., 2022). In addition, there is growing evidence that changes in membrane integrity can play an important role as a trigger that allows the interaction between the oxidative enzymes and their phenolic substrates to occur as the browning process progresses (Yuan et al., 2025).

Thanks to recent development of high throughput "omics" technologies, the study of post-harvest physiology and enzymatic browning has changed. The use of integrated methods with transcriptomic, proteomic, metabolomic and systems biology has provided insights into the identification of important genes, pathways and regulatory networks that underlie browning susceptibility and resistance. Multi-omics analyses have given unprecedented insights into the molecular basis of enzymatic browning in various crop species, and have helped to identify candidate biomarkers and regulatory genes of post-harvest quality maintenance (Wang et al., 2024). In a similar manner, omics studies have improved the understanding of the physiology and metabolism of fruit and vegetables in post-harvest and allowed the development of targeted strategies of intervention (Habibi et al., 2024).

In fruit crops, the use of omics technologies has been particularly valuable, and integrated genomic, transcriptomic and metabolomic studies have helped to clarify key molecular events involved in ripening and in the biosynthesis of VOCs and in the development of quality during post harvest storage in peach (Sirangelo et al., 2022a). Further multi-omic studies have further illustrated the power of systems-level analyses to discover underlying regulatory mechanisms that control fruit physiology and post-harvest responses and help lay the groundwork for functional genomics-based crop improvement (Sirangelo et al., 2022b).

This review focuses on the latest developments regarding the molecular genetics of enzymatic browning after harvest in fruit, especially in regard to gene expression changes, regulatory networks, and functional genomics. The review consolidates the available information obtained from transcriptomic, proteomic, metabolomic, epigenetic and genome-editing studies to give a complete overview of the mechanisms underlying browning development. It also provides an insight into new molecular approaches for browning avoidance and outlines future research areas that could help create cultivars with browning resistance and enhance post-harvest processing.

2. Biochemical and Physiological Foundations of Enzymatic Browning

2.1 Mechanisms of Enzymatic Browning in Fruits

Enzymatic browning is one of the processes which have been subject to much scientific study in relation to their effects on the quality of fruits and their marketability. Enzymatic browning starts with disruption of cellular compartmentation due to factors such as harvest, mechanical damage, processing, aging, and environmental stress. Oxidative enzymes and the phenolic substrate exist in two separate cells under normal physiological conditions. Disruption of cells causes them to react in the presence of oxygen to produce oxidative reaction and the formation of brown pigments from phenols. The quinones produced by polyphenol oxidase (PPO) undergo polymerization reaction forming melanins which are the cause of the dark color observed in tissues. Factors influencing this process include enzyme activity, substrate concentration, presence of oxygen, tissue structure, and storage conditions. The direct impact of this process on visual quality and nutrition makes it important in post-harvest physiology research (Sultan et al., 2025).

2.2 Oxidative Enzymes and Phenolic Metabolism

The biochemical basis for enzymatic browning involves the activity of oxidative enzymes in combination with phenolic metabolites. The two major enzymes involved in this process are polyphenol oxidase and peroxidase, which help catalyze oxidation reactions that transform phenolic substrates into quinone products. Quinones then undergo a number of non-enzymatic condensation and polymerization reactions that result in the formation of pigments. Thus, sensitivity to enzymatic browning among fruits is correlated with the quantity and quality of oxidative enzymes, as well as the presence of various phenolic substrates in tissue. Recent studies on metabolic pathways related to browning development have shown that several interacting pathways, such as phenylpropanoid biosynthesis, flavonoid metabolism, and oxidation resistance-related pathways, can cause browning. Consequently, it appears that browning development does not depend solely on one pathway, but rather results from the regulation of several metabolic pathways (Qi et al., 2022).

2.3 Reactive Oxygen Species and Membrane Integrity

Reactive oxygen species (ROS) are fundamental components during post-harvest browning. Accumulation of superoxide radicals, hydrogen peroxide, and hydroxyl radicals leads to an imbalance within cells, promoting lipid peroxidation and loss of membrane integrity. Deterioration of membranes results in the interaction of oxidative enzymes and phenolic compounds, thus hastening the process of browning. Recent research has shown that controlling the levels of ROS contributes significantly to preventing enzymatic browning and ensuring high-quality post-harvest products. For instance, exposure to nitric oxide has been shown to help control oxidation stress, ROS scavenging mechanisms, and reduce browning in post-harvest mushrooms by preserving cellular redox state (Gao et al., 2023). Also, the signaling role of nitric oxide via S-nitrosylation of proteins in plants has been established as an important strategy in improving stress tolerance and extending shelf-life by modulating ethylene biosynthesis and oxidative processes at low temperatures (Sougrakpam et al., 2023).

2.4 Environmental and Post-Harvest Factors Influencing Browning

The incidence and extent of enzymatic browning depend greatly on the surrounding and post-harvest environments. Environmental factors including temperature variations, chilling injuries, mechanical injuries, infection with fungi, availability of oxygen, and duration of storage are known to influence cell metabolism and oxidation reactions. The infection of harvested fruits and vegetables with post-harvest fungal pathogens has gained much importance since they damage tissues, induce oxidative stress responses, and expedite senescence-induced deteriorations. Amongst these fungal pathogens, B. cinerea has emerged to be the most deleterious contributor to post-harvest decay in produce using its pathogenic strategies for causing tissue deterioration (Hua et al., 2018). On the contrary, the use of exogenous application of biologically active compounds such as melatonin has become an area of major interest in preserving fruit quality. Various studies have shown that melatonin administration improves antioxidant activities, reduces oxidative damages, and decreases the rate of post-harvest decay, hence reducing the development of browning symptoms in fruits (Chen et al., 2020).

2.5 Species-Specific Browning Responses

The degree to which fruits become susceptible to enzymatic browning depends on different factors for various fruit species and varieties. These factors include genetic makeup, phenolic content, antioxidative status, and the body's response to stress. Species-specific control of ROS generation and antioxidative defenses is important when considering the susceptibility of fruits to enzymatic browning. Specifically, the relationship between melatonin and ROS is relevant in establishing antioxidant defense and resistance to post-harvest stresses (Li et al., 2023). The biochemical events that lead to enzymatic browning are illustrated in Figure 1.

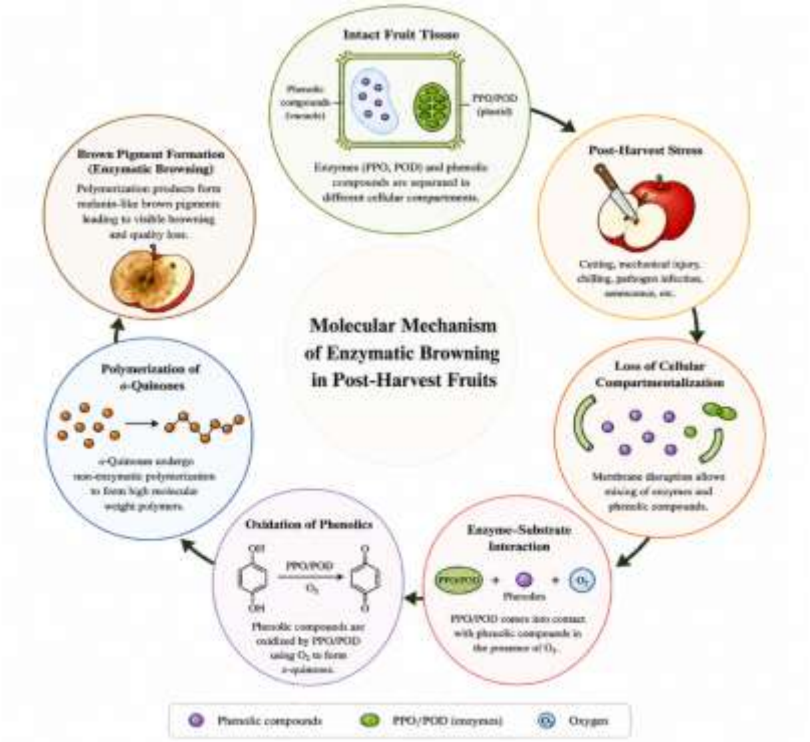

Figure 1. Molecular mechanism of enzymatic browning in post-harvest fruits

As shown in Figure 1 below, enzymatic browning results from the occurrence of a series of biochemically-coordinated reactions following exposure to post-harvest stress. Other than these physiological mechanisms, genes and gene regulation are major contributors that influence the extent to which fruits become susceptible to browning.

3. Genetic Architecture and Gene Expression Dynamics of Enzymatic Browning

3.1 Genetic Determinants of Browning Susceptibility

Susceptibility to enzyme-brownings varies significantly depending on the genetic makeup of the fruit. This genetic makeup will determine the presence and functioning of oxidative enzymes, phenolic compounds, and antioxidant defense systems. Browning is not a monogenic trait but is controlled by many genes. The variation in susceptibility to enzyme-browning seen in different varieties of fruits and fruits species is often due to variations in gene expressions responsible for maintaining cellular structure and membranes, phenolic metabolism, and physiological and biochemical response to stresses post-harvesting. Research work done on peaches suggests that susceptibility to cold storage disorder is dependent on coordinated expressions of many genes involved in the maintenance of cellular structure and metabolic activities (Pons et al., 2016).

3.2 Expression Profiles of Browning-Related Genes

Recent advancements in transcriptomics technologies have greatly enhanced knowledge concerning the role of genes in enzymatic browning. The differential expression of genes involved in the process of browning has shown that the process is characterized by considerable transcriptional modifications related to oxidative metabolism, phenylpropanoid metabolism, antioxidant mechanisms, membrane transport, and cellular stress response systems. Transcriptome analysis in peach fruits subjected to cold storage showed large-scale variations in the expression levels of the genes involved in the process of browning, indicating that chilling-induced browning is controlled via transcriptional modulation in relation to multiple metabolic processes (Badrunnesa et al., 2025). Similarly, transcriptome studies on fresh-cut eggplants have identified a number of genes responsible for the process of browning through their involvement in oxidative reactions and phenol metabolism, thus enhancing understanding of the mechanism of susceptibility to browning (Liu et al., 2021). Likewise, investigations on the transcriptional responses to various stresses in pineapples have provided useful information on the use of gene expression profiles as molecular markers for post-harvest physiological changes (Sinaga & Marpaung, 2024).

3.3 Stress-Responsive and Hormone-Regulated Genes

Hormones in plants are crucially important for the regulation of physiology after harvest and the regulation of processes associated with browning. Hormonal signaling cascades regulate ripening, senescence, stress response, antioxidant capacity, and metabolism, which altogether affect the maintenance of the quality during post-harvesting. The latest research conducted on a transcriptome level revealed different ripening mechanisms regulated by the interaction between phytohormones, physiological conditions, and gene expressions in kiwi fruits (Lin et al., 2024), which underlines the importance of the regulation of physiology by hormones during post-harvesting. The role of ethylene response genes is especially significant since they control multiple processes associated with ripening and susceptibility to chilling injuries and oxidative stress. It was also shown that the regulation of the ripening process of kiwifruit occurs through ethylene signaling pathway at the level of the transcriptional network (Salazar et al., 2021). The genome analysis of bananas also revealed an extensive abscisic acid (ABA) regulatory network affecting development, ripening, and stress adaptation (Hu et al., 2017).

3.4 Comparative Transcriptomic Insights Across Fruit Species

Comparative transcriptomic analysis provides many chances for understanding both common and unique aspects of molecular mechanisms involved in post-harvest browning and quality control processes. The combination of transcriptomic and metabolomic data provided insights into complex interactions between the regulation of gene expression, metabolite biosynthesis, and environmental changes occurring during storage. It was found that the application of methyl jasmonate in prune fruits contributes to the mitigation of chilling injury due to the regulation of gene expression and metabolic processes linked to cellular protection (Zhao et al., 2025). In grapes, the use of a combined analysis of transcriptional and metabolic changes allowed finding how UV-C exposure causes transcriptional and metabolic adaptations related to maintaining quality characteristics of fruit during storage (Zhang et al., 2021). In addition, transcriptome analysis of lotus seeds after low-temperature storage revealed the involvement of many genes in response to storage-related stress factors (Chen et al., 2024).

3.5 Candidate Genes, QTLs, GWAS Findings, and Molecular Markers

Identification of genes and molecular markers related to post-harvest traits has been among the primary goals of fruit genetics and breeding programs. Genome-wide association studies, QTL mapping, and marker-assisted methodologies allow researchers to identify the genomic regions involved in complex traits such as browning vulnerability, shelf-life duration, firmness, and stress tolerance. Recent studies of genome-wide association have revealed the complex genetic makeup behind pre- and post-harvest traits in grapevines, discovering many loci connected to fruit quality and storage properties (García-Abadillo et al., 2024). In tomato, gene-based studies have identified potential candidates for maintaining firmness, increasing shelf-life duration, and resistance to pre- and post-harvest stress conditions, making such genes promising molecular markers in future improvement programs (Nie et al., 2024). Altogether, it can be stated that contemporary transcriptomics, genomics, and association-mapping studies have demonstrated that browning is controlled by a combination of oxidative enzyme activity, stress response genes, hormone-based signal transduction pathways, and molecular markers. The main genetic factors and molecular techniques used in browning-related research on post-harvest fruits are summarized in Table 1.

Table 1. Major Genetic Factors and Molecular Approaches Associated with Enzymatic Browning in Post-Harvest Fruits

Category	**Representative Genes/Factors**	**Role in Browning Regulation**	**Key Reference**
Oxidative Enzymes	PPO gene family	Catalyzes phenolic oxidation leading to browning	Sultan et al., 2025
Phenolic Metabolism	Phenylpropanoid pathway genes	Regulate synthesis of browning substrates	Qi et al., 2022
Stress-Responsive Genes	Cold- and oxidative stress-related genes	Influence chilling-induced browning and quality deterioration	Badrunnesa et al., 2025
Hormone-Regulated Genes	Ethylene- and ABA-responsive genes	Control ripening, stress adaptation, and browning susceptibility	Lin et al., 2024; Hu et al., 2017

Candidate Genes & Molecular Markers	QTLs, GWAS loci, marker-associated genes	Enable identification of browning-resistance traits for breeding	García-Abadillo et al., 2024; Nie et al., 2024

4. Molecular Regulatory Networks Controlling Post-Harvest Browning

4.1 Transcription Factors and Gene Regulatory Circuits

Transcription Factors (TFs) act as the main gene expression regulators and play a vital role in orchestrating the physiological activities of post-harvest response associated with browning processes. These regulatory molecules influence the transcription of genes participating in oxidative activity, phenylpropanoid metabolism, stress tolerance, antioxidants, and hormonal regulation. Regulation in the expression of certain transcription factors decides whether a fruit tissue responds to environmental stimuli or storage-related stresses. Recent research on post-harvest pepper has shown that metabolic remodeling due to bioactive molecules is followed by coordinated transcription regulation of genes linked with carbon metabolism, antioxidants, and quality preservation. These findings indicate the significance of the gene regulatory network in post-harvest adaptation (Zhang et al., 2025).

4.2 Hormonal Signaling Pathways

Plant hormones play a pivotal role in regulating physiological phenomena which have direct or indirect consequences on post-harvest browning. These hormones mediate plant growth and development by coordinating ripening, senescence, stress tolerance, defence response, and antioxidant metabolism via highly coordinated signal transduction pathways. One hormone, in particular, which is gaining increasing recognition because of its unique qualities is salicylic acid due to its role in strengthening oxidative stress tolerance, maintaining membrane stability, and improving post-harvest quality. Laboratory studies have shown that treatment with salicylic acid could successfully affect antioxidant enzyme activity and delay quality loss in horticultural produce by delaying the onset of browning disorders (Wang et al., 2022).

4.3 Reactive Oxygen and Stress Signaling Networks

ROS not only serve as toxic byproducts of biological metabolism but are essential components of the cell signaling cascade responsible for the regulation of various biological processes including stress response and adaptation. Post-harvest stresses result in the generation of ROS and the activation of various signal transduction cascades that regulate defence response, antioxidant activities, and repair processes. Some of the most prominent stresses causing adverse effects on the fruit quality after harvest include chilling injury, infections from pathogens, and other changes to environmental conditions. In loquat fruit, the study of regulatory mechanisms has shown that the combined effect of oxidative stress responses, chilling response, and diseases affects the development of various disorders (Zhang et al., 2022). Similarly, studying the processes associated with fungal pathogens, it was found that cellular communication in this process results in various metabolic, defensive, and deterioration responses, leading to browning (Zhang et al., 2021).

4.4 Epigenetic Regulation and Non-Coding RNAs

The importance of epigenetic phenomena in the regulation of post-harvest traits, which involve control of the expression of genes without changing the composition of the DNA, is gaining increasing importance. These have come to the fore as important regulators of fruit development, ripening, senescence and stress adaptation – DNA methylation, histone modifications, chromatin remodeling and non-coding RNAs. The dynamic nature of epigenetic regulation in post-harvest tomato fruit has been highlighted by extensive epigenetic changes induced by post-harvest handling that are linked to modifications in gene expression and metabolic activity, as revealed by integrative methylome and transcriptome analyses of tomato fruit (Zhou et al., 2024). Likewise, a wide range of studies on fruit and vegetable quality attributes have emphasised the significance of epigenetic regulation in post-harvest performance and stress tolerance (Kumar et al., 2024). As post-transcriptional regulation mechanisms, microRNAs (miRNAs) and long non-coding RNAs (lncRNAs) have been gaining more and more attention due to their fine-tuning power in the regulation of gene expression networks. Several target genes that are regulated by browning-related miRNAs are associated with oxidative metabolism, stress response and cellular homeostasis, which makes the pathways involved in browning processes complex (Xu et al., 2018). Besides, lncRNAs are involved in a variety of biological processes, such as, signal transduction, chromatin modification, and transcriptional regulation and are known to play a vital role in modulating fruit quality and post-harvest physiology (Zhao et al., 2024). Histone modifications also have important regulatory functions: Studies indicate that H3K27me3-mediated chromatin repression is linked to the suppression of colour and aroma development in strawberry fruit during storage (Baldwin et al., 2025).

4.5 Integrated Regulatory Network Models

Finally, post-harvest browning is regulated by a complex network of regulatory mechanisms that are closely interconnected and include signals from transcription factors, hormones, ROS metabolism, epigenetic modification and environment. The use of systems biology methods is becoming more and more important to understand these complex interactions, as they allow to integrate multi-layered biological data into comprehensive network models. In papaya fruit, studies have shown the coordinated interaction between ethylene signalling, metabolic pathways and gene regulatory networks involved in fruit ripening and quality maintenance through systems-level analyses (Soares et al., 2021). This type of integrated regulation enables to build a broader picture of processes involved in browning and could be useful for the identification of potential regulatory points which can be addressed by breeding, biotechnology or post-harvest management strategies. Complex interactions between transcription factors, hormonal pathways, ROS signaling, epigenetic modifications and non-coding RNAs regulate the post-harvest browning. Major regulatory interactions during browning development are shown in Figure 2.

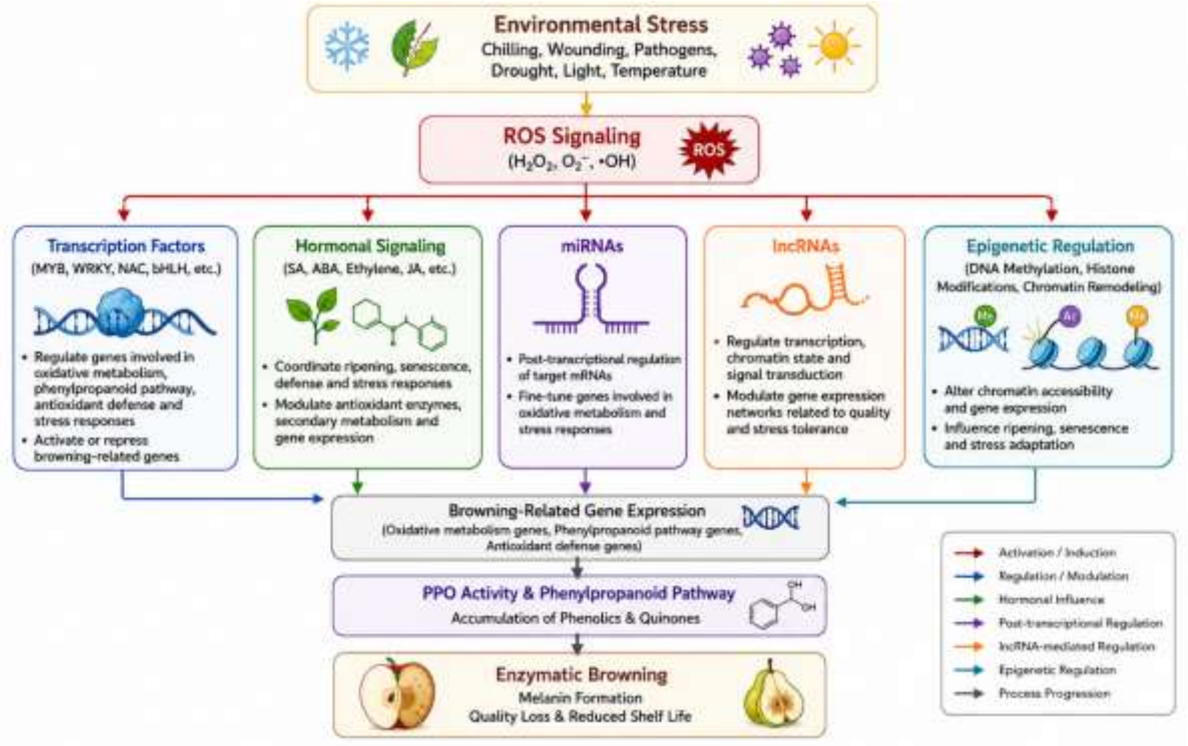

Figure 2. Molecular regulatory network of post-harvest browning

Figure 2 illustrates the interrelated regulatory networks involved in the regulation of genes associated with browning and oxidative metabolism. The molecular pathways offer possibilities for targeting improvement through breeding programs and genetic engineering, as well as after harvesting.

5. Functional Genomics Approaches in Browning Research

5.1 Transcriptomics, Proteomics, and Metabolomics

Functional genomics has greatly advanced the study of post-harvest browning due to its capability of allowing researchers to undertake a comprehensive analysis of gene expression, proteins, and metabolites at a systems-level scale. Out of the various strategies used in this study, transcriptomics, proteomics, and metabolomics have emerged as the major tools that help in understanding the molecular processes associated with browning development and degradation in horticultural produce. The transcriptome analysis can help in identifying the genes that are up- or down-regulated in association with oxidative processes, stress responses, biosynthesis of phenolics, and other defence mechanisms. Similarly, proteomics is a powerful approach to studying proteins.

Recent research involving integration of transcriptomics and proteomics in post-harvest litchi fruits has shown that the combination of transcriptional and translational regulation is important for the mitigation of browning as well as delaying senescence through the use of citric acid and L-cysteine treatments (Xiao et al., 2025). Likewise, the analysis of the transcriptomic profile of strawberries and application of the network analysis approach has indicated the potential role of ultrasonic treatments in the suppression of post-harvest browning, which is achieved through alterations in pyruvate metabolism and amino acids balance (Chen et al., 2025). Additionally, proteomics has shown that temperature-related changes in the expression pattern play an important role in the physiology of fruits, as seen from studies on strawberries under thermal stress conditions similar to those encountered after harvesting (Lv et al., 2022).

5.2 Epigenomics and RNA-Based Regulatory Mechanisms

Apart from transcriptional control, post-harvest browning also involves a series of post-transcriptional and post-translational regulations that affect the activity of genes and the physiological response of cells. The application of epigenomics enables us to better understand the role of chromatin configuration, changes in DNA structure, and different regulatory factors in the control of fruit development and maintenance of quality. Furthermore, post-translational modifications (PTMs) of proteins are considered an important regulatory process, which affects the functioning of enzymes, signal transduction, protein stability, and stress tolerance. As recent research reveals, PTMs are critical in controlling the processes related to fruit ripening and their interaction with different post-harvest environmental factors, hence impacting the characteristics of fruits' quality and longevity (Li et al., 2024).

5.3 Multi-Omics Integration and Systems Biology

While informative data can be gained from individual omics platforms, the complexity of post-harvest browning requires integrated approaches that can capture interactions among genes, proteins, metabolites and physiological processes.

Combining multi-omics has become a useful approach to build a regulatory network that accounts for the interplay of the various molecular components involved in browning development. Integrated omics analyses have significantly advanced the knowledge regarding chilling injury and related quality disorders in pome and stone fruits, uncovering complex regulatory networks linked to stress response, metabolic processes, and cellular homeostasis (Rodrigues et al., 2024). These systems-level approaches help identify important regulatory nodes, allow prediction of physiological responses and serve as a basis for precision interventions for better post-harvest quality.

5.4 Functional Validation Through RNAi, VIGS, and Genome Editing

Candidate genes identified for browning and quality traits should be followed by functional validation to make the genotype-phenotype correlation. The silencing methods such as RNA interference (RNAi), virus-induced gene silencing (VIGS), and genome-editing technologies are now essential for studying gene function in horticultural crops. These methods allow for specific manipulation of particular genes related to oxidative metabolism, hormone signaling, stress adaptation and phenolic biosynthesis. Genome editing, especially CRISPR-based technologies, has shown great promise in minimising post-harvest losses in fruits and vegetables through enhanced shelf life, stress tolerance and quality attributes (Kumari et al., 2022). Moreover, the improvement of horticultural cultivars is becoming faster with the development of novel improved techniques of genome editing, which has opened the door to more precise modification of genes that are related to nutritional quality, storage performance and post-harvest deterioration resistance (Sharma et al., 2023).

5.5 Emerging Technologies in Functional Genomics

Functional genomics continues to grow in its scope and applications in post-harvest biology and is rapidly expanding due to technological advancements. There are new opportunities for understanding complex biological systems using high throughput sequencing platforms, powerful bioinformatics pipelines, machine-learning-assisted analyses, and integrated approaches to molecular phenotyping. Functional genomics has become a more common approach for translating a gene's discovery into real crop improvement, such as the recent efforts to incorporate genomic information into breeding and biotechnology programs for the economically important crop potato (Qu et al., 2024). Concurrently, the increasing use of genomic, transcriptomic and proteomic approaches in edible fungi research underscores the importance of functional genomics in the study of various biological systems and offers essential methodological insights that can be leveraged in post-harvest quality research (Xie et al., 2025). The future of browning resistance cultivars and precision post-harvest management is likely to involve these emerging technologies as a central piece. Table 2 provides a summary of the main functional genomics approaches and their impact on the study of browning.

Table 2. Functional Genomics Tools and Their Applications in Enzymatic Browning Research

Functional Genomics Approach	**Major Application**	**Contribution to Browning Research**	**Key Reference**
Transcriptomics	Gene expression profiling	Identification of browning-associated genes and pathways	Badrunnesa et al., 2025
Proteomics	Protein abundance and modification analysis	Understanding enzyme activity and stress responses	Lv et al., 2022
Metabolomics	Metabolite profiling	Characterization of phenolic compounds and metabolic changes	Qi et al., 2022
Epigenomics	DNA methylation and chromatin studies	Regulation of post-harvest quality traits and gene expression	Zhou et al., 2024
Multi-Omics Integration	Systems-level analysis	Identification of interconnected regulatory networks	Rodrigues et al., 2024
RNAi/VIGS	Functional gene validation	Verification of candidate browning-related genes	Kumari et al., 2022
CRISPR/Cas Genome Editing	Targeted gene modification	Development of browning-resistant cultivars	Sharma et al., 2023
AI-Assisted Functional Genomics	Predictive modeling and data integration	Accelerated discovery of molecular targets	Qu et al., 2024

6. Comparative Molecular Insights into Browning Across Fruit Crops

6.1 Apple and Pear

Apple and pear are two important model systems that have been extensively researched regarding post-harvest browning due to their economic significance and vulnerability to degradation. In both cases, browning is linked to enzymatic reactions like polyphenol oxidase, availability of phenolic substrates, oxidative stress, and damage to cellular membranes. Pears vary in texture, aroma compounds, sugar metabolism, and their antioxidant capabilities. Research has revealed that stress-responsive genes, hormones, and metabolic controls are the most important factors that determine the quality of harvested fruits (Zhang et al., 2024). The same holds for apples, except that the phenolic profile may vary between cultivars.

6.2 Peach, Nectarine, and Plum

Peach, nectarine, and plum (Prunus spp.) exhibit some similar physiological and biochemical processes related to their quality after harvest. These fruits are particularly vulnerable to chilling damage, oxidative stress, tissue softening, and browning upon storage. Studies involving genomics, transcriptomics, and metabolomics have shown how the development process, hormone interactions, stresses, and secondary metabolism contribute to determining the fruit's quality (García-Gómez et al., 2020). Networks of genes involved in ripening, antioxidant defense, and stress response have also been established (Ortuno-Hernandez et al., 2025). In addition, preservation techniques may further impact on such processes (Cao et al., 2025).

6.3 Litchi, Pomegranate, and Kiwifruit

Litchi, pomegranate, and kiwi often suffer from rapid post-harvest decay due to their high metabolic activity and susceptibility to environmental stresses. Browning is often associated with membrane damage, oxidative stress, phenolic oxidation, and imbalance in redox status within cells. For example, studies using metabolomics in pomegranate have revealed that phenylpropanoid biosynthesis, antioxidant defense systems, and oxidative stress responses play critical roles in pericarp browning (Qi et al., 2022). In kiwi fruit, significant changes in gene expression, including responses to hormone signaling, stress, and fruit ripening processes, affect post-harvest quality (Lin et al., 2024).

6.4 Grape, Banana, and Other Tropical Fruits

Grape, banana, and certain tropical fruit varieties exhibit differential physiological behavior during the post-harvest period, affecting their browning process and storage ability. Transcriptome and metabolome analysis conducted in grape has shown that stress-related genes, antioxidants, and secondary metabolites play a vital role in regulating the browning process and retaining quality attributes (Zhang et al., 2021). For banana, oxidative stress and hormonal signals play critical roles in the ripening process and shelf-life determination. Research into less-studied tropical fruits has identified that bioactive compounds and adaptive physiological characteristics play important roles (Cordeiro et al., 2024).

6.5 Comparative Synthesis of Conserved and Species-Specific Browning Pathways

Comparative studies have shown that enzymes responsible for enzymatic browning involve similar yet distinct molecular mechanisms. Some common molecular pathways in enzymatic browning are the polyphenol oxidase pathway, phenylpropanoid pathway, production of reactive oxygen species, antioxidant pathway, preservation of cellular membranes, and stress-responsive signaling pathways. Differences in gene expression profiles, hormone sensitivity, metabolite content, and antioxidant activity between different fruit species have been observed. Comparative omics studies help understand the different browning mechanisms between species, and thereby aid in developing fruit crop-specific and universal techniques for browning prevention. A summary of the major drivers of browning and molecular attributes in fruit crops is given in Table 3.

Table 3. Comparative Molecular Mechanisms of Enzymatic Browning in Major Fruit Crops

Fruit Group	Major Browning Trigger	Key Molecular Factors	Representative Reference
Apple & Pear	PPO activity, oxidative stress	PPO, phenolic compounds, antioxidant pathways	Zhang et al., 2024; Sultan et al., 2025
Peach, Nectarine & Plum	Chilling injury	Stress-responsive genes, antioxidant defense, secondary metabolism	García-Gómez et al., 2020; Ortuno-Hernandez et al., 2025
Litchi & Pomegranate	Membrane damage, phenolic oxidation	Phenylpropanoid metabolism, ROS signaling	Qi et al., 2022
Kiwifruit	Ripening-associated stress	Ethylene signaling, hormone-regulated genes	Lin et al., 2024; Salazar et al., 2021
Grape	Storage and environmental stress	Transcriptomic and metabolomic adjustments, antioxidant pathways	Zhang et al., 2021
Banana	Ripening and oxidative stress	ABA-regulated networks, stress-signaling pathways	Hu et al., 2017
Tropical Fruits	Environmental and physiological stress	Bioactive compounds, antioxidant systems	Cordeiro et al., 2024

7. Molecular Strategies for Browning Mitigation and Quality Improvement

7.1 Conventional Breeding and Marker-Assisted Selection

Conventional breeding is still one of the best and effective ways to achieve improvement in post harvest quality and susceptibility to browning in fruit crop. Traditionally, breeding programs have focussed on traits that indirectly affect browning development during storage and distribution, such as shelf life, firmness, texture, nutritional quality, disease resistance and stress tolerance. The availability of genomic resources has made conventional breeding much more efficient, as genes and quantitative trait loci (QTLs) and molecular markers of desirable post-harvest traits could be identified. In tropical fruit crops, genomic tools have also helped identify the genetic factors that influence fruit quality, nutrient content and storage attributes and are thus useful for marker-assisted selection and cultivar improvement (Mathiazhagan et al., 2021). Molecular markers can be used to introduce them in breeding programmes to select superior cultivars with more precision and to shorten the time for cultivar development.

7.2 Genome Editing and Genetic Engineering Approaches

The post-harvest quality attributes can now be modified thanks to the recent development of genome editing technologies. pathways in ripening, oxidative stress responses, cell wall degradation and enzymatic browning are now open for unprecedented manipulation with tools like CRISPR/Cas systems. The major benefit of genome editing over traditional breeding is that it can be used to modify specific genes without large changes in the genome. For durian, genome editing has been suggested to manipulate genes that are involved in pericarp softening so as to prolong post-harvest longevity by targeted gene editing (Wang, 2025). These methods show great promise in the development of fruit cultivars with improved storage quality, low tendency to browning, and consumer acceptance.

7.3 Targeting Regulatory Networks and Signaling Pathways

The understanding of molecular regulatory networks has facilitated the formulation of specific strategies to tackle post-harvest browning by targeting specific signalling pathways. These methods aim at regulating oxidative stress, hormone signaling, antioxidant metabolism, and cellular defence mechanisms which affect fruit quality during storage. Melatonin has been studied as a multifunctional signaling molecule that can play a role in regulating cellular redox homeostasis, antioxidant defence, and slowing down senescence. Among the various signaling molecules studied, it is particularly promising. Experimental evidence indicates that melatonin regulation of physiological and biochemical processes could be an effective strategy to improve post-harvest preservation and alleviate the quality decay of fruits and vegetables (Xu et al., 2019). The targeting of these regulatory pathways represents a promising approach to develop innovative browning-control strategies that are based on endogenous molecular mechanisms.

7.4 Omics-Assisted Precision Breeding

The use of genomics, transcriptomics, proteomics and metabolomics in breeding programs has led to precision breeding methods that can advance crop improvement at a more rapid pace. Omics-assisted breeding facilitates the identification of molecular signatures of quality, shelf life, stress tolerance and browning resistance and hence, the comprehensive characterization of complex traits. The use of both high-throughput molecular and phenotypic data will allow the better prediction of desirable genotypes, and the development of cultivars with improved post -harvest performance. The importance of incorporating both genomic information and physiological and biochemical analysis to develop better fruit and vegetable varieties with extended storage ability and quality parameters has been recently highlighted with molecular approaches (Kumar & Choudhary, 2024).

7.5 Integration with Post-Harvest Management Technologies

While genetic improvement can offer long-term solutions in reducing the susceptibility to browning, genetic improvement can be combined with post-harvest management technologies to increase its effectiveness. Modern post-harvest biotechnology brings the molecular knowledge together with the technologies of storage, preservation treatments and quality monitoring systems to reduce losses and to preserve the quality of the products during the supply chain. The shelf life has been extended and less food waste has been produced by using genetic engineering techniques as an additional tool for increasing resistance to post-harvest deterioration. The technologies allow for the manipulation of genes related to ripening, senescence, oxidative and stress responses, and hence improve the effectiveness of conventional post-harvest interventions (Ninama et al., 2024). The future of post-harvest quality management is likely to be in the direction of an integrated approach using molecular breeding, biotechnology and advanced storage technology for sustainable improvement of fruit quality and shelf life. The main molecular approaches currently used to prevent browning and enhance post-harvest quality are shown in Figure 3.

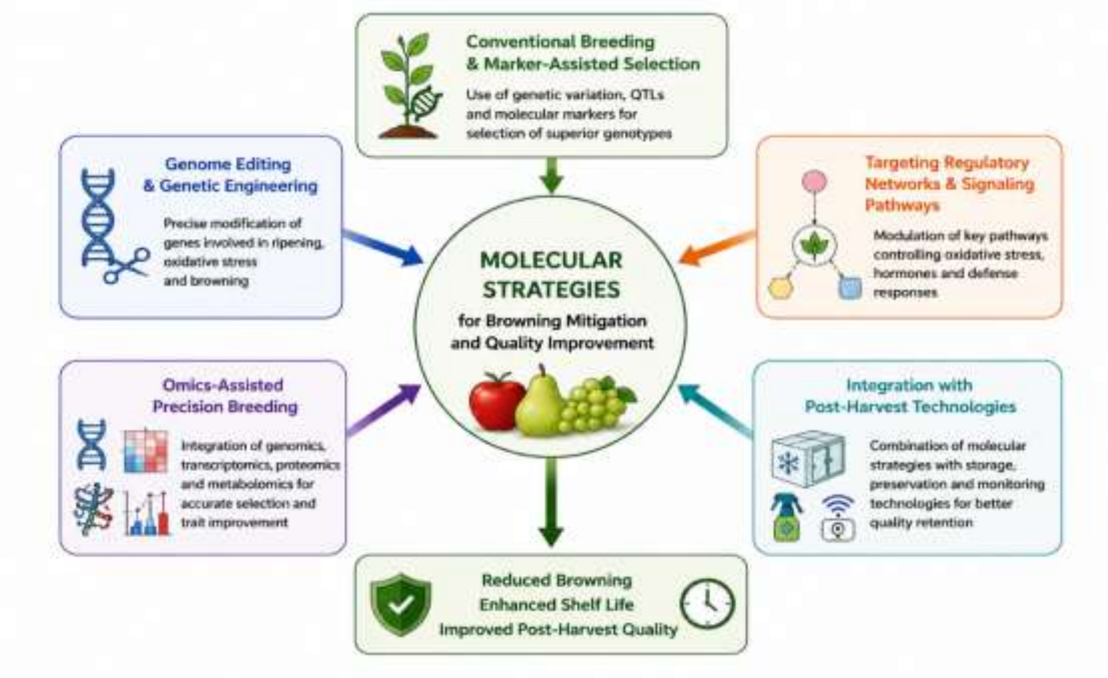

Figure 3. Molecular Strategies for Browning Mitigation

Figure 3 shows that mitigating browning needs a multifaceted strategy involving genetics, molecular biology, and technology. With recent breakthroughs in the fields of genome editing, omics-assisted breeding, and regulation of biochemical pathways, there is great potential for breeding better-performing fruit varieties. At the same time, the use of post-harvest techniques can add value to these genetic gains, thus ensuring quality throughout the logistics process.

8. Challenges, Knowledge Gaps, and Future Perspectives

Despite significant advancement made in the discovery of the molecular mechanism underlying browning, many challenges still exist. The occurrence of browning is a multifactorial trait that is regulated by complex interactions involving oxidative enzymes, phenolic biosynthesis, ROS, hormones, and environment, thus making the determination of universal markers quite challenging. Furthermore, most research studies target individual pathways without considering how browning occurs as a result of the functioning of regulatory pathways.

A key challenge is the inability to translate basic science to applied technology in terms of browning control. This implies that although many candidate genes, markers, and pathways involved in browning have been discovered, there has not been significant effort invested in harnessing the discoveries for use in breeding and post-harvest handling of fruits.

New technologies are coming that may be able to overcome these restrictions. Progress in multi-omics platforms, systems biology, AI and machine learning approaches are helping to explore further gene regulation and their ability to predict browning susceptibility and storage performance. All of these can help speed up identifying important molecular targets and facilitate precision breeding strategies.

Future studies should focus on genomic selection, functional genomics and genome-editing technologies to develop cultivars that are resistant to browning. To enhance fruit quality and minimize post-harvest losses, a much tighter integration of molecular genetics with post-harvest physiology, storage technology and computational biology will be required. Collaborative, multidisciplinary approaches will be key factors in the development of sustainable post-harvest biology and the long-term food quality and security.

9. CONCLUSIONS

Browning caused by enzyme activity is one of the key aspects that affect the post-harvest quality and commercial success of fruit crops globally. As can be gathered from this review, browning is a complicated process with a genetic basis that results from the interplay between oxidative enzymes, phenols, ROS, hormone-mediated signaling, and stressors. The breakthroughs made within molecular genetics prove that there are specific gene networks that control browning susceptibility through the regulation of phenolic metabolism, antioxidative system, plasma membrane integrity, and stress responses. Moreover, transcriptomics, proteomics, metabolomics, and epigenomics approaches allowed to learn much more about the molecular mechanisms of browning onset and identified many candidate genes and pathways associated with the post-harvest response. One significant outcome derived from current scientific research is that the regulation of enzymatic browning involves very complex regulatory networks and not simple genes or pathway activities alone. The combined effect of hormone signaling, redox reactions, transcription factors, noncoding RNAs, and epigenetics determines whether browning occurs or is avoided in fruits. Functional genomics techniques like multi-omics analysis, RNAi, and gene editing technologies have further increased the rate at which molecular targets can be discovered and validated for browning resistance. The comparison of various mechanisms of browning sensitivity in different fruit varieties provides both commonalities and unique differences that can serve as targets for developing resistant fruits through precision breeding and biotechnological manipulation. Going forward, the convergence of functional genomics, artificial intelligence, and breeding technologies should enable researchers to develop browning resistant varieties.

REFERENCES

1. Qi, X., Zhao, J., Jia, Z., Cao, Z., Liu, C., Li, J., ... & Qin, G. (2022). Potential metabolic pathways and related processes involved in pericarp browning for postharvest pomegranate fruits. *Horticulturae*, *8*(10), 924.
2. Wang, C., Meng, L., Zhang, G., Yang, X., Pang, B., Cheng, J., ... & Sun, F. (2024). Unraveling crop enzymatic browning through integrated omics. *Frontiers in Plant Science*, *15*, 1342639.
3. Rodrigues, M., Ordoñez-Trejo, E. J., Rasori, A., Varotto, S., Ruperti, B., & Bonghi, C. (2024). Dissecting postharvest chilling injuries in pome and stone fruit through integrated omics. *Frontiers in Plant Science*, *14*, 1272986.
4. García-Gómez, B. E., Salazar, J. A., Nicolás-Almansa, M., Razi, M., Rubio, M., Ruiz, D., & Martínez-Gómez, P. (2020). Molecular bases of fruit quality in Prunus species: An integrated genomic, transcriptomic, and metabolic review with a breeding perspective. *International journal of molecular sciences*, *22*(1), 333.
5. Sultan, M. Z., Farouk, K. A., Elbagoury, M. M., & Yahia, E. M. (2025). Trends in biochemical, anatomical mechanisms and molecular aspects in enzymatic browning of apples: a review. *European Food Research and Technology*, *251*(10), 3305-3326.
6. Xiao, L., Huang, H., Liu, W., Li, X., Zhao, J., Liang, S., ... & Chen, Y. (2025). Integrated transcriptome and proteome analysis reveals the regulatory mechanisms of citric acid and L-Cysteine treatment in mitigating browning and senescence of postharvest litchi fruit. *LWT*, *221*, 117604.
7. Sirangelo, T. M., Rogers, H. J., & Spadafora, N. D. (2022). Multi-omic approaches to investigate molecular mechanisms in peach post-harvest ripening. *Agriculture*, *12*(4), 553.
8. Habibi, F., Boakye, D. A., Chang, Y., Casorzo, G., Hallman, L. M., Madison, M., ... & Liu, T. (2024). Molecular mechanisms underlying postharvest physiology and metabolism of fruit and vegetables through multi-omics technologies. *Scientia Horticulturae*, *324*, 112562.
9. Kumari, C., Sharma, M., Kumar, V., Sharma, R., Kumar, V., Sharma, P., ... & Irfan, M. (2022). Genome editing technology for genetic amelioration of fruits and vegetables for alleviating post-harvest loss. *Bioengineering*, *9*(4), 176.

10. García-Abadillo, J., Barba, P., Carvalho, T., Sosa-Zuñiga, V., Lozano, R., Carvalho, H. F., ... & y Sánchez, J. I. (2024). Dissecting the complex genetic basis of pre-and post-harvest traits in Vitis vinifera L. using genome-wide association studies. *Horticulture Research*, *11*(2), uhad283.
11. Yuan, X., Zhan, Z., Lin, W., Zhang, C., & Wang, B. (2025). The membrane may be a key factor influencing browning: a mini review on browning mechanisms of fresh-cut fruit and vegetables from a multi-omics perspective. *Frontiers in Nutrition*, *12*, 1534594.
12. Pons, C., Martí, C., Forment, J., Crisosto, C. H., Dandekar, A. M., & Granell, A. (2016). A genetic genomics-expression approach reveals components of the molecular mechanisms beyond the cell wall that underlie peach fruit woolliness due to cold storage. *Plant molecular biology*, *92*(4), 483-503.
13. Sirangelo, T. M., Rogers, H. J., & Spadafora, N. D. (2022). Molecular investigations of peach post-harvest ripening processes and VOC biosynthesis pathways: A review focused on integrated genomic, transcriptomic, and metabolomic approaches. *Chemistry Proceedings*, *10*(1), 8.
14. Badrunnesa, A., Zhan, W., Duan, W., Meng, J., Li, A., Yao, Z., ... & Zeng, W. (2025). Transcriptome analysis reveals the mechanism of peach fruit browning during cold storage. *New Zealand Journal of Crop and Horticultural Science*, *53*(5), 2696-2715.
15. Zhao, Y., Hou, Y., Xiao, X., Wu, Y., Zhang, X., Li, B., ... & Chen, J. (2025). Integration of transcriptomics and metabolomics reveals the role of methyl jasmonate in alleviating chilling injury of postharvest prune fruit. *Postharvest Biology and Technology*, *229*, 113713.
16. Zhou, J., Zhou, S., Chen, B., Sangsoy, K., Luengwilai, K., Albornoz, K., & Beckles, D. M. (2024). Integrative analysis of the methylome and transcriptome of tomato fruit (Solanum lycopersicum L.) induced by postharvest handling. *Horticulture Research*, *11*(6), uhae095.
17. Kumar, A., Gautam, S., Smakaria, S., Negi, N., & Abrol, D. (2024). Epigenetic Regulation of Pre-And Postharvest Quality Traits in Fruits and Vegetables. In *Bioengineered Fruit and Vegetables* (pp. 185-218). Apple Academic Press.
18. Gao, X., Wu, W., Chen, H., Niu, B., Han, Y., Fang, X., ... & Gao, H. (2023). Nitric oxide treatment delays quality deterioration and enzymatic browning of Agaricus bisporus via reactive oxygen metabolism regulation. *Food Frontiers*, *4*(1), 447-458.
19. Li, T., Zeng, J., Yang, X., Garcia-Caparros, P., & Duan, X. (2024). The role of protein post-translational modifications in fruit ripening. *Horticulturae*, *10*(10), 1042.
20. Lin, M., Gao, Z., Wang, X., Mao, J., Pan, L., Gong, X., ... & Huo, H. (2024). Identification of two postharvest ripening regulatory models in kiwifruit: based on plant hormones, physiology, and transcriptome analysis. *BMC Plant Biology*, *24*(1), 1121.
21. Chen, B., Hu, Y., Xu, S., Li, F., Chen, L., Wu, H., ... & Jiang, Y. (2025). Ultrasound treatment inhibits postharvest browning of Lyophyllum decastes by regulating pyruvate metabolism and amino acid homeostasis: A transcriptomic and network analysis. *Scientia Horticulturae*, *349*, 114238.
22. Cao, S., Zhang, G., Luo, Y., Qiu, J., Ba, L., Xu, S., ... & Ren, Y. (2025). Recent advances in postharvest physiology and preservation technology of peach fruit: A systematic review. *Horticulturae*, *11*(9), 1007.
23. Zhang, Z. Q., Chen, T., Li, B. Q., Qin, G. Z., & Tian, S. P. (2021). Molecular basis of pathogenesis of postharvest pathogenic fungi and control strategy in fruits: progress and prospect. *Molecular horticulture*, *1*(1), 2.
24. Zhang, J., Zeng, J., Zheng, J., Chen, H., Chen, X., Tian, X., ... & Zhou, Y. (2025). Transcriptional Coordination of Metabolic Reprogramming in Chlorogenic-and Gamma Aminobutyric Acid-Treated Pepper During Postharvest Storage. *LWT*, 118989.
25. Mathiazhagan, M., Chidambara, B., Hunashikatti, L. R., & Ravishankar, K. V. (2021). Genomic approaches for improvement of tropical fruits: fruit quality, shelf life and nutrient content. *Genes*, *12*(12), 1881.
26. Zhang, K., Li, W., Ju, Y., Wang, X., Sun, X., Fang, Y., & Chen, K. (2021). Transcriptomic and metabolomic basis of short-and long-term post-harvest UV-C application in regulating grape berry quality development. *Foods*, *10*(3), 625.
27. Wang, H. (2025). Enhancing Postharvest Characteristics in Durian via Genome Editing: Regulation of Pericarp Softening and Shelf-Life Extension. *Molecular Plant Breeding*, *16*.
28. Zhang, S., Sun, H., Wang, J., Shen, J., He, F., Chen, D., & Wang, Y. (2022). The regulatory mechanisms and control technologies of chilling injury and fungal diseases of postharvest loquat fruit. *Plants*, *11*(24), 3472.
29. Ninama, N., Gangal, L., Khayum, A., SB, H., HM, S., & Singh, A. (2024). Post-harvest biotechnology or genetic engineering solutions: Extending shelf life and reducing food waste. *Journal of Advances in Biology & Biotechnology*, *27*(4), 1-26.
30. Martínez-González, M. E., Balois-Morales, R., Alia-Tejacal, I., Cortes-Cruz, M. A., Palomino-Hermosillo, Y. A., & López-Gúzman, G. G. (2017). Postharvest fruits: maturation and biochemical changes. *Revista mexicana de ciencias agrícolas*, *8*(SPE19), 4075-4087.
31. Chen, L., Dong, G., Song, H., Xin, J., Su, Y., Cheng, W., ... & Sun, H. (2024). Unveiling the molecular dynamics of low temperature preservation in postharvest lotus seeds: a transcriptomic perspective. *BMC plant biology*, *24*(1), 755.
32. Kumar, J., & Choudhary, K. (2024). Enhancing Postharvest Stability and Shelf Life of Perishable Fruits and Vegetables Using Molecular Approaches. In *Bioengineered Fruit and Vegetables* (pp. 75-92). Apple Academic Press.
33. Nie, H., Yang, X., Zheng, S., & Hou, L. (2024). Gene-based developments in improving quality of tomato: focus on firmness, shelf life, and pre-and post-harvest stress adaptations. *Horticulturae*, *10*(6), 641.
34. Qu, L., Huang, X., Su, X., Zhu, G., Zheng, L., Lin, J., ... & Xue, H. (2024). Potato: from functional genomics to genetic improvement. *Molecular Horticulture*, *4*(1), 34.
35. Liu, X., Zhang, A., Zhao, J., Shang, J., Zhu, Z., Wu, X., & Zha, D. (2021). Transcriptome profiling reveals potential genes involved in browning of fresh-cut eggplant (Solanum melongena L.). *Scientific reports*, *11*(1), 16081.

36. Sinaga, A. O. Y., & Marpaung, D. S. S. (2024). Abiotic stress-induced gene expression in pineapple as a potential genetic marker. *Advanced Agrochem*, *3*(2), 133-142.

37. Xu, Y., Liu, Z., Lou, L., & Su, X. (2018). Identification of browning-related microRNAs and their targets reveals complex miRNA-mediated browning regulatory networks in Luffa cylindrica. *Scientific Reports*, *8*(1), 16242.

38. Sharma, P., Pandey, A., Malviya, R., Dey, S., Karmakar, S., & Gayen, D. (2023). Genome editing for improving nutritional quality, post-harvest shelf life and stress tolerance of fruits, vegetables, and ornamentals. *Frontiers in Genome Editing*, *5*, 1094965.

39. Sougrakpam, Y., Babuta, P., & Deswal, R. (2023). Nitric oxide (NO) modulates low temperature-stress signaling via S-nitrosation, a NO PTM, inducing ethylene biosynthesis inhibition leading to enhanced post-harvest shelf-life of agricultural produce. *Physiology and Molecular Biology of Plants*, *29*(12), 2051-2065.

40. Hua, L., Yong, C., Zhanquan, Z., Boqiang, L., Guozheng, Q., & Shiping, T. (2018). Pathogenic mechanisms and control strategies of Botrytis cinerea causing post-harvest decay in fruits and vegetables. *Food Quality and Safety*, *2*(3), 111-119.

41. Zhang, Y., Cheng, Y., Ma, Y., Guan, J., & Zhang, H. (2024). Regulation of pear fruit quality: A review based on Chinese pear varieties. *Agronomy*, *15*(1), 58.

42. Salazar, J., Zapata, P., Silva, C., González, M., Pacheco, I., Bastías, M., ... & Infante, R. (2021). Transcriptome analysis and postharvest behavior of the kiwifruit 'Actinidia deliciosa'reveal the role of ethylene-related phytohormones during fruit ripening. *Tree Genetics & Genomes*, *17*(1), 8.

43. Baldwin, A., Lechon, T., Marchbank, A., Scofield, S., Lieu, K., Wilson, C. L., ... & Rogers, H. J. (2025). The H3K27me3 histone mark correlates with repression of colour and aroma development post-harvest in strawberry fruit. *Journal of Experimental Botany*, *76*(9), 2487-2499.

44. Xu, T., Chen, Y., & Kang, H. (2019). Melatonin is a potential target for improving post-harvest preservation of fruits and vegetables. *Frontiers in plant science*, *10*, 1388.

45. Chen, Y., Zhang, Y., Nawaz, G., Zhao, C., Li, Y., Dong, T., ... & Xu, T. (2020). Exogenous melatonin attenuates post-harvest decay by increasing antioxidant activity in wax apple (Syzygium samarangense). *Frontiers in plant science*, *11*, 569779.

46. Yang, C., Xu, Y., Xie, X., Wu, Y., Gao, Z., Li, K., ... & Liu, M. (2025). Post-harvest physiology of vegetable crops and its regulation. In *Growth Regulation and Quality Improvement of Vegetable Crops: Physiological and Molecular Features* (pp. 495-557). Singapore: Springer Nature Singapore.

47. Wang, J., Allan, A. C., Wang, W. Q., & Yin, X. R. (2022). The effects of salicylic acid on quality control of horticultural commodities. *New Zealand Journal of Crop and Horticultural Science*, *50*(2-3), 99-117.

48. Li, N., Zhai, K., Yin, Q., Gu, Q., Zhang, X., Melencion, M. G., & Chen, Z. (2023). Crosstalk between melatonin and reactive oxygen species in fruits and vegetables post-harvest preservation: An update. *Frontiers in Nutrition*, *10*, 1143511.

49. Xie, M., Wang, J., Wang, F., Wang, J., Yan, Y., Feng, K., & Chen, B. (2025). A review of genomic, transcriptomic, and proteomic applications in edible fungi biology: current status and future directions. *Journal of Fungi*, *11*(6), 422.

50. Cordeiro, M. C. R., da Silva, F. R., Faleiro, F. G., Junqueira, N. T. V., & Costa, A. M. (2024). Towards an Improved Vita Fruit (Passiflora tenuifila BRS VT): Functional Properties Basis for a Better Post-Harvest. *Preservation*, *23*(3).

51. Zhao, X., Li, F., Ali, M., Li, X., Fu, X., & Zhang, X. (2024). Emerging roles and mechanisms of lncRNAs in fruit and vegetables. *Horticulture Research*, *11*(4), uhae046.

52. Soares, C. G., do Prado, S. B. R., Andrade, S. C., & Fabi, J. P. (2021). Systems biology applied to the study of papaya fruit ripening: the influence of ethylene on pulp softening. *Cells*, *10*(9), 2339.

53. Lv, J., Zheng, T., Song, Z., Pervaiz, T., Dong, T., Zhang, Y., ... & Fang, J. (2022). Strawberry proteome responses to controlled hot and cold stress partly mimic post-harvest storage temperature effects on fruit quality. *Frontiers in Nutrition*, *8*, 812666.

54. Hu, W., Yan, Y., Shi, H., Liu, J., Miao, H., Tie, W., ... & Jin, Z. (2017). The core regulatory network of the abscisic acid pathway in banana: genome-wide identification and expression analyses during development, ripening, and abiotic stress. *BMC plant biology*, *17*(1), 145.

55. Ortuno-Hernandez, G., Sandoval-Belmar, P., Ruiz, D., Martinez-Gomez, P., Meneses, C., & Salazar, J. A. (2025). Insights into the molecular basis of fruit development in Prunus species. *Plant Molecular Biology Reporter*, *43*(3), 1397-1413.