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Review

Regulation of Pear Fruit Quality: A Review Based on Chinese Pear Varieties

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Abstract: Fruit quality is one of the most important economic traits of fruit crops, directly influencing market prices and orchard revenues. Enhancing fruit quality has therefore become a critical objective in both fruit production and scientific research. External quality traits of fruits typically include size, coloration, shape, uniformity, and consistency. Internal quality traits refer to the nutritional value of fruits, which largely determine their flavor and palatability. Over the past decade, significant progress has been made in understanding the formation and regulatory mechanisms of fruit quality, with numerous key functional genes associated with quality traits being identified. While substantial advancements have been achieved in studying specific aspects of fruit quality, there remains a lack of comprehensive and systematic reviews addressing the overall physiology of fruit quality, the interplay among various quality traits, and the diversity of regulatory mechanisms. Using Chinese pears as an example, this review summarizes the research progress in fruit quality regulation over the past five years. Key aspects include metabolic regulation of fruit traits such as sweetness, color, texture, and physiological disorders; factors influencing stone cell formation; sugar content regulation; roles of plant hormones including ethylene, gibberellins, and abscisic acid; translational regulation and post-translational modifications such as ubiquitination, methylation, and acetylation; as well as the application of genomic sequencing technologies. Furthermore, the review offers practical suggestions for improving pear fruit quality and provides insights for researchers in related fields. Finally, future trends in fruit quality research are discussed, offering a forward-looking perspective for advancing the field.

Keywords: fruit; quality; pear; stone cells; sugar content

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1. Introduction

Fresh fruits serve as an essential dietary component, providing humans with vitamins, minerals, essential amino acids, antioxidants, and bioactive compounds with specialized physiological functions. China ranks first globally in fruit production; however, post-harvest losses account for as much as 30%, leading to annual economic losses of several hundred billion yuan, significantly undermining agricultural efficiency and farmers' incomes. Consequently, improving post-harvest storage quality and minimizing losses have become critical issues requiring urgent solutions [1–3]. Fruit quality encompasses various

attributes, including color, aroma, flavor, and texture, all of which are regulated by both internal and external factors. Plant hormones, environmental conditions, and epigenetic modifications are among the primary factors affecting fruit quality [4]. Both applied and basic research have demonstrated that the quality traits of specific cultivars can vary significantly due to differences in pre-harvest (growth and development) and post-harvest treatments/technologies. In addition to genetic differences, the regulatory mechanisms of fruit quality traits influenced by pre- and post-harvest treatments remain a hot research topic. However, numerous theoretical questions remain unresolved. The mechanisms underlying the maintenance of post-harvest quality traits, the regulatory networks governing fruit ripening and senescence, the interactions between environmental factors and intrinsic fruit factors, and the similarities and differences in quality maintenance and regulation mechanisms across different fruit types are still unclear. Notably, research attention is uneven across various quality traits and regulatory mechanisms. For instance, anthocyanin metabolism is a popular focus, whereas studies on translational regulation, protein modifications, and microRNAs remain relatively underexplored [5,6].

China is the origin center for pears, boasting a rich diversity of pear germplasm resources and accounting for over 70% of the global pear cultivation area and production. Despite this, traditional local cultivars still dominate China's pear production, failing to meet the diverse quality demands of modern consumers [7,8]. Pear, as a perennial fruit tree, exhibits a long juvenile phase and typical self-incompatibility, making traditional cross-breeding approaches time-consuming and inefficient. This underscores the need for molecular breeding technologies to achieve efficient genetic improvement of key traits [9–11]. Key traits for evaluating pear germplasm include three yield and edibility traits (fruit transverse diameter, longitudinal diameter, and core size), five morphological and external quality traits (skin color, russeting, lenticel prominence, fruit shape, and pedicel length), and nine internal quality traits (flesh color, juiciness, aroma, flavor, texture, flesh type, soluble solids content, titratable acidity, and overall internal quality) [12]. Due to the perennial nature of pear trees, their breeding cycle is lengthy [13,14]. Additionally, pear hybrid breeding in China started relatively late. As a result, the main cultivars (such as 'Dangshan Su' 'Xuehua' etc.) are still traditional local varieties, often exhibiting poor comprehensive quality, such as bland flavor and coarse flesh texture [15]. Many traditional Chinese pear varieties have not undergone artificial breeding or targeted genetic improvement, leading to high stone cell content in the fruit, which causes a coarse texture and significantly reduces fruit quality and market acceptance [7,16–18]. Over the past decade, substantial progress has been made in understanding the formation and regulatory mechanisms of fruit quality, with several key functional genes and transcription factors identified. This review focuses on recent advances in Chinese pear fruit quality research over the past five years, providing a reference for researchers in related fields and offering insights into future research directions.

2. Metabolic Regulation of Pear Fruit Quality

Pear is crisp and delicious, rich in proteins, sugars, crude fiber, vitamins, and minerals such as calcium, phosphorus, and iron [19]. It offers various health benefits, including aiding digestion, soothing the lungs and cough, alleviating hangovers, reducing inflammation, and improving blood pressure and heart health [20]. In recent years, the breeding of ultra-early maturing pears has optimized industrial structure, reduced labor costs, and met consumer demands by bringing the fruit to market earlier. However, ultra-early maturing pears often suffer from bland flavor and low sweetness. The flavor quality of fruit directly affects consumer preference and market competitiveness, making the improvement of ultra-early maturing pear fruit quality a key focus for breeders and researchers [21–23].

Several fruit characteristics critical for pear quality, which have been the focus of genetic studies, include sweetness, color, texture, and physiological disorders.

2.1. Sweetness

Sugars represent the primary biochemical constituents of pears, with both the species and concentration of sugars exerting a direct impact on fruit flavor attributes, including the intensity and quality of sweetness. Furthermore, they play a pivotal role in determining overall fruit quality. A recent study reported a novel member of the S1-bZIP transcription factor family, *PpbZIP44*, which is significantly upregulated during fruit development. Overexpression of *PpbZIP44* notably increases the sugar content, enhances the sugar-to-acid ratio, and elevates levels of amino acids, fatty acids, and flavonoids in fruit. Conversely, silencing *PpbZIP44* has the opposite effects [24]. Furthermore, PpbZIP44 directly binds to the promoter of *PpSDH9* and induces its expression, facilitating the conversion of sorbitol to fructose. Additionally, PpbZIP44 interacts with the promoter of *PpProDH1*, thereby accelerating the proline cycle. Overexpression of *PpbZIP44* promotes the consumption of intermediates in the tricarboxylic acid (TCA) cycle and increases the levels of amino acids and fatty acids. PpbZIP44 also directly binds to the promoters of *PpADT* and *PpF3H*, directing carbon flux toward the phenylpropanoid biosynthesis pathway and enhancing the contents of phenylalanine and flavonoids [24]. This study provides a comprehensive understanding of the metabolic regulatory network mediated by *PpbZIP44* and offers valuable insights for genetic improvement and breeding strategies aimed at enhancing pear fruit quality [24] (Figure 1).

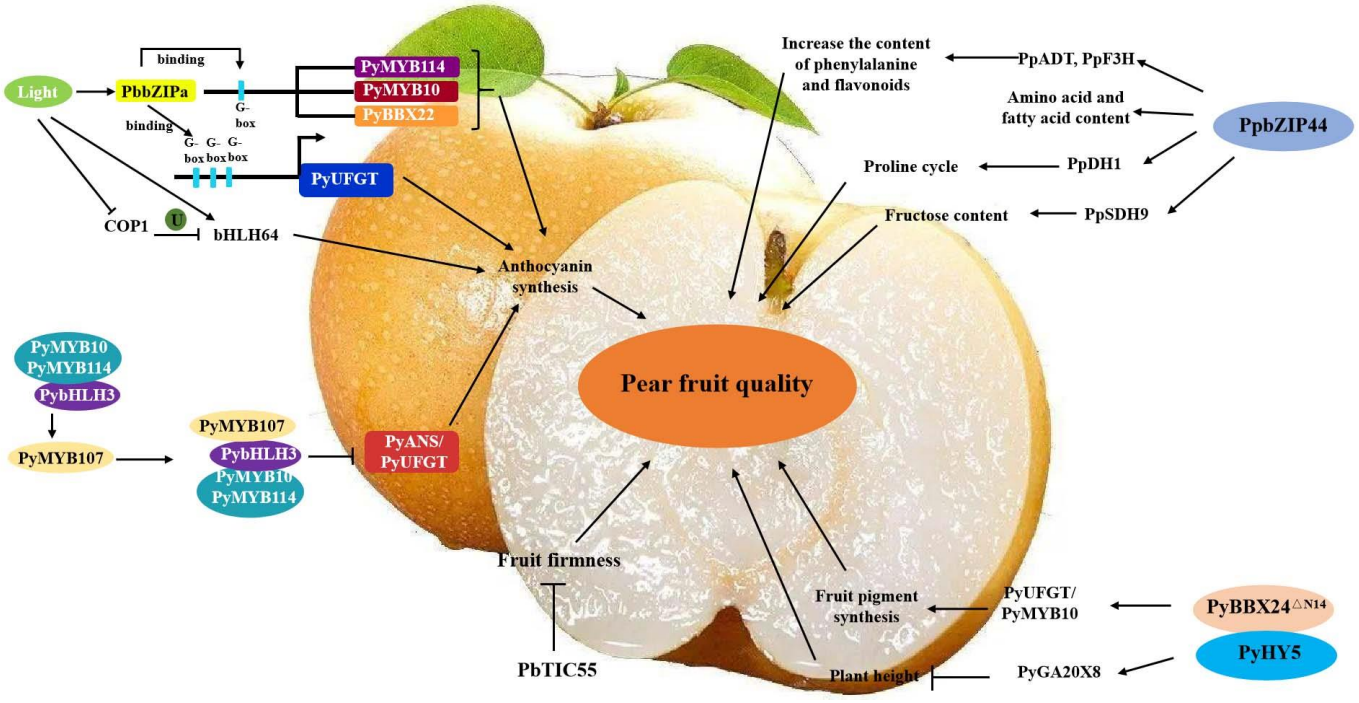

Figure 1. A network that regulates metabolic processes, color, anthocyanin synthesis, and dwarfism in *P.*

2.2. Color

Color is a critical determinant of fruit appearance quality [25,26]. The pear fruit surface exhibits three distinct phenotypes—fully russeted, partially russeted with green patches, and fully green—depending on the accumulation of the cork layer. The presence of anthocyanins introduces varying degrees of red coloration across these three phenotypes.

Partially russeted skin, also known as russeted skin, is a crucial target for elimination in both pear and apple breeding programs. Previous studies on the mechanisms underlying the brown skin phenotype have predominantly focused on this aspect [27,28]. The cork layer, which overlays secondary tissues, serves as a protective barrier that deters pathogen invasion and mitigates water loss. In addition to analyzing the metabolic characteristics associated with cork layer formation, recent studies have identified the germin-like protein (*GLP*) and Patatin-like protein (*PLP*) gene families, each containing four members, as being responsive during pear skin suberization. These genes are implicated in initiating cellular pathogen response pathways. Three potential defense mechanisms against pathogen and pest invasion have been proposed in suberized tissues: a physical barrier formed by the cork layer, a chemical barrier constituted by antimicrobial metabolites such as triterpenes; and basal plant resistance conferred by disease-resistance genes such as *GLP*, *PLP*, and *RPM1*. The wax layer on the surface of suberized pear skin is often compromised, leading to significantly increased water loss. In brown-skinned pears, aquaporin genes are downregulated, suggesting an emergency cellular response to rapid dehydration, which plays a crucial role in mitigating water loss from russeted fruits [29].

In China, the dominant pear species—*Pyrus bretschneideri* 'White Pear', *Pyrus pyrifolia* 'Sand Pear', and *Pyrus ussuriensis* 'Qiuzi Pear'—mainly produce green or brown-skinned fruits. Red-skinned pear resources are rare and confined to a few regions like Yunnan and southern Sichuan. The red coloration in pears primarily stems from anthocyanin accumulation, which not only benefits human health but also significantly enhances the fruit's commercial value [30,31]. Overexpression of *PyMYB107* suppressed anthocyanin biosynthesis in pear calli and fruit, while virus-induced silencing of *PyMYB107* increased anthocyanin accumulation. This study revealed the "activation-inhibition" loop regulatory mechanism of anthocyanin synthesis in red-skinned pear fruit. The transcription of the inhibitor *PyMYB107* is activated by the activators PyMYB10/MYB114. PyMYB107 prevents excessive anthocyanin accumulation by competitively binding to *PybHLH3* with PyMYB10/MYB114 [32]. The variation in anthocyanin synthesis in pear fruits provides valuable genetic resources for pear breeding. Meanwhile, dwarfing is an important agronomic trait that helps reduce management costs and address issues of tree canopy shading. This, in turn, improves the light conditions for fruit development, benefiting both the internal and external quality of the fruit.

Furthermore, studies have shown that overexpression of $PyBBX24^{\Delta N14}$ promotes anthocyanin accumulation in pear, strawberry, *Arabidopsis*, tobacco, and tomato, whereas the overexpression of the full-length PyBBX24 does not [33]. $PyBBX24^{\Delta N14}$ interacts with PyHY5 to directly activate the expression of *PyUFGT* and *PyMYB10*. Stable overexpression of $PyBBX24^{\Delta N14}$ also induces a dwarf phenotype in *Arabidopsis*, tobacco, and tomato by directly binding to the promoter of *PyGA2ox8*, which inactivates bioactive gibberellins, thus reducing plant height. Interestingly, this premature termination mutation in PyBBX24 is also present in several European red pear bud sport varieties, identifying PyBBX24 as a key gene linking pigmentation and dwarfing traits [33]. To further explore the role of BBX proteins in anthocyanin biosynthesis, it identified a *bHLH* gene with high expression levels in *BBX18* overexpression lines, named bHLH64. bHLH64 acts as a positive regulator of anthocyanin biosynthesis by forming a complex with MYB10 to activate structural genes [34]. Its expression is induced by light and is targeted for degradation by COP1 in the dark via the 26S proteasome pathway. Light exposure inhibits COP1, enhancing bHLH64 protein stability under light conditions. This discovery makes bHLH64 the first non-IIIf sub-group bHLH transcription factor involved in anthocyanin biosynthesis, expanding the understanding of the bHLH family's role and enriching the molecular network of light-induced coloration in red pear fruits [34] (Figure 1). Environmental factors also

influence the stability of pear coloration, with light being one of the most critical factors. Understanding the light-induced coloration mechanism in pears is therefore of great scientific and practical importance [35,36]. A study investigating bagged and unbagged fruit peels of the red-skinned pear cultivar 'Mantianhong' combined metabolomic and transcriptomic analyses. This research identified a novel transcript, *PybZIPa*, whose expression was strongly light-responsive post-bag removal and positively correlated with cyanidin content [37]. Unlike the regulatory mechanisms in *Arabidopsis*, apple, and rice, *PybZIPa* in pear not only activated the promoters of transcription factors *PyMYB114*, *PyMYB10*, and *PyBBX22* but also enhanced its promoter activity. Moreover, PybZIPa directly regulated the anthocyanin structural gene *PyUFGT*, promoting anthocyanin biosynthesis. Further analysis revealed that genes regulated by *PybZIPa* contained G-box elements. The *PyUFGT* promoter of 'Mantianhong' features three tandem G-box elements. Mutational analysis showed that the transcriptional activation of *PyUFGT* by *PybZIPa* depended on the number of G-box elements, fewer G-box elements led to reduced activation [37].

2.3. Texture

Pears are typically classified into two main categories—European and Asian pears—based on their geographic distribution [38]. European pears, primarily belonging to *Pyrus communis*, are characterized by their soft, juicy flesh, and strong aroma [39]. In contrast, the principal cultivars of Asian pears are derived from *P. pyrifolia*, *P. bretschneideri*, *P. sinkiangensis*, and *P. ussuriensis* [39]. Most Asian pears exhibit a crisp texture, abundant juice content, and a more subtle aroma. A recent study reported the genomic variation maps of 113 wild and cultivated pear germplasm materials from around the world. The distinct selective sweep signatures observed between Asian and European pears, in conjunction with co-localized quantitative trait loci (QTLs) and differentially expressed genes, highlight the genetic basis for various phenotypic traits such as flesh texture. The research team found that in Asian pears, eleven genes associated with cell wall degradation were identified within regions undergoing selective sweeps, whereas no such genes were detected in the selective sweep regions of European pears. These domestication-related genes may contribute to the characteristic crisp texture of Asian pear flesh, in contrast to the softer, finer texture typical of European pears [39]. In addition to geographical differences in texture, texture depends on many factors: the time of harvest, the conditions and duration of storage, and the ripening conditions after storage. A chilling period following harvest is required for the proper initiation of ripening in many winter pear varieties [40]. Once the chilling requirements are met, the typical ripening process involves a loss of firmness, the degradation of green pigments, a reduction in organic acids, and an increase in protein and water-soluble polyuronides, all of which are triggered by elevated ethylene levels. Pears exhibit a high sensitivity to storage temperature. For instance, 'Anjou' and 'Bartlett' pears demonstrate approximately a 40% longer storage life when stored at 1 °C compared to 0 °C. Heat treatment of fruit can lead to changes in fruit texture by stimulating various enzyme activities. In the case of African pears, heat-induced softening has been attributed to the activation of cell wall-degrading enzymes, including cellulase (Cel), polygalacturonase (PG), and pectin methylesterase (PME), following heat treatment at temperatures ranging from 60 to 85 °C. Proper maturity at harvest is crucial for ensuring a long storage life. Pears harvested at full maturity are less prone to physiological disorders and are more likely to ripen appropriately after storage. In addition, the balance of oxygen and carbon dioxide determines the texture of the fruit. Low oxygen levels can slow the ripening process of many fruits. Studies have shown that Carbon dioxide treatment helped to preserve fruit quality by delaying the loss of firmness and promoting the accumulation of total soluble

solids (TSS) [41]. Both high concentrations of CO_2 and low O_2 levels appear to inhibit the ethylene biosynthetic pathway with respect to ethylene production.

2.4. Physiological Disorders

Superficial scald is a widespread postharvest disease affecting several globally cultivated pear varieties, including 'Anjou', 'Red Bartlett', 'Yali', 'Dangshan Su', and 'Nanguo'. It manifests as dark blemishes on the fruit surface, severely reducing commercial value and often rendering the fruit unsellable. Given its extensive damage and the irreversibility of symptoms post-onset, superficial scald poses a significant economic burden on the global pear industry and remains a critical issue requiring urgent resolution [42,43]. Traditional theories attribute superficial scald to the excessive accumulation of α-farnesene, which disrupts the cellular membrane system. This disruption facilitates the enzymatic oxidation of phenolic compounds by polyphenol oxidase, producing brown quinones that result in scald symptoms [44,45]. However, the potential involvement of alternative pathways remains unclear. Recent research has clarified that superficial scald in certain European pear cultivars, such as 'Red Bartlett' does not depend on excessive α-farnesene accumulation. Instead, the primary enzymatic browning reactions in these pears are mediated by laccase rather than polyphenol oxidase. Moreover, a laccase-encoding gene, *PcTT10*, has been identified as being highly correlated with scald development [46]. Additionally, studies have revealed that scald-susceptible cultivars like 'Red Bartlett' accumulate substantial amounts of epicatechin and anthocyanins. These phenolic compounds rapidly form brown enzymatic products under the catalytic action of laccase, leading to scald development [46].

3. Stone Cells Affect Fruit Quality of Pears

Pear is a globally significant fruit, particularly favored by consumers for its crisp and sweet taste. The quality of pear fruit is determined by various factors, among which a unique type of lignified cell, the stone cell, plays a critical role. An excessive presence of stone cells results in a coarse fruit texture and inferior taste. While the transcription factors involved in stone cell formation in pear have been preliminarily identified, the mechanisms underlying their coordinated regulation remain unclear [47,48]. Recent research identified *PbrMYB24* through co-expression network and transcriptome analyses. This gene exhibits a significant positive correlation with stone cell, lignin, and cellulose content across different pear cultivars [49]. Transient overexpression and gene silencing experiments in pear fruit have confirmed that *PbrMYB24* promotes the accumulation of lignin and cellulose in stone cells. Overexpression of *PbrMYB24* in transgenic pear callus and *Arabidopsis* inflorescence stems significantly increased lignin and cellulose content, as evidenced by enhanced phloroglucinol-HCl staining, safranin-fast green staining, and Calcofluor white fluorescence, along with substantial thickening of the secondary cell wall. PbrMYB24 directly activates lignin and cellulose synthesis genes by binding to different cis-elements (AC-I, AC-II, and MBS). Additionally, *PbrMYB24* regulates the expression of *PbrNSC* and *PbrMYB169*, which in turn can activate *PbrMYB24*, forming a hierarchical regulatory network that synergistically modulates lignin and cellulose biosynthesis in stone cells [49]. This study advances our understanding of the molecular mechanisms and regulatory networks underlying lignin and cellulose synthesis in pear stone cells. It provides a theoretical foundation and genetic resources for the future genetic improvement of stone cell traits in pear fruits [49] (Figure 2).

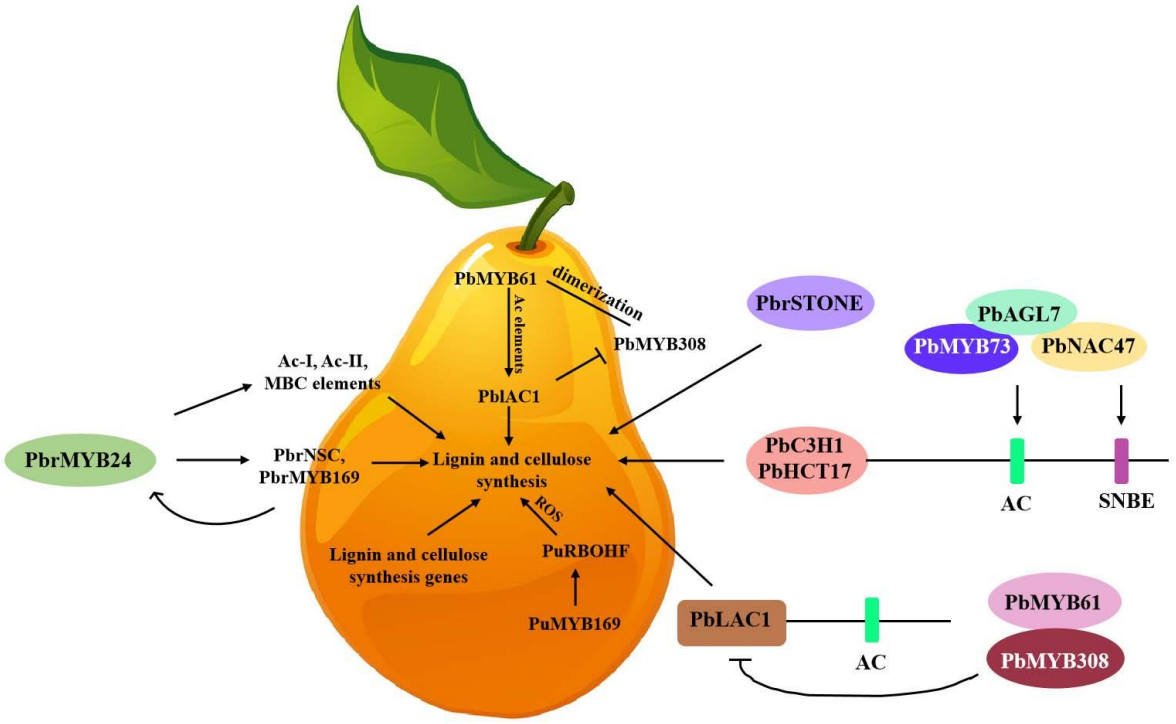

Figure 2. A network that regulates lignin and cellulose synthesis of pear.

'Qiuzi' pears are characterized by a high stone cell content, making the investigation of stone cell formation and its influencing factors crucial for improving fruit quality [50]. Stone cells are formed through secondary cell wall thickening and lignin deposition, with reactive oxygen species (ROS) generated by respiratory burst oxidase homologs (RBOHs) playing a key role in lignin polymerization. However, the specific role of ROS in stone cell development in pear remains unclear [51]. Studies have demonstrated a close correlation between ROS accumulation and lignification of stone cells in pear fruit. Confocal microscopy and transmission electron microscopy have shown spatial consistency between ROS distribution and cell wall lignification [51]. Lignification of stone cells in pear can be inhibited by the RBOH inhibitor diphenyleneiodonium chloride (DPI), providing physiological evidence for the critical role of RBOH-mediated ROS in lignin biosynthesis. In situ hybridization analysis has identified *PuRBOHF* as the *RBOH* family member most likely involved in stone cell lignification in pear. Transient expression in young pear fruit and stable transformation in fruit callus revealed that overexpression of *PuRBOHF* significantly increased lignin content in both fruit and callus tissues, whereas silencing *PuRBOHF* suppressed lignin accumulation [51]. Dual-Luciferase assays confirmed that the transcription factor PuMYB169 activates the *PuRBOHF* promoter. GUS reporter gene assays demonstrated that the promoters of lignin polymerization-related structural genes (*PuPOD2*, *PuLAC2*) can be induced by exogenous ROS [51]. These findings indicate that *PuRBOHF* can be activated by PuMYB169, and it regulates the transcription of lignin polymerization-related genes through ROS production. This study is the first to elucidate the molecular mechanism of *PuRBOHF* in pear fruit lignin metabolism, providing a theoretical basis for strategies to regulate stone cell content in pear fruit [51] (Figure 2).

Recent studies have identified 25 PDCB genes in pear, showing a conserved evolutionary relationship with the PDCB family in *Arabidopsis*. Pear PDCB proteins consist of five conserved domains. Among them, *PbPDCB16* exhibits a negative correlation with lignin content during pear fruit development [52]. Transient expression in 'Dangshan Su' pear fruit at 35 days after flowering and stable expression in pear fruit callus revealed that *PbPDCB16* overexpression significantly increased gene expression and callose content

while reducing lignin accumulation. Conversely, silencing *PbPDCB16* resulted in decreased callose content and increased lignin levels. In *Arabidopsis*, overexpression of *PbPDCB16* led to dwarf plants, enhanced callose accumulation in stems, and reduced expression of lignin biosynthesis genes, lowering lignin content. Additionally, the number of plasmodesmata (PD) in transgenic stems was reduced, with simplified and obstructed structures [52]. These findings suggest that PbPDCB16 promotes callose accumulation in PD and modulates the lignification of stone cells in pear fruit by altering PD structure, thereby reducing secondary cell wall thickness. This highlights a cell cooperation pathway in the formation of pear fruit stone cells [52].

Stone cells in pear fruit are characterized by thickened cell walls due to secondary growth and lignin deposition, which severely impact the fruit's edible quality [53]. A transcriptomic analysis of five developmental stages of 'Shannong Su' pear identified 35,874 differentially expressed genes. Weighted Gene Co-expression Network Analysis (WGCNA) revealed two stone cell-associated modules and identified 42 lignin biosynthesis genes, including nine hub genes in the lignin synthesis network. Furthermore, WGCNA identified two key transcription factors, *PbMYB61* and *PbMYB308*, involved in regulating lignin biosynthesis [53]. PbMYB61 activates gene transcription by binding to the AC element in the *PbLAC1* promoter, promoting lignin biosynthesis. PbMYB308 forms a dimer with PbMYB61, thereby inhibiting its activation of *PbLAC1* and negatively regulating stone cell lignin synthesis [53]. This reveals the molecular mechanism by which the PbMYB308-PbMYB61-PbLAC1 module regulates lignin biosynthesis in pear fruit. This expands our understanding of the transcriptional regulatory mechanisms of lignin biosynthesis in pear fruit [53] (Figure 2).

Recent research has identified critical factors initiating stone cell formation in pear, including PbMC1a/1b and PbRD21, which serve as "switches" to trigger cell lignification [54]. A subsequent study unveiled the molecular mechanism of stone cell formation, highlighting the PbAGL7-PbNAC47-PbMYB73 module that coordinates the response to programmed cell death (PCD) in regulating this process [55]. Using transcriptomic analysis of pear varieties with differing stone cell content, *PbAGL7* was identified as a key transcription factor associated with stone cell formation. Transient expression of *PbAGL7* in pear fruit and stable expression in *Arabidopsis* demonstrated its ability to increase stone cell and lignin content, enhance secondary cell wall thickness, and upregulate key lignin biosynthesis genes *PbC3H1* and *PbHCT17*. However, *PbAGL7* lacks direct transcriptional activation activity and does not bind directly to the promoters of these genes [55]. Further screening through a yeast library revealed that PbNAC47 and PbMYB73 interact with PbAGL7 in the nucleus. After transient expression in pear fruit and stable expression in *Arabidopsis*, *PbNAC47* and *PbMYB73* also increased stone cell and lignin content, promoted secondary cell wall thickening, and raised the expression of key lignin biosynthesis genes *PbC3H1* and *PbHCT17*. PbNAC47 and PbMYB73 upregulated the expression of *PbC3H1* and *PbHCT17* by binding to the SNBE and AC elements, respectively. At the same time, the interaction between PbNAC47 and PbMYB73 forms the PbAGL7-PbNAC47-PbMYB73 complex, which significantly activates the expression of *PbC3H1* and *PbHCT17*, promoting stone cell formation in pear fruit. Additionally, the PCD process proteins PbMC1a/1b interact with PbAGL7, suggesting that this complex may be influenced by the PCD process mediated by PbMC1a/1b, thereby promoting lignin biosynthesis in stone cells of pear fruit. This study provides new insights into the molecular mechanism by which transcription factors, influenced by the PCD process, collaboratively regulate stone cell formation in pear fruit, expanding our understanding of plant cell wall lignification and laying a foundation for future genetic engineering to improve pear fruit quality [55] (Figure 2).

4. Sugar Affects Pear Fruit Quality

Among the many factors influencing fruit quality, sweetness is a key determinant of pear fruit flavor. Understanding the genetic basis and molecular regulatory mechanisms underlying variations in sugar content among different pear cultivars is crucial for improving sweetness and overall fruit quality. Sweetness is one of the primary indicators of fruit quality, and sucrose, as the main substance transported from "source" to "sink" in plants, plays a pivotal role in determining fruit sweetness. Unraveling the mechanisms of sucrose transport and sugar accumulation in fruit is essential [56,57]. Numerous studies have highlighted the importance of sugar transport proteins, particularly SWEET proteins, in the transportation of sugars within plants. SWEET proteins mediate the transmembrane transport of monosaccharides or disaccharides driven by concentration gradients, without requiring energy. This protein family comprises four evolutionary clades, with each clade responsible for transporting different types of sugars. In higher plants, *SWEET* genes perform additional roles beyond sugar transport during various developmental stages [58]. As sugar content is a critical indicator of fruit quality, increasing sugar levels remains a major breeding goal for fruit crops. Sucrose is the primary transport form of photosynthetic products in plants [59,60]. By enhancing our understanding of sugar transport and metabolism, particularly through key regulators such as SWEET proteins, targeted breeding strategies can be developed to improve the sweetness and quality of pear fruit.

'Nanguo' pear, a distinctive local variety of sand pear native to Liaoning Province, China [61,62], has been the subject of research investigating the differences in sugar content between the standard 'Nanguo' pear (NG) and its high-sugar bud mutant (BNG). This study identified an essential sugar transporter, PuSWEET15, and a regulatory transcription factor, PuWRKY31, which influence sugar content [63]. WRKY transcription factors play a crucial role in plants' stress resistance, but their involvement in regulating sucrose accumulation in fruits has not been reported. Using Nanguo pear (NG) and its high-sugar bud mutant (BNG) fruit as materials, a transcriptome sequencing study identified the high expression of the sugar transporter *PuSWEET15* in BNG fruit. By silencing or overexpressing *PuSWEET15* in the fruit, it was found that *PuSWEET15* functions in sucrose transport. The transcription factor *PuWRKY31* is also highly expressed in BNG fruit. Overexpressing *PuWRKY31* in the fruit and validating its effect showed that PuWRKY31 can directly bind to the promoter of the *PuSWEET15* gene both in vivo and in vitro, thereby upregulating its expression. The high expression of *PuWRKY31* in BNG fruit is associated with a high acetylation level of its promoter. This study reveals the relationship between WRKY transcription factors and sucrose transport in fruits, which contributes to a deeper understanding of the role of the sugar transport network in plant growth and development [63] (Figure 3).

A study investigating the transcriptome during pear fruit development identified PbrbZIP15 as a transcription factor highly positively correlated with sugar content. PbrbZIP15 promotes the accumulation of fructose, sucrose, glucose, and total sugars in pear fruits, thereby enhancing fruit sweetness [64]. The *PbrbZIP15* gene shares high sequence similarity with homologous genes in *Arabidopsis*, tobacco, and tomato, all of which contain a conserved upstream open reading frame. This leader peptide can participate in sucrose-induced translation repression. Co-expression analysis of *PbrbZIP15* with structural genes related to sugar metabolism and transport revealed that *PbrXylA1*, a direct downstream target gene of *PbrbZIP15*, can be transcriptionally activated by PbrbZIP15 [65]. XylA catalyzes the isomerization of D-glucose to D-fructose, which is widely used in the industry to produce high-fructose corn syrup. Most reported glucose isomerases are derived from bacteria, and there are few reports of them in plants. This study performed evolutionary analysis and sequence comparison of XylA from different plants and bacteria, finding that plant XylA proteins originated 177 million years ago. Compared to bacterial XylA, the

plant XylA protein contains a leucine-rich signal peptide at its N-terminus, which may play a role in its endoplasmic reticulum localization. Further studies revealed that *PbrXylA1* can catalyze the isomerization of glucose to fructose, while also promoting the accumulation of sucrose and total sugars, thereby enhancing the sweetness of pear fruit [65]. PbrbZIP15 activates the transcription of PbrXylA1, thereby increasing fructose content in pears through the glucose isomerization pathway, and promoting the accumulation of sucrose and total sugars, which ultimately improves fruit sweetness. This study provides new insights into the mechanism of sugar accumulation in pear fruits and expands the sugar metabolism regulatory network in pears. At the same time, this study is the first to demonstrate the mutual isomerization process of glucose and fructose in horticultural fruits [65] (Figure 1).

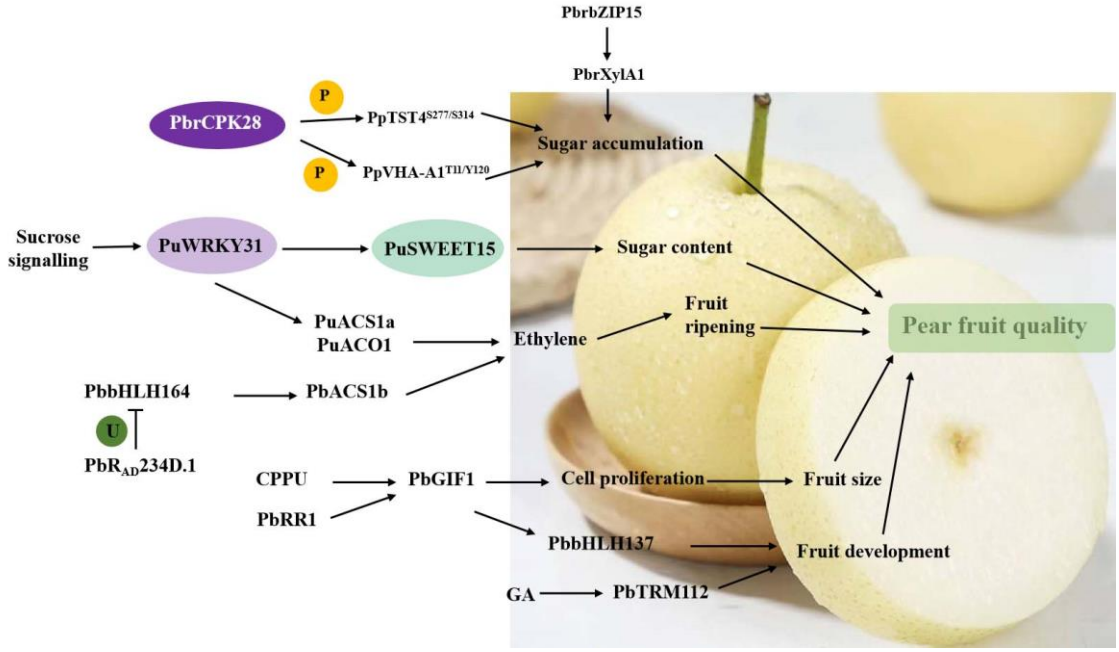

Figure 3. A network that regulates sugar and hormones of pear.

A study constructed a high-density genetic linkage map of pears and located a major QTL for soluble solid content in pear fruit on linkage group LG15 [66]. By combining transcriptome data from different pear varieties and phenotypic data of sugar content at fruit maturity, an important candidate gene related to sugar content in pear fruit, *PbCPK28*, was located in this region [67]. It was also found that this gene is located in a selective scan region and exhibits selective domestication features in both wild and cultivated varieties. The study found that PbCPK28 interacts with the vacuolar membrane sugar transporter PbTST4 and undergoes phosphorylation, thereby activating the transport activity of PbTST4. At the same time, PbCPK28 can phosphorylate the vacuolar membrane proton pump PbVHA-A1, enhancing the transport of hydrogen ions into the vacuole. The resulting electrochemical gradient provides energy for PbTST4 to transport sugars, thereby promoting sugar accumulation in fruit. The study also found that the residues S277 and S314 of PbTST4 are crucial for its function, and the phosphorylation sites T11 and Y120 in VHA-A1 are essential for its function [68]. Association analysis showed that a single nucleotide polymorphism ($SNP13^{T/C}$) in the promoter region of PbCPK28 affects its expression in different pear varieties, leading to differences in fructose content in pears. The discovery of this regulatory pathway improves the molecular mechanism and action network of sugar quality regulation in pear fruit, providing a theoretical foundation and genetic resources for future genetic improvement of sugar quality traits in pear fruit. At the same time, the identified sugar content-related variation loci will provide targets for

the development of molecular markers for pear fruit quality traits and molecular-assisted breeding [68] (Figure 3).

5. Regulation of Pear Fruit Quality by Plant Hormones

5.1. Cytokinin

Cytokinins (CK) play a pivotal role in plant growth and development, particularly in regulating cell division and proliferation across various tissues [69,70]. GRF-INTERACTION FACTOR 1 (GIF1) is a key transcription factor involved in the regulation of cell proliferation. While GIF1 has been reported to regulate leaf and floral organ development, its role in fruit development has not been well documented [70,71]. Recent research has shown that PbGIF1 promotes cell proliferation in pear fruit [72]. Transgenic tomato plants overexpressing *PbGIF1* exhibited increased fruit size due to enhanced cell proliferation. Similarly, accelerated cell proliferation was observed in callus tissues of transgenic pear overexpressing *PbGIF1*. Furthermore, treatment with the CK analog CPPU was found to induce the transcription of *PbGIF1* in pear fruits. Subsequent studies revealed that *PbGIF1* can be activated by the CK response regulator B-RR PbRR1, implicating *PbGIF1* in the CK signaling pathway that regulates pear fruit development. This research elucidates the function of the transcriptional co-activator *PbGIF1* in regulating fruit cell proliferation and uncovers the molecular mechanisms through which CK influences pear fruit development, providing theoretical foundations and genetic resources for studies on fruit development and molecular breeding [72]. Growth-regulating factors (GRF) and GIF, as plant cell proliferation regulators, control the development of different tissues. A study investigated the role of the *PbGIF1* gene in pear fruit development [73]. By constructing a fruit cDNA yeast library, a transcription factor PbbHLH137 involved in regulating pear fruit development was identified. Interaction between PbbHLH137 and PbGIF1 was confirmed. Tracking the entire fruit development process revealed a strong correlation between fruit size and the expression level of *PbbHLH137*, which is highly involved in the later stages of pear fruit development. Further research demonstrated that heterologous expression of *PbbHLH137* and *PbGIF1* positively regulates cell volume and cell number, respectively, promoting fruit expansion. Moreover, *PbGIF1* enhances the transcriptional activation of *PbbHLH137*. As a key transcription factor regulating fruit development, *PbbHLH137* works in tandem with *PbGIF1*, which promotes fruit development by activating *PbbHLH137* expression, marking *PbGIF1* as a potential positive regulator of pear fruit growth [73] (Figure 3).

5.2. Gibberellin

Fruit shape and size are key economic factors in the pear industry, and appropriate fruit size and similar shape are beneficial for mechanical harvesting. Fruit size and shape are regulated by various hormones. Gibberellin (GA) plays an important role in regulating fruit size. A study applied exogenous GA to the pedicel during the full bloom stage of 'Sheng Shui' pear and explored the regulatory mechanism of exogenous GA on pear fruit development at the physiological, cellular, and molecular levels [74]. The single fruit weight (Fw) of pear fruits in the GA treatment group significantly increased on days 4, 8, 12, 16, 20, 24, 28, 38, 53, 68, 83, 98, 113, and 128 post-treatment, and remained higher than the control group, indicating that GA plays a positive regulatory role in increasing fruit size. The fruit shape index of pears treated with GA remained higher than the control group, suggesting that GA may regulate fruit shape by affecting longitudinal elongation. The study analyzed the transcriptional levels of 13 differentially expressed genes related to cell growth and expansion, suggesting that GA may regulate fruit development by altering the transcription levels of these genes [74]. A total of 50 TRM genes were identified in the pear genome, which can be classified into three subfamilies. The PyTRM proteins were predicted

to be localized in the nucleus, chloroplasts, and mitochondria, implying that PyTRM may function in various cellular locations and regulate various biological processes [74]. Among the 50 *PyTRM* genes, 9 genes were expressed in all transcriptome samples (FPKM > 0). After GA treatment, the transcriptional levels of *PyTRM13-2*, *PyTRM13-1A*, and *PyTRM112* were higher. qRT-PCR showed that *PyTRM112* had the highest expression level in the fruit flesh samples on day 12 after GA treatment. Generally, changes in gene expression precede changes in physiological phenotypes. Given that the expression level of *PyTRM112* in the GA treatment group was significantly higher than in the control group, it is hypothesized that *PyTRM112* plays an important role in pear fruit development. A total of 8 *PyTRM112* genes were identified, and the *PyTRM112* gene with the highest expression level after GA treatment was selected for further research. The *PyTRM112* overexpression *Arabidopsis* T3 transgenic lines were obtained using Agrobacterium-mediated transformation. Compared to the Col-0 line, *PyTRM112* overexpressing lines showed significantly increased plant height, a higher number of siliques, a larger ratio of silique length to width, and earlier flowering. This indicates that overexpression of the *PyTRM112* gene promotes growth and development in *Arabidopsis* [74]. The *PyTRM112* overexpression Arabidopsis T3 transgenic lines were obtained using Agrobacterium-mediated transformation. Compared to the Col-0 line, *PyTRM112* overexpressing lines showed significantly increased plant height, a higher number of siliques, a larger ratio of silique length to width, and earlier flowering. This indicates that overexpression of the *PyTRM112* gene promotes growth and development in *Arabidopsis*. Additionally, potential protein interactions with PyTRM112 were predicted, suggesting that PyTRM112 may interact with other proteins to regulate pear growth and development [74]. In this study, GA was applied to pear peduncles during full bloom, and differentially expressed genes were identified through transcriptome sequencing. Fifty *TRM* family genes were identified in pear, among which *PyTRM112* exhibited the highest expression level on the 12th day after exogenous GA treatment. *PyTRM112* was subsequently introduced into the model plant *Arabidopsis* to elucidate its function, showing that overexpression of *PyTRM112* increased plant height, promoted earlier flowering, and enhanced silique growth. This study provides important insights for further investigation into the role of *TRM* genes in pear fruit growth and development [74] (Figure 3).

5.3. Ethylene

Ethylene plays a crucial role in the ripening process of climacteric fruits, while sucrose is essential in various plant developmental processes. The regulatory mechanisms between ethylene and sucrose are complex. Previous studies have shown that exogenous sucrose treatment can promote ethylene synthesis [75–77]. A study using 'Nanguo' pear (NG) and its high-sugar bud mutant (BNG) fruits as materials investigated the molecular mechanism by which the transcription factor PuWRKY31 promotes ethylene production in response to sugar signaling, uncovering the sucrose-induced ethylene biosynthesis mechanism. The study found that BNG fruits accumulated more sucrose during development and ripening than NG, and the ethylene release peak occurred earlier in BNG fruits. Exogenous sucrose treatment of pear fruits also revealed that sucrose promotes ethylene biosynthesis. The study demonstrated that *PuWRKY31* and key ethylene biosynthesis genes *PuACS1a* and *PuACO1* were highly expressed in BNG fruits during ripening. Silencing and overexpressing *PuWRKY31* in fruits revealed that *PuWRKY31* can directly bind to the promoters of *PuACS1a* and *PuACO1* both in vivo and in vitro, upregulating their expression, which ultimately led to an earlier ethylene release peak in BNG. This study revealed that PuWRKY31 responds to sucrose signaling to promote ethylene biosynthesis in pear fruits, facilitating further investigation into the roles of ethylene and sucrose signaling in fruit ripening [78]. The plant hormone ethylene plays a crucial role in fruit ripening. Another study, based

on transcriptome analysis of fruits at different developmental and ripening stages from two pear cultivars, 'Sucui No.1′ and 'Cuiguan,' identified a novel transcription factor, PbbHLH164. Compared to developing fruits, PbbHLH164 was more highly expressed in ripening fruits and positively correlated with ethylene production in both cultivars. PbbHLH164 can directly bind to the promoter of 1-aminocyclopropane-1-carboxylate synthase (*PbACS1b*), enhancing its expression, which increases ethylene production and accelerates fruit ripening [79] (Figure 3).

Ethylene induces the synthesis of anthocyanins in apples, grapes and other fruits, and some studies have found that ethylene inhibits the synthesis of pear anthocyanins [80]. It was found that ethylene induced the expression of the transcription factor *PpERF105*. *PpERF105* further activated the expression of the repressive transcription factor *PpMYB140*, which inhibited the expression of the promoter of anthocyanin synthesis-related structural genes by forming the M(140)BW repressor complex and affecting the formation of the activated MBW complex, and finally inhibited the anthocyanin synthesis of pear fruits [81]. Further studies identified the ethylene-induced inhibitory transcription factor PpERF9, which directly binds to the promoter of *PpMYB114* and inhibits its expression, thereby inhibiting the synthesis of anthocyanins in pear peel [82]. The active transcription factor *PpRAP2.4* repressed by ethylene was also identified, which directly binds to the promoter of *PpMYB114* to promote its expression, thereby promoting the accumulation of anthocyanins in pear peel, and the expression of *PpRAP2.4* is also repressed by the transcription of PpERF9, thus forming a regulatory pathway of ethylene-PpERF9-PpRAP2.4-PpMYB114-anthocyanins. It was further found that PpERF9 recruited the TOPLESS protein PpTPL1 through the EAR motif in its protein structure to form the PpERF9-PpTPL1 co-repressor complex, which mediated the histone deacetylation process, reduced the level of histone H3 acetylation on the PpMYB114 and PpRAP2.4 loci, inhibited the expression of target genes, and finally inhibited the synthesis of anthocyanins in pear peel. This study systematically elucidated the molecular mechanism by which ethylene inhibits the expression of *PpRAP2.4* and *PpMYB114* through the histone deacetylation mediated by the PpERF9-PpTPL1 co-inhibitory complex, thereby inhibiting the synthesis of anthocyanins in pear peel [82].

5.4. ABA

ABA is an important plant hormone that promotes pear fruit ripening by increasing the levels of soluble sugars, including sucrose and glucose, and enhancing ethylene release [83]. DNA methylation may regulate pear fruit development by influencing ABA biosynthesis. Pear pulp treated with 5′-Aza under the peel showed decreased DNA methylation levels in both the peel and pulp compared to the control. The 5′-Aza-treated peel exhibited increased chlorophyll accumulation, while the pulp showed higher accumulations of ABA, β-carotene, and lutein, indicating that DNA methylation participates in carotenoid metabolism and promotes fruit ripening by enhancing ABA production [84]. Real-time quantitative PCR analysis of carotenoid metabolic pathway genes and related transcription factors (TFs) in treated and wild-type pulp revealed upregulation of *PbPSY*, *PbHYB1*, and *PbAAO*, while *PbZDS1* and *PbSDR2* showed no significant changes. This suggests that DNA methylation in the pulp inhibits ABA production by suppressing the expression of *PbPSY*, *PbHYB1*, and *PbAAO*. Among the identified TFs, the expression of *PbZFP1*, *PbHB3*, *PbERF*, *PbB3.1*, *PbZFP4*, *PbbZIP1*, *PbGRAS3*, *PbbHLH3*, and *PbNAC1* was upregulated in the treated pulp compared to the control, while *PbZFP2*, *PbHB1*, *PbHB2*, *PbIAA2*, *PbIAA3*, *PbbHLH2*, and *PbbHLH1* showed no significant changes. This implies that the reduction in DNA methylation may promote the expression of these TFs, thereby inducing *PbPSY*, *PbHYB1*, and *PbAAO* expression [84]. Additionally, *PbZFP1*, which exhibits nuclear localization, was selected for functional verification in ABA biosynthesis. Overexpression of *PbZFP1* in

pear fruit callus driven by the 35S promoter significantly increased the expression of key ABA biosynthesis genes, including *PbHYB1*, *PbSDR2*, and *PbAAO*, as well as ABA content. Conversely, VIGS-mediated silencing of *PbZFP1* in 'Dangshan Su' pear fruits resulted in significantly decreased expression of these genes and reduced ABA content compared to the control. These findings demonstrate that PbZFP1 promotes ABA biosynthesis in pear pulp [84].

5.5. Salicylic Acid

Salicylic acid (SA) can delay the ripening and senescence of various fruits, including pear, banana, sweet cherry, and mango, thereby extending their shelf life [85]. Studies have shown that pre-harvest SA treatment on 'Huangjin' pear increases fruit hardness, with higher chlorophyll content in the peel and reduced anthocyanin content compared to the control, resulting in delayed fruit ripening. Post-harvest SA treatment slows the decline in fruit hardness, maintains freshness, and delays senescence. In bananas treated with SA, fruit softening is delayed, with reduced levels of reducing sugars and a decrease in respiration rate. Additionally, the activity of major cell wall-degrading enzymes, including cellulase, polygalacturonase, and xylanase, decreased, further delaying fruit ripening. Post-harvest treatment of citrus fruit with SA reduces rot by inducing the accumulation of H_2O_2, primary metabolites, and lipophilic polymethoxyflavonoids in response to SA signals, thereby delaying fruit senescence. Most of these studies have focused on the physiological and biochemical aspects, while the molecular mechanisms by which SA regulates fruit ripening and senescence remain largely unknown. A study utilizing RNA sequencing technology analyzed and compared the transcriptomic profiles of pear fruit before and after SA treatment [86]. After 12 and 24 h of SA treatment, the expression levels of 159 and 419 genes were significantly altered, respectively. Among these differentially expressed genes (DEGs), 125 genes showed differential expression at both time points and were identified as potential candidate genes related to SA regulation of fruit ripening and senescence. These DEGs are mainly associated with plant hormone biosynthesis and metabolism, cell wall metabolism and modification, antioxidant systems, and senescence-related transcription factors. Additionally, qRT-PCR was used to further validate the expression of several candidate DEGs in pear fruit after SA treatment. This study helps deepen the understanding of the comprehensive mechanisms by which SA regulates pear fruit ripening and senescence [86].

'Huangjin' Pear a cultivar within the sand pear system, is known for its excellent fruit quality. However, its short shelf life severely limits its industrial development. SA has been shown to delay fruit senescence, thereby extending shelf life. Recent studies identified 22 COL (CONSTANS-LIKE) genes in 'Sand pear', including 4 COL genes (*PpCOL8*, *PpCOL9a*, *PpCOL9b*, and *PpCOL14*) identified through RNA-Seq and 18 COL genes identified via whole-genome analysis. Based on the structural domains of COL proteins, these genes were classified into three subfamilies. PpCOL8, which contains two B-box motifs and a CCT domain, belongs to the first subfamily and is predominantly expressed during the early stages of fruit development. Exogenous SA treatment suppressed the expression of *PpCOL8*. Interestingly, PpCOL8 interacts with PpMADS, a MADS-box protein gene that is highly expressed in fruits and whose expression is upregulated by SA. Overexpression of the *PpCOL8* gene in sand pear fruits increased ethylene production and malondialdehyde (MDA) content. Additionally, the activity of antioxidant enzymes (POD and SOD) and the expression of their corresponding genes (*PpPOD1* and *PpSOD1*) were downregulated, indicating that *PpCOL8* promotes fruit senescence. Conversely, overexpression of *PpMADS* in sand pear fruits led to opposite effects, suggesting that *PpMADS* delays fruit senescence. Moreover, co-expression of *PpCOL8* and *PpMADS* was found to delay fruit senescence.

This study highlights the critical role of the interaction between PpCOL8 and PpMADS via the SA signaling pathway in regulating pear fruit senescence [87].

6. Post-Translational Modifications in Regulating Pear Fruit Quality

6.1. Ubiquitination

Post-translational modifications (PTMs) play a crucial role in regulating protein activity and have been reported to be associated with fruit ripening. Among these, ubiquitination facilitates the degradation of target proteins via the 26S proteasome pathway, which is critical for numerous physiological processes. Ubiquitination may occur concurrently with protein phosphorylation. For instance, jasmonic acid-induced phosphorylation of CsMYC2 by CsMPK6 leads to CsMYC2 degradation, inhibiting the biosynthesis of red carotenoids in citrus fruit [88]. Similarly, Ca^{2+}-induced phosphorylation of MdCRF4 by MdCaM2 and MdMADS5 by MdCDPK7 promotes their degradation, suppressing ethylene biosynthesis in apple fruits [89]. Ethylene-induced phosphorylation of MdNAC72 by MdMAPK3 results in MdNAC72 degradation by MdPUB24, accelerating apple fruit softening [90,91]. These findings suggest that transcription factor ubiquitination, potentially triggered by phosphorylation, plays a critical role in fruit ripening. However, the specific transporters that transfer ubiquitinated proteins to the UPS (ubiquitin-proteasome system) during fruit ripening remain unclear. Recent studies using yeast two-hybrid (Y2H) screening identified RAD23C/D.1. Co-immunoprecipitation (Co-IP) analysis revealed that while PbRAD23C/D.1 does not increase PbbHLH164 ubiquitination, it likely facilitates the transfer of polyubiquitinated PbbHLH164 to the 26S proteasome for degradation. This discovery fills a gap in understanding how ubiquitinated proteins are transferred to the UPS during fruit ripening [79]. Notably, phosphorylation can also enhance the activity of target proteins. Light-induced phosphorylation of MdMYB1 and MdERF17 increases their transcriptional regulatory activities, resulting in changes in apple peel coloration [92]. Similarly, phosphorylation of MabZIP21 by MAPK6-3 enhances its transcriptional activity, accelerating banana fruit ripening [93]. Apart from ubiquitination and phosphorylation, PTMs also include acetylation, methylation, and hydroxylation. However, the roles of acetylation, methylation, and hydroxylation in fruit development and ripening are still poorly understood, highlighting the need for further research to elucidate the molecular networks regulating fruit ripening. This study revealed that PbbHLH164 directly binds to *PbACS1b*, enhancing its expression and increasing ethylene production during pear fruit ripening. PbRAD23C/D.1 interacts with PbbHLH164, promoting its degradation. High *PbbHLH164* expression coupled with low *PbRAD23C/D.1* expression results in excessive ethylene accumulation and accelerated fruit ripening. These findings significantly advance the understanding of the regulatory network controlling ethylene biosynthesis during fruit ripening [79] (Figure 3).

6.2. Methylation Modifications

As a globally cultivated fruit tree, the mechanisms by which DNA methylation influences pear fruit flesh development remain insufficiently understood. Recent studies have employed comprehensive analyses of metabolomics, proteomics, transcriptomics, DNA methylomics, and small RNA from pear fruit flesh across 11 developmental stages (from young fruit to ripened fruit) to explore the relationship between metabolites and DNA methylation during fruit development. This research not only fills gaps in understanding the metabolic regulatory networks of perennial fruit trees but also provides new strategies for improving pear fruit quality [84]. The research compared pear flesh tissue at 11 developmental stages, identifying 449 metabolites with differential accumulation across different stages, including plant hormones, anthocyanins, amino acids, and their deriva-

tives, carbohydrates, flavonols, hydroxycinnamic acid derivatives, lipids, nucleotides, and their derivatives across 32 categories. By integrating proteomic and transcriptomic data, a correlation database was constructed, covering 439 metabolites and 14,399 genes, revealing the molecular network regulating pear flesh metabolism. Further exploration of the relationship between DNA methylation and fruit metabolism revealed that DNA methylation levels gradually increased during fruit development and correlated with the accumulation trends of several metabolites, particularly with abscisic acid (ABA), which promotes fruit ripening. Using the DNA methylation inhibitor 5′-deoxycytidine (5′-Aza) on developing pear fruit, the study revealed that DNA methylation inhibits the accumulation of chlorophyll in the peel and the accumulation of ABA, β-carotene, and lutein in the flesh. Additionally, a novel zinc finger protein, PbZFP1, was identified, this protein directly acts on the promoter of the key gene *PbAAO* in the ABA biosynthesis pathway, regulating its expression and thereby promoting ABA synthesis. The study also found that the downregulation of the DNA demethylase gene ROS1 during flesh development is the main reason for the continuous increase in DNA methylation levels, indicating that the dynamic balance between DNA methylation and demethylation determines DNA methylation levels during pear fruit development [84]. This research provides new insights into understanding epigenetic regulation during the fruit development of perennial fruit trees. DNA methylation participates in the regulation of pear flesh metabolism by controlling the expression of key genes, particularly playing an important role in the ABA biosynthesis pathway. These findings not only enhance the understanding of the regulatory mechanisms of pear fruit development but also offer potential strategies for improving fruit quality and extending storage life [84].

6.3. Acetylation Modifications

As a common modification mode of PTM, lysine acetylation plays an important role in regulating various physiological functions and substance metabolism in plants. However, the key regulatory sites and mechanisms of fruit quality formation in perennial woody plants are still unclear. Firstly, the acetylation modification omics of proteins at three key stages of fruit development were systematically detected, and 4280 acetylation modification proteins were identified, including 15,195 acetylation modification sites. Among them, 981 acetylated proteins were differentially modified, and were mainly enriched in carbohydrate metabolism, energy metabolism, terpene and ketone metabolism, lipid metabolism, amino acid metabolism, and other metabolic pathways related to fruit quality [94]. Focusing on 19 acetylated proteins whose acetylation levels were continuously upregulated with fruit development, it was found that the up-regulation of acetylation levels of sucrose synthase (SuS1) was the most significant. Enzyme activity analysis, RNA-seq and proteomic analysis showed that the up-regulation of SuS enzyme activity was not related to its transcription and protein levels, and may be regulated by acetylation level, which ultimately regulates the accumulation of sucrose [94]. This study systematically elucidated the regulatory role of lysine acetylation modification proteins in the development of Rosa roxburghii fruit for the first time, which provided a new idea for better understanding the acetyl proteome of Rosa roxburghii fruit, and also revealed a new mechanism of acetylated sucrose synthase mediating plant sucrose metabolism [94].

bHLH and MYB transcription factors are involved in the regulation of anthocyanin biosynthesis in plants, but their joint involvement in fruit sugar transport has rarely been reported. In some studies, yeast functional complementation analysis, silencing and overexpression in fruits were used to identify the *PuSUT4-like* gene with the function of transporting sucrose [95]. Through the analysis of transcriptome data, *PuMYB12* was found to be highly expressed in ‘Nanhong Pear’, *PuPRE6* and *PuHDAC9-like* were highly expressed

in 'Nanguo Pear', *PuPRE6* and *PuMYB12* antagonized the transcription of *PuSUT4-like* and sucrose accumulation, *PuMYB12* promoted the transcription of *PuSUT4-like* and further promoted the accumulation of sucrose, while *PuPRE6* inhibited the expression of *PuSUT4-like* and thus inhibited the accumulation of sucrose. Further studies revealed that PuPRE6 was upstream of PuMYB12 and inhibited its transcription. Histone acetylation level analysis showed that the histone deacetylation level of PuMYB12 and PuSUT4-like promoters in 'Nanguo pear' was higher than that of 'Nanhong pear', and yeast monohybrid analysis showed that histone deacetylase PuHDAC9-like binds to PuMYB12 and PuSUT4-like promoters. This study provides new evidence for the involvement of bHLH and MYB transcription factors in sucrose accumulation in pear fruits, and opens up a new perspective for understanding fruit quality formation [95].

7. Genomic Sequencing Technologies in the Study of Pear Fruit Quality

Another study focused on the rich genetic diversity of sand pear varieties, analyzing whole-genome genetic variation in 312 natural populations, obtaining 2.15T resequencing data and identifying 3.4 M SNPs [96]. Population analysis of local pear varieties and artificially bred varieties revealed a strong signal in an 11.2Mb interval during the improvement process. The genetic population analysis of traditional local pear varieties and artificially domesticated varieties found that traits such as stone cells, sugar, and acid in pear fruits were subject to continuous selection during domestication and improvement, while traits like fruit size were only selected during domestication [39,96]. Further whole-genome association analysis (GWAS) of eight quality traits, including single fruit weight, color, stone cells, and three phenological traits, such as fruit development days, identified 42 associated intervals. These included known functional genes, some of which overlapped with known QTL loci for certain traits. The association analysis also identified several unknown functional genes related to important pear fruit traits. To explore the impact of unknown genes on trait formation, the study focused on stone cells—an important trait affecting pear quality—by conducting gene function validation. By combining phenotypic data, transcriptomics, and phylogenetic analysis, a new gene, *PbrSTONE*, was identified. Using a transient transformation system in pear fruits and a stable transformation system in *Arabidopsis*, it was confirmed that *PbrSTONE* can regulate the formation of stone cells and their main component, lignin, in pear fruits, and it was clarified that PbrSTONE interacts with a key gene in the lignin synthesis pathway, *PbrC3H*, to collaboratively regulate the lignin synthesis mechanism in stone cells [96]. The research on genetic variation and GWAS of pear fruit traits not only provides abundant genetic loci information for the population genetic characteristics of pears and the development of molecular markers for quality traits but also offers an effective pathway for discovering new genes with unknown functions. The study will provide valuable references for developing molecular breeding technologies for perennial fruit trees and unraveling the regulatory mechanisms of complex traits [96] (Figure 2).

A study reported the resequencing and SNP identification of 176 pear F1 hybrid populations [66]. Using a "sliding window" strategy of 500 kb, the SNP markers with identical genotypes within the window were merged, creating 5515 merged Bin markers for constructing a genetic linkage map. The final map contained 3190 Bin markers (including 1.93 M SNPs) and covered the pear genome to a length of 1358.5 cM, with an average marker spacing of 0.43 cM, creating a saturated genetic map [66]. This high-quality Bin marker map was used to re-anchor Scaffold sequences in the first published version of the 'Dangshan Su' pear genome, increasing the chromosome anchoring rate from 75.5% to 83.7%. The assembly of chromosomes 1, 4, and 7 was improved by 110.1%, 75.7%, and 57.6%, respectively, effectively enhancing the quality of the reference genome [66]. The

study further evaluated the phenotypic data of 18 traits, including single fruit weight, stone cell content, hardness, soluble solids, sugar (fructose, sucrose, glucose, sorbitol) content, acid (citric acid, malic acid, oxalic acid, quinic acid, shikimic acid) content, over two years in this hybrid population. Based on the constructed Bin marker map, QTL mapping was performed, identifying 148 QTLs with 180 significant markers. For the first time in pears, QTLs for stone cell content, four soluble sugar contents, and five organic acid contents were identified. Some QTLs showed reproducibility across different years or contained candidate genes with known functions. By screening genes in QTL intervals using transcriptome data during fruit development in different pear varieties, 399 potential candidate genes were obtained. To explore the impact of candidate genes on pear fruit trait formation, a gene function validation was performed for sugar content traits. Through transient transformation in pear fruit, it was demonstrated that the candidate gene *PbrtMT1* can promote the accumulation of fructose in pear fruit [66]. The development of high-density genetic maps based on Bin markers and QTL mapping of fruit traits not only provides solutions for constructing genetic maps and accurate trait localization in the context of sequencing technology but also serves as a bridge for comparison between maps with different genetic backgrounds. Additionally, genetic maps based on Bin markers provide a wealth of genetic loci information for analyzing population genetic characteristics, mining important functional genes, and developing molecular markers for agronomic traits. This research will provide valuable references for molecular breeding and the analysis of complex traits in perennial fruit trees like pears [66].

Gene interaction through interspecific hybridization during plant domestication is an important pathway for trait improvement. Pear exhibits typical gametophytic self-incompatibility, with gene interactions occurring between wild and cultivated pear species. The fruit hardness of cultivated pear is lower than that of wild pear, and the softening rate of Asian cultivated pear is slower than that of European cultivated pear. Fruit hardness may be a characteristic independently domesticated in Asian and European pears. A study used Identity by Descent (IBD) analysis to investigate the genomes of 113 pear varieties and identified a total of 3,320,796 IBD segments [97]. The study found that Asian and European cultivated varieties share a 3 Mb IBD-enriched region (IBD-ER) on chromosome 15. Genome-wide association study (GWAS) analysis indicated that this IBD-ER contains the *PbTIC55* gene, which is significantly associated with fruit softening. This gene consists of three exons and two introns and encodes a protein with 575 amino acid residues. It was discovered that compared to European cultivars, Asian cultivars have a 12-bp tandem repeat sequence in the first exon of *PbTIC55*, a unique insertion mutation found in seven Asian pear germplasms. To further investigate the effect of the 12-bp tandem repeat sequence on *TIC55*, researchers compared the expression levels of *TIC55* in nine Asian pear cultivars and six European pear cultivars using real-time fluorescence quantitative PCR [97]. The results showed that *PbTIC55* expression levels in Asian pears were significantly higher than in European pears, which may be a key reason for the difference in fruit hardness between Asian and European pears. This study identifies candidate genes that regulate fruit hardness, with significant implications for quality breeding and trait improvement in pear and other fruit trees [97] (Figure 1).

'Yulu Xiang' pear, as a flagship variety of the rural revitalization initiative and a billion-dollar brand, aggregates numerous advantageous traits from its parentage. It is characterized by a large fruit size, distinct aroma, a red blush on the fruit surface, a small seed core, near-round shape, and juicy crisp texture. However, the persistence of the sepals leads to an increased number of stone cells, which negatively impacts the fruit's quality. Although several pear genomes have been sequenced, the genome of a single species does not represent the genetic diversity of the genus Pyrus as a whole. Therefore, it

is necessary to integrate multiple pear genomes into a pan-genome framework with the 'Yulu Xiang' pear as the core and explore the genetic variation of its important traits. A study has assembled the known haploid genome of the 'Yulu Xiang' pear parents and constructed a pan-genome framework based on its haplotype, PsbM. Simultaneously, the study investigated the function of the sepal abscission gene *PsbMGH3.1*, providing new insights into the genomic research of key agronomic traits in "Yuluxiang" pear [98].

Pear cultivation has a long history, with over 22 varieties and more than 5000 cultivars, each exhibiting distinct morphological, physiological, and adaptive characteristics. Currently, eight pear genomes have been released in the GDR (Rosaceae Genomics Database) and NCBI. These genomes have advanced functional genomics and further guided pear breeding. However, due to technical limitations, many gaps remain in the pear genomes, resulting in the loss of genetic information and hindering a comprehensive understanding of pear genome structure and evolution. A study used the representative cultivar 'Yunhong 1' of sand pear to establish the world's first high-quality, gap-free pear T2T-level genome. The assembled genome revealed the formation and functional differentiation of repetitive genes driven by fragmental replication and whole-genome duplication, and further explored the regulatory mechanisms of duplicated gene functional differentiation on important fruit traits in pear [99].

8. Conclusions and Perspective

Over the years, extensive research has been conducted on the physiological, biochemical, and molecular bases of fruit quality formation, but the signal networks governing this process remain largely unknown. The shift in modern fruit production from quantity-oriented to quality-oriented production is an inevitable trend in the global fruit industry [100,101]. China has become a leading fruit producer, with about one-fifth of the world's total fruit production and planting area. Additionally, there has been a significant shift in China's fruit production model, moving from a single-crop mode under a planned economy to a market-driven commodity economy. Producers and managers are increasingly focused on market demands, leading to significant improvements in the appearance of products and a better alignment of taste and flavor with consumer preferences, resulting in a substantial increase in fruit quality [102]. As China joined the World Trade Organization and with the growing need for the development of pollution-free agriculture, there has been an increased focus on fruit quality and safety. With intense global competition in fruit production and quality, improving fruit quality has become a critical issue for China's fruit industry, both now and in the foreseeable future. High-quality fruit production demands in-depth research into the physiology of fruit quality development, as well as the development of techniques that promote superior quality, to produce fruit with both attractive external traits and rich nutritional content. The development of techniques that promote fruit quality, based on an understanding of the inherent rules of fruit quality formation is a quantitative expression of theory guiding practice. On the other hand, scientifically explaining the physiological basis of high-quality fruit cultivation represents a qualitative leap from practice to theory. While factors such as tree species, varieties, ecological environments, and site conditions are important for fruit quality, the biological characteristics of the tree itself and agricultural management practices cannot be overlooked. In particular, the large-scale implementation of protected fruit cultivation and bagging in recent years has led to issues such as a decline in fruit flavor, severe physiological disorders, and poor nutritional value, which have significantly hindered the improvement of fruit quality [2,103–105].

There are several challenges in pear production and storage. For instance, although the breeding of extremely early-ripening pear varieties has optimized the industry structure,

these varieties often suffer from bland taste and low sweetness. Traditional varieties such as 'Dangshan Su' and 'Xuehua' exhibit excellent overall quality, but their high stone cell content negatively affects texture. Compared to European pears, the widely cultivated Chinese pear varieties, such as white pears and sand pears, tend to have a mild aroma, and there are few red-skinned pear cultivars. The increasingly popular 'Yulu Xiang' pear has a very low fruit set rate, which severely impacts economic returns. Additionally, 'Qiuyue' is not resistant to post-harvest storage, significantly reducing its market value. Therefore, addressing existing problems in pear production, such as sugar-to-acid ratio, stone cell content, aroma, fruit color, and endogenous hormones, is crucial. Based on recent molecular biology studies, the goal is to achieve efficient genetic improvement of these key traits through molecular-assisted breeding techniques.

The development of pear fruit quality is jointly regulated by genetic factors and environmental conditions. Obtaining superior varieties through hybrid breeding and molecular-assisted breeding is crucial, but environmental conditions cannot be overlooked. Fruit quality development is often associated with light exposure, as good sunlight promotes carbohydrate formation, which in turn affects the accumulation of sugars and starches in the fruit. Light also influences fruit enlargement, as sugars serve as the molecular foundation for aroma compounds and anthocyanin formation. Therefore, light exposure affects pear size, flavor, aroma, and fruit color, and improving light energy utilization is key to enhancing fruit quality. In recent years, through artificial pruning for the dwarfing and densification of pear trees, both yield and quality have significantly improved, although labor costs remain high. To fundamentally achieve pear tree dwarfing, obtaining dwarfing rootstocks or dwarf varieties is essential. Dwarfing rootstocks can be selected from seedling populations, and the molecular mechanisms underlying dwarfism and dwarfing can be analyzed through molecular biology techniques. By creating dwarf genetic resources through genetic transformation and combining plant tissue culture and factory-based seedling production, mass propagation and application in production can be achieved. This approach not only improves pear fruit quality comprehensively but also addresses labor-related bottlenecks faced by the pear industry.

It is well known that pears are highly nutritious, containing various bioactive components such as polysaccharides, chlorogenic acid, and arbutin. Fresh pears or pear products (such as pear paste and pear soup) are known for their health benefits. However, the specific bioactive compounds responsible for these health effects remain unclear. Identifying the functional components in pears that have therapeutic properties, such as cough suppression and anti-inflammatory effects, is crucial. Further improvement of specific pear varieties, such as Anli pear (a traditional Chinese cultivar from the autumn pear system, which is highly cold-resistant and disease-resistant but has poor fresh eating quality and is often used in processing), through genetic engineering or molecular breeding techniques, could increase the content of these functional components. This would lead to the development of pear products with enhanced health benefits. Additionally, integrating pear breeding with disciplines such as medicine and pharmacology could maximize the value of pears and contribute to human health.

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References

1. Barthwal, R.; Negi, A.; Kathuria, D.; Singh, N. Ozonation: Post-harvest processing of different fruits and vegetables enhancing and preserving the quality. *Food Chem.* **2025**, *463*, 141489. [CrossRef] [PubMed]
2. Abdel Moniem, H.; Yusuf, M.S.; Chen, G. Ecology and population structure of some indigenous geese breeds and the impact of four GH and Pit-1 SNPs on their body weights. *Environ. Sci. Pollut. Res. Int.* **2021**, *28*, 37603–37615. [CrossRef] [PubMed]
3. Orrego, C.E.; Salgado, N.; Botero, C.A. Developments and trends in fruit bar production and characterization. *Crit. Rev. Food Sci. Nutr.* **2014**, *54*, 84–97. [CrossRef] [PubMed]
4. Muhammad, N.; Liu, Z.; Wang, L.; Yang, M.; Liu, M. The underlying molecular mechanisms of hormonal regulation of fruit color in fruit-bearing plants. *Plant Mol. Biol.* **2024**, *114*, 104. [CrossRef] [PubMed]
5. Arji, I.; Hassany, B.; Ghamarnia, H. The effects of water stress on apple qualities and quantities (Golden delicious variety). *J. Hortic. Sci.* **2016**, *29*, 610–620.
6. Beier, S.; Marella, N.C.; Yvin, J.C.; Von Wiren, N.; Hosseini, S.A. Silicon mitigates potassium deficiency by enhanced remobilization and modulated potassium transporter regulation. *Environ. Exp. Bot.* **2022**, *198*, 104849. [CrossRef]
7. Dong, X.; Wang, Z.; Tian, L.; Zhang, Y.; Qi, D.; Huo, H.; Xu, J.; Li, Z.; Liao, R.; Shi, M.; et al. De novo assembly of a wild pear (*Pyrus betuleafolia*) genome. *Plant Biotechnol. J.* **2020**, *18*, 581–595. [CrossRef] [PubMed]
8. Liu, C.; Li, H.; Ren, A.; Chen, G.; Ye, W.; Wu, Y.; Ma, P.; Yu, W.; He, T. A comparison of the mineral element content of 70 different varieties of pear fruit (*Pyrus ussuriensis*) in China. *PeerJ* **2023**, *11*, e15328. [CrossRef] [PubMed]
9. Liu, H.; Wang, G.; Yang, Z.; Wang, Y.; Zhang, Z.; Li, L.; Waqas, M.; Hong, N.; Liu, H.; Wang, G.; et al. Identification and Characterization of a Pear Chlorotic Leaf Spot-Associated Virus, a Novel Emaravirus Associated with a Severe Disease of Pear Trees in China. *Plant Dis.* **2020**, *104*, 2786–2798. [CrossRef]
10. Sun, W.; Gong, P.; Zhao, Y.; Ming, L.; Zeng, Q.; Liu, F. Current Situation of Fire Blight in China. *Phytopathology* **2023**, *113*, 2143–2151. [CrossRef] [PubMed]
11. Wang, P.; Wu, X.; Shi, Z.; Tao, S.; Liu, Z.; Qi, K.; Xie, Z.; Qiao, X.; Gu, C.; Yin, H.; et al. A large-scale proteogenomic atlas of pear. *Mol. Plant* **2023**, *16*, 599–615. [CrossRef] [PubMed]
12. Zhang, Y.; Cao, Y.-F.; Huo, H.-L.; Xu, J.-Y.; Tian, L.-M.; Dong, X.-G.; Qi, D.; Liu, C. An assessment of the genetic diversity of pear (*Pyrus* L.) germplasm resources based on the fruit phenotypic traits. *J. Integr. Agric.* **2022**, *21*, 2275–2290. [CrossRef]
13. Gottschalk, C.; Bell, R.L.; Volk, G.M.; Dardick, C. Over a century of pear breeding at the USDA. *Front. Plant Sci.* **2024**, *15*, 1474143. [CrossRef] [PubMed]
14. Saito, T. Advances in Japanese pear breeding in Japan. *Breed. Sci.* **2016**, *66*, 46–59. [CrossRef] [PubMed]
15. Khan, M.K.U.; Zhang, X.; Ma, Z.; Huang, M.; Yang, C.; Wang, X.; Liu, M.; Peng, J. Contribution of the LAC Genes in Fruit Quality Attributes of the Fruit-Bearing Plants: A Comprehensive Review. *Int. J. Mol. Sci.* **2023**, *24*, 15768. [CrossRef]
16. Cho, G.; Burckhardt, D.; Inoue, H.; Luo, X.; Lee, S. Systematics of the east Palaearctic pear psyllids (Hemiptera: Psylloidea) with particular focus on the Japanese and Korean fauna. *Zootaxa* **2017**, *4362*, 75–98. [CrossRef] [PubMed]
17. Kan, J.; Yuan, N.; Lin, J.; Li, H.; Yang, Q.; Wang, Z.; Shen, Z.; Ying, Y.; Li, X.; Cao, F. Seed Germination and Growth Improvement for Early Maturing Pear Breeding. *Plants* **2023**, *12*, 4120. [CrossRef]
18. Mo, R.; Li, Y.; Yuan, Q.; He, M.; Xu, X.; Chen, G.; Zhang, W.; Duan, Y. Nest-Site Features and Breeding Ecology of Chestnut-Vented Nuthatch Sitta nagaensis in Southwestern China. *Animals* **2023**, *13*, 2034. [CrossRef]
19. Blattný, C. PEARS. In *Encyclopedia of Food Sciences and Nutrition*, 2nd ed.; Caballero, B., Ed.; Academic Press: Oxford, UK, 2003; pp. 4428–4433.
20. Reiland, H.; Slavin, J. Systematic Review of Pears and Health. *Nutr. Today* **2015**, *50*, 301–305. [CrossRef] [PubMed]
21. Bai, L.; Zhang, L.; Lv, J.; Zhang, Y.; Sun, M.; Chen, J.; Ge, Y. Effects of 1-methylcyclopropene (1-MCP) treatment on ethanol fermentation of Nanguo pear fruit during ripening. *J. Food Biochem.* **2022**, *46*, e14035. [CrossRef] [PubMed]
22. Li, J.M.; Huang, X.S.; Li, L.T.; Zheng, D.M.; Xue, C.; Zhang, S.L.; Wu, J. Proteome analysis of pear reveals key genes associated with fruit development and quality. *Planta* **2015**, *241*, 1363–1379. [CrossRef] [PubMed]
23. Song, B.; Yu, J.; Li, X.; Li, J.; Fan, J.; Liu, H.; Wei, W.; Zhang, L.; Gu, K.; Liu, D.; et al. Increased DNA methylation contributes to the early ripening of pear fruits during domestication and improvement. *Genome Biol.* **2024**, *25*, 87. [CrossRef] [PubMed]

24. Wang, H.; Xu, K.; Li, X.; Blanco-Ulate, B.; Yang, Q.; Yao, G.; Wei, Y.; Wu, J.; Sheng, B.; Chang, , Y.; et al. A pear S1-bZIP transcription factor PpbZIP44 modulates carbohydrate metabolism, amino acid, and flavonoid accumulation in fruits. *Hortic Res.* **2023**, *10*, uhad140. [CrossRef] [PubMed]
25. Ali, M.M.; Anwar, R.; Yousef, A.F.; Li, B.; Luvisi, A.; De Bellis, L.; Aprile, A.; Chen, F. Influence of Bagging on the Development and Quality of Fruits. *Plants* **2021**, *10*, 358. [CrossRef] [PubMed]
26. Wang, L.; Gao, F.S.; Xu, K.; Xu, N. Effects of fruit bag color on the microenvironment, yield and quality of tomato fruits. *Ying Yong Sheng Tai Xue Bao* **2013**, *24*, 2229–2234. [PubMed]
27. Wang, H.; Zhang, S.; Fu, Q.; Wang, Z.; Liu, X.; Sun, L.; Zhao, Z. Transcriptomic and metabolomic analysis reveals a protein module involved in preharvest apple peel browning. *Plant Physiol.* **2023**, *192*, 2102–2122. [CrossRef]
28. Zhao, J.; Zou, Q.; Bao, T.; Kong, M.; Gu, T.; Jiang, L.; Wang, T.; Xu, T.; Wang, N.; Zhang, Z.; et al. Transcription factor MdbZIP44 targets the promoter of MdPPO2 to regulate browning in Malus domestica Borkh. *Plant Physiol. Biochem.* **2024**, *214*, 108934. [CrossRef] [PubMed]
29. Wang, Y.; Dai, M.; Cai, D.; Shi, Z. Proteome and transcriptome profile analysis reveals regulatory and stress-responsive networks in the russet fruit skin of sand pear. *Hortic. Res.* **2020**, *7*, 16. [CrossRef] [PubMed]
30. Feng, S.; Sun, S.; Chen, X.; Wu, S.; Wang, D.; Chen, X. PyMYB10 and PyMYB10.1 Interact with bHLH to Enhance Anthocyanin Accumulation in Pears. *PLoS ONE* **2015**, *10*, e0142112. [CrossRef]
31. Feng, S.; Wang, Y.; Yang, S.; Xu, Y.; Chen, X. Anthocyanin biosynthesis in pears is regulated by a R2R3-MYB transcription factor PyMYB10. *Planta* **2010**, *232*, 245–255. [CrossRef]
32. Yang, G.; Xue, Z.; Lin-Wang, K.; Chen, G.; Zhao, Y.; Chang, Y.; Xu, S.; Sun, M.; Xue, C.; Li, J.; et al. An 'activator-repressor' loop controls the anthocyanin biosynthesis in red-skinned pear. *Mol. Hortic.* **2024**, *4*, 26. [CrossRef] [PubMed]
33. Yang, G.; Sun, M.; Brewer, L.; Tang, Z.; Nieuwenhuizen, N.; Cooney, J.; Xu, S.; Sheng, J.; Andre, C.; Xue, C.; et al. Allelic variation of BBX24 is a dominant determinant controlling red coloration and dwarfism in pear. *Plant Biotechnol. J.* **2024**, *22*, 1468–1490. [CrossRef] [PubMed]
34. Tao, R.; Yu, W.; Gao, Y.; Ni, J.; Yin, L.; Zhang, X.; Li, H.; Wang, D.; Bai, S.; Teng, Y. Light-Induced Basic/Helix-Loop-Helix64 Enhances Anthocyanin Biosynthesis and Undergoes CONSTITUTIVELY PHOTOMORPHOGENIC1-Mediated Degradation in Pear. *Plant Physiol.* **2020**, *184*, 1684–1701. [CrossRef] [PubMed]
35. Liu, H.; Shu, Q.; Lin-Wang, K.; Allan, A.C.; Espley, R.V.; Su, J.; Pei, M.; Wu, J. The PyPIF5-PymiR156a-PySPL9-PyMYB114/MYB10 module regulates light-induced anthocyanin biosynthesis in red pear. *Mol. Hortic.* **2021**, *1*, 14. [CrossRef] [PubMed]
36. Yao, G.; Gou, S.; Zhong, T.; Wei, S.; An, X.; Sun, H.; Sun, C.; Hu, K.; Zhang, H. Persulfidation of transcription factor MYB10 inhibits anthocyanin synthesis in red-skinned pear. *Plant Physiol.* **2023**, *192*, 2185–2202. [CrossRef] [PubMed]
37. Liu, H.; Su, J.; Zhu, Y.; Yao, G.; Allan, A.C.; Ampomah-Dwamena, C.; Shu, Q.; Lin-Wang, K.; Zhang, S.; Wu, J. The involvement of PybZIPa in light-induced anthocyanin accumulation via the activation of PyUFGT through binding to tandem G-boxes in its promoter. *Hortic. Res.* **2019**, *6*, 134. [CrossRef]
38. Wu, X.; Chen, Y.; Wang, X.; Qi, K.; Qiao, X.; Li, Q.; Xie, Z.; Cao, P.; Zhang, S.; Yin, H. New insights into aroma regulation in pear peel and flesh under methyl jasmonate treatment obtained by metabolite and whole-transcriptome RNA sequencing analyses. *Postharvest Biol. Technol.* **2023**, *201*, 112347. [CrossRef]
39. Wu, J.; Wang, Y.; Xu, J.; Korban, S.S.; Fei, Z.; Tao, S.; Ming, R.; Tai, S.; Khan, A.M.; Postman, J.D.; et al. Diversification and independent domestication of Asian and European pears. *Genome Biol.* **2018**, *19*, 77. [CrossRef] [PubMed]
40. Gerasopoulos, D.; Richardson, D.G. Effects of exogenous propylene and fruit calcium on ripening of non-chilled and chilled Anjou pears. *Postharvest Biol. Technol.* **1996**, *8*, 111–120. [CrossRef]
41. Wang, D.; Ma, Q.; Belwal, T.; Li, D.; Li, W.; Li, L.; Luo, Z. High Carbon Dioxide Treatment Modulates Sugar Metabolism and Maintains the Quality of Fresh-Cut Pear Fruit. *Molecules* **2020**, *25*, 4261. [CrossRef] [PubMed]
42. Sun, X.; Wang, F.; Wang, Y.; Zhang, Y.; Zhang, Y.; Liu, Y.; Sun, X.; Qi, K.; Xie, Z.; Zhang, S. Transcription factors Pbr3RAV2 and PbrTTG1 regulate pear resistance to Botryosphaeria dothidea via the autophagy pathway. *Plant Physiol.* **2024**, *195*, 3024–3038. [CrossRef] [PubMed]
43. Yang, Y.; He, Y.; Lv, S.; Zhu, H.; Wang, T.; Wang, G.; Hong, N.; Wang, L. The PcMYB44-mediated miR397-PcLACs module regulates defence-induced lignification in pear resistance to fungal disease. *Mol. Plant Pathol.* **2023**, *24*, 1107–1125. [CrossRef] [PubMed]
44. Ding, R.; Du, B.; Zhang, Y. Conjugated trienols and programmed cell death are more closely related to superficial scald than reactive oxygen species in apple fruit stored at low temperature. *Sci. Hortic.* **2019**, *246*, 597–603. [CrossRef]
45. He, J.; Feng, Y.; Cheng, Y.; Karuppanapandian, T.; Wang, J.; Guan, J. Changes in α-Farnesene and Phenolic Metabolism and the Expression of Associated Genes during the Development of Superficial Scald in Two Distinct Pear Cultivars. *Int. J. Mol. Sci.* **2022**, *23*, 12088. [CrossRef] [PubMed]
46. Zhai, R.; Xiang, F.; Song, J.; Wang, Z.; Yang, C.; Xu, L. Roles of laccase and cultivar-specific phenolic composition in scald-like disorder development in pears. *Postharvest Biol. Technol.* **2021**, *181*, 111651. [CrossRef]

47. Xue, C.; Yao, J.L.; Qin, M.F.; Zhang, M.Y.; Allan, A.C.; Wang, D.F.; Wu, J. *PbrmiR397a* regulates lignification during stone cell development in pear fruit. *Plant Biotechnol. J.* **2019**, *17*, 103–117. [CrossRef] [PubMed]
48. Xue, C.; Yao, J.L.; Xue, Y.S.; Su, G.Q.; Wang, L.; Lin, L.K.; Allan, A.C.; Zhang, S.L.; Wu, J. PbrMYB169 positively regulates lignification of stone cells in pear fruit. *J. Exp. Bot.* **2019**, *70*, 1801–1814. [CrossRef] [PubMed]
49. Xue, Y.; Shan, Y.; Yao, J.L.; Wang, R.; Xu, S.; Liu, D.; Ye, Z.; Lin, J.; Li, X.; Xue, C.; et al. The transcription factor PbrMYB24 regulates lignin and cellulose biosynthesis in stone cells of pear fruits. *Plant Physiol.* **2023**, *192*, 1997–2014. [CrossRef] [PubMed]
50. Peco, J.D.; Rapoport, H.F.; Centeno, A.; Pérez-López, D. Does Regulated Deficit Irrigation Affect Pear Fruit Texture by Modifying the Stone Cells? *Plants* **2023**, *12*, 4024. [CrossRef] [PubMed]
51. Wang, X.; Liu, S.; Sun, H.; Liu, C.; Li, X.; Liu, Y.; Deguo, L.; Du, G. Production of reactive oxygen species by PuRBOHF is critical for stone cell development in pear fruit. *Hortic. Res.* **2021**, *8*, 249. [CrossRef] [PubMed]
52. Li, W.; Yuan, K.; Ren, M.; Xie, Z.; Qi, K.; Gong, X.; Wang, Q.; Zhang, S.; Tao, S. PbPDCB16-mediated callose deposition affects the plasmodesmata blockage and reduces lignification in pear fruit. *Plant Sci. Int. J. Exp. Plant Biol.* **2023**, *337*, 111876. [CrossRef]
53. Zhu, Y.; Wang, Y.; Jiang, H.; Liu, W.; Zhang, S.; Hou, X.; Zhang, S.; Wang, N.; Zhang, R.; Zhang, Z.; et al. Transcriptome analysis reveals that PbMYB61 and PbMYB308 are involved in the regulation of lignin biosynthesis in pear fruit stone cells. *Plant J.* **2023**, *116*, 217–233. [CrossRef] [PubMed]
54. Gong, X.; Xie, Z.; Qi, K.; Zhao, L.; Yuan, Y.; Xu, J.; Rui, W.; Shiratake, K.; Bao, J.; Khanizadeh, S.; et al. PbMC1a/1b regulates lignification during stone cell development in pear (*Pyrus bretschneideri*) fruit. *Hortic. Res.* **2020**, *7*, 59. [CrossRef] [PubMed]
55. Gong, X.; Qi, K.; Zhao, L.; Xie, Z.; Pan, J.; Yan, X.; Shiratake, K.; Zhang, S.; Tao, S. PbAGL7-PbNAC47-PbMYB73 complex coordinately regulates PbC3H1 and PbHCT17 to promote the lignin biosynthesis in stone cells of pear fruit. *Plant J.* **2024**, *120*, 1933–1953. [CrossRef]
56. Cheng, R.; Cheng, Y.; Lü, J.; Chen, J.; Wang, Y.; Zhang, S.; Zhang, H. The gene PbTMT4 from pear (Pyrus bretschneideri) mediates vacuolar sugar transport and strongly affects sugar accumulation in fruit. *Physiol. Plant* **2018**, *164*, 307–319. [CrossRef] [PubMed]
57. Gu, C.; Wu, R.F.; Yu, C.Y.; Qi, K.J.; Wu, C.; Zhang, H.P.; Zhang, S.L. Spatio-temporally expressed sorbitol transporters cooperatively regulate sorbitol accumulation in pear fruit. *Plant Sci.* **2021**, *303*, 110787. [CrossRef]
58. Li, J.; Qin, M.; Qiao, X.; Cheng, Y.; Li, X.; Zhang, H.; Wu, J. A New Insight into the Evolution and Functional Divergence of SWEET Transporters in Chinese White Pear (Pyrus bretschneideri). *Plant Cell Physiol.* **2017**, *58*, 839–850. [CrossRef] [PubMed]
59. Li, J.M.; Zheng, D.M.; Li, L.T.; Qiao, X.; Wei, S.W.; Bai, B.; Zhang, S.L.; Wu, J. Genome-Wide Function, Evolutionary Characterization and Expression Analysis of Sugar Transporter Family Genes in Pear (*Pyrus bretschneideri* Rehd). *Plant Cell Physiol.* **2015**, *56*, 1721–1737. [CrossRef]
60. Nishio, S.; Hayashi, T.; Shirasawa, K.; Saito, T.; Terakami, S.; Takada, N.; Takeuchi, Y.; Moriya, S.; Itai, A. Genome-wide association study of individual sugar content in fruit of Japanese pear (*Pyrus* spp.). *BMC Plant Biol.* **2021**, *21*, 378. [CrossRef]
61. Katayama, H.; Amo, H.; Wuyun, T.; Uematsu, C.; Iketani, H. Genetic structure and diversity of the wild Ussurian pear in East Asia. *Breed. Sci.* **2016**, *66*, 90–99. [CrossRef] [PubMed]
62. Peng, F.; Ren, X.; Du, B.; Yang, Y. *Pyrus ussuriensis* Maxim 70% ethanol eluted fraction ameliorates inflammation and oxidative stress in LPS-induced inflammation in vitro and in vivo. *Food Sci. Nutr.* **2023**, *11*, 458–469. [CrossRef] [PubMed]
63. Li, X.; Guo, W.; Li, J.; Yue, P.; Bu, H.; Jiang, J.; Liu, W.; Xu, Y.; Yuan, H.; Li, T.; et al. Histone Acetylation at the Promoter for the Transcription Factor PuWRKY31 Affects Sucrose Accumulation in Pear Fruit. *Plant Physiol.* **2020**, *182*, 2035–2046. [CrossRef] [PubMed]
64. Lü, J.; Tao, X.; Yao, G.; Zhang, S.; Zhang, H. Transcriptome Analysis of Low- and High-Sucrose Pear Cultivars Identifies Key Regulators of Sucrose Biosynthesis in Fruits. *Plant Cell Physiol.* **2020**, *61*, 1493–1506. [CrossRef] [PubMed]
65. Jia, L.; Zhang, X.; Zhang, Z.; Luo, W.; Nambeesan, S.U.; Li, Q.; Qiao, X.; Yang, B.; Wang, L.; Zhang, S. PbrbZIP15 promotes sugar accumulation in pear via activating the transcription of the glucose isomerase gene PbrXylA1. *Plant J. Cell Mol. Biol.* **2024**, *117*, 1392–1412. [CrossRef]
66. Qin, M.F.; Li, L.T.; Singh, J.; Sun, M.Y.; Bai, B.; Li, S.W.; Ni, J.P.; Zhang, J.Y.; Zhang, X.; Wei, W.L.; et al. Construction of a high-density bin-map and identification of fruit quality-related quantitative trait loci and functional genes in pear. *Hortic. Res.* **2022**, *9*, uhac141. [CrossRef] [PubMed]
67. Lin, Q.; Chen, J.; Liu, X.; Wang, B.; Zhao, Y.; Liao, L.; Allan, A.C.; Sun, C.; Duan, Y.; Li, X.; et al. A metabolic perspective of selection for fruit quality related to apple domestication and improvement. *Genome Biol.* **2023**, *24*, 95. [CrossRef] [PubMed]
68. Li, J.L.; Wang, S.B.; Li, Y.J.; Hao, X.Y.; Zong, Y.Z.; Zhang, D.S.; Shen, J.; Shi, X.R.; Li, P. Effects of elevated CO(2) concentration on cell structure and stress resistance physiology of Setaria italica under drought stress. *Ying Yong Sheng Tai Xue Bao = J. Appl. Ecol.* **2023**, *34*, 1281–1289.
69. Kieber, J.J.; Schaller, G.E. Cytokinin signaling in plant development. *Development* **2018**, *145*, dev149344. [CrossRef] [PubMed]
70. Laburthe, M.; Couvineau, A.; Rouyer-Fessard, C. Study of species specificity in growth hormone-releasing factor (GRF) interaction with vasoactive intestinal peptide (VIP) receptors using GRF and intestinal VIP receptors from rat and human: Evidence that Ac-Tyr1hGRF is a competitive VIP antagonist in the rat. *Mol. Pharmacol.* **1986**, *29*, 23–27.

71. Zhang, M.; Li, H.; Zhu, H.; Zhao, H.; Zhang, K.; Ge, W. Molecular Mechanisms of the miR396b-GRF1 Module Underlying Rooting Regulation in *Acer rubrum* L. *Evol. Bioinform. Online* **2023**, *19*, 11769343231211071. [CrossRef]
72. Wang, H.; Sha, G.; Gao, R.; Pang, J.; Zhai, R.; Yang, C.; Wang, Z.; Xu, L. PbGIF1 promoting cell-proliferation in pear fruit is transcriptionally activated by PbRR1. *Hortic. Plant J.* **2024**, *10*, 689–697. [CrossRef]
73. Sha, G.; Cheng, J.; Wang, X.; Xue, Q.; Zhang, H.; Zhai, R.; Yang, C.; Wang, Z.; Xu, L. PbbHLH137 interacts with PbGIF1 to regulate pear fruit development by promoting cell expansion to increase fruit size. *Physiol. Plant* **2024**, *176*, e14451. [CrossRef] [PubMed]
74. Liu, X.; Sun, W.; Zhang, N.; Zhang, S.; Bie, Y.; Deng, C.; Liu, H.; Song, L.; Manzoor, M.A.; Wang, J.; et al. PyTRM112 is involved in the regulation of GA-mediated fruit size and shape in *Pyrus pyrifolia*. *Sci. Hortic.* **2024**, *333*, 113248. [CrossRef]
75. Haydon, M.J.; Mielczarek, O.; Frank, A.; Román, Á.; Webb, A.A.R. Sucrose and Ethylene Signaling Interact to Modulate the Circadian Clock. *Plant Physiol.* **2017**, *175*, 947–958. [CrossRef]
76. Lao, T.D.; Nguyen, N.H.; Le, T.A.H.; Nguyen, P.D.T. Insights into Sucrose Metabolism and Its Ethylene-Dependent Regulation in *Cucumis melo* L. *Mol. Biotechnol.* **2023**. [CrossRef] [PubMed]
77. Lee, B.R.; Zaman, R.; La, V.H.; Bae, D.W.; Kim, T.H. Ethephon-Induced Ethylene Enhances Starch Degradation and Sucrose Transport with an Interactive Abscisic Acid-Mediated Manner in Mature Leaves of Oilseed rape (*Brassica napus* L.). *Plants* **2021**, *10*, 1670. [CrossRef]
78. Li, X.; Guo, W.; Xu, M.; Zhao, J.; Wang, G.; Yuan, H.; Wang, A. PuWRKY31 affects ethylene production in response to sucrose signal in pear fruit. *Hortic. Res.* **2022**, *9*, uhac156. [CrossRef] [PubMed]
79. Guo, Z.; Liu, H.; Zheng, S.; Qi, K.; Xie, Z.; Wang, X.; Hong, Y.; Cui, Y.; Liu, X.; Gu, C.; et al. The transcription factor PbbHLH164 is destabilized by PbRAD23C/D.1 and mediates ethylene biosynthesis during pear fruit ripening. *J. Adv. Res.* **2024**, *66*, 119–131. [PubMed]
80. Ni, J.; Zhao, Y.; Tao, R.; Yin, L.; Gao, L.; Strid, Å.; Qian, M.; Li, J.; Li, Y.; Shen, J.; et al. Ethylene mediates the branching of the jasmonate-induced flavonoid biosynthesis pathway by suppressing anthocyanin biosynthesis in red Chinese pear fruits. *Plant Biotechnol. J.* **2020**, *18*, 1223–1240. [CrossRef] [PubMed]
81. Ni, J.; Premathilake, A.T.; Gao, Y.; Yu, W.; Tao, R.; Teng, Y.; Bai, S. Ethylene-activated PpERF105 induces the expression of the repressor-type R2R3-MYB gene PpMYB140 to inhibit anthocyanin biosynthesis in red pear fruit. *Plant J.* **2021**, *105*, 167–181. [CrossRef]
82. Ni, J.; Wang, S.; Yu, W.; Liao, Y.; Pan, C.; Zhang, M.; Tao, R.; Wei, J.; Gao, Y.; Wang, D.; et al. The ethylene-responsive transcription factor PpERF9 represses *PpRAP2.4* and *PpMYB114* via histone deacetylation to inhibit anthocyanin biosynthesis in pear. *Plant Cell* **2023**, *35*, 2271–2292. [CrossRef] [PubMed]
83. Luo, Y.; Ge, C.; Ling, Y.; Mo, F.; Yang, M.; Jiang, L.; Chen, Q.; Lin, Y.; Sun, B.; Zhang, Y.; et al. ABA and sucrose co-regulate strawberry fruit ripening and show inhibition of glycolysis. *Mol. Genet. Genom.* **2020**, *295*, 421–438. [CrossRef] [PubMed]
84. Gu, C.; Pei, M.S.; Guo, Z.H.; Wu, L.; Qi, K.J.; Wang, X.P.; Liu, H.; Liu, Z.; Lang, Z.; Zhang, S. Multi-omics provide insights into the regulation of DNA methylation in pear fruit metabolism. *Genome Biol.* **2024**, *25*, 70. [CrossRef]
85. Fatmi, M.; Bougsiba, M.; Saoud, H. First Report of Fire Blight Caused by Erwinia amylovora on Pear, Apple, and Quince in Morocco. *Plant Dis.* **2008**, *92*, 314. [CrossRef]
86. Shi, H.Y.; Cao, L.W.; Yue, X.U.; Yang, X.; Chen, L. Transcriptional profiles underlying the effects of salicylic acid on fruit ripening and senescence in pear (*Pyrus pyrifolia* Nakai). *J. Integr. Agric.* **2021**, *20*, 2424–2437. [CrossRef]
87. Xu, Y.; Song, S.; Wang, H.; Cao, X.; Zhao, X.; Wang, W.; Huo, L.; Li, Y.; Wassie, M.; Lu, B.; et al. Genome-wide identification of the CONSTANS-LIKE (COL) family and mechanism of fruit senescence regulation by PpCOL8 in sand pear (*Pyrus pyrifolia*). *J. Integr. Agric.* **2024**, *23*, 1222–1237. [CrossRef]
88. Yue, P.; Jiang, Z.; Sun, Q.; Wei, R.; Yin, Y.; Xie, Z.; Larkin, R.M.; Ye, J.; Chai, L.; Deng, X. Jasmonate activates a CsMPK6-CsMYC2 module that regulates the expression of β-citraurin biosynthetic genes and fruit coloration in orange (*Citrus sinensis*). *Plant Cell* **2023**, *35*, 1167–1185. [CrossRef] [PubMed]
89. Xu, Y.; Liu, Z.; Lv, T.; Wei, Y.; Liu, W.; Wei, Y.; Yang, G.; Liu, L.; Li, T.; Wang, A. Exogenous Ca2+ promotes transcription factor phosphorylation to suppress ethylene biosynthesis in apple. *Plant Physiol.* **2023**, *191*, 2475–2488. [CrossRef] [PubMed]
90. Sriskantharajah, K.; El Kayal, W.; Ayyanath, M.M.; Saxena, P.K.; Sullivan, A.J.; Paliyath, G.; Subramanian, J. Preharvest Spray Hexanal Formulation Enhances Postharvest Quality in 'Honeycrisp' Apples by Regulating Phospholipase D and Calcium Sensor Proteins Genes. *Plants* **2021**, *10*, 2332. [CrossRef]
91. Wei, Y.; Liu, Z.; Lv, T.; Xu, Y.; Wei, Y.; Liu, W.; Liu, L.; Wang, A.; Li, T. Ethylene enhances MdMAPK3-mediated phosphorylation of MdNAC72 to promote apple fruit softening. *Plant Cell* **2023**, *35*, 2887–2909. [CrossRef]
92. Jiang, S.; Wang, N.; Chen, M.; Zhang, R.; Sun, Q.; Xu, H.; Zhang, Z.; Wang, Y.; Sui, X.; Wang, S.; et al. Methylation of MdMYB1 locus mediated by RdDM pathway regulates anthocyanin biosynthesis in apple. *Plant Biotechnol. J.* **2020**, *18*, 1736–1748. [CrossRef]
93. Wu, C.; Deng, W.; Shan, W.; Liu, X.; Zhu, L.; Cai, D.; Wei, W.; Yang, Y.; Chen, J.; Lu, W.; et al. Banana MKK1 modulates fruit ripening via the MKK1-MPK6-3/11-4-bZIP21 module. *Cell Rep.* **2023**, *42*, 112832. [CrossRef] [PubMed]

94. Zhang, X.; Lu, M.; An, H. Lysine acetylproteome analysis reveals the lysine acetylation in developing fruit and a key acetylated protein involved in sucrose accumulation in Rosa roxburghii Tratt. *J. Proteom.* **2024**, *305*, 105248. [CrossRef] [PubMed]
95. Gao, S.; Yin, M.; Xu, M.; Zhang, H.; Li, S.; Han, Y.; Ji, S.; Li, X.; Du, G. Transcription factors PuPRE6/PuMYB12 and histone deacetylase PuHDAC9-like regulate sucrose levels in pear. *Plant Physiol.* **2024**, *194*, 1577–1592. [CrossRef] [PubMed]
96. Zhang, M.Y.; Xue, C.; Hu, H.; Li, J.; Xue, Y.; Wang, R.; Fan, J.; Zou, C.; Tao, S.; Qin, M.; et al. Genome-wide association studies provide insights into the genetic determination of fruit traits of pear. *Nat. Commun.* **2021**, *12*, 1144. [CrossRef]
97. Song, B.; Li, X.; Cao, B.; Zhang, M.; Korban, S.S.; Yu, L.; Yang, W.; Zhao, K.; Li, J.; Wu, J. An identical-by-descent segment harbors a 12-bp insertion determining fruit softening during domestication and speciation in Pyrus. *BMC Biol.* **2022**, *20*, 215. [CrossRef] [PubMed]
98. Ding, B.; Hu, H.; Cao, Y.; Xu, R.; Lin, Y.; Muhammad, T.u.Q.; Song, Y.; He, G.; Han, Y.; Guo, H.; et al. Pear genomes display significant genetic diversity and provide novel insights into the fruit quality traits differentiation. *Hortic. Plant J.* **2024**, *10*, 1274–1290. [CrossRef]
99. Sun, M.; Yao, C.; Shu, Q.; He, Y.; Chen, G.; Yang, G.; Xu, S.; Liu, Y.; Xue, Z.; Wu, J. Telomere-to-telomere pear (*Pyrus pyrifolia*) reference genome reveals segmental and whole genome duplication driving genome evolution. *Hortic. Res.* **2023**, *10*, uhad201. [CrossRef] [PubMed]
100. Serra, S.; Borghi, S.; Mupambi, G.; Camargo-Alvarez, H.; Layne, D.; Schmidt, T.; Kalcsits, L.; Musacchi, S. Photoselective Protective Netting Improves "Honeycrisp" Fruit Quality. *Plants* **2020**, *9*, 1708. [CrossRef]
101. Tas, A.; Gundogdu, M.; Ercisli, S.; Orman, E.; Celik, K.; Marc, R.A.; Buckova, M.; Adamkova, A.; Mlcek, J. Fruit Quality Characteristics of Service Tree (*Sorbus domestica* L.). *Genotypes. ACS Omega* **2023**, *8*, 19862–19873. [CrossRef] [PubMed]
102. Munné-Bosch, S.; Bermejo, N.F. Fruit quality in organic and conventional farming: Advantages and limitations. *Trends Plant Sci.* **2024**, *29*, 878–894. [CrossRef]
103. Fallik, E.; Ziv, C. How rootstock/scion combinations affect watermelon fruit quality after harvest? *J. Sci. Food Agric.* **2020**, *100*, 3275–3282. [CrossRef] [PubMed]
104. Fredes, A.; Roselló, S.; Beltrán, J.; Cebolla-Cornejo, J.; Pérez-de-Castro, A.; Gisbert, C.; Picó, M.B. Fruit quality assessment of watermelons grafted onto citron melon rootstock. *J. Sci. Food Agric.* **2017**, *97*, 1646–1655. [CrossRef]
105. Wang, N.; Yang, C.; Pan, Z.; Liu, Y.; Peng, S. Boron deficiency in woody plants: Various responses and tolerance mechanisms. *Front. Plant Sci.* **2015**, *6*, 916. [CrossRef] [PubMed]