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Omics-Based Study of Salt Stress Mechanisms in Mountain Peach (*Prunus davidiana* Carr.) in Northwest China

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Abstract: Long-term field evidence shows that peach trees grafted onto mountain peach (*Prunus davidiana* Carr.) rootstocks exhibit superior salt tolerance in Northwest China's saline-alkali soils compared to those on hairy peach (*Prunus persica* L.) rootstocks, yet the mechanism is unclear. This study compared physiological and transcriptomic analysis, providing a theoretical basis for understanding breeding responses of 'Longmi 9' peach to salt stress. Mountain peach effectively restricted leaf Na^+ accumulation (up to 36.36% reduction) and Cl^- influx, maintained a higher K^+/Na^+ ratio, and showed only half the reduction in stomatal aperture under high stress, thereby preserving photosynthesis. In contrast, hairy peach exhibited sensitive ion accumulation. Transcriptomics revealed a more targeted response in mountain peach, with 256 differentially expressed genes (DEGs) across three stress levels versus 1,196 in hairy peach. Both varieties activated phenylpropanoid and α-linolenic acid metabolism pathways. Notably, mountain peach uniquely coordinated glutathione, nitrogen, and pyruvate metabolism into a synergistic network, whereas hairy peach relied more on flavonoid biosynthesis. Quantitative real-time PCR (qRT-PCR) validation of ten co-enriched DEGs, such as *PRX44*, *OPR2* and *CCR2*, confirmed expression trends consistent with the transcriptome data, thereby verifying its reliability. This work elucidates the multilevel, coordinated regulatory mechanism conferring salt tolerance in mountain peach, providing robust theoretical foundations for the development of salt-tolerant peach cultivars.

Keywords: mountain peach, hairy peach, salt stress, physiological response, transcriptome analysis

Introduction

Salt stress, as one of the major abiotic stressors limiting crop growth and productivity, is commonly encountered in fruit tree cultivation systems worldwide. The global extent of saline-alkali land reaches approximately 954 million hectares, with China accounting for around 36.7 million hectares-nearly 3.8% of the total-and 12.3 million hectares of which possess significant potential for agricultural development[1]. In the Loess Plateau of northwest China, a core production region for high-quality and distinctive peaches, soil salinization poses a particularly severe challenge to sustainable agriculture. The loessal soils, widely distributed across this region, typically exhibit pH values exceeding 8.0, leading to reduced availability of essential nutrients and increased risk of sodium ion toxicity, both of which impose significant physiological stress on fruit tree root systems. In

practical production systems, it is precisely this unique soil environment that renders improper rootstock selection highly susceptible to inducing tree chlorosis, diminished tree vigor, reduced yield and quality, and even catastrophic orchard-wide failure.

Prunus davidiana Carr., a deciduous small tree of the genus *Prunus* (Rosaceae), is widely distributed across North, Northwest, and Southwest China. As a heliophilous species, it exhibits tolerance to cold, drought, and saline-alkali conditions, with well-developed root systems and strong sprouting capacity[2]. Owing to its vigorous growth, high productivity, and superior fruit quality, this species is extensively used as a grafting rootstock for various stone fruit crops in northwestern China[3]. *Prunus persica* L., commonly referred to as the hairy peach, is native to northern and central China and has been widely cultivated across diverse regions. This species exhibits cold and drought tolerance but is sensitive to waterlogging[4]. In long-term production practices, it has been observed that peach trees grafted onto hairy peach rootstocks are prone to developing chlorosis after fruiting, leading to reduced yields. In contrast, those grafted onto mountain peach rootstocks exhibit normal growth and fruiting performance, making them widely adopted in commercial orchard systems. Most fruit trees are propagated through grafting; the selection of rootstocks with high salt-alkali tolerance is critical for improving the salt-alkali resistance of fruit trees. Zhao et al.[5] conducted a comparative study on the salt-alkali tolerance of peach trees across different habitats and found that mountain peach rootstocks exhibit strong tolerance. Salt stress severely disrupts physiological activities and molecular processes in fruit trees through mechanisms including ion toxicity, osmotic stress, and oxidative stress. Liu et al.[6] reported that salt stress causes significant changes in plant chlorophyll content and photosynthesis performance. Zhai et al.[7] further demonstrated that saline-alkali stress significantly inhibits the growth and development of 'M9-T337' seedlings; reduces photosynthetic performance; induces ion accumulation, thereby disrupting the osmotic adjustment system, endogenous hormone system, antioxidant system. Transcriptomics further revealed that the Kyoto Encyclopedia of Genes and Genomes (KEGG) pathways of *Actinidia chinensis* Planch. under 4% salt stress are mainly enriched in glycine metabolism, serine and threonine metabolism, glutathione metabolism, and pyruvate metabolism[8]. Chen et al.[9] reported that under salt stress, 1,968 and 4,700 (DEGs) were identified in grapevines following short-term and long-term salt treatments, respectively, when compared to the control group. The study highlighted significant enrichment of key metabolic pathways associated with salt stress responses, including flavonoid biosynthesis, starch and sucrose biosynthesis, phenylpropanoid biosynthesis, and terpenoid biosynthesis. Although mountain peach is widely recognized as a tree species with strong salt-alkali tolerance, research into the underlying physiological and molecular mechanisms of this trait remains limited; its comparative advantages over hairy peach rootstocks in terms of stress responses and regulatory pathways have not yet been clearly elucidated.

Therefore, this study employed mountain peach and hairy peach as experimental materials to systematically compare their physiological responses and transcriptomic regulatory networks under salt stress. The aim was to elucidate the intrinsic mechanisms underlying their differential salt tolerance through integrated analyses of leaf anatomical structure, ion homeostasis, antioxidant defense systems, and differential gene expression regulation. These findings not only provide a robust theoretical foundation for understanding the physiological and molecular basis of the superior salt tolerance in

mountain peach but also offer valuable insights for the development of salt-tolerant rootstocks in peach breeding programs.

Results

Effects of salt stress on Na^+, K^+, Cl^- concentrations and Na^+/K^+ ratio in mountain peach and hairy peach rootstocks

The effects of different salt stress treatments on the ion contents of the rootstocks of mountain peach and hairy peach are shown in Fig. 1. Salt stress significantly decreased Na^+ concentration in mountain peach rootstocks, compared with the control (CK), treatments T1-T3 induced significant reductions of 31.81%, 36.36%, and 31.81%, respectively. In contrast, Na^+ concentration in hairy peach rootstocks increased gradually, with the highest level observed under T3 treatment (an 82.00% increase relative to CK, Fig. 1A). Under salt stress, the K^+ concentration of both peach rootstock varieties exhibited a trend of first increasing, then decreasing, and then increasing again. Specifically, the K^+ concentration in mountain peach rootstocks was highest under T3 treatment, showing a 14.72% increase relative to the CK. For hairy peach rootstocks, the K^+ concentration under T1 treatment was significantly higher than that of the CK, with an increase of 34.41% (Fig. 1B). As salt stress concentration increased, the Cl^- concentration of both peach rootstock varieties increased significantly. For mountain peach rootstocks, the Cl^- concentration peaked under T2 treatment, showing a 33.09% increase relative to the CK, in contrast, the Cl^- concentration of hairy peach rootstocks reached its maximum under T3 treatment (Fig. 1C). Salt stress decreased the Na^+/K^+ ratio in mountain peach rootstocks while increasing it in hairy peach rootstocks. Notably, the Na^+/K^+ ratio for hairy peach rootstocks reached its maximum under T3 treatment (Fig. 1D).

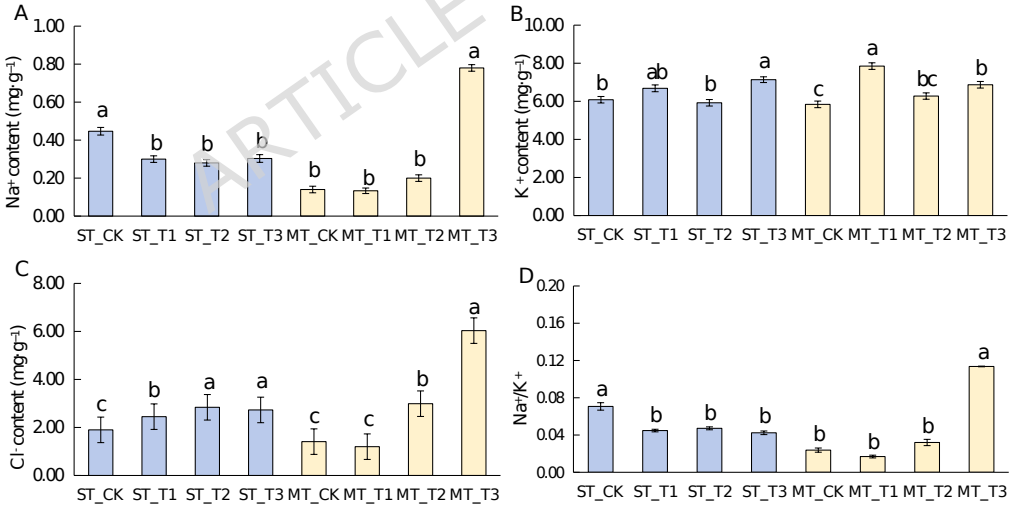

Fig. 1. Ion accumulation in mountain peach and hairy peach rootstocks under salt stress. The abscissa represents the CK, T1, T2, and T3 treatments applied to mountain peach and hairy peach rootstocks. (A) Na^+ concentration in mountain peach and hairy peach rootstocks under different treatments. (B) K^+ concentration in mountain peach and hairy peach rootstocks under different treatments. (C) Cl^- concentration in mountain peach and hairy peach rootstocks under different treatments. (D) Na^+/K^+ ratio in mountain peach and hairy peach rootstocks under different treatments. Different lowercase letters indicate significant

differences (P < 0.05), while the same lowercase letters indicate no statistically significant difference. For each rootstock separately, different lowercase letters indicate a significant difference (*P < 0.05*) compared with its own CK control within that same rootstock, not between the two rootstocks. Abbreviations: MT, mountain peach; ST, hairy peach (the same below).

Effects of salt stress on chlorophyll concentration in mountain peach and hairy peach rootstocks

The chlorophyll contents in the two peach rootstocks varieties under different salt stress treatments are presented in Fig. 2. As salt stress intensity increased, chlorophyll a concentration in both rootstocks gradually rose, with the rate of increase declining after the T2 treatment. In mountain peach rootstocks, chlorophyll a concentration peaked at the T2 treatment, showing a 29.41% increase relative to the CK. In contrast, hairy peach rootstocks exhibited maximal chlorophyll a concentration under both T2 and T3 treatments, with a consistent 3.44% increase compared to CK (Fig. 2A). Chlorophyll b concentrations in both mountain peach and hairy peach rootstocks increased progressively with rising salt stress intensity. Notably, hairy peach rootstocks achieved the highest leaf chlorophyll b level under T3 treatment, representing a 50% increase over the CK (Fig. 2B). While the chlorophyll a/b ratio in mountain peach remained stable across T1–T3 treatments, that in hairy peach was significantly higher under T2 than under all other treatments (Fig. 2C).

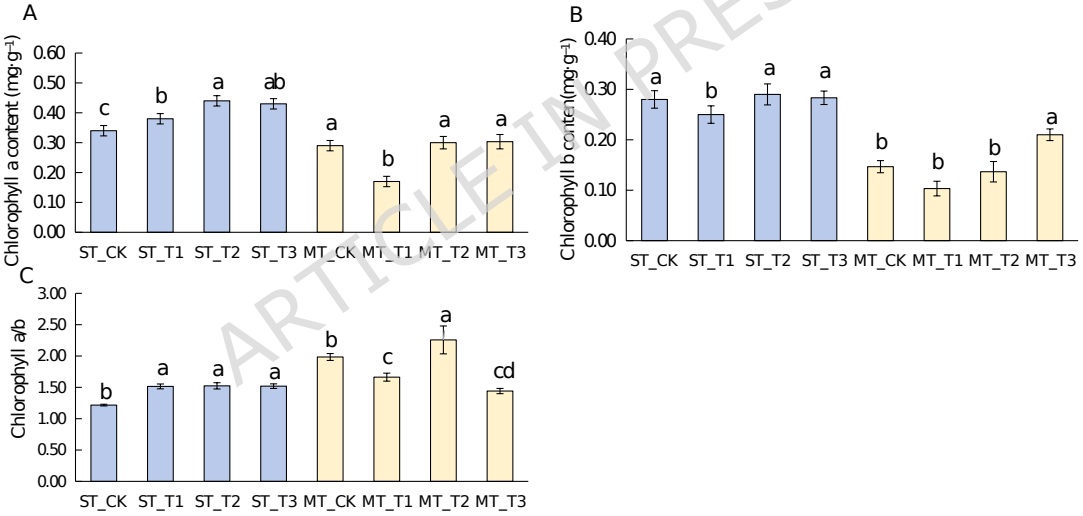

Fig. 2. Changes in chlorophyll content of mountain peach and hairy peach rootstocks under salt stress. The x-axis represents the CK, T1, T2, and T3 treatments applied to both rootstock varieties. (A) Chlorophyll a concentrations in mountain peach and hairy peach rootstocks across different treatments. (B) Chlorophyll b concentrations in mountain peach and hairy peach rootstocks across different treatments. (C) Chlorophyll a/b ratios in mountain peach and hairy peach rootstocks across different treatments. Different lowercase letters denote significant differences (P < 0.05), whereas identical lowercase letters indicate no statistically significant difference. For each rootstock separately, different lowercase letters indicate a significant difference (*P < 0.05*) compared with its own CK control within that same rootstock, not between the two rootstocks.

Effects of salt stress on soluble sugar content and enzyme activities in mountain peach and hairy peach rootstocks

The changes in soluble sugar content of the two peach rootstocks varieties under different salt stress treatments are presented in Figure 3. In mountain peach rootstocks, soluble sugar content under T2 treatment significantly increased by 93.00% compared to the CK, while the increase under T3 treatment was 21.02%. In hairy peach rootstocks, soluble sugar content peaked at 34.52 g·kg^{-1} under T3 treatment, representing a significant 16.26% increase over CK. In contrast, T1 and T2 treatments resulted in significant reductions of 29.03% and 30.51%, respectively, relative to CK (Fig. 3A).

In mountain peach rootstock, POD activity was highest under T2 treatment, showing a 72.10% increase compared to the CK. In hairy peach rootstocks, POD activity reached its maximum under T3 treatment, with an 87.19% increase relative to CK (Fig. 3B). Across both rootstock varieties, SOD activity progressively increased with elevated salt stress intensity, Mountain peach exhibited peak SOD activity under T2 treatment, while hairy peach showed maximal activity under T3 treatment (Fig. 3C). As salt concentration increased, NOX activity in mountain peach rootstocks gradually decreased, whereas that in hairy peach rootstocks it reached its maximum under T3 treatment, showing a 72.96% increase relative to the CK (Fig. 3D).

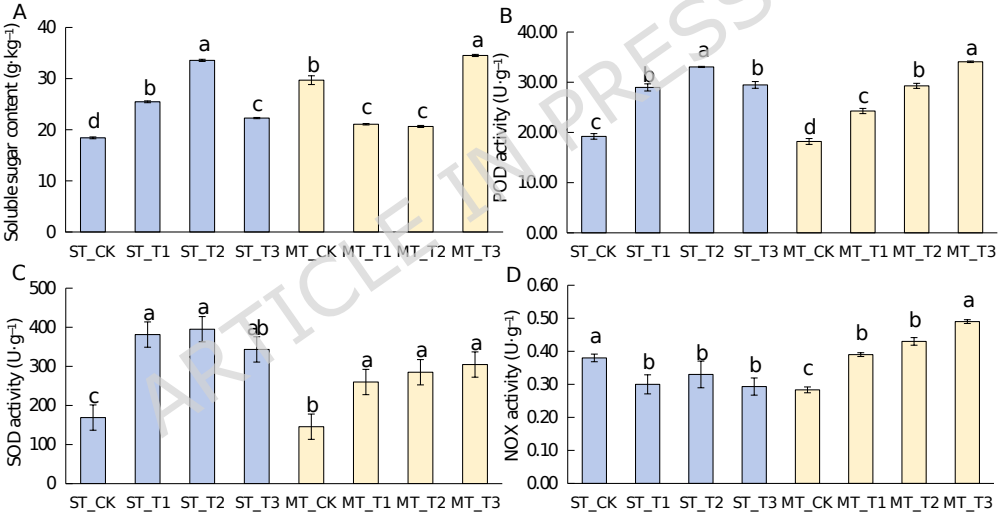

Fig. 3. Changes in soluble sugar content and enzyme activities of mountain peach and hairy peach rootstocks under salt stress. The abscissa represents CK, T1, T2, and T3 treatments for both rootstock varieties. (A) Soluble sugar content of mountain peach and hairy peach rootstocks under different treatments. (B) POD activity of mountain peach and hairy peach rootstocks under different treatments. (C) SOD activity of mountain peach and hairy peach rootstocks under different treatments. (D) NOX activity of mountain peach and hairy peach rootstocks under different treatments. Different lowercase letters indicate significant differences ($P < 0.05$), while the same lowercase letters indicate no significant statistical differences. For each rootstock separately, different lowercase letters indicate a significant difference ($P < 0.05$) compared with its own CK control within that same rootstock, not between the two rootstocks.

Effects of salt stress on leaf phenotype, anatomical structure, and stomatal traits of mountain peach and hairy peach rootstocks

Leaf phenotype analysis of mountain peach and hairy peach rootstocks revealed that under the CK treatment, leaves of both rootstock varieties remained green (Fig. 4A). With increasing salt stress concentration, leaves of hairy peach rootstocks exhibited yellowing progressing to light yellow discoloration under all salt treatments, accompanied by necrosis at the leaf margins and tips. In contrast, mountain peach rootstocks showed minimal phenotypic changes across T1–T3 treatments, although leaves under T1 treatment displayed a light green discoloration with necrosis at the leaf tips.

The effects of salt stress on the leaf anatomical structure of the two peach rootstocks varieties are presented in (Fig. 4B) and (Supplementary Table S1) With increasing salt stress intensity, palisade tissue thickness, spongy tissue thickness, and leaf thickness exhibited an overall increasing trend in both mountain peach and hairy peach rootstocks. The palisade tissue thickness of both rootstock varieties reached maximum values under T3 treatment, at 56.20 μm and 74.50 μm, respectively. In mountain peach, leaf spongy tissue thickness peaked at 66.67 μm under T2 treatment, whereas in hairy peach, it reached a maximum of 54.00 μm under T3 treatment. In hairy peach, the CTR value showed an overall decreasing trend across T1–T3 treatments, while the SR value increased continuously. In contrast, in mountain peach, the CTR value first decreased and then increased, with the SR value also exhibiting an upward trend.

With increasing salt stress intensity, the stomatal aperture of hairy peach rootstock leaves gradually decreased, reaching the minimum value under T3 treatment, representing a significant reduction 44.64% compared to CK. In contrast, the stomatal aperture of mountain peach rootstock leaves only decreased by 22% under T3 treatment relative to CK, with a much smaller reduction amplitude than that of hairy peach (Fig. 4D).

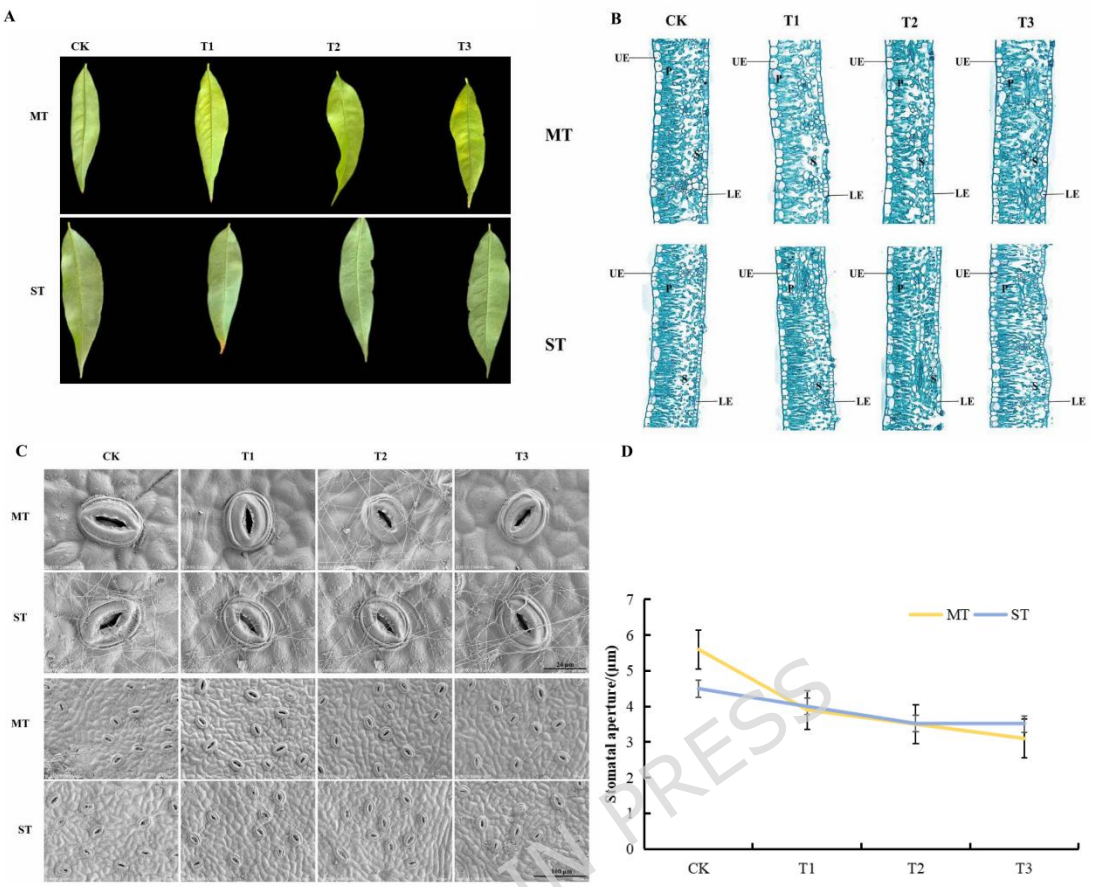

Fig. 4. Changes in leaf phenotype, anatomical structure, and stomatal traits of mountain peach and hairy peach rootstocks under salt stress. **(A)** Leaf phenotypes of mountain peach and hairy peach rootstocks under CK, T1, T2, and T3 treatments. **(B)** Paraffin sections (20×) of mountain peach and hairy peach rootstocks under different treatments. UE: Upper epidermis; LE: Lower epidermis; P: Palisade tissue; S: Spongy tissue. **(C)** Scanning electron microscopy (SEM) images of stomata from mountain peach and hairy peach rootstock leaves under different treatments. Scale bars = 200 μm and 20 μm, respectively. **(D)** Stomatal aperture of mountain peach and hairy peach rootstocks under different treatments. X-axis: CK, T1, T2, and T3 treatments (from left to right); Y-axis: Stomatal aperture.

Overview of RNA Sequencing (RNA-Seq) data

Transcriptome sequencing was performed on eight samples from two peach rootstock varieties using the DNBSEQ platform. After raw read filtering, a total of 1,069,964,526 clean reads and 156.62 G clean bases were obtained. The GC content was approximately 45%, and the Q30 base percentage exceeded 96% in all samples, indicating that the transcriptome sequencing data was of high quality and reliability, and thus suitable for downstream analyses (Supplementary Table S2).

Screening and analysis of DEGs

As shown in Fig. 5A and Fig. 5B, the first two principal components (PC1 and PC2) explained 78.3% of the total variance. Data points for the same material under different treatments were distributed in distinct clusters, indicating significant changes in gene expression between treated groups and CK following salt stress. Additionally, the three replicates of each treatment clustered closely together, demonstrating good reproducibility. As shown in (Fig. 5B), correlation analysis across the 24 samples further confirmed strong correlations between biological replicates of the salt stress treatments, validating that the sequencing data were highly reliable and suitable for subsequent analyses.

The ST_CK vs ST_T2 comparison yielded the largest number of DEGs, with a total of 3,317 DEGs including 2,816 upregulated genes and 501 downregulated genes. The second largest number of DEGs was observed in the mountain peach T3 treatment, with 1,222 DEGs comprising 350 upregulated genes and 872 downregulated genes. For the peach rootstock hairy peach, the T3 treatment resulted in the largest number of DEGs compared to the CK, with a total of 11,625 DEGs including 5,448 upregulated genes and 6,117 downregulated genes. Among different rootstock cultivars subjected to the same treatment, the T3 treatment induced the largest number of DEGs, with a total of 11,646 DEGs including 5,489 upregulated genes and 6,157 downregulated genes. Among the DEGs, 256 DEGs were common to the three stress treatments (ST_CK vs ST_T1, ST_CK vs ST_T2, and ST_CK vs ST_T3) of mountain peach (Fig. 5C). For hairy peach, 1,196 DEGs were shared across its three stress treatments (MT_CK vs MT_T1, MT_CK vs MT_T2, and MT_CK vs MT_T3) (Fig. 5D). Additionally, 863 DEGs were common to the four cultivar comparison groups (MT_CK vs ST_CK, MT_T1 vs ST_T1, MT_T2 vs ST_T2, and MT_T3 vs ST_T3) under respective treatments (Fig. 5E).

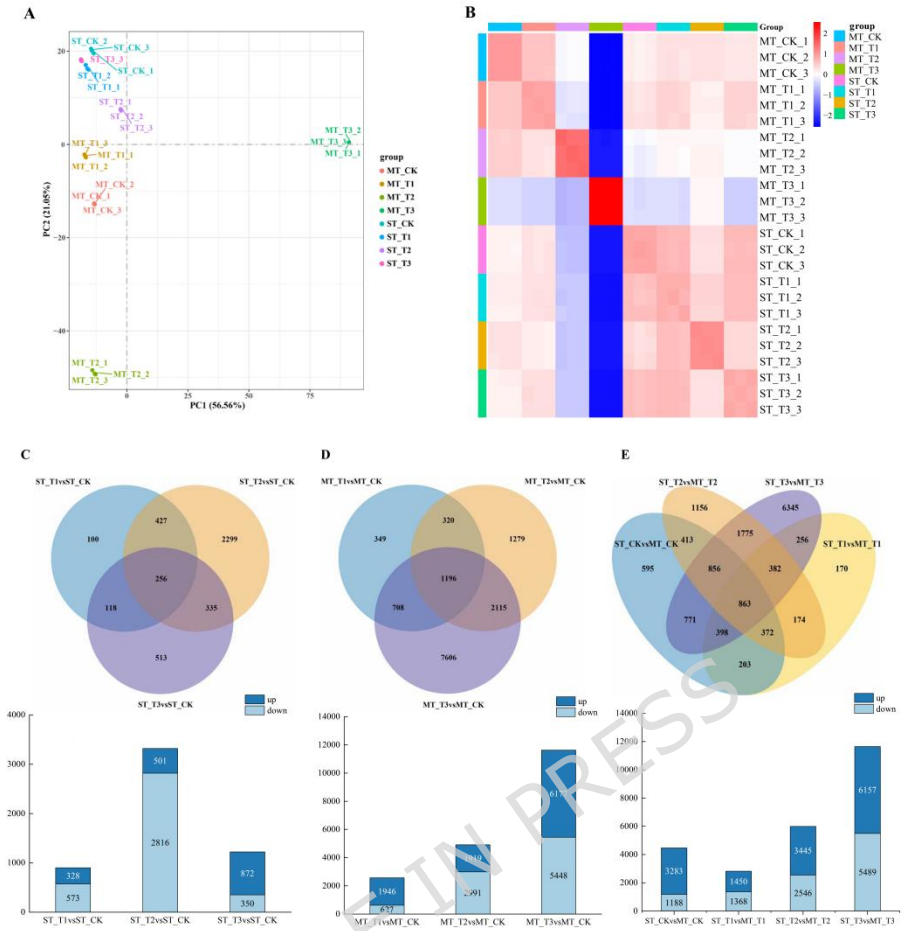

Fig. 5. Comparative analysis of DEGs between two peach rootstocks cultivars under salt stress. **(A)** Two-dimensional principal component analysis (PCA) plot of all samples. Each point represents one sample, with three replicates of the same treatment sharing the same color. The position of each point reflects its score on the first two principal components. **(B)** Pearson correlation analysis between samples. A value close to 1 indicates a strong positive correlation, close to - 1 indicates a strong negative correlation, and close to 0 indicates no linear relationship. **(C)** Venn diagram showing common and unique DEGs among ST_T1 vs ST_CK, ST_T2 vs ST_CK, and ST_T3 vs ST_CK comparisons. In the bar chart, dark blue represents upregulated genes and light blue represents downregulated genes. **(D)** Venn diagram showing common and unique DEGs among MT_T1 vs MT_CK, MT_T2 vs MT_CK, and MT_T3 vs MT_CK comparisons. In the bar chart, dark blue represents upregulated genes and light blue represents downregulated genes. **(E)** Venn diagram showing common and unique DEGs among MT_CK vs ST_CK, MT_T1 vs ST_T1, MT_T2 vs ST_T2, and MT_T3 vs ST_T3 comparisons. In the bar chart, dark blue represents upregulated genes and light blue represents downregulated genes.

GO enrichment and KEGG pathway analysis of DEGs

GO enrichment analysis of the three comparison groups in mountain peach (ST_T1 vs ST_CK, ST_T2 vs ST_CK, and ST_T3 vs ST_CK) revealed that: for cellular component (CC), the most significantly enriched terms were "integral component of membrane" and "intrinsic component of membrane". Molecular function (MF), dominant terms included

"carbon-oxygen lyase activity" and "terpene synthase activity". Biological process (BP), key enriched terms were "amine metabolic process" and "defense response". In hairy peach (MT_T1 vs MT_CK, MT_T2 vs MT_CK, and MT_T3 vs MT_CK), GO enrichment analysis showed that for CC, "integral component of membrane" and "intrinsic component of membrane" were also significantly enriched MF, the main terms were "tetrapyrrole binding" and "heme binding". BP, the most prominent terms were "response to stress" and "defense response". Furthermore, comparative GO enrichment analysis across the four inter-cultivar comparison groups (MT_CK vs ST_CK, MT_T1 vs ST_T1, MT_T2 vs ST_T2, and MT_T3 vs ST_T3)-representing the two rootstock cultivars under identical treatment conditions-revealed distinct functional patterns. CC, the primary enriched terms were "external encapsulating structure" and "cell wall". MF, key terms included "tetrapyrrole binding" and "heme binding"; and for BP, the dominant terms were "response to stress" and "defense response".

Analysis of the top 20 significantly enriched KEGG pathways for DEGs in mountain peach and hairy peach showed the following for mountain peach (ST_T1 vs ST_CK, ST_T2 vs ST_CK, and ST_T3 vs ST_CK), 150 out of 256 DEGs were enriched in 47 pathways, with alpha-Linolenic acid metabolism, Biosynthesis of secondary metabolites, and Metabolic pathways being significantly enriched. For hairy peach (comparison groups: MT_T1 vs MT_CK, MT_T2 vs MT_CK, and MT_T3 vs MT_CK), 526 out of 1,196 DEGs were enriched in 90 pathways, with Biosynthesis of secondary metabolites, Phenylpropanoid biosynthesis, and Cyanoamino acid metabolism being significantly enriched. For the four cultivar comparison groups between the two peach rootstock cultivars under the same treatment (MT_CK vs ST_CK, MT_T1 vs ST_T1, MT_T2 vs ST_T2, and MT_T3 vs ST_T3), 276 out of 863 DEGs were enriched in 76 pathways, with Biosynthesis of secondary metabolites, Sesquiterpenoid and triterpenoid biosynthesis, and Plant-pathogen interaction being significantly enriched.

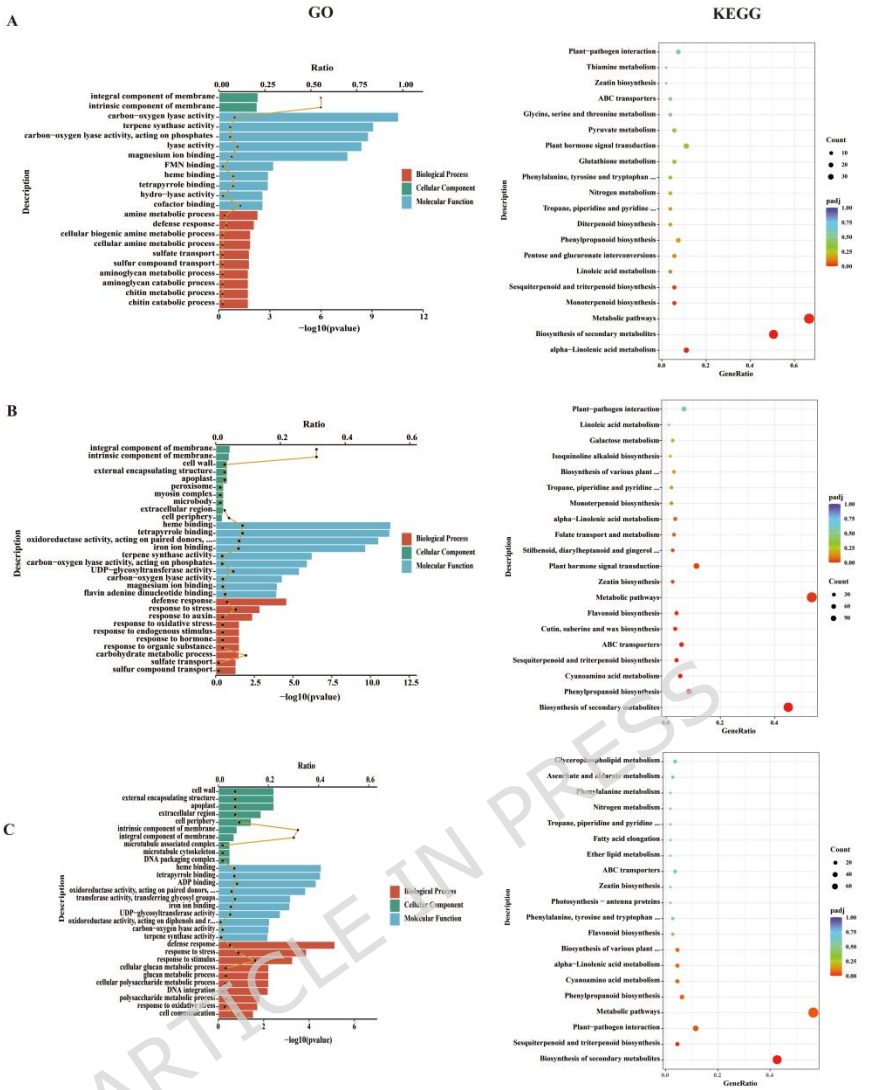

Fig. 6. GO and KEGG enrichment analysis of DEGs. GO enrichment is categorized into three functional classes: cellular component (CC), biological process (BP), and molecular function (MF). In the GO enrichment bar chart, the bar height represents the number of DEGs annotated to each term, while the line represents the -log$_{10}$ (p-value). For KEGG enrichment, the top 20 significantly enriched pathways were selected; the size of the dots indicates the number of DEGs mapped to each pathway, and the color gradient from blue to red indicates increasing significance (blue = less significant, red = more significant). **(A)** GO and KEGG enrichment of DEGs from ST_T1 vs ST_CK, ST_T2 vs ST_CK, and ST_T3 vs ST_CK comparisons. **(B)** GO and KEGG enrichment of DEGs from MT_T1 vs MT_CK, MT_T2 vs MT_CK, and MT_T3 vs MT_CK comparisons. **(C)** GO and KEGG enrichment of DEGs from MT_CK vs ST_CK, MT_T1 vs ST_T1, MT_T2 vs ST_T2, and MT_T3 vs ST_T3 comparisons.

Cultivar-specific KEGG pathways of the two peach rootstocks

KEGG enrichment analysis revealed that mountain peach and hairy peach were co-significantly enriched in the alpha-Linolenic acid metabolism and Phenylpropanoid biosynthesis pathways. In the Phenylpropanoid biosynthesis pathway, hairy peach exhibited 18 significantly downregulated genes, substantially more than the 4 in mountain peach,

Among these, *CCR2*, *PRXA21*, and *PRX44* were identified as significantly co-enriched genes (Fig. 7A). In the alpha-Linolenic acid metabolism pathway, hairy peach showed enrichment of 7 DEGs, with 1 upregulated (*OPR2*) and 6 downregulated, whereas mountain peach displayed enrichment of 6 DEGs, including one upregulated (*ADH*) and 5 downregulated genes (Fig. 7B). Mountain peach specifically enriched the Glutathione metabolism, Nitrogen metabolism, and Pyruvate metabolism pathways. Meanwhile, hairy peach was uniquely enriched in the Flavonoid biosynthesis and Cutin, suberin, and wax biosynthesis pathways (Supplementary Table S3).

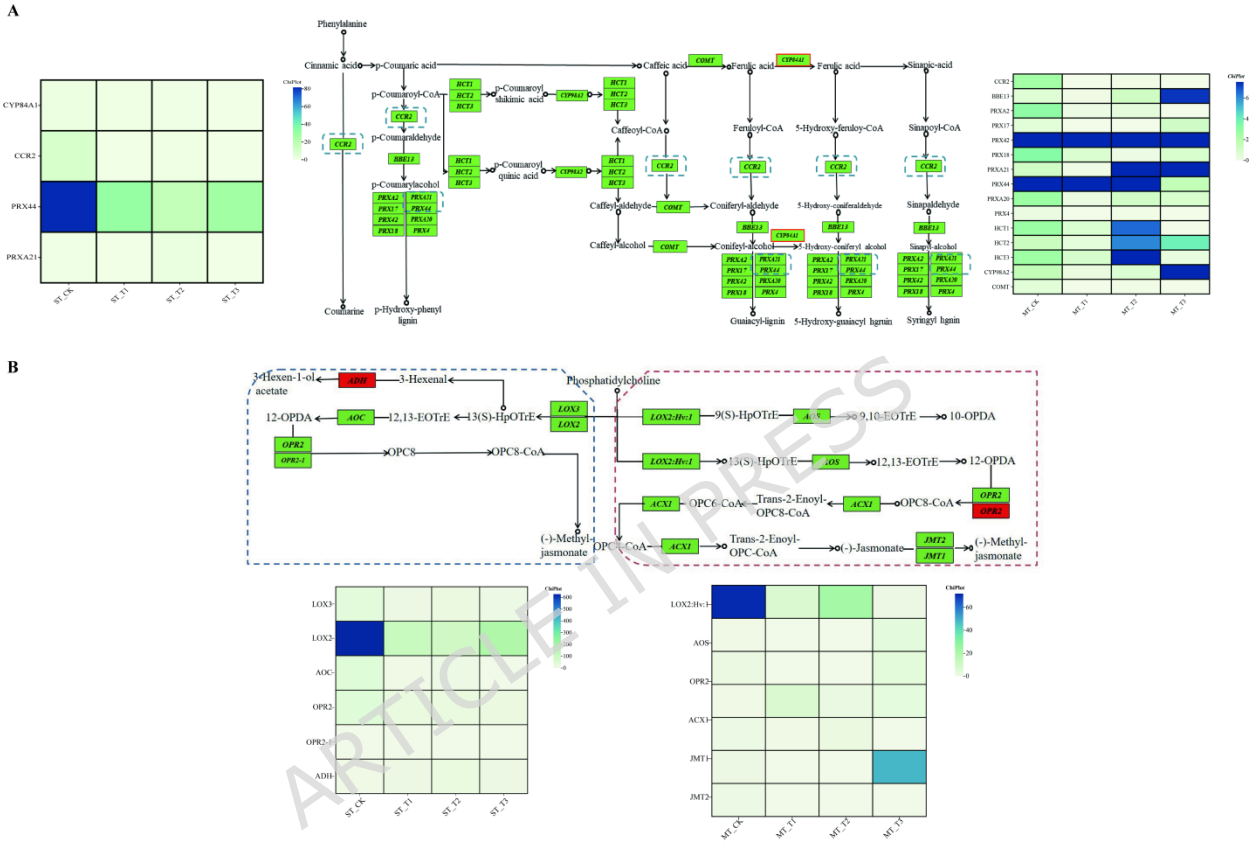

Fig. 7. KEGG pathway enrichment analysis of co-differentially expressed genes (co-DEGs) between mountain peach (MT) and hairy peach (ST). (**A**) The Phenylpropanoid biosynthesis pathway was co-enriched in the comparison groups MT_T1 vs MT_CK, MT_T2 vs MT_CK, MT_T3 vs MT_CK (hairy peach) and ST_T1 vs ST_CK, ST_T2 vs ST_CK, ST_T3 vs ST_CK (mountain peach). Green icons represent downregulated genes in mountain peach, and red boxes represent downregulated genes in hairy peach. Blue dashed boxes represent genes shared by mountain peach and hairy peach. (**B**) The alpha-Linolenic acid metabolism pathway was analyzed for the same comparison groups as in (**A**). Blue dashed boxes denote the sub-pathways enriched in mountain peach (green icons = downregulated genes; red icons = upregulated genes). Red dashed boxes denote the sub-pathways enriched in hairy peach (green icons = downregulated genes; red icons = upregulated genes).

qRT-PCR validation of DEGs

To validate the sequencing results, ten DEGs were selected based on the aforementioned pathway enrichment analysis for qRT-PCR verification. Among these, six

genes showed expression trends consistent with the transcriptome data (Fig. 8a) , confirming the accuracy and reliability of the RNA-seq results. The remaining four genes, although exhibiting qPCR expression patterns not fully consistent with the FPKM trends, still showed significant differential expression under salt stress conditions, providing additional validation from a broader perspective .

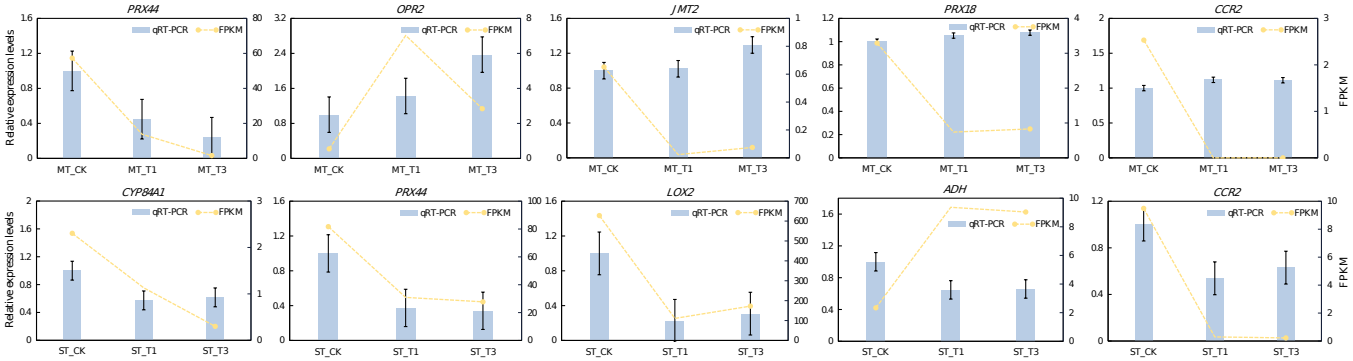

Fig. 8. qRT-PCR validation of DEGs. The abscissa in the figure denotes the CK, T1, T2, and T3 treatments applied to the mountain peach and hairy peach rootstocks varieties.

Discussion

The color change of plant leaves serves as an intuitive indicator of salt tolerance, primarily regulated by chlorophyll content. Under salt stress, a reduction in chlorophyll levels leads to leaf yellowing and wilting. When stress intensity exceeds a critical threshold, it can result in plant death[10, 11]. Aazami et al.[12] reported that the levels of chlorophyll a and b in grape leaves decline with increasing salt stress intensity. This study revealed that the leaves of both mountain peach and hairy peach under CK treatment exhibited a bright green color, with chlorophyll a content in mountain peach slightly higher than that in hairy peach, indicating a greater inherent stability of the photosynthetic system in mountain peach. In response to increasing salt concentration, a clear divergence was observed between the two rootstocks: hairy peach leaves progressively developed from marginal yellowing to extensive chlorosis, whereas mountain peach leaves exhibited only slight scorching at the tips and margins while maintaining green coloration in the main leaf area (Fig. 4). This phenotypic difference aligns with changes in chlorophyll content: the chlorophyll a/b ratio of hairy peach exhibited a decreasing trend under intensified salt stress, whereas that of mountain peach initially increased before stabilizing. These findings suggest that mountain peach mitigates salt stress through enhanced photosynthetic activity, demonstrating greater salt tolerance compared to hairy peach.

Salt stress impairs plant growth and physiological functions through multiple mechanisms, including salt ion toxicity, osmotic stress, and ionic imbalance in the rhizosphere[13]. Therefore, the capacity of plants to maintain intracellular ionic homeostasis under saline conditions is critical for mitigating salt-induced damage[14]. The present study demonstrated that, with increasing salt stress intensity, the accumulation of Na^+ and Cl^- in mountain peach was significantly lower than those in hairy peach, while the K^+/Na^+ ratio was notably higher. These findings highlight a fundamental difference in ion regulation capacity between the two rootstocks, with mountain peach exhibiting superior ability to restrict ion accumulation. This difference likely reflects a more efficient ion exclusion or compartmentalization mechanism in mountain peach, enabling it to maintain ionic balance

under salt stress. Similar findings were reported by Wu et al.[15] in hairy peach, suggesting that the capacity for selective ion uptake and compartmentalization in mountain peach likely constitutes the key physiological basis for its superior salt tolerance. The mechanism underlying such ionic balance differences may be attributed to divergent structural responses in leaves of the two rootstocks under salt stress. A higher palisade-to-spongy mesophyll ratio, along with the presence of leaf trichomes, cuticular wax, and specialized stomatal traits, is associated with enhanced adaptability to adverse environmental conditions. Wu et al.[16] demonstrated that under 6.0 $g \cdot L^{-1}$ NaCl treatment, the leaf epidermal cell layer, cuticle, and spongy mesophyll of two cherry cultivars exhibited significant thickening, whereas the palisade mesophyll showed reduced thickness. Liu et al.[17] reported that abiotic stress induced increased leaf thickness, higher stomatal density, and cuticular thickening in mountain peach. In this study, with the increase of salt concentration, the thicknesses of palisade tissue, spongy tissue and leaves of both mountain peach and hairy peach gradually increased. However, the CTR of mountain peach leaves first decreased and then increased with the enhancement of salt stress, while that of hairy peach leaves gradually decreased (Fig. 4). These distinct structural responses suggest that mountain peach adopts a more flexible and adaptive leaf architecture under salt stress, whereas hairy peach exhibits a more rigid structural response that may limit its ability to cope with increasing stress intensity. The compact mesophyll structure of mountain peach may restrict ion transport, enable efficient ion compartmentalization, and thereby enhance its salt tolerance. Collectively, the superior ion regulation capacity of mountain peach, coupled with its adaptive leaf structural modifications, provides a synergistic basis for its stronger salt tolerance compared to hairy peach.

Ionic and osmotic stresses induced by salt stress trigger metabolic disturbances and the toxic accumulation of reactive oxygen species (ROS) in plants, leading to cellular oxidative damage and thereby severely impairing normal growth and development in fruit trees[18, 19.] Plants typically induce the expression of antioxidant enzymes to scavenge ROS-induced cellular damage[20]. Studies have demonstrated that the activities of POD and SOD in melon exhibit varying degrees of elevation under salt stress of different concentrations[21]. Zong et al.[22] reported that the POD activity of Pyrus betulifolia Batal. (yellow-fruited genotype) seedlings shows an upward trend under salt stress. Our study revealed that with increasing salt stress concentration, SOD and POD activities in mountain peach initially increased and then declined, whereas those in hairy peach exhibited a progressive elevation. This contrasting pattern reflects a fundamental difference in antioxidant defense strategies between the two rootstocks: mountain peach activates its antioxidant system rapidly but downregulates it upon reaching a threshold, whereas hairy peach maintains a sustained antioxidant response throughout the stress period. NOX serves as a key component in the initiation of adaptive signaling pathways in plants; however, its uncontrolled activity can trigger oxidative damage[23, 24]. Under salt stress induction, NOX activity in mountain peach leaves progressively declined, whereas in hairy peach, NOX activity increased concomitantly with escalating stress intensity. This difference in NOX regulation further distinguishes the two rootstocks, suggesting distinct regulatory mechanisms for managing oxidative stress. These findings suggest that mountain peach responds to salt stress by rapidly activating its antioxidant system and then reducing it after reaching a threshold, thereby avoiding unnecessary energy consumption, whereas hairy peach maintains a continuously elevated antioxidant response throughout the stress

period. Taken together, the data demonstrate that mountain peach possesses stronger salt tolerance than hairy peach, which can be attributed to its more efficient and balanced antioxidant defense system.

Transcriptome analysis further elucidated the molecular mechanisms underlying salt tolerance divergence among peach rootstock cultivars. In this study, transcriptomic profiling identified distinct metabolic pathways in mountain peach and hairy peach under salt stress, with phenylalanine metabolism and α-linolenic acid metabolism emerging as shared core pathways. However, within these shared pathways, the two rootstocks exhibited markedly different expression patterns. Notably, phenylalanine metabolism functions as a central hub of plant secondary metabolism, giving rise to downstream products such as lignin and phenolic compounds that play critical roles in cell wall fortification, stress resistance responses, and flavor compound biosynthesis25, 26. Within the phenylpropanoid biosynthesis pathway, hairy peach harbored 18 downregulated genes, whereas mountain peach contained only 4 downregulated genes. This substantial difference suggests that the phenylpropanoid pathway is more severely suppressed in hairy peach under salt stress. The co-downregulated genes CCR2, PRXA21, and PRX44 suggest that lignin polymerization and peroxidase-mediated cell wall remodeling play critical roles in the salt stress response27. α-Linolenic acid is a key unsaturated fatty acid in plants, which is involved in the transduction of stress resistance signals and the establishment of antioxidant defense systems28, 29. In this study, 6 and 7 DEGs were identified to be enriched in the α-linolenic acid metabolic pathway in mountain peach and hairy peach, respectively. Notably, the ADH gene in mountain peach and OPR2 gene in hairy peach were both upregulated (Fig. 6). These findings suggest that mountain peach and hairy peach both activate the jasmonic acid (JA) signaling pathway under salt stress, though they may utilize different downstream components to achieve stress tolerance30, 31. Furthermore, the enrichment of mountain peach-specific pathways-glutathione metabolism, nitrogen metabolism, and pyruvate metabolism-constitutes a coordinated network that integrates antioxidant defense, nitrogen assimilation, and energy supply32. By contrast, the enrichment of hairy peach-specific pathways-including flavonoid biosynthesis, cutin/suberin/wax biosynthesis, and plant-pathogen interaction-reveals a defense strategy that relies on physical barrier reinforcement, secondary metabolite accumulation, and stress signal transduction. Taken together, mountain peach relies more on active metabolic adjustments (antioxidant defense and energy metabolism) to mitigate salt stress, whereas hairy peach depends more on structural reinforcement and secondary metabolite accumulation. This fundamental divergence in pathway enrichment patterns explains the intrinsic molecular mechanism underlying the stronger salt tolerance of mountain peach relative to hairy peach.

To summarize, under salt stress, mountain peach maintains a high K^+/Na^+ ratio and chlorophyll a/b ratio, while its antioxidant enzyme activity first increases and then decreases, reflecting an efficient and balanced stress response. In contrast, hairy peach shows continuously elevated antioxidant enzyme activity and a decreasing chlorophyll a/b ratio, indicating a less efficient response. In addition, mountain peach has more compact leaf structure and specifically activates the glutathione metabolic pathway, which helps maintain leaf function under stress. Hairy peach, on the other hand, appears to depend more on structural reinforcement and the accumulation of secondary metabolites. These combined differences explain why mountain peach has stronger salt tolerance than hairy

peach (Fig. 9). Future studies should focus on validating the molecular functions of salt stress-responsive DEGs and reconstructing their regulatory and protein-protein interaction networks.

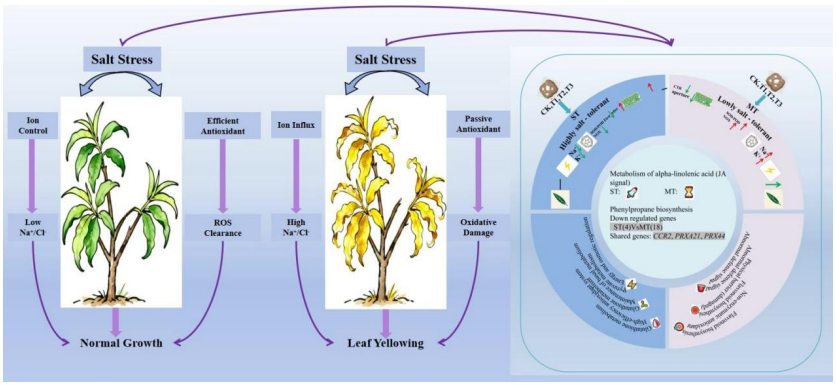

Fig. 9. Mechanisms underlying salt stress adaptation in mountain peach and hairy peach

Conclusions

This study elucidates how two peach rootstock genotypes achieve efficient adaptation to salt stress through multi-layered coordinated regulatory mechanisms. At the physiological level, mountain peach rootstock maintain growth and suppress chlorosis under salinity by implementing a coordinated strategy characterized by enhanced ion homeostasis regulation and an inducible antioxidant defense system. At the molecular level, mountain peach precisely regulates the phenylpropanoid metabolic pathway and concurrently activates key metabolic routes such as glutathione and nitrogen metabolism, thereby constructing a robust and integrated defense network. Collectively, these findings reveal the mechanistic basis of the superior salt tolerance in mountain peach from both physiological and molecular perspectives, offering substantial theoretical support for the development of salt-tolerant peach cultivars.

Materials and methods

Plant materials

The experiment was conducted in a multi-span greenhouse for seedling propagation at the Gansu Academy of Agricultural Sciences. One-year-old grafted seedlings using mountain peach and hairy peach as rootstocks with ‘Longmi 9’ as scions were transplanted into 20 cm × 20 cm plastic pots filled with a mixed substrate in August 2024. The substrate consisted of perlite, vermiculite, and peat in a 1:1:1 volume ratio, with each pot containing 4 kg of the mixture. Salt stress treatments at varying levels were initiated when the seedlings reached a height of approximately 40 cm.

The mountain peach (*Prunus davidiana* (Carr.) Franch.) and hairy peach (*Prunus persica* (L.) Batsch var. davidiana) used in this study were obtained from the germplasm repository of the Institute of Forestry, Fruits and Floriculture, Gansu Academy of Agricultural Sciences. These two rootstocks are commonly used in Northwest China. These two materials were selected as rootstocks for grafting with the self-bred cultivar ‘Longmi 9’, developed by the same institute. Under saline-alkali soil conditions, the leaves of ‘Longmi 9’ grafted onto mountain peach rootstock appeared normal (left), whereas those grafted onto hairy peach rootstock exhibited chlorosis (right) (Fig. S1). Mountain peach exhibits drought

resistance, cold hardiness, and tolerance to saline-alkali soils, whereas hairy peach is heliophilous and performs poorly under alkaline or heavy clay soil conditions. Prior to large-scale propagation, a tissue culture-based micropropagation system was established based on field-observed phenotypes of salt-alkali tolerance and sensitivity, enabling the production of clonal tissue-cultured plantlets for both species. These plantlets were acclimatized through batch transplantation, and all experimental materials were uniformly cultivated and managed under controlled environmental conditions in the institute's tissue culture facility and greenhouse. The environmental parameters during the treatment period were as follows: daytime temperature ranged from 21 °C to 25 °C, nighttime temperature ranged from 15 °C to 18 °C, and relative humidity was maintained at 60% ± 5%.

Experimental design

A randomized complete block design (RCBD) was employed. NaCl solutions with concentrations of 0.075% (CK, control), 0.15%, 0.3%, and 0.6%. The 0.075% concentration was designated as the control based on field observations: in Northwest China, where typical soil pH is 8.2, the corresponding salt concentration averages approximately 0.075%. Rootstock type (mountain peach or hairy peach) served as a grouping factor, and each concentration was applied to grafted seedlings on both rootstocks, resulting in eight treatment combinations. Mountain peach treatments included the control (ST_CK), 0.15% NaCl (ST_T1), 0.3% NaCl (ST_T2), and 0.6% NaCl (ST_T3). hairy peach treatments included the control (MT_CK), 0.15% NaCl (MT_T1), 0.3% NaCl (MT_T2), and 0.6% NaCl (MT_T3). Each treatment was assigned to 10 pots of plants, and the experiment was replicated three times. The treatment cycle lasted 25 days, with applications administered every 5 days. Specifically, 320 mL of NaCl solution at designated concentrations was applied to each pot at 6:00 p.m. on each treatment day. In the later stages, all leachate collected in the trays was returned to the substrate the day after each treatment. After 25 days of treatment, the second to fourth fully expanded mature leaves from new shoots were collected. One portion was used for measuring leaf chlorophyll content, osmotic ion concentration, antioxidant enzyme activity, and stress resistance-related physiological indices. Another portion was subjected to morphological trait monitoring and resin embedding for sectioning. The remaining samples were immediately flash-frozen in liquid nitrogen and stored at -80°C for subsequent transcriptomic analysis.

Physiological index measurement

Leaf soluble sugar and chlorophyll contents were quantified by ethanol extraction. Fresh leaf tissue was homogenized and extracted with 95% ethanol. Sugar content was measured by the anthrone method, while chlorophyll content was determined spectrophotometrically[33]. Potassium (K^+) and sodium (Na^+) contents were quantified by flame atomic absorption spectrometry, while chloride (Cl^-) content was measured via silver nitrate titration[34].

Paraffin sectioning and scanning electron microscopy

For each variety and treatment group, five leaves were randomly sampled and excised into 5 mm × 5 mm tissue segments. The segments were immediately fixed in (Formalin-Aceto-Alcohol) FAA fixative solution and maintained under low - temperature conditions, then submitted to Seville Biotechnology Co., Ltd (Wuhai). for paraffin section preparation.

Leaf thickness, palisade tissue thickness, and spongy tissue thickness were quantified using CaseViewer 4.0 software, with reference to the leaf anatomical structure maps generated from the sections.

Leaf cell structural compactness ratio (CTR) = Palisade tissue thickness / Leaf thickness

Leaf cell structural looseness ratio (SR) = Spongy tissue thickness / Leaf thickness

For each variety and treatment, five leaves were randomly selected and excised into 5 mm × 5 mm tissue segments. These samples were immediately fixed in glutaraldehyde fixative and maintained under low-temperature conditions before being submitted to Seville Biotechnology Co., Ltd (Wuhai). for scanning electron microscopy (SEM) analysis. Stomatal aperture was quantified using ImageJ 2.0 software based on the obtained micrographs.

RNA extraction and detection

RNA-seq was performed on leaves from mountain peach and hairy peach rootstock varieties with three biological replicates per treatment group through collaboration with Jizhi (Tianjin) Biotechnology Co., Ltd. Total RNA was isolated using a standardized protocol, and RNA integrity was rigorously assessed using the Agilent 2100 Bioanalyzer to ensure high-quality input material for downstream analysis.

Library construction and sequencing

Following library construction, initial quantification was performed using a Qubit 2.0 Fluorometer, and the library was diluted to a final concentration of 1.5 $ng \cdot \mu L^{-1}$. The insert size of the library was assessed via the Agilent 2100 Bioanalyzer. Upon confirmation that the insert size met the expected range, the effective concentration of the library was accurately quantified using qRT-PCR, with the requirement that the effective concentration exceed 2 $nmol \cdot L^{-1}$ to ensure library quality.

Data quality control and sequence alignment

The raw sequencing reads contained adapter sequences and low-quality reads. Thus, quality control was performed using Fastp with default parameters, and only reads passing the filtering criteria were retained for subsequent analyses. The filtering rules were defined as follows:

(1) Trimming of adapter sequences from reads;

(2) Exclusion of paired-end reads if a single-end read contained more than 5 ambiguous (N) bases;

(3) Exclusion of paired-end reads if the proportion of low-quality bases (Phred quality score $Q \leq 15$) in a single-end read exceeded 40% of the total read length.

DEGs expression and functional enrichment analysis

Reads with alignment quality scores < 10, unpaired alignments, and those mapping to multiple genomic regions were filtered out using feature Counts[35]. Fragments per kilobase of transcript per million mapped fragments (FPKM) values were then calculated. Raw read counts were normalized to account for differences in sequencing depth. P-values were computed via statistical hypothesis testing, followed by multiple hypothesis testing correction to derive false discovery rate (FDR) values. Functional enrichment analyses for GO and KEGG pathways were performed on the DEGs set using clusterProfiler[36].

qRT-PCR validation of DEGs

Six DEGs were selected from the two KEGG pathways co-enriched in mountain peach and hairy peach under CK, T1, and T3 treatments for qRT-PCR validation.

The qRT-PCR assays were performed using kits from Yeasen Biotechnology Co., Ltd. (Shanghai, China). First-strand cDNA synthesis was carried out with the Hifair® Ⅲ 1st Strand cDNA Synthesis SuperMix for qPCR (gDNA digester plus) (Cat. No. 11141ES60). Quantitative fluorescence detection utilized the Hieff® qPCR SYBR Green Master Mix (Low Rox Plus). Gene-specific primers for the six target genes and the Actin reference gene were designed using the PrimerQuest tool (http://sg.idtdna.com/Primerquest/Home/Index) (Supplementary Table S4).

The 20 μL reaction mixture contained 8 μL of ddH_2O, 1.2 μL of cDNA template, 0.4 μL each of forward and reverse primers, and 10 μL of SYBR Green Master Mix. Thermal cycling conditions were as follows: initial denaturation at 95 °C for 5 min; followed by 40 cycles of denaturation at 95 ℃ sidu for 10 s and extension at 60 ℃ for 30 s. Relative gene expression levels were calculated using the $2^{-\Delta\Delta CT}$ method[37]. The *Actin* gene was selected as the internal reference for qRT-PCR because it showed stable expression levels in our preliminary experiments and is widely used as a housekeeping gene in gene expression studies of Prunus species under stress conditions[38].

Statistical and bioinformatic data analysis

Data collation and statistical summarization were performed using Excel 2010, subsequent data analysis was conducted with SPSS 23.0 software, Duncan's multiple range test was applied for significance assessment Different lowercase letters indicate significant differences ($P < 0.05$), while identical lowercase letters indicate no statistically significant differences, and data visualization was implemented using Origin 2021.

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Author contributions

F.Z.: Conceptualization, Methodology, Investigation, Data curation, Formal analysis, Writing-original draft. J.R: Conceptualization, Validation, Software, Writing-review & editing. C.W.: Methodology, Software, Validation, Writing-review & editing. H.C.: Formal analysis, Statistical analysis, Writing-review & editing. Y.L.: Supervision, Writing-review & editing. All authors listed have made direct, considerable, and intellectual contributions to the research. All authors have read and approved the final manuscript.

Data availability

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request. The datasets supporting the conclusions of this article are available in the NCBI Sequence Read Archive (SRA) under the accession number PRJNA1379919.

Declarations

Competing interests

The authors declare no competing interests.

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Additional information

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Ethics approval and consent to participate

This study did not involve any human tissue materials or animal tissue materials. It did not require ethical approval. The plant materials used in this study—including mountain peach (*Prunus davidiana* (Carr.) Franch.), hairy peach (*Prunus persica* (L.) Batsch var. davidiana), and the scion cultivar ‘Longmi 9’—were obtained from the germplasm repository of the Institute of Forestry, Fruits and Floriculture, Gansu Academy of Agricultural Sciences. We confirm that the use of these materials complies with relevant institutional, national, and international guidelines and legislation. Neither of the rootstock species is listed under the IUCN Red List or CITES appendices, and no specific collection permits were required because all materials were sourced from the institute’s established germplasm collection. Voucher specimens, if required, are retained at the same institute.