

Research Paper

Transcriptomic and metabolomic analysis of the effects of grafting on melon fruit development and volatile flavor compounds

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ABSTRACT

Melon fruit texture and flavor are key sensory characteristics that affect consumer preference and market competitiveness. Grafting technology can significantly regulate fruit quality and flavor, but the molecular mechanisms underlying rootstock-mediated melon flavor modification remain unclear. In this study, we compared and analyzed the flavor-related metabolites and transcription profiles of grafted and self-rooted melons using three different pumpkin rootstocks. In total, 301 specific primary metabolites and 1882 differentially expressed genes were identified in grafted compared with self-rooted melons. A metabolomics analysis revealed that grafting significantly altered the contents of major metabolites, such as sugars, vitamins, and organic acids. A transcriptome analysis indicated that high expression levels of genes related to key metabolic pathways were essential for flavor compound formation. Among the rootstocks, 'Sizhuang' up-regulated genes associated with sugar metabolism, amino acid metabolism, and fatty acid metabolism, thereby promoting the accumulation of key flavor metabolites, such as (2E,6Z)-nona-2,6-dienal and methyl jasmonate. This study clarifies the metabolic pathways behind grafting-induced flavor changes in melon fruit, provides a theoretical basis for the improvement of melon quality, and deepens our understanding of the molecular mechanisms by which grafting regulates fruit flavor.

1. Introduction

Melon (*Cucumis melo* L.) is a trailing herbaceous plant widely cultivated in temperate and tropical regions, and it is an economically significant horticultural crop worldwide. According to the Food and Agriculture Organization, in 2023, the global annual production of melon reached approximately 14 million tons. This fruit is widely acclaimed for its sweet and succulent characteristics. Due to natural causes, such as soil erosion and salinization, as well as human activities,

such as deforestation, overgrazing, and unsustainable irrigation methods, global soil degradation has intensified, and global agriculture faces severe challenges (FAO, 2025). Supply dynamics and weather conditions affect the quantities and prices of various melon types in different regions. Melon is generally planted in spring and autumn, and it is susceptible to weather conditions such as high temperature, drought, and flood. These conditions greatly reduce fruit yield and also lead to unpredictable changes in fruit quality. Consumer surveys have highlighted that taste, sweetness, and texture are critical factors

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influencing consumer preference for melon, with taste being particularly emphasized (Vallone et al., 2013). The principal flavors of fruit and vegetables consist of series of volatile substances (esters, alcohols, and phenols) and non-volatile substances (carbohydrates, amino acids, and lipids))(Xu et al., 2022). How to use limited and lower-quality land to produce more and better crops remains a persistent problem for agricultural scientists. Fruit yield and quality are crucial to improving the economic value of fruit. However, breeders generally focus on improving productivity and pay less attention to fruit quality (Wang et al., 2023)

Grafting is a widely applied horticultural technique in which different rootstock–scion combinations are used to differentially regulate scion growth to achieve purposeful production. Grafting can maintain the excellent characteristics of varieties, promote early fruiting, overcome vegetative propagation-associated difficulties in some species, enhance disease resistance and immunity, prevent pests, expand cultivation areas, improve yield and quality, and dwarf or arborize fruit trees. It is of great significance for improving soil utilization rate and for addressing problems associated with continuous cropping obstacles, secondary salinization, soil-borne diseases, and soil acidification and hardening (Babu et al., 2026). Notably, grafting exerts a significant impact on fruit quality by modulating fruit morphology, texture, sweetness, acidity, and aroma. Grafting can alter the composition of primary metabolites in fruit, including sugars, vitamins, nucleotides, organic acids, lipids, phenolic acids, and volatile compounds (Wang et al., 2024; Kaleem et al., 2022). Compared with non-grafted tomato, grafted tomato has higher levels of soluble solids and a higher titratable acid content (Flores et al., 2010). Similarly, rootstocks significantly impact the compositional characteristics of grafted tomato peels, particularly the concentrations of sugars, acids, and volatile compounds. These changes are likely due to rootstock–scion interactions, with the grafting method itself influencing metabolic changes in grafted plants (Zhou et al., 2022). The effects of grafting on fruit quality vary with different rootstock–scion combinations. Specifically, grafting with different pumpkin rootstocks can induce significant changes in the physiological characteristics of cucumber fruit, as well as the metabolism of sugars and α -linolenic acid. The proportions of volatile organic compounds in both the peel and pulp of fruit can also be altered, thereby affecting fruit aroma and taste. These findings highlight the high degree and complexity of grafting-induced effects on fruit quality (Miao et al., 2019). Grafting serves as a core strategic tool to advance the transformation and upgrading of modern agriculture and resolve the conflict between yield improvement and ecological conservation. By combining the superior traits of rootstocks and scions, it effectively modifies crop growth characteristics, increases land productivity per unit area, and achieves quality and efficiency improvement in intensive agricultural production (Babu et al., 2026). Grafting exerts effects on crops mainly through regulatory networks mediated by rootstocks. It improves fruit quality, extends shelf life and enhances plant disease resistance (Singh et al., 2020; Thies, 2021). While cutting the costs of field management and transportation, it also generates greater social and economic benefits via superior fruit quality. Rootstocks impose multiple regulatory effects on grafted plants. Eggplant rootstocks promote aerenchyma formation and improve vascular connectivity, thereby alleviating the inhibition of nutrient uptake and transport, cell division and vegetative growth caused by root hypoxia under waterlogging conditions. Meanwhile, the enhanced waterlogging tolerance of grafted tomato plants mediated by rootstocks relies on the maintenance of photosynthetic efficiency, plant water status and antioxidant defense systems, which facilitates nutrient translocation and fruit retention in tomato scions (Bhatt et al., 2015; Mote et al., 2025). Rootstocks enhance salt tolerance of scions by restricting the transport of Na^+ and Cl^- and maintaining the K^+/Na^+ ratio. The rootstock-mediated regulation of ion homeostasis, together with the activated antioxidant pathways and ROS-scavenging enzymes, further strengthens salt resistance (Coşkun et al., 2025; Elsheery et al., 2020; Khapte et al., 2026; Huihui Zhang et al., 2018).

Rootstock-mediated regulation of photosynthesis and salicylic acid signaling pathways improves powdery mildew resistance in grafted cucumber (Chen et al., 2026). Additionally, rootstocks modulate the accumulation of antioxidant compounds in fruits to prolong shelf life and preserve fruit appearance, flavor and nutritional quality (Darré et al., 2022; Lo'ay and Doaa, 2020). Robust root systems of vigorous rootstocks feature larger root surface areas and higher nutrient uptake efficiency, which increases nitrogen use efficiency, reduces fertilizer application and mitigates environmental pollution (Huang et al., 2016; Noor et al., 2019). Previous studies have demonstrated that grafting fully conforms to the development of global circular economy and the transition toward sustainable food systems. As a low-cost, low-input, eco-friendly and resource-efficient core technology, grafting simultaneously achieves pesticide reduction, carbon sequestration, water conservation, quality improvement, shelf-life extension and resource recycling.

In recent years, transcriptomics and metabolomics have emerged as powerful tools for deciphering the intricate mechanisms underlying plant fruit flavor traits in crops such as tomatoes, cucumbers, and grapes (Carrari, 2006; He et al., 2023; Zhang et al., 2022; Zhao et al., 2023; Zhou et al., 2022). By integrating metabolomics and transcriptomics, researchers have identified genetic loci associated with key flavor-related metabolites, including sugars, acids, and volatiles, in both modern and wild crop varieties (Tiemann et al., 2017; Zhao et al., 2021). Comprehensive analyses have elucidated the regulatory networks governing flavor formation in kiwifruit (Wang et al., 2022). Transcriptome profiling alone has revealed the molecular mechanisms responsible for increases in fruit size, peel firmness and soluble solids content in watermelon and gourd after grafting (Garcia-Lozano et al., 2020). Metabolomics has also been applied to explore how rootstock–scion interactions affect the flavor of grafted tomato fruits. Different rootstocks and grafting methods have been found to alter the content of sugars, acids, and volatile metabolites, thereby affecting fruit flavor (Zhou et al., 2022). For blood oranges, the integration of metabolomics and transcriptomics has revealed the impact of rootstocks on fruit quality, with the transcription factor NAC identified as a key regulator of anthocyanin content, offering potential for variety improvement (Yang et al., 2023). These studies highlight that selecting appropriate rootstocks through grafting can enhance fruit quality and flavor, primarily by influencing sugar and volatile compound metabolism. To date, a range of volatile components including esters, alcohols, aldehydes and alkenes have been detected in grafted fruits via multi-omics combined analysis (Kaleem et al., 2025; Yan et al., 2023).

In this study, the independently bred melon cultivar ‘Cuixue’ was grafted onto three Cucurbita moschata rootstocks, and self-grafted melon plants were set as controls. Fruit quality was evaluated via comprehensive metabolomic and transcriptomic analyses. We analyzed the metabolic pathways of sugars, acids, and volatile compounds, along with related differential gene expression, to elucidate the molecular mechanisms of flavor formation in grafted melon fruits. Our study identifies the key candidate genes and metabolic pathways involved in the melon fruit flavor formation of melon grafted onto different rootstock, and may provide references for optimizing rootstock selection in melon breeding.

2. Materials and methods

2.1. Plant materials and growth conditions

This study was conducted in a plastic greenhouse at the Yangdu Base of the Zhejiang Academy of Agricultural Sciences, China. The experimental materials consisted of melon cultivars independently bred by the Zhejiang Academy of Agricultural Sciences. The melon cultivar ‘Cuixue’ was used as the scion, while ‘Cuixue’, ‘Shenzhen’, ‘Changzhen’, and ‘Sizhuang’ were used as rootstocks. The scion and rootstock seeds were separately sown in 50-well polystyrene trays (54 × 28 × 9 cm) filled

with a commercial organic substrate (V - peat: vermiculite: perlite = 1:1:1). Seedlings were raised in an environmentally - controlled growth chamber maintained at 26–28 °C with a relative humidity of 80%–85%. At the two-leaf stage, the hole-insertion grafting method was applied for grafting (Miao et al., 2019). Grafted and non-grafted (self-rooted) plants were cultivated under consistent conditions using a randomized complete block design (RCBD). Each grafting combination served as one treatment, with three biological replicates containing 40 plants per replicate. Five fruits from were harvested from each replicate at 35 days after flowering and pooled for subsequent analysis. Partial samples were used for physiological index determination, and the remaining samples were immediately frozen in liquid nitrogen. Peeled fruits were cut for GC - MS and RNA - seq analysis.

2.2. Physical measurements

Fruit morphological and quality traits were systematically evaluated. Individual fruit weight was measured using an electronic balance. Dimensional characteristics, including seed cavity dimensions (length and width), longitudinal diameter, and transverse diameter, were measured using digital calipers. For cross-sectional observation, fruits were cut longitudinally to determine mesocarp and exocarp thickness. Texture profile analysis (TPA) was conducted using a texture analyzer to determine viscosity, cohesiveness, adhesiveness, hardness, and toughness at three longitudinal positions. Soluble solids content was measured in both central and peripheral flesh using a digital refractometer. Considering material availability, 5–7 fruits were harvested from each grafting combination. Among them, five fruits were randomly selected for each grafting for subsequent index determination.

2.3. Soluble solid analysis

Changes in sugar and organic acids during fruit ripening were analyzed. Peeled melon fruits from each grafting combination were sliced, and 4–5 slices were pressed to extract juice. The obtained juice was measured with a digital refractometer (PR-100, ATAGO, Japan). Considering sample availability, five fruits were randomly chosen from each group. Pulp tissues taken from the same position of each fruit were divided into 12 equal portions, among which 3 portions were randomly sampled. The soluble solids content (SSC) of these samples was determined using the Brix method.

2.4. Sample extraction and GC–MS analysis

Five fruits of each rootstock-scion combination were peeled, and the central pulp of the peeled melon fruit was cut into uniform small pieces, mixed and sub-packed into a 50 mL cryopreservation tube, and then stored at $-80\text{ }^{\circ}\text{C}$ for ≤ 7 days for analysis. The samples were crushed in liquid nitrogen at low temperature using a mortar and a mortar. 500 mg (1 mL) of the powder was transferred immediately to a 20 mL headspace vial (Agilent, Palo Alto, CA, USA), containing NaCl saturated solution, to inhibit any enzyme reaction. The vials were sealed using crimp-top caps with TFE-silicone headspace septa (Agilent). At the time of SPME analysis, each vial was placed in $60\text{ }^{\circ}\text{C}$ for 5 min, then a 120 m DV B/CWR/PDMS fibre (Agilent) was exposed to the headspace of the sample for 15 min at $60\text{ }^{\circ}\text{C}$.

After sampling, desorption of the VOCs from the fibre coating was carried out in the injection port of the GC apparatus (Model 8890; Agilent) at $250\text{ }^{\circ}\text{C}$ for 5 min in the splitless mode. The identification and quantification of VOCs was carried out using an Agilent Model 8890 GC and a 7000D mass spectrometer (Agilent), equipped with a 30 m $\times$ 0.25 mm $\times$ 0.25 μm DB-5MS (5% phenyl-polymethylsiloxane) capillary column. Helium was used as the carrier gas at a linear velocity of 1.2 mL/min. The injector temperature was kept at $250\text{ }^{\circ}\text{C}$ and the detector at $280\text{ }^{\circ}\text{C}$. The oven temperature was programmed from $40\text{ }^{\circ}\text{C}$ (3.5 min), increasing at $10\text{ }^{\circ}\text{C}/\text{min}$ to $100\text{ }^{\circ}\text{C}$, at $7\text{ }^{\circ}\text{C}/\text{min}$ to $180\text{ }^{\circ}\text{C}$, at

$25\text{ }^{\circ}\text{C}/\text{min}$ to $280\text{ }^{\circ}\text{C}$, hold for 5 min. Mass spectra were recorded in electron impact (EI) ionisation mode at 70 eV. The quadrupole mass detector, ion source and transfer line temperatures were set, respectively, at 150, 230 and $280\text{ }^{\circ}\text{C}$. The MS was selected ion monitoring (SIM) mode was used for the identification and quantification of analytes.

Four independent biological replicates were analyzed. Specific analysis, refer to previous articles (Miao et al., 2019).

2.5. RNA extraction, cDNA library preparation, and RNA sequencing

The RNAprep Pure Plant Plus Kit (Tiangen, Beijing, China) was used for total RNA extraction. Genomic DNA was eliminated from the total RNA using RNase-free DNase I. The RNA integrity was confirmed by 1.0% agarose gel electrophoresis. RNA concentrations were determined by NanoDrop™ 2000 spectrophotometer (Thermo Scientific, Waltham, MA, USA), samples with an A260/A280 ratio of 1.8–2.2 and an A260/A230 ratio >2.0 were used for further analyses. Five fruits were randomly selected from each grafting combination to mix the pulp, and each combination was subjected to three independent biological replicates. After quality assessment, 3 μg RNA was extracted from each sample for cDNA library construction. First-strand cDNA synthesis was performed using a FastQuant cDNA Synthesis kit (Tiangen, Beijing, China) according to the manufacturer's instructions. Sequencing libraries were constructed by NEBNext® Ultra™ RNA Library Prep Kit for Illumina® (NEB, Ipswich, MA, USA) following the manufacturer's instructions. Then, the prepared library was sequenced on an Illumina HiSeq 2000 platform (San Diego, CA, USA). The specific analysis is based on the previous article (Miao et al., 2019).

2.6. Weighted correlation network analysis (WGCNA)

WGCNA is a powerful analytical approach for dissecting complex traits governed by multigene regulation and nonlinear interactions. It overcomes the limitations of analyzing individual differentially expressed genes, and fully captures nonlinear gene relationships across four aspects: network structure, module coordination, weighted topology and central regulation (Horvath and Dong, 2008; Zhang and Horvath, 2005). Complex traits, such as flavor, are determined by gene synergy networks rather than isolated genes and cannot be fully captured by analyzing a single differentially expressed gene (Klee and Tieman, 2018; Zhu et al., 2023). Based on gene co-expression correlations, WGCNA characterizes nonlinear patterns of gene synergy and antagonism, varying association strengths, and indirect interactions. Genes are grouped into co-expression modules with distinct expression patterns, and these modules are further linked to phenotypic traits. Based on intra-module connectivity, module membership, and gene significance, hub genes are screened to determine key drivers. This makes WGCNA a powerful tool for generating hypotheses and identifying key regulatory "central genes" in biological networks (Horvath and Dong, 2008; Langfelder et al., 2008; Langfelder and Horvath, 2008). We constructed a co-expression network of melon differentially expressed genes (DEGs) and correlated it with phenotypic traits via WGCNA on the Omicshare Platform (<https://www.omicshare.com>). The network was established based on scale-free topology principles, where individual DEGs served as nodes and edges represented Pearson correlation coefficients between gene expression profiles. Network construction parameters included a soft threshold power (β) of 9, minimum module size of 30, merge cut height of 0.25, and minimum KME (kME) threshold of 0.3. Hub genes within modules were identified through network topology analysis using default parameters for intra-module connectivity (≥ 30) and edge weight (≥ 0.02). Network visualization revealed gene-gene interactions, with node size proportional to connectivity degree, reflecting the number and strength of gene interactions. Module-trait associations were established by integrating gene co-expression modules with phenotypic data, enabling the identification of biologically relevant modules and their constituent genes associated

with specific traits. The analysis method refers to previous articles (Kaleem et al., 2025).

2.7. Statistical analysis

Gene expression and metabolite profiling data were normalized through log2 transformation and standardized as Z-scores. Principal component analysis (PCA) and Pearson correlation coefficients (PCCs) were calculated using the normalized datasets. Significant gene-metabolite correlations were screened with a dual threshold ($PCC > 0.8$ and $p\text{-value} < 0.05$) for comparisons across groups: GSZ vs. AC, GCZ vs. AC, and GS vs. AC. Physiological parameters are presented as mean $\pm$ standard deviation ($n = 3$ biological replicates). Statistical analysis was performed using one-way analysis of variance (ANOVA) implemented in SAS software (version 9.4, SAS Institute Inc., Cary, NC, USA), with post-hoc comparisons conducted using Fisher's least significant difference (LSD) test at $\alpha = 0.05$ significance level. Data visualization was performed using Microsoft Excel 2018 (Microsoft Corporation, Redmond, WA, USA).

3. Results

3.1. Effects of four different rootstocks on growth and fruit quality of 'Cuixue' oriental melon

We systematically evaluated morphological and quality attributes of melon fruits grafted onto different rootstocks, including fruit weight, flesh and rind thickness, fruit diameters, and seed cavity dimensions (Fig. S1). The results revealed that grafting with the selected pumpkin rootstocks significantly reduced single fruit weight and fruit diameter at maturity, particularly for plants grafted onto GS (Fig. S1). TPA demonstrated that rootstocks markedly altered the textural properties of fruit pulp. Grafting increased adhesiveness and hardness in the upper pulp but decreased those in the lower pulp. Rootstocks 'GSZ' and 'GCZ' significantly increased the toughness of the upper pulp. By contrast, 'GS' markedly raised hardness and toughness in both upper and lower pulp.

Nevertheless, rootstock grafting exerted no significant effects on textural parameters of the middle pulp (Fig. S2). Measurement of mature fruit showed that rootstock grafting significantly increased soluble sugar content in the pulp. The GS rootstock produced the most prominent increase, with soluble sugar content rising by 13.7% in the upper pulp, 10.1% in the middle pulp, and 7.1% in the lower pulp (Fig. 1B). Metabolic profiling further revealed changes in key quality-related compounds: succinic acid and malic acid accumulated to significantly higher levels after grafting, especially in fruits grafted onto 'GS' (Fig. 1, C-D). In comparison, the contents of glucose, sucrose and citric acid showed no significant differences between grafted and autografted melons (Fig. 1, C-D). Ascorbic acid (Vc) content also remained unchanged, whereas grafting significantly increased the sugar-acid ratio (Fig. 1E-F). Overall, these results underscored that rootstocks exert strong effects on both external and internal quality traits of grafted melons.

3.2. Transcriptomics reveals the crucial role of metabolism in flavor alteration of grafted oriental melon

We performed RNA-seq on developmentally synchronized samples to explore transcriptome alterations induced by grafting. Compared with the self-rooted controls, distinct DEGs were detected in fruits from each pumpkin rootstock (Fig. 2A). Notably, grafting induced widespread transcriptional reprogramming. The 'GS' rootstock produced 1709 DEGs, a number far higher than those of the other rootstocks (Fig. 2B). GO enrichment functional annotation of DEGs in each treatment revealed rootstock-specific metabolic changes: 'GSZ' and 'GCZ' mainly affected categories related to molecular function and cellular components, while 'GS' mainly changed categories related to biological processes and cellular components (Fig. S3). KEGG pathway enrichment analysis of DEGs showed that all grafting treatments showed significant differential regulation in three key metabolic pathways compared with the self-rooted control, including 'metabolic pathway', 'biosynthesis of secondary metabolites', 'phenylpropanoid biosynthesis' (Fig. 3C-E). These findings clearly underscored the vital roles of metabolic pathways

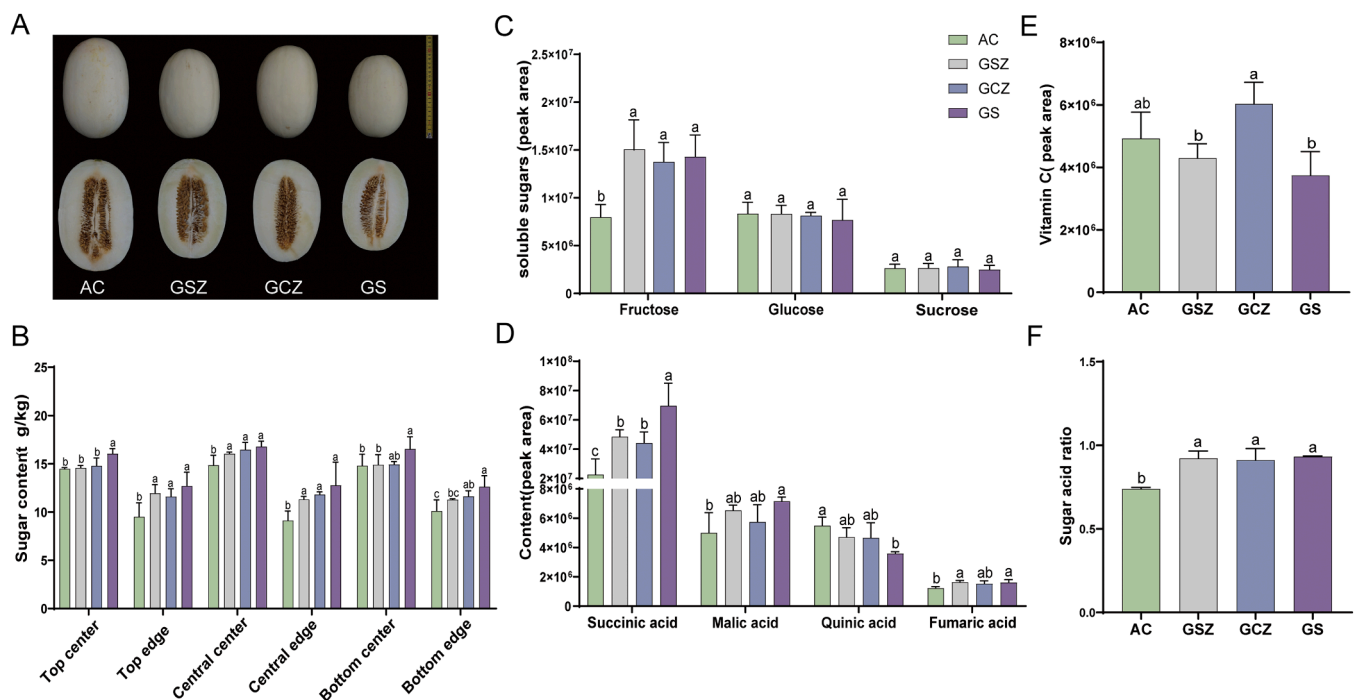


Fig. 1. Physiological indices of melon cultivar Cuixue grafted onto different pumpkin rootstock. (A) Morphological characterization of different grafted fruits. (B) Sugar content in different parts of fruits. (C) Glucose, fructose, sucrose content of different grafted fruits. (D-F) Acid content, Vitamin C content and sugar-acid ratio of different grafted fruits. AC, autografted Cuixue; GSZ, Cuixue grafted onto Shenzhen; GCZ, Cuixue grafted onto Changzhen; GS, Cuixue grafted onto Sizhuang.

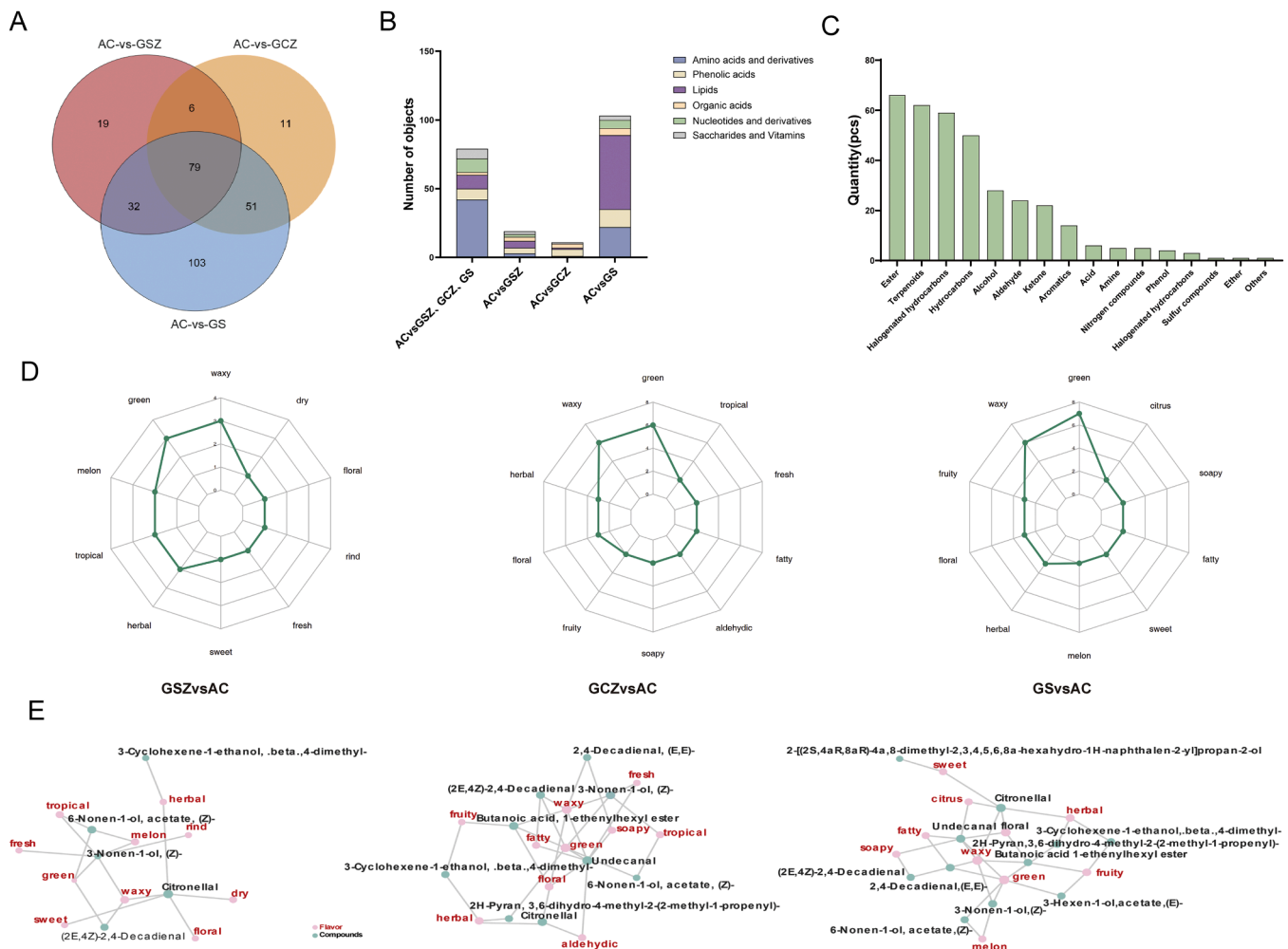


Fig. 2. Transcriptome analysis of melon grafted on four rootstocks at maturity stage. (A)The Venn diagram of different treatments. (B)Total numbers of upregulated and downregulated DEGs about different comparison groups. (C-E)KEGG enrichment analysis of differential genes treated with GSZ vs AC, GCZ vs AC, GS vs AC.

in regulating fruit quality and flavor in pumpkin rootstock grafted melons. In 'GS' rootstocks, DEGs were specifically enriched in 'amino sugar and nucleotide sugar metabolism' and 'MAPK signaling pathway'. Notably, among the three key pathways, 'GS' had the significantly largest number of annotated DEGs. This result strongly suggested that grafting with the GS rootstock exerted a more pronounced effect on the biosynthesis and regulation of fruit metabolic compounds.

3.3. Correlation analysis between primary metabolites and traits based on WGCNA

To systematically clarify the correlations between differentially expressed genes (DEGs) and differentially accumulated metabolites (DMs), we integrated transcriptomic and metabolomic datasets via correlation analysis. A dual threshold of Pearson correlation coefficient ($PCC > 0.8$ and $p < 0.05$) was applied to screen the co-expression network. Single-threshold strategies based solely on PCC or p-value tend to produce numerous false-positive associations, whereas the combined criteria markedly reduced false positives. Subsequently, a soft thresholding power (β) was adopted for adjacency matrix transformation, with the adjacency coefficient calculated as $|r|^\beta$. This transformation amplifies strong correlations, suppresses weak correlations and attenuates negative correlations, enabling the network to conform to the scale-free topology. Such a strategy effectively retains biologically meaningful network edges associated with scion-rootstock communication (Langfelder and Horvath, 2008; Owaresat et al., 2026; Perkins

and Langston, 2009; Xia and Zhang, 2020). Finally, multiple DEGs potentially involved in carbohydrate metabolism, amino acid metabolism and fatty acid metabolism were identified. A co-expression network was constructed using WGCNA with 14,764 genes, leading to the identification of six distinct modules (Fig. 3A). The 'mediumpurple3' module contained the highest number of genes (10,157), while the 'grey' module contained the fewest (4) (Fig. 3B). Combined GO and KEGG enrichment analyses revealed the core biological functions of each module. The mediumpurple3 module was mainly involved in the synthesis and metabolism of cytoplasmic nitrogen-containing compounds; the midnightblue module participated in protein phosphorylation; the darkgreen module was associated with energy metabolism and ATP hydrolysis; the paleturquoise module functioned in carbon metabolism and glycolysis; and the skyblue3 module mediated substance transport, as well as ion phosphorus transport and assimilation. Module-trait association analysis revealed that the 'mediumpurple3' module significantly correlated with trehalose content and negatively with β -ketoglutaric acid content. Conversely, the 'midnightblue' module showed a significant positive correlation with β -ketoglutaric acid and glucosephosphate isomerase levels, but a negative correlation with trehalose. The 'skyblue3' module was significantly associated with isoleucine content (Fig. 3C). The genes in the six modules were mapped to the KEGG database for enrichment and classification (Fig. 3D). The interaction between different pathways was plotted according to the pathway information of gene enrichment in the module 'mediumpurple3' and 'midnightblue'. Functional analysis of genes was

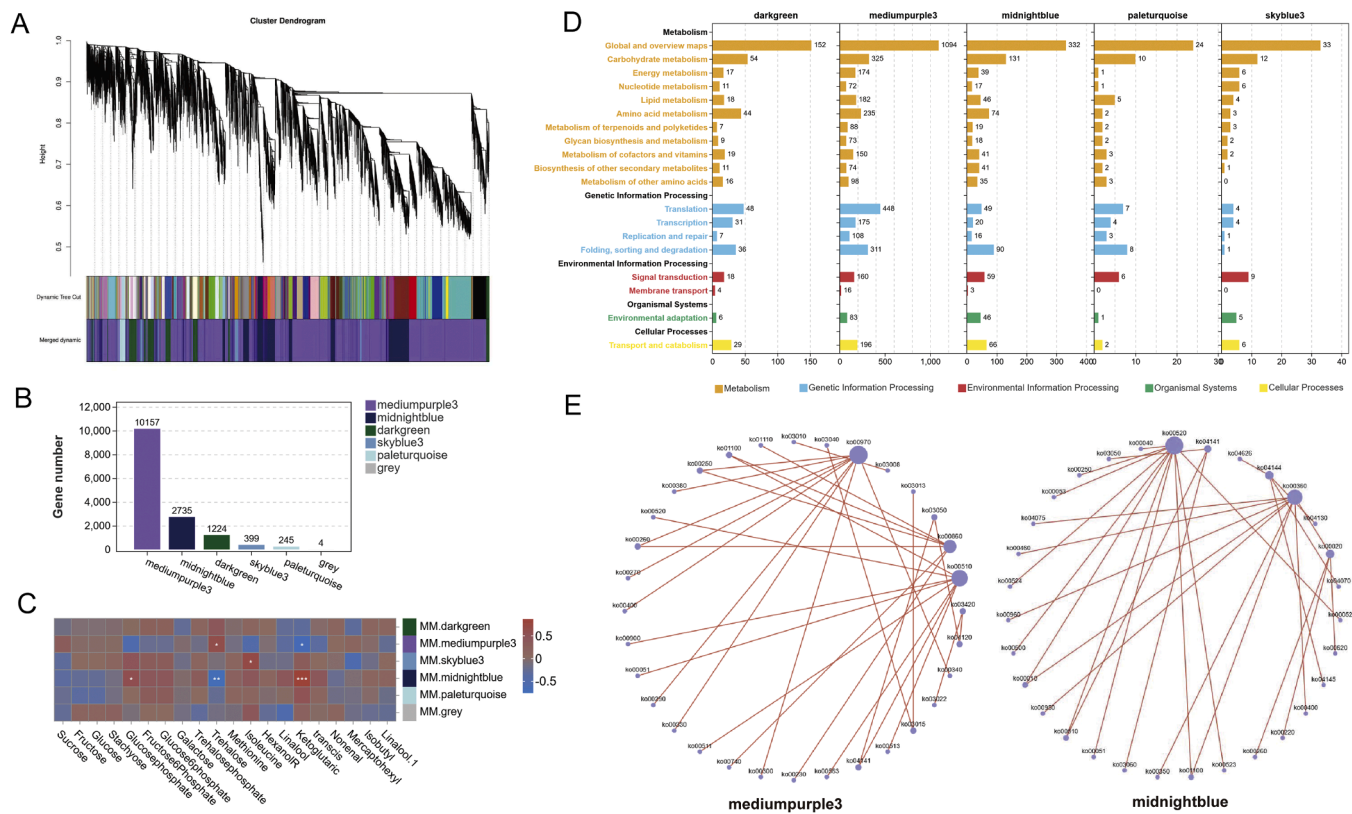


Fig. 3. Weighted gene co-expression network analysis (WGCNA). (A) Dendrogram clustering presenting modules having co-expressed genes. Each leaflet in the tree corresponds to an individual gene. (B) The number of genes in different co-expression modules. (C) Module-trait associations based on Pearson correlations. (D) Distribution of genes in KEGG metabolic pathway. (E) Interactions between different pathways.

performed by Melon Information Resource (Xu et al., 2025), including Aminoacyl-tRNA biosynthesis (KO00970), Porphyrin metabolism (KO00860), N-Glycan biosynthesis (KO00510), Amino sugar and nucleotide sugar metabolism (KO00520), and Phenylalanine metabolism (KO00360), which is consistent with our previous KEGG results (Fig. 3E). Consequently, we focused on sugar and amino acid metabolic pathways. This approach effectively narrowed down thousands of genes to a few candidate functional modules for further investigation (Table S1).

3.4. Metabolic reprogramming in 'Cuixue' oriental melon induced by four rootstocks

Comprehensive metabolic profiling via GC-MS was performed on mature fruits to investigate grafting-induced changes, focusing on primary metabolites and volatile organic compounds. This effort identified 976 primary metabolites, spanning multiple classes such as phenolic acids, lipids, nucleotides, amino acids, organic acids, vitamins, sugars, and alcohols. A comparative analysis uncovered 79 metabolites commonly altered by all rootstocks. Additionally, rootstock-specific comparisons with the self-rooted control identified 19, 11, and 103 unique metabolites for 'GSZ', 'GCZ', and 'GS', respectively, highlighting distinct metabolic reprogramming induced by each rootstock (Fig. 4A). Lipids and amino acids served as the main precursors of flavor compounds in melon fruit. Lipid-derived metabolites were mainly ethyl acetate and benzyl acetate, whereas amino acid-derived compounds included proline and isoleucine etc. (Jia et al., 2022; Kaleem et al., 2022; Miao et al., 2019). In this study, the specific metabolites in the 'GSZ' group included 8 amino acids and their derivatives (e.g., N-formyl-L-methionine, N⁶,N⁶-dimethyl-L-lysine), 2 phenolic acids (2-formamidobenzoic acid, 3-hydroxybenzaldehyde), 3 organic acids, 4 nucleotides and their derivatives, as well as 2 sugars and vitamins. The

specific metabolites in the 'GCZ' group consisted of 1 amino acid derivative (L-homocysteine), 5 phenolic acids, 1 lipid (1-octadecanoylglycerol), 3 organic acids, and 1 vitamin. The 'GS' group exhibited the most pronounced metabolic profile, with a total of 22 amino acids and derivatives (such as Phe-Ile, Leu-Glu-Phe), 13 phenolic acids (e.g., acetophenone, vanillic acid), 54 lipids (including triglyceric acid, monolinolenin), 5 organic acids, 6 nucleotides and their derivatives, and 3 sugars and vitamins (Table S2). Classification analysis of metabolites across different treatment groups revealed that grafting significantly altered the relative abundance of major metabolite categories, including sugars and vitamins, nucleotides and derivatives, organic acids, lipids, and phenolic acids (Fig. 4B). Notably, the 'GS' rootstock yielded the highest number of differential metabolites compared to the self-rooted control. The majority of these metabolites were lipids, and they were consistently significantly upregulated (Table S2).

Profiling of VOCs in mature fruits revealed 352 compounds, chiefly esters, terpenoids, heterocyclics, hydrocarbons, alcohols, aldehydes, ketones, and aromatics, among them alcohols and aldehydes were differential in grafted fruits largely (Fig. 4C, Table S2). The distinctive metabolites were identified in 'GS' grafted fruit compared with auto-selfed and other rootstock grafted fruit, and it is clearly demonstrated by the results of the PCA and OPLS-DA analysis (Fig. S4). Flavor characteristic analysis of differential metabolites in 'GSZ', 'GCZ', and 'GS' was conducted, and the results are visualized via radar charts and correlation network diagrams (Fig. 4D). All three rootstock treatments exhibited distinct profiles associated with green, waxy, floral, and herbal flavors, each linked to specific metabolic signatures. Notably, the 'GS' treatment was characterized by two unique flavor-related metabolites: (3E)-hex-3-en-1-yl acetate (imparting fresh pear, banana, apple, and green notes, and known as a key ester defining the core flavor of many fruits), and 2-[(2S,4aR,8aR)-4a,8-dimethyl-2,3,4,5,6,8a-hexahydro-1H-naphthalen-2-yl]propan-2-ol (ledol, associated with sweetness).

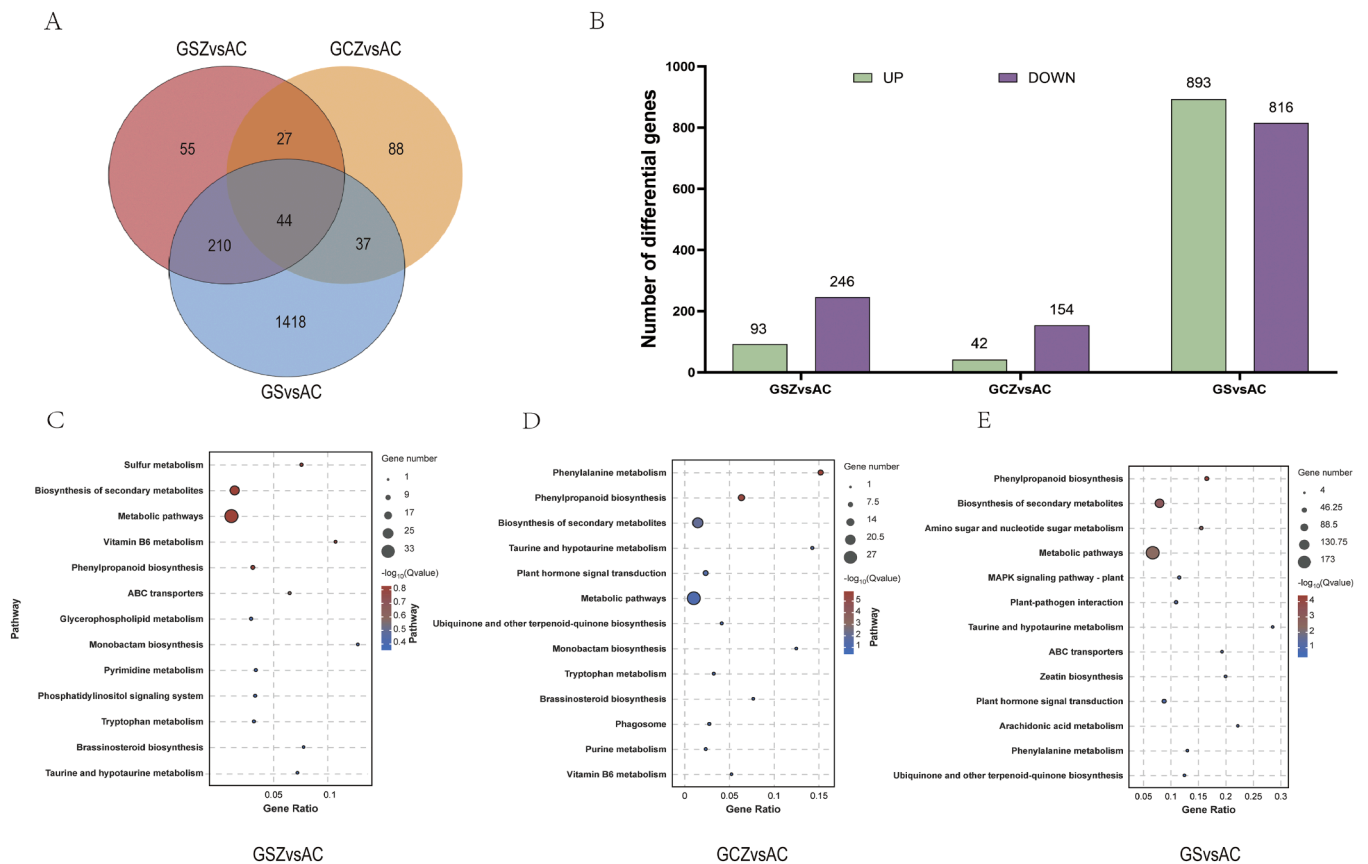


Fig. 4. Metabolomics changes of four rootstocks grafted melon at mature stage. (A) The Venn diagram of different treatments of differential metabolites. (B) Metabolite composition diagram in each treatment. (C) Volatile substance content of grafted mature fruit. (D) Sensory flavor characteristics analysis radar chart of differential metabolites. (E) Sensory flavor characteristics and differential substance correlation network diagram.

Citronellal, a compound imparting a strong lemon and citronella aroma—a signature note in citrus and many herbs—was uniquely detected in grafted fruits but absent in the self-rooted control. Its concentration was significantly higher in the ‘GS’ treatment than in all others. These differential primary and volatile metabolites collectively shaped the unique flavor characteristics of grafted fruits. Furthermore, these compounds laid a metabolic foundation for the improved fruity flavor and sweetness of melons grafted with ‘GS’ (Fig. 4E).

3.5. Multi-omics reveals the impact of amino acid and fatty acid metabolism on flavor in grafted melon

To clarify the correlation between metabolic and transcriptional networks in grafted melon fruits, an integrated multi-omics analysis was performed via O2PLS. A comprehensive loading map was constructed based on the squared loadings of the first two principal components for selected genes and metabolites (Fig. 5). The analysis revealed a cluster of amino acid metabolism-related genes—such as proteases and peptide transporters—that were negatively correlated with a group of amino acid-derived metabolites across all grafting treatments, underscoring the central role of amino acid metabolism. Given the distinct phenotypic differences observed in the ‘GS’ group, we further compared ‘GS’ with self-rooted controls. In primary metabolism, lipids and key lipid-related enzymes, namely IAA-amino acid hydrolase ILR1 (*CmILR1*) and peroxidase (*CmGSTU17*), changed significantly in ‘GS’, which might improve fruit aroma and prolong shelf life. Increased expression of aminotransferase (*CmABAT1*) further promoted secondary metabolism and phenylpropanoid biosynthesis, consistent with earlier KEGG results. RNA-seq data revealed that grafting reshaped metabolic pathways to regulate fruit flavor. Key volatile metabolites, such as (3Z)-non-3-en-1-ol,

(2E,4Z)-deca-2,4-dienal, and citronellal, served as critical nodes in flavor metabolism. Concurrent changes in amino acid and lipid metabolism-related genes, along with compounds like carvone and 1-tridecene, and the expression of hydrolase (*CmEH2*), transferase (*CmBGLU*), and dehydrogenase (*CmFQR1*), collectively underpinned the flavor alterations in ‘GS’. Notably, several genes and their corresponding metabolites involved in aromatic hydrocarbon synthesis and fatty acid metabolism exhibited high loadings in ‘GS’, indicating pathway co-activation. This synergy promoted the accumulation of flavor-related metabolites and ultimately enhanced the distinct flavor profile of ‘GS’ grafted melons (Table S3).

3.6. Changing of glucose metabolism, amino acid and fatty acid metabolism induced by grafting

Sugar metabolism largely determines the sweetness of melon fruit. Integrated transcriptomic and metabolomic analyses revealed that grafting affected numerous genes and metabolites related to sugar metabolism. By integrating data from prior WGCNA and O2PLS analyses, 16 key differential genes in sugar metabolism were identified (Fig. 6A). Pathway analysis showed that stachyose and raffinose family oligosaccharides (RFOs) were sequentially degraded into sucrose. During this process, key genes (AAG, NAG, UGGP) were upregulated in fruits grafted with ‘GS’. Sucrose was then hydrolyzed by sucrose synthase to produce fructose and glucose, which further participated in oxidative pathways. Notably, the ‘GS’ rootstock exhibited the highest expression levels of fructokinase (FK) and hexokinase-1 (HK1), concomitant with increased levels of fructose-6-phosphate (F6P) and glucose-6-phosphate (G6P). These molecular findings were consistent with the high sugar accumulation detected in melons grafted with ‘GS’.

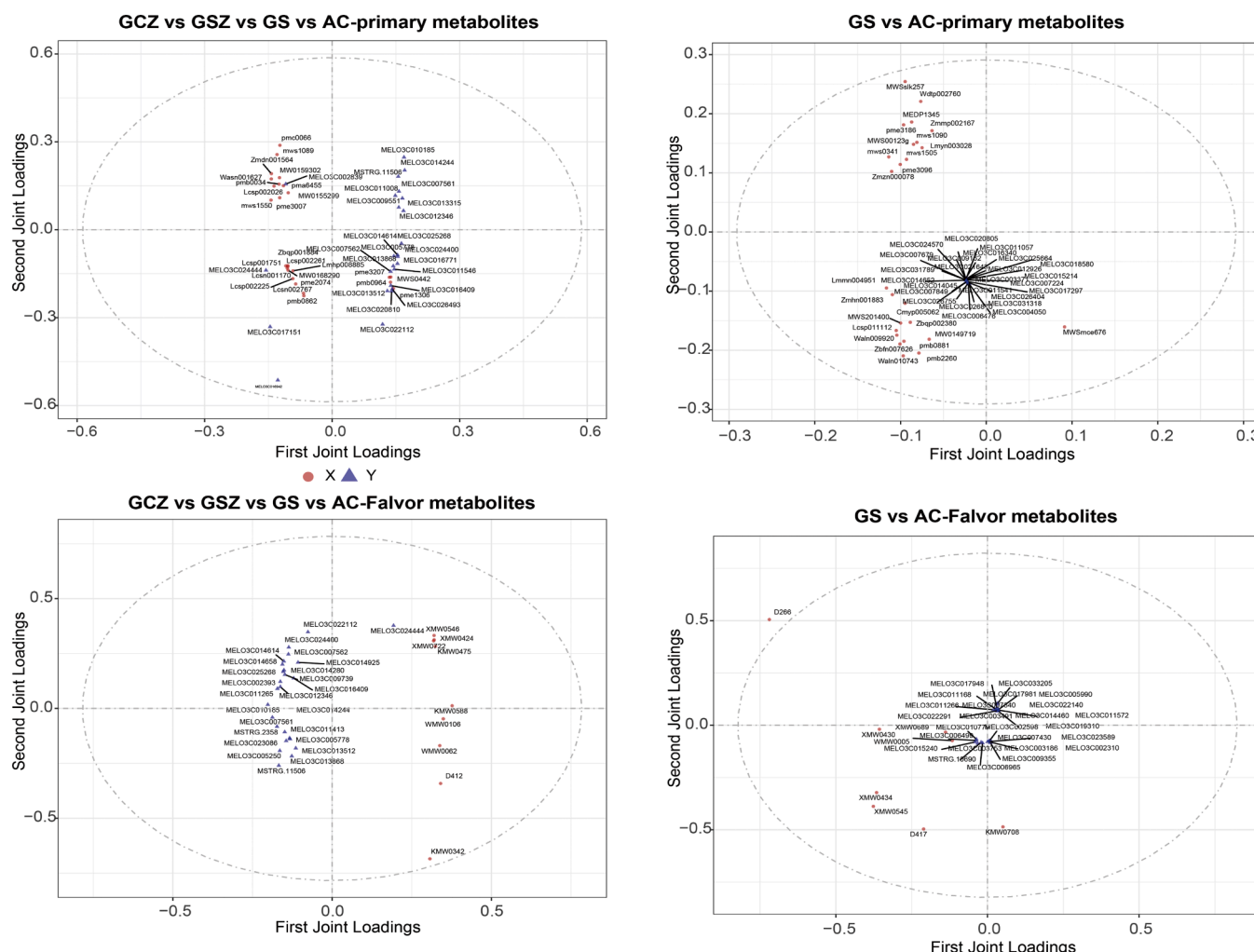


Fig. 5. O2PLS combined analysis of transcriptome and metabolome association trends Red dots represent metabolites, and blue triangles represent genes.

Volatile compounds are key determinants of fruit flavor and essential component of fruit quality. Our findings revealed that grafting markedly modulated metabolic synthesis in these two core pathways (Fig. 6). The amino acid pathway acted as a major route for the biosynthesis of aromatic compounds. In the lipoxygenase (LOX) pathway, unsaturated fatty acids were oxidized to produce hydroperoxides, which were then cleaved by hydroperoxide lyase into (2E,6Z)-nona-2,6-dienal. TVolatile esters were finally formed via reduction by alcohol dehydrogenase (ADH) and esterification by alcohol acyltransferase (AAT) (Zhou et al., 2015b). The monoterpene biosynthesis pathway used geranyl pyrophosphate (GPP) and farnesyl pyrophosphate (FPP) as precursors to produce characteristic aromatic compounds (Mendez-Perez et al., 2017). Meanwhile, β -carotene-derived apocarotenoids affected both pigmentation and aroma development (Hou et al., 2016). In the amino acid metabolic pathway, fruits grafted onto the 'GS' rootstock exhibited decreased levels of phenylalanine and L-branched-chain amino acids, along with reduced expression of related metabolic genes (CmArAT and CmBCAT1). Conversely, an increased concentration of methionine and its cleavage product by methionine lyase (MAL) was observed, indicating an enhanced flux through the L-isoleucine biosynthetic pathway via the α -ketobutyrate intermediate. This metabolic alteration likely facilitated the synthesis of volatile aldehydes, which were further oxidized to aromatic alcohols. In the fatty acid metabolism pathway, linolenic acid was oxidized by lipoxygenase (LOX) to generate (2E, 6Z)-nona-2,6-dienal, which was further converted into volatile esters through the coordinated activities of ADH and AAT. The 'GS' group had

the highest transcript levels of CmADH and CmAAT, accompanied by the maximum accumulation of esters. Furthermore, (2E,6Z)-nona-2, 6-dienal was previously identified as a key metabolic node in the 'GS' profile. In addition, upregulated expression of monoterpene synthase genes *CmTPS4* and *CmTPS7* in the GPP pathway, together with increased contents of linalool, 1,8-cineole, and terpineol, collectively account for the superior flavor characteristics observed in 'GS' grafted fruits compared to other treatments (Fig. 6A).

4. Discussion

4.1. The fruit quality of melon was significantly affected by grafting

Grafting has been widely used to enhance the stress resistance of melon scions and improve fruit quality, exerting positive effects on flavor, aroma and nutrient content (Condurso et al., 2012; Lecholocho et al., 2022). An important factor for successful grafting is rootstock selection. Rootstocks with vigorous growth, well-developed roots, relevant environmental adaptability, desirable resistance traits (such as cold tolerance, drought resistance, salt-alkali tolerance, and strong disease and pest resistance), and high scion compatibility have positive effects on grafting performance. In this study, grafting significantly increased the soluble solids content in the mesocarp and altered the levels of soluble sugars and vitamin C (VC), thereby improving the nutritional value of melon fruit. Among the treatments, the GS rootstock exhibited the most significant effects. The core reason for sweeter fruit after



grafting is that the rootstock optimizes sugar metabolism across four key processes: synthesis, transport, accumulation, and conversion (Ma et al., 2025; Nie et al., 2026; Sun et al., 2023; Xue et al., 2023). Essentially, grafting optimizes the source–flow–sink system (Falchi et al., 2020; Lemoine et al., 2013). Grafted rootstocks develop more extensive root systems with greater numbers of fine roots, enabling more efficient uptake of water, nitrogen, phosphorus, potassium, and other micronutrients. These mineral nutrients support a higher photosynthetic efficiency in leaves and promote the production of larger amounts of carbohydrates, which serve as precursors for sugars (Glanz-Idan and Wolf, 2020). Moreover, superior rootstocks can promote scion leaf

growth, resulting in larger and thicker leaves with higher chlorophyll contents and enhanced photosynthetic capacities. The total synthesis of photosynthetic products (sucrose and starch) increases, providing a solid material basis for fruit sweetness (Ugur et al., 2024; Zhu et al., 2025). Most importantly, rootstocks facilitate the transport and distribution of photosynthates toward fruit by altering plant hormone levels (e.g., auxin, cytokinin, and abscisic acid) (Carraro, 2025; Duan et al., 2024; Guo et al., 2021; Kawaguchi et al., 2022; Nanda and Melnyk, 2018). By regulating the source-sink relationship, rootstocks direct more photosynthetic products to be preferentially transported into fruit instead of being consumed in vegetative growth. They also improve

phloem transport efficiency, allowing sugars to move more smoothly from leaves to fruit and to accumulate more rapidly (Jegatheeswaran et al., 2026; Zhao et al., 2022; Zhou et al., 2023). Our results showed that the significantly increased fructose content in fruit after grafting may be due to the inhibition of excessive scion growth by rootstocks and the reduction of nutritional competition, making fruit more dominant in 'sugar grabbing'. Transcriptome data showed that the expression levels of genes encoding amylase and sucrose phosphate synthase in the sugar metabolism pathway was up-regulated, which accelerated the decomposition of starch into sugars (Sun et al., 2023). Comprehensive transcriptome and metabolome data indicated that the increase in organic acid metabolic enzyme activity levels led to a decrease in citric acid content and an increase in the sugar-acid ratio, resulting in a significant increase in the soluble solids content of grafted fruit. In addition, rootstocks can moderately adjust water supply, thereby increasing sugar concentration. The direction and degree of each change depends on the rootstock genotype (Camalle et al., 2023; Kaleem et al., 2022). Studies have shown that the flavor profile of grafted melons is shaped by the rootstock genotype, with significant variations in sugar composition observed in the scion (Kaleem et al., 2025). Similar rootstock-mediated influences on fruit quality have also been reported in other cucurbit crops (Devi et al., 2020; Liu et al., 2025; Sun et al., 2023). Here, we found that there was a potential relationship between the texture characteristics of the pulp and the sugar content (Zepeda et al., 2018). Grafting also improves nutrient absorption, especially sugar assimilation, thereby improving the texture characteristics and sweetness of grafted melon fruit (Liu et al., 2011). While previous studies have reported no significant effect of pumpkin rootstocks on melon fruit size (Camalle et al., 2023; Ye et al., 2025), our observations indicated that all three pumpkin rootstocks used here significantly reduced fruit size and single fruit weight (Fig. S1). Such discrepancies have also been noted in earlier work (Kaleem et al., 2022). A trade-off between fruit quality and size was observed in this experiment, meaning that in some cases, rootstocks may redistribute resources at the expense of fruit volume, such as preferentially promoting sugar accumulation or secondary metabolite synthesis, thereby, highlighting the complexity of scion-rootstock interactions. These results indicated that the improvement in melon fruit quality induced by grafting was determined by both rootstock and scion varieties. A metabolomics analysis showed that the improvement in GS fruit sweetness was associated with increased soluble sugar and SSC contents, which was related to the significant accumulations of key glycolysis intermediates, such as D-fructose-1,6-diphosphate and D-fructose-6-phosphate (Table S2). In the glucose metabolism pathway, related metabolic genes (Fig. 3C; Fig. 6; Tables S1 and S2) play vital roles.

4.2. Effects of grafting on the metabolism of fruit flavor substances

Sucrose serves as the primary determinant of melon fruit quality (Burger and Schaffer, 2007). During fruit maturation, sucrose accumulation is accompanied by a relative decrease in fructose, glucose, and trehalose concentrations. The elevated hexose/sucrose ratio observed in grafted plants, characterized by increased glucose and fructose levels alongside reduced sucrose content, suggests that grafting may modulate fruit ripening processes (Sun et al., 2023). Organic acid profiling revealed that malic acid constitutes the predominant component in grafted fruits, followed by citric acid and succinic acid. As a key respiratory substrate, malic acid contributes to both flavor development and energy metabolism, with its increased concentration in grafted fruits aligning with previous findings (Chen et al., 2023). The change of sugar content in apple interspecies grafting was related to the differential expression of sugar metabolism related genes (Chen et al., 2020). In eggplant grafting, the sweetness of ungrafted eggplant fruit was higher (Arvanitoyannis et al., 2005). Our results showed that grafting could significantly increase the fructose content of melon fruit, increase the sugar-acid ratio, and significantly increase the content of organic acids such as malic acid and succinic acid.

The biosynthesis of volatile compounds in melon fruit proceeds through the following well-established pathways: (1) amino acid metabolism, (2) fatty acid (linolenic acid) metabolism, (3) the GPP pathway, (4) the FPP pathway, and (5) β -carotene degradation. Among them, amino acid and fatty acid metabolism serve as the primary routes. In our study, a volatile organic compound analysis identified alcohols and aldehydes as the main volatile substances in grafted fruit, with the highest concentrations in the GS treatment group. The key aroma components included benzaldehyde, phenylacetaldehyde, (2E)-non-2-enal, (2E,6Z)-nona-2,6-dienal, citronellal, cis-citral, and a variety of alcohols [ethanol, 2-hexanol, (3Z)-hex-3-en-1-ol, (2E)-hex-2-en-1-ol, and linalool]. Ethyl acetate, phenylmethyl acetate, and 2-methylbutyl acetate are recognized as characteristic aroma substances of melon (Kaleem et al., 2025; Verzera et al., 2011). Ester compounds (especially phenylethyl acetate and trans-3-hexenyl acetate) provide the unique fruity and sweet flavor characteristic of melon aroma (Lignou et al., 2014; Wang, 2025). Methyl jasmonate, as a plant hormone and signal molecule, is a key regulator of sugar metabolism that aids in improving the postharvest quality of grafted fruit (Hakeem et al., 2025; Li et al., 2022; Luo et al., 2021; Wang et al., 2025; Xu et al., 2020). This was also reflected in our research. Benzaldehyde, a characteristic volatile substance in mature plums and grafted peach fruit, was significantly reduced in our work (El-Sayed et al., 2018; Seker et al., 2017). The decrease in this substance, which has a weak bitter almond aroma and slightly sweet background note, made the fresh and sweet flavor of grafted melon fruit more prominent. Citronellal, which provides the fresh citrus aroma of rhododendrons and oranges, was significantly increased in our grafting combinations (Johnson et al., 2022; Qian et al., 2019). While it is commonly found in citrus fruit, it has rarely been reported in melon fruit. It may be the result of signal transduction or induction produced by rootstock specificity, and it may endow grafted melons with a unique flavor that is more popular among consumers. The differential accumulation of alcohols and esters induced by different rootstock treatments, especially GS, formed unique aroma characteristics, which was consistent with the results of previous studies on rootstock-mediated flavor improvement (D. Huang et al., 2025). These findings together clarify the internal factors behind the improved fruit quality of GS grafted melon.

The reciprocal exchange of substances between rootstocks and scions mainly relies on water and diverse metabolites, including mineral nutrients, small organic molecules, and functional signaling components. The structural basis for grafting communication lies in vascular reconnection and intercellular channel formation. Specifically, the phloem enables bidirectional transport of phytohormones, small RNAs, mRNAs, and metabolites, while the xylem mediates the unidirectional upward translocation of water and minerals. Plant phytohormones act as core messengers for graft union healing and growth regulation, exhibiting crucial regulatory effects on grafting performance. Auxin (IAA) is essential for graft junction recovery, which synergizes with cytokinin (CK) to promote cell dedifferentiation, cell proliferation, and vascular reconnection (Park et al., 2021; Serivichyaswat et al., 2024). Absciscic acid (ABA) participates in graft union repair, salt stress response, long-distance signal transduction, and plant organ development in grafted plants (Niu et al., 2019; Peng et al., 2023; Huihui Zhang et al., 2018). Mobile small RNAs undergo long-distance transportation via phloem sieve tubes, mediating DNA methylation and developmental regulation (Lewsey et al., 2016). In tomato, mobile mRNAs have been confirmed to be closely associated with leaf metabolic processes (Huihui Zhang et al., 2018). Furthermore, small RNAs cooperate with phytohormones and metabolites to coordinately regulate stress tolerance and fruit quality of grafted crops (Jeynes-Copper and Catoni, 2023; Kapazoglou et al., 2021; Ning et al., 2025). Multiple metabolic precursors, including sucrose, trehalose, raffinose, citric acid, succinic acid, amino acids, phenylalanine, and fatty acids, have been verified to undergo long-distance transport in grafted plants (Jeynes-Copper and Catoni, 2023)). Consistent with these findings, the present study also

confirms extensive substance exchange and signal crosstalk in grafted melon plants. These mobile substances serve as key driving factors that trigger genome-wide transcriptional reprogramming and metabolic remodeling in grafted fruits.

4.3. Regulation of sugar metabolism and volatile substance metabolism genes in grafted melon fruit

Extensive research has demonstrated that grafting induces significant transcriptional reprogramming in fruit metabolic pathways. In grafted cucumber systems, key genes associated with glycolytic metabolism, including glycoside hydrolase (GH), pectinesterase (PE), and trehalose-6-phosphate phosphatase (TPP), have been identified as differentially regulated (Miao et al., 2019). Similarly, in grafted grapevines, multiple transcription factor families (MYB, AP2/ERF, C2C2, and WRKY) have been shown to regulate phenolic compound biosynthesis through transcriptional and post-transcriptional mechanisms (Zhang et al., 2022). Our transcriptome analysis revealed extensive differential expression of genes involved in central carbon metabolism, including glycolysis/gluconeogenesis, fructose metabolism, and α -linolenic acid metabolism. Invertases (IAI), sucrose synthase (SuSy), and SPSs are recognized enzyme families associated with sugar metabolism in cucurbits (Liu et al., 2013). Two key enzymes involved in sucrose accumulation in fruits are sucrose phosphate synthase (SPS) and sucrose synthase (SUS). SPS must first catalyze fructose-6-phosphate (F6P) and uridine diphosphate glucose (UDPG), after which sucrose phosphatase (SPP) irreversibly converts sucrose-6-phosphate (S6P) into sucrose (Shah et al., 2025). Notably, in our study, GS treatment resulted in low expression of SUS and SPP, while SPS1 was upregulated. Sucrose phosphate synthase (SPS1), which catalyzes sucrose biosynthesis, and various sucrose synthase (SuSy) isoforms with distinct roles in reversible sucrose metabolism (Aslam et al., 2020; Gao et al., 2018) were differentially regulated. Particularly striking was the upregulation of fructokinase (FK), a key enzyme in fructose phosphorylation and the regulation of glycolytic flux. This transcriptional reprogramming, coupled with increased SPS1 expression, may underlie the enhanced soluble sugar accumulation and improved texture properties in GS-grafted fruits. These findings are consistent with previous reports on rootstock-mediated regulation of sugar metabolism and aroma-related gene expression (Zhao et al., 2018), particularly the role of acid invertases in phloem unloading and sucrose accumulation (Aslam et al., 2020).

The synthesis of volatile esters via the lipoxygenase (LOX) pathway is a key determinant of aroma quality in melons (Zhou et al., 2015a). This pathway involves four key enzymatic steps: LOX-mediated oxidation, hydroperoxide lyase (HPL) cleavage, alcohol dehydrogenase (ADH) reduction, and alcohol acyltransferase (AAT) esterification. In the fatty acid pathway, linoleic acid and linolenic acid can be cleaved by HPL into hydroperoxides and converted to hexenal or hexenoic acid. ADH subsequently reduces the aldehydes to their corresponding alcohols. AAT catalyzes the final linkage of acyl-CoA with an alcohol to produce aromatic esters. Transaminases convert amino acids into ammonia, which is then decarboxylated to formaldehyde by the pyruvate dehydrogenase system and ultimately converted to alcohol via ADH (Tang et al., 2023). ADH is involved in ripening regulation and aroma development in various fruit, including apricot and pear (González-Agüero et al., 2009; Luo et al., 2021). C6 aldehydes, as direct products of the LOX-HPL pathway, form the grassy aroma of immature fruit and serve as crucial contributors to mature fruit flavor formation. During fruit ripening, bursts of ethylene synthesis (Li et al., 2016; Zhu et al., 2005) and activated ripening-related transcription factors (e.g., RIN and ERF) de-repress the fatty acid metabolism pathway (Fujisawa et al., 2013; Griffiths et al., 1999; He et al., 2020; Li et al., 2023). Additionally, the gradual disintegration of the cell wall and membrane system releases large amounts of membrane-derived unsaturated fatty acids, including linoleic and linolenic acids (Yu et al., 2021). The up-regulated LOX binds

to these substrates and triggers oxidative cleavage, leading to the formation of the 'green' astringent fruit taste. Sufficient aldehyde substrates generated by unsaturated fatty acid oxidative cleavage induce high-level ADH expression. The ADH enzyme catalyzes the reduction of aldehydes to alcohols, whereas AAT utilizes the produced alcohols and acyl-CoA to synthesize fruit esters. This cascade eliminates the 'green' astringent taste and facilitates the rapid accumulation of the characteristic fruit aroma. Acyl-CoA for ester synthesis is primarily derived from basal metabolic pathways, including fatty acid β -oxidation, glycolysis, the tricarboxylic acid cycle, the upstream fatty acid oxidation branch of the LOX pathway, and amino acid catabolism (D'Auria, 2006; Lin and Oliver, 2008; Wei et al., 2022), which enables efficient coupling of fruit aroma metabolism. At the stable ripening stage, declined ethylene accumulation and attenuated ethylene signaling directly repress the transcription of CmLOX9/18. Accumulated abscisic acid further suppresses LOX transcription via ABRE cis-element-mediated inhibition of the LOX promoter. In late ripening stages, reduced jasmonic acid accumulation and accumulated JAZ repressors block jasmonic acid-induced LOX activation (Ju et al., 2018; Kang et al., 2021; Zhang et al., 2015). Combined with progressive membrane lipid degradation, decreased LOX substrates, and transcriptional and enzymatic feedback inhibition of LOX, the generation of LOX-dependent oxidative aldehyde products is restricted. Additionally, LOX-derived aldehydes exert substrate feedback inhibition on LOX expression to prevent excessive lipid peroxidation (Wasternack and Song, 2016). Collectively, these regulatory changes decelerate the biosynthesis of aroma precursors and the interconversion between aldehydes and alcohols. Constitutively high AAT expression sustains low but stable ester synthesis, ultimately maintaining the overall flavor stability of ripe fruit. In the melon-squash grafting system, rootstock-induced alterations in the expression of CmADH and CmAAT significantly influence the biosynthesis of volatile esters and fruit flavor. Amino acid metabolism pathways, such as phenylalanine metabolism, and alanine and tyrosine metabolism, play roles in regulating nitrogen and volatile compound synthesis (Li et al., 2025; Xing et al., 2023). Our results revealed the differential expression of genes encoding relevant enzymes in the phenylalanine pathway, branched-chain amino acid pathway, and methionine pathway among the different treatments. The down-regulation of CmLOX in GS-grafted fruit was feedback-coordinated with aldehyde accumulation, and the buildup of alcohol substrates induced CmAAT expression. Excess aldehydes suppress CmLOX activity to maintain metabolic homeostasis. This accounted for the low CmLOX expression in ripe GS-grafted fruit, along with the abundant accumulations of alcohol- and aldehyde-derived flavor compounds. The coordinated expression patterns of CmLOX, CmADH, and CmAAT genes and their corresponding volatile metabolite profiles indicated that these aroma biosynthesis pathways were evolutionarily conserved in species (Chen et al., 2016). Furthermore, grafting enhances fruit quality traits, such as SSC/TA ratio, contents of ascorbic acid, β -carotene, amino acid, lutein, and volatile organic compounds, and antioxidant scavenging activity, thereby improving the sensory characteristics of grafted fruit (Camalle et al., 2021; Lecholocholo et al., 2022). These factors collectively determine the fruit flavor provided by grafted rootstocks.

This study elucidated the grafting-induced reprogramming of flavor metabolism in melon based on transcriptomic data. However, transcript abundance cannot fully reflect protein accumulation, enzyme activity, and final metabolic phenotypes, resulting in widespread multi-layered decoupling between gene transcription and metabolic traits. Such decoupling is primarily attributed to post-transcriptional splicing, translational regulation, protein post-translational modifications, enzyme allosteric regulation, substrate limitation, and subcellular compartmentalization of metabolic pathways (Guo et al., 2026; Jiang et al., 2023; Zhang et al., 2023). O2PLS-based multi-omics analysis revealed significant covariation between flavor-related structural genes and metabolites, whereas the overall correlation between

transcriptomic and metabolomic profiles was non-linear. This evidence indicates that post-transcriptional regulation, protein modification, and enzyme activity modulation serve as the core regulatory layers governing the fine accumulation of flavor compounds in melon fruit (Kaleem et al., 2020). The transcriptional upregulation of key flavor synthesis genes (CmLOX, CmAAT, CmADH) and sugar metabolism genes (SPS, FK) did not drive the linear accumulation of corresponding metabolites. This inconsistency is caused by substrate competition and product feedback inhibition within flavor metabolic pathways, dynamic fluctuations in enzyme activity induced by phosphorylation and deubiquitination of key enzymes, and subcellular compartmentalization that spatially isolates sequential metabolic reactions. Collectively, these factors lead to evident deviations between transcriptional signals and final metabolic phenotypes (Van De Ven et al., 2026; Huabin Zhang et al., 2018). This also explains why the present study successfully identified representative gene-metabolite association modules but failed to construct a high-precision predictive model for flavor metabolic flux.

Furthermore, the regulatory mechanism underlying rootstock-induced accumulation of novel aromatic volatiles remains unclear. Rootstock–scion long-distance communication operates via two distinct regulatory modes: rootstocks can directly supply scion metabolic pools by transporting small molecular substances, or reshape scion transcriptional networks and activate downstream flavor synthetic pathways through mobile RNAs and hormonal signals (Fan and Zhao, 2022; Paajanen et al., 2025). Therefore, whether the accumulation of specific volatiles such as benzaldehyde and citronellal originates from direct rootstock transport or inducible *de novo* synthesis in scions requires further verification, which represents a critical breakthrough for future research on rootstock-mediated flavor regulation mechanisms in melon.

Future studies will adopt quantitative enzyme activity detection, Western blot assay, protein post-translational modification identification, and subcellular localization analysis to verify the protein expression patterns and functional activities of core hub genes. This approach will clarify the hierarchical correlations among transcription, protein, and metabolism, elucidate the molecular mechanisms responsible for phenotype decoupling, and ultimately facilitate the construction of an accurate predictive model for flavor metabolic flux.

It is worth noting that the weighted gene co-expression network analysis (WGCNA) adopted in this study has inherent technical limitations associated with correlation-based algorithms. First, this approach only identifies correlative co-expression relationships among genes and cannot determine the upstream and downstream causal relationships of gene regulation (Langfelder and Horvath, 2008). The gene modules and core hub genes identified in this study merely reflect transcriptional correlation patterns and cannot be directly regarded as definitive molecular regulatory mechanisms. Second, WGCNA network construction, module segmentation, and hub gene screening are sensitive to key parameters, including soft-thresholding power and minimum module size, and variations in parameter settings may introduce statistical biases in module partitioning and gene identification. In addition, the screening of hub genes solely based on intramodular connectivity tends to retain constitutively highly expressed and functionally non-specific transcripts, thereby causing potential screening errors in the identification of functional core genes (Van Dam et al., 2017). We standardized analytical parameters across all samples and validated the stability of key modules through repeated network reconstruction. Genes with high intramodular association were screened by combining two indicators: gene differential expression levels and intramodular connectivity. This strategy effectively eliminated the interference of highly expressed background genes and improved the reliability of our results. Despite these optimizations to the analytical workflow, the inherent limitations of correlation-based analysis cannot be fully resolved. Accordingly, the flavor regulatory network associated with rootstock–scion crosstalk identified in this study is merely an exploratory correlative result. The causal regulatory mechanisms and biological functions of genes with high intramodular relevance remain to be further verified via

subsequent molecular functional experiments.

4.4. Economic value of grafted rootstock-mediated fruit flavor quality

Grafting is often used as an effective means to control soil-borne diseases by using rootstock genetic resistance. Rootstock can help in disease resistance by producing root exudates that inhibit bacteria, activating plant defense mechanisms, and blocking pathogen transmission paths. The effective control of common soil-borne diseases of melons directly reduces plant death and yield declines caused by soil problems. In addition to controlling soil-borne diseases, grafting increases the single fruit weight and total yield of crops by improving the scion root system and reducing the planting density, thereby decreasing the cost of manual management and harvesting costs and increasing farmer incomes (Musa et al., 2020; Ricárdez-Salinas et al., 2010). Grafting-based resistance can replace chemical agents to reduce the harm of soil-borne diseases to crops, and the use of fewer chemicals can reduce the harm to soil, air, and other environments. Selecting suitable rootstocks for grafting can significantly improve irrigation water- and nitrogen-use efficiencies in melon production. Improved sandy soil planting also aids in achieving efficient resource utilization (Djidonou et al., 2013). Effective rootstock-use strategies can enhance the resistance of scions to spring frost and reduce the related damage (C. Huang et al., 2025). In our study, the fruit quality of the GS rootstock grafting combination was outstanding. The rootstock specifically induced the fruit to produce citronellal, a rare fresh and fragrant volatile compound in melon fruit, which gave the grafted fruit a unique and sweet quality and directly improved the market competitiveness of the product. In addition, thin-skinned melon is prone to cracking during transportation, resulting in economic loss. The GS rootstock grafting combination increased the peel and pulp toughness levels, as well as the viscosity of grafted fruit, thereby improving the transport resistance and reducing losses. At the nutritional level, GS fruit was rich in phyloquinone (Vitamin K1) and riboflavin (Vitamin B2). These increases not only met the needs of consumers in terms of taste and nutritional value, but also created more social and economic benefits by reducing losses during management, harvesting, and transportation. This work provides a reference for the study of melon cultivation methods and the changes in related varieties of grafted fruit. Currently, the application of grafted rootstocks has evolved from focusing solely on disease resistance and yield improvement toward the multidimensional and collaborative optimization of plant stress tolerance, fruit quality, and metabolic regulation. This study employed a single thin-skinned melon cultivar ‘Cuixue’ as the scion material grafted onto three pumpkin rootstock genotypes, and all experiments were conducted under controlled greenhouse conditions. Accordingly, the findings of this study have certain limitations in terms of applicability and universality. First, the use of a single scion genotype cannot fully represent rootstock–scion interaction effects across diverse melon cultivars, and cultivar-specific variations may restrict the generalization of the present conclusions to all melon grafting systems. Second, the stable greenhouse conditions with controlled temperature, light, water, and soil nutrients excluded the complex field climate, soil microenvironment, and various field stress factors, failing to reflect the genotype-by-environment interactions and natural phenotypic variations under large-scale field cultivation. Furthermore, this study only investigated the short-term variations in plant growth and fruit metabolic transcription, without monitoring the long-term agronomic performance and flavor stability of grafted plants under continuous multi-year cultivation.

To overcome these limitations, future research will be optimized and supplemented from multiple perspectives. First, multi-site and multi-year field experiments will be conducted under natural field conditions and environmental gradients to systematically dissect the genotype-by-environment interaction mechanisms of rootstock–scion crosstalk and verify the field stability of greenhouse-derived results. Second, reciprocal grafting combinations and multiple scion cultivars

will be included to eliminate the interference of genetic background and clarify the independent regulatory contributions of rootstocks and scions. Third, spatial transcriptomics will be applied to precisely characterize the tissue-specific gene expression patterns in graft union tissues, vascular tissues, and different fruit regions, thereby elucidating the spatial regulatory characteristics of long-distance signal communication between rootstocks and scions. Fourth, through further study of the screened core hub genes, in vivo functional verification was carried out through gene overexpression and CRISPR-Cas9 gene editing, and the causal relationship between transcriptional regulation and fruit flavor substance accumulation was clarified from the genetic level, so as to further improve the molecular mechanism of rootstock regulation of melon flavor metabolism.

5. Conclusion

This study showed that pumpkin rootstock grafting significantly improved melon fruit quality through a variety of metabolic pathways. The comparative analysis showed that the grafted fruit of ‘Sizhuang’ had the most desirable characteristics, including increased soluble sugar and aromatic substance contents, viscosity, and ascorbic acid level, as well as decreased flesh hardness, that improved the commodity competitiveness and transportation capacity of grafted fruit, reduced the production and transportation costs, and increased the production income. The improved metabolism was associated with the up-regulated expression of key biosynthetic genes, including those encoding fructokinase, sucrose phosphate synthase, and ADH. In addition, methyl jasmonate and citronellal, known regulators of fruit quality and aroma, respectively, produced by non-melon rootstocks, were detected and gave the fruit a unique flavor. In this study, the molecular mechanisms of rootstock-mediated fruit quality improvement of grafted melon were elucidated by integrating metabolomics and transcriptomics analyses. This study provides new insights into the regulatory network of flavor substance metabolism and identifies key metabolic pathways affected by rootstock grafting. These findings help us to understand the physiological and molecular mechanisms by which rootstock selection regulates fruit quality traits in grafted melon.

CRediT authorship contribution statement

Jianan Zhang: Data curation, Writing – original draft. **Shaoshuai Fan:** Supervision. **Qiong Luo:** Writing – review & editing. **Lixiang Zheng:** Writing – review & editing. **Yeliya Fu:** Data curation. **Wenjia Lv:** Software. **Xiaonuan Chen:** Data curation. **Min Guan:** Investigation. **Chengze Du:** Investigation. **Dong Wang:** Data curation. **Ying Duan:** Writing – review & editing. **Li Miao:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Project administration, Supervision, Writing – review & editing. **Huasen Wang:** Funding acquisition, Project administration, Resources, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

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Data availability

Data will be made available on request.

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