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The UDP-dependent glycosyltransferase *MdUGT88F4* of apple (*Malus domestica*) functions in drought tolerance by promoting the accumulation of isosalipurposide and amino acids

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Abstract

Members of the UDP-dependent glycosyltransferase (UGT) family play critical roles in plant stress responses. *MdUGT88F4*, a key UDP-glucose: phloretin 2'-O-glucosyltransferase gene in *Malus* spp., was previously identified to catalyze the biosynthesis of the dihydrochalcone compound isosalipurposide, but its role in abiotic stress tolerance remains unexplored. In this study *MdUGT88F4* expression was found to be upregulated by drought stress. Overexpression of *MdUGT88F4* alleviated drought-induced growth inhibition of transgenic apple plants. Under drought conditions, transgenic lines overexpressing *MdUGT88F4* (OX) exhibited reduced leaf wilting, along with significantly lower relative electrolyte leakage and malondialdehyde content compared to wild type (WT). Conversely, OX plants showed higher relative water content and total chlorophyll levels. Notably, OX plants displayed enhanced photosynthetic capacity and reduced reactive oxygen species (ROS) accumulation under drought conditions. Drought stress induced isosalipurposide accumulation in apple plants, with OX plants showing significantly higher levels than WT. Furthermore, most amino acids and their derivatives were detected at higher concentrations in the OX plants, which also exhibited enhanced accumulation of amino acids under drought conditions, implying presence of a more robust metabolic adjustment. RNA-seq analysis revealed that differences in metabolic processes, particularly amino acid metabolism, contributed to the enhanced drought tolerance in the OX plants. Collectively, these findings indicate that *MdUGT88F4* positively modulates drought tolerance in apple by promoting isosalipurposide synthesis and coordinating amino acid metabolism.

Keywords Apple, Drought stress, UDP-dependent glycosyltransferase gene, Metabolite accumulation

Introduction

The escalating greenhouse effect driven by climate change has imposed multifaceted abiotic stresses on

vegetation, including drought, extreme temperatures (both low and high), and other environmental pressures (Cavagnaro et al. 2016). Drought, as one of the most significant limitations to agricultural productivity, disrupts a plant's water balance, reduces its ability to efficiently utilize water, and ultimately alters growth patterns and biochemical pathways (Asrar and Elhindi 2011; Hussain et al. 2009). These effects compromise plant development, decrease agricultural yield, and, in severe cases, lead to widespread plant mortality (Sharma et al. 2020). Nearly 30% of the world's arable land is now too arid to

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support normal plant growth and productivity (Golldack et al. 2014). To withstand prolonged drought, plants have developed complex adaptive mechanisms. For example, they reduce water loss by closing stomata, a process that also limits CO₂ uptake—a crucial survival trade-off (Li et al. 2022a, b; Pilon et al. 2018; Farooq et al. 2009). On the molecular level, drought triggers widespread transcriptional reprogramming, activating stress-responsive genes to enhance drought tolerance, while post-translational modifications refine cellular drought responses (Zhang et al. 2022; Zong et al. 2019; Fu et al. 2018). Drought stress also leads to significant changes in secondary metabolites and phytohormones. Key compounds such as polyphenols, flavonoids, cinnamic acid, amino acids, and heterocyclic organic molecules accumulate dynamically under water-deficient conditions (Khan et al. 2019; Ackah et al. 2021).

UDP-glycosyltransferases (UGTs) represent a major gene family in higher plants. The first comprehensive identification of *UGT* genes was conducted in *Arabidopsis thaliana*, where Li et al. (2001) characterized 119 members, grouping them into 14 distinct phylogenetic families. Later, Zhou et al. (2017) identified 237 UGTs in the apple genome, further classified into 16 evolutionary clades based on phylogenetic analysis. Functionally, plant UGTs catalyze the final glycosylation step in the biosynthesis of various secondary metabolites (Caputi et al. 2012). For example, *UGT74F2* catalyzes the glycosylation of anthranilic acid and salicylic acid in *A. thaliana* (Dean and Delaney 2008; Quiel and Bender 2003), and *UGT72L1* is crucial for epicatechin 3'-O-glycosylation in the alfalfa seed coat, a key step in proanthocyanidin production (Pang et al. 2008). Moreover, *MdUGT88F1* has been linked to phenylpropanoid accumulation in apples, acting as a phloretin 2'-O-glucosyltransferase (Zhou et al. 2019).

UGTs play a pivotal role in regulating diverse metabolic pathways that govern plant growth and development while enhancing resistance to biotic and abiotic stressors. A prominent example is *Arabidopsis AtUGT76B1*, which binds isoleucine and strengthens plant immunity against pathogenic infections (Veronica et al. 2011). Similarly, *AtUGT74E2* catalyzes the glycosylation of indole-3-butyric acid (IBA), contributing to plant adaptation to drought conditions (Tognetti et al. 2010). Genome-wide studies on apple *UGT* genes have identified *MdUGT83L3* as a stress-responsive gene. Transgenic apple calli and regenerated plants overexpressing *MdUGT83L3* exhibit enhanced stress tolerance, a process regulated by *MdMYB88* (Li et al. 2022a, b). In another study, a novel glycosyltransferase (GT), *MdUGT83K2*, was found to aid in plant detoxification by glycosylating and inactivating herbicides (Li et al. 2023). The *MsUGT* gene displays distinct regulatory

roles under drought stress and ABA treatment, with *MsUGT003* and *MsUGT024* specifically enhancing drought resistance (Ao et al. 2022). Additionally, salt stress upregulates *PhUGTSI* expression, and its overexpression significantly improves salinity tolerance in *Petunia hybrida* (Dong et al. 2022). *UGT86A1* confers drought tolerance through multiple mechanisms: (1) increasing osmoprotectant levels (e.g. soluble sugars), (2) enhancing oxidative stress mitigation via improved reactive oxygen species (ROS) scavenging, and (3) upregulating key stress-responsive genes, thus minimizing cellular damage (Ma et al. 2025). Parallel research on *AhUGT75A* demonstrated that overexpression in *Arabidopsis* significantly reduced oxidative stress markers (MDA and superoxide), improving drought adaptation (Ouyang et al. 2023). Further studies revealed that *UGT71B6*, along with its homologs *UGT71B7* and *UGT71B8*, is crucial for ABA homeostasis in *Arabidopsis*, promoting tolerance to drought, osmotic stress, and high salinity (Dong et al. 2014).

Apple (*Malus domestica*) is an economically significant fruit crop worldwide. Previous research characterized *MdUGT88F4*, a GT gene in the apple genome, encoding an enzyme responsible for synthesizing isosalipurposide rather than phloretin (Zhou et al. 2019; Ye et al. 2024). Isosalipurposide possesses potent anti-inflammatory and analgesic properties and has been shown to protect against HCl/EtOH-induced gastric ulcers (Ghribi et al. 2021). To explore the role of isosalipurposide in drought stress responses, functional analyses were performed on *MdUGT88F4*-overexpressing apple plants under water-deficient conditions. Our findings indicated that overexpression of *MdUGT88F4* significantly improved drought tolerance in transgenic plants. This increased resilience was associated with reduced ROS accumulation and enhanced osmotic adjustment. Elevated phenolic acid levels likely contributed to ROS scavenging, while increased amino acid accumulation may have facilitated osmotic regulation during drought stress. These results provide valuable insights into harnessing plant UGTs to modulate key metabolic pathways involved in drought adaptation. Furthermore, the transgenic apple plants represent a potential source for large-scale isosalipurposide extraction, with promising applications in pharmaceutical development.

Materials and Methods

Plant materials and treatments

The GL-3 plant tissue cultures and transgenic lines used in this study were derived from previous experiments conducted in our laboratory (Dai et al. 2013; Ye et al. 2024).

After 35 days in the rooting medium, GL-3 plants were transferred to small pots (8×8×7 cm) containing a vermiculite-loam-perlite mixture (1:3:1, *v/v/v*) and acclimatized in an artificial growth chamber. For dehydration stress assays, detached leaves were placed in dry petri dishes and weighed at 10-min intervals for 50 min (0, 10, 20, 30, 40, and 50 min). Phenotypic images were captured at three time points: pre-treatment, 30 min, and 60 min post-dehydration. For drought stress experiments, plants were initially grown in a controlled-environment growth chamber for 45 days before being transplanted into outdoor pots (5 kg of soil per pot) for acclimation. After a two-week adjustment period, the plants were moved to a greenhouse for further treatment. Two months of greenhouse cultivation resulted in plants reaching an average height of 85–95 cm. Healthy plants of overexpression lines (OX2, OX4), and wild type (WT) with comparable growth vigor were randomly divided into drought treatment and control groups with (45 plants in each group). Prior to drought treatment, all plants were fully irrigated. The drought treatment group was then subjected to drought stress by withholding water for nine days, while the control group was applied with normal irrigation. Greenhouse conditions were maintained at 25°C with 70% relative humidity.

RNA extraction and qRT-PCR analysis

RNA extraction and qRT-PCR analysis followed the method described by Ye et al. (2024). Total RNA was isolated from the samples with a Wolact Plant RNA Isolation Kit (Wolact, Hong Kong, China). First-strand cDNA was then reverse-transcribed from 1 µg of total RNA using the RevertAid First Strand cDNA Synthesis Kit (Thermo Scientific, Waltham, MA, USA). Quantitative real-time PCR (qRT-PCR) was subsequently carried out with SYBR Green qPCR kits (Takara, Tokyo, Japan) on an iQ5 Multicolor Detection System (Bio-Rad Laboratories, Hercules, USA).

Physiological measurements

Leaf relative electrolyte leakage (REL) and chlorophyll concentrations were determined according to the protocol outlined by Ye et al. (2022). Relative water content (RWC) was assessed using established protocols (Huo et al. 2020; Shao et al. 2019). Enzymatic activities of superoxide dismutase (SOD) and peroxidase (POD), along with concentrations of malondialdehyde (MDA), superoxide radicals (OFR), and hydrogen peroxide (H₂O₂), were measured using commercial kits (Suzhou, China). Histochemical staining with nitro blue tetrazolium (NBT) and 3,3'-diaminobenzidine (DAB) was conducted to visualize O₂⁻ and H₂O₂ accumulation, respectively, in leaves.

Evaluation of photosynthetic characteristics

Leaf gas exchange parameters, including net photosynthetic rate (P_n), transpiration rate (Tr), and stomatal conductance (G_s)—were measured between 9:00 and 11:00 AM with a CIRAS-3 portable photosynthesis system (CIRAS, Amesbury, MA, USA). For each treatment group, 4–5 uniformly growing plants were randomly selected, and measurements were taken on mature leaves from a consistent position. Chlorophyll fluorescence parameters were assessed using a Dual-PAM-100 fluorometer (Heinz Walz, Germany). The maximum quantum yield of PSII (*F_v/F_m*) was determined after 20 min of dark adaptation. At the experimental endpoint, leaves of uniform expansion from a standardized node were sampled, sectioned into small pieces, and processed according to the protocol of Huo et al. (2020). Stomatal morphology was examined using a JSM-6360LV scanning electron microscope (SEM) (JEOL, Japan).

Measurements of amino acids and phenolic acids

The amino acid and phenolic acid profiles of both WT and OX plants were quantified *via* UPLC-MS, following the methodology outlined by Ye et al. (2024). The resulting supernatant was passed through a 0.22 µm membrane filter, and a 50 µL aliquot was diluted with 950 µL methanol in an amber vial prior to LC-MS analysis. Metabolite separation was achieved using an Inertsil ODS-4 C18 column on a SCIEX QTRAP5500 system (AB SCIEX, the United States).

Measurements of isosalipurposide

Isosalipurposide was extracted following the protocol established by Zhou et al. (2017). The extraction process involved sequential shaking at 30°C—first at 1,000 rpm for 30 min, followed by 10 min at 12,000 rpm. This procedure was repeated in triplicate, and the resulting extracts were pooled. The stock solution was filtered through an organic membrane and diluted to a final concentration of 0.22 µmol before being transferred to an HPLC vial. Dihydrochalcone detection was performed using an Agilent 1200 HPLC system (Agilent Technologies, Palo Alto, CA, USA). Isocratic elution was carried out with a mobile phase consisting of methanol and 0.3% trifluoroacetic acid in water (1:1, *v/v*). Quantification of isosalipurposide and phenolic acids was achieved by comparing retention times and peak areas against standards.

RNA-Seq analyses

Following drought treatment, leaf samples were collected and subjected to transcriptomic analysis by Beijing Tsingke Biotech Co., Ltd. Raw sequencing data were aligned to the apple genome (GDDH13_v1.1_GDR) using HISAT2 (Hierarchical Indexing for Spliced

Alignment of Transcripts), followed by transcriptome assembly and quantification with StringTie (v2.1.3b). Differentially expressed genes (DEGs) were identified using DESeq2, with statistical significance defined as adjusted $P < 0.05$ and $\log_2FC \geq 1$, corresponding to a two-fold expression difference.

Statistical analysis

All data are presented as mean $\pm$ standard deviation (SD). Statistical significance was evaluated using one-way ANOVA (SPSS 23.0), with post-hoc Duncan's multiple range test to identify significant differences ($P < 0.05$) between WT and OX plants under different treatments.

Results

Overexpression of *MdUGT88F4* leads to enhanced dehydration tolerance in apple plants

qPCR was performed to assess the responsiveness of *MdUGT88F4* to drought stress. The analysis revealed that drought treatment significantly upregulated

MdUGT88F4 expression, with the highest expression observed on the 6th day (Fig. 1a). Next, two transgenic apple lines (OX2/OX4) previously developed were used for leaf dehydration experiments. During the entire dehydration process, WT exhibited significantly greater water loss compared to transgenic OX plants, with notable differences emerging as early as 30 min post-dehydration initiation (Fig. 1b). Upon completion of dehydration, WT leaves displayed more pronounced wilting compared to OX leaves (Fig. 1c).

The dynamic modulation of stomatal aperture are crucial for regulating osmotic homeostasis and facilitating carbon fixation. Stomatal movement was observed under dehydration using Tungsten filament SEM. Under control conditions, there was no significant difference in stomatal morphology between OX and WT plants (Fig. 2a). However, leaf water loss led to changes in stomatal morphology, causing a reduction in stomatal aperture. WT plants exhibited larger stomatal apertures compared to OX plants (Fig. 2b). Overexpression of *MdUGT88F4* resulted in greater stomatal closure during leaf dehydration,

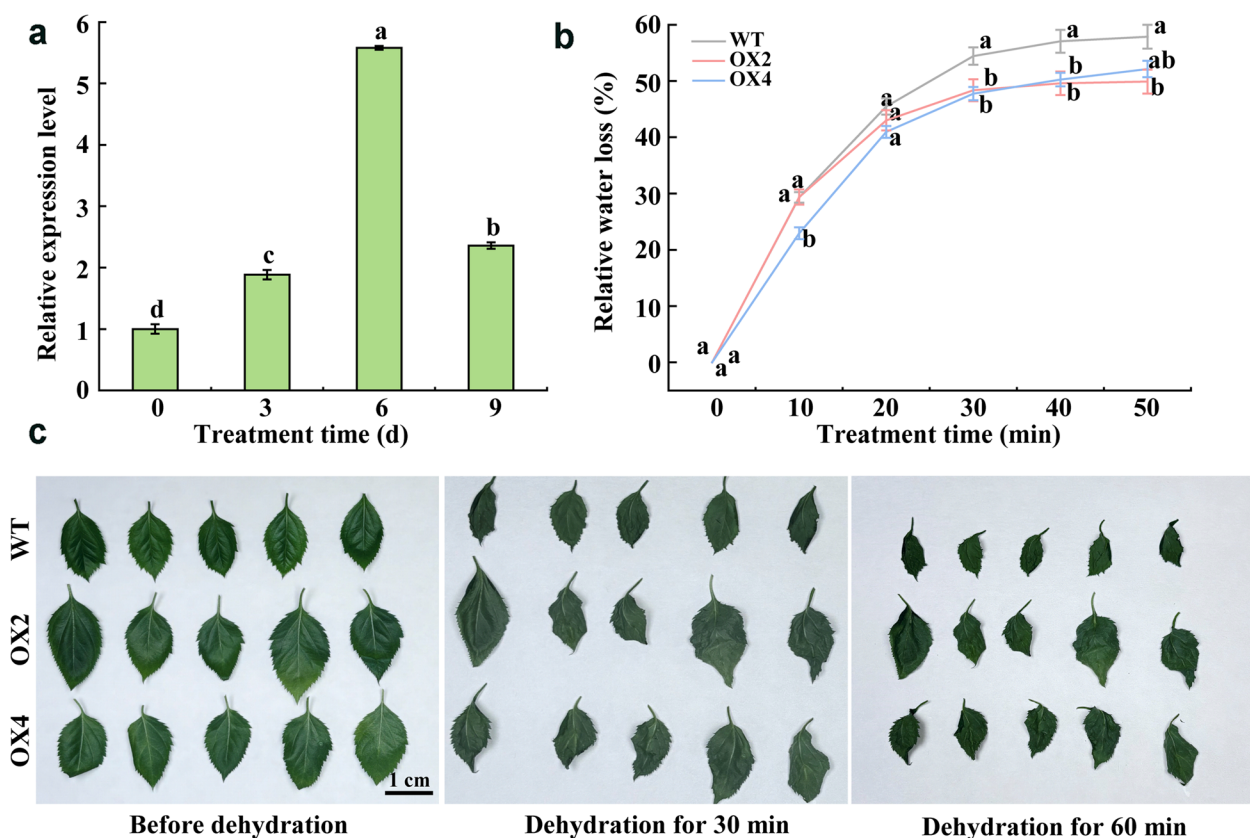


Fig. 1 *MdUGT88F4* overexpression enhances dehydration tolerance in apple plants. **a** Differential expression of *MdUGT88F4* under drought stress in apple (*Malus domestica*). **b** Comparison of water loss rates between transgenic lines overexpressing *MdUGT88F4* (OX) and wild type (WT) during 50-min dehydration. **c** Phenotypic comparison of OX and WT leaves before and after 60-min dehydration. Data are presented as mean $\pm$ SE ($n \geq 3$). Letters denote statistically distinct groups ($P < 0.05$). OX2/OX4, two transgenic apple lines overexpressing *MdUGT88F4*

leading to reduced water loss under drought stress in OX plants compared to WT plants.

Overexpression of *MdUGT88F4* confers enhanced drought tolerance in apple plants

Both WT and OX plants underwent a 9-day drought treatment. Under control conditions, there were no notable phenotypic differences between the two groups. Following drought stress, however, OX plants displayed significantly less leaf wilting compared to WT plants (Fig. 3a). Under normal conditions, REL, RWC, and MDA content of WT and OX plants did not differ significantly. However, after drought treatment, OX plants exhibited significantly lower REL and MDA levels, and significantly higher RWC compared to WT plants (Fig. 3b–d). Additionally, after drought treatment, OX plants had significantly higher levels of chlorophyll a, chlorophyll b, and total chlorophyll compared to WT plants (Fig. 3e–g).

Drought stress significantly reduced photosynthetic efficiency in all plants. Under control conditions, no significant differences in Pn, Gs, or Tr were observed between WT and OX plants. As drought treatment progressed, Pn, Gs, and Tr gradually declined in all plants. Notably, on day 3 of drought exposure, the Gs and Tr values of OX plants remained significantly higher than those of WT plants, although this difference diminished by the end of the treatment period. Moreover, under drought conditions, Pn remained significantly higher in OX plants compared to WT plants (Fig. 4a–c). Under control conditions, no significant differences in Fv/Fm were found between the two groups. However, after drought treatment, OX plants showed a significantly higher Fv/Fm value than WT plants (Fig. 4d). These results suggest that

MdUGT88F4 overexpression in transgenic plants reduces photosystem damage under drought stress, implying a protective role for *MdUGT88F4* in maintaining photosynthetic efficiency.

In summary, these findings demonstrate that overexpression of *MdUGT88F4* enhances drought tolerance in transgenic apple plants.

MdUGT88F4 affected the ROS scavenging in apple plants under drought stress

NBT and DAB staining of both WT and OX leaves under normal and drought conditions revealed a significant increase in the intensity of blue and brown spots following drought treatment. Notably, the number of blue and brown spots was considerably lower on OX leaves compared to WT leaves (Fig. 5a). Under control conditions, H₂O₂ and OFR levels showed no notable differences between WT and OX plants. However, drought treatment led to a marked increase in H₂O₂ and OFR levels across all strains, with OX plants showing significantly lower levels than WT plants (Fig. 5b–c). POD and SOD are critical enzymes involved in mitigating ROS accumulation during stress responses (Zhou et al. 2021; Zhang et al. 2022). Under drought stress, POD and SOD activities were elevated in all plant types compared to control conditions, with OX lines exhibiting significantly higher activities than WT plants (Fig. 5d–e).

Previous research has demonstrated a direct relationship between phenolic accumulation and enhanced antioxidant activity (Chisté et al. 2012; Surjadinata et al. 2021). To assess the phenolic acid content in both WT and OX2 plants, UPLC-MS-based metabolomics was employed (Ye et al. 2024). The levels of 16 phenolic acids

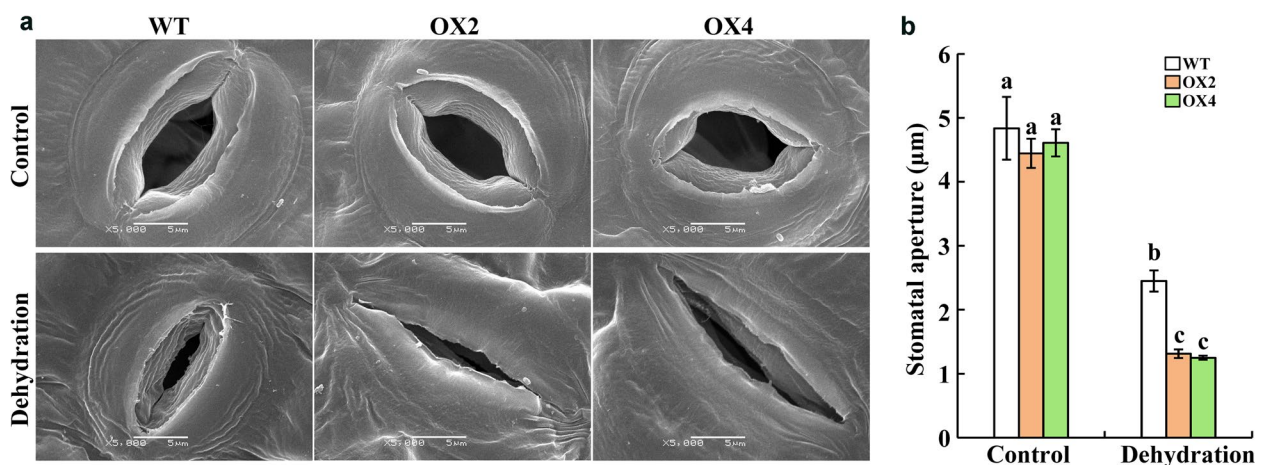


Fig. 2 *MdUGT88F4* overexpression induces stomatal opening under drought stress in apple plants. **a** Scanning electron microscope (SEM) images of stomata before and after dehydration. Scale bar = 5 μm. **b** Variation in stomatal aperture before and after dehydration. Data are presented as mean ± SE (n ≥ 3). Different letters indicate that the values are significantly different (P < 0.05). WT, wild type; OX2/OX4, two transgenic apple lines overexpressing *MdUGT88F4*

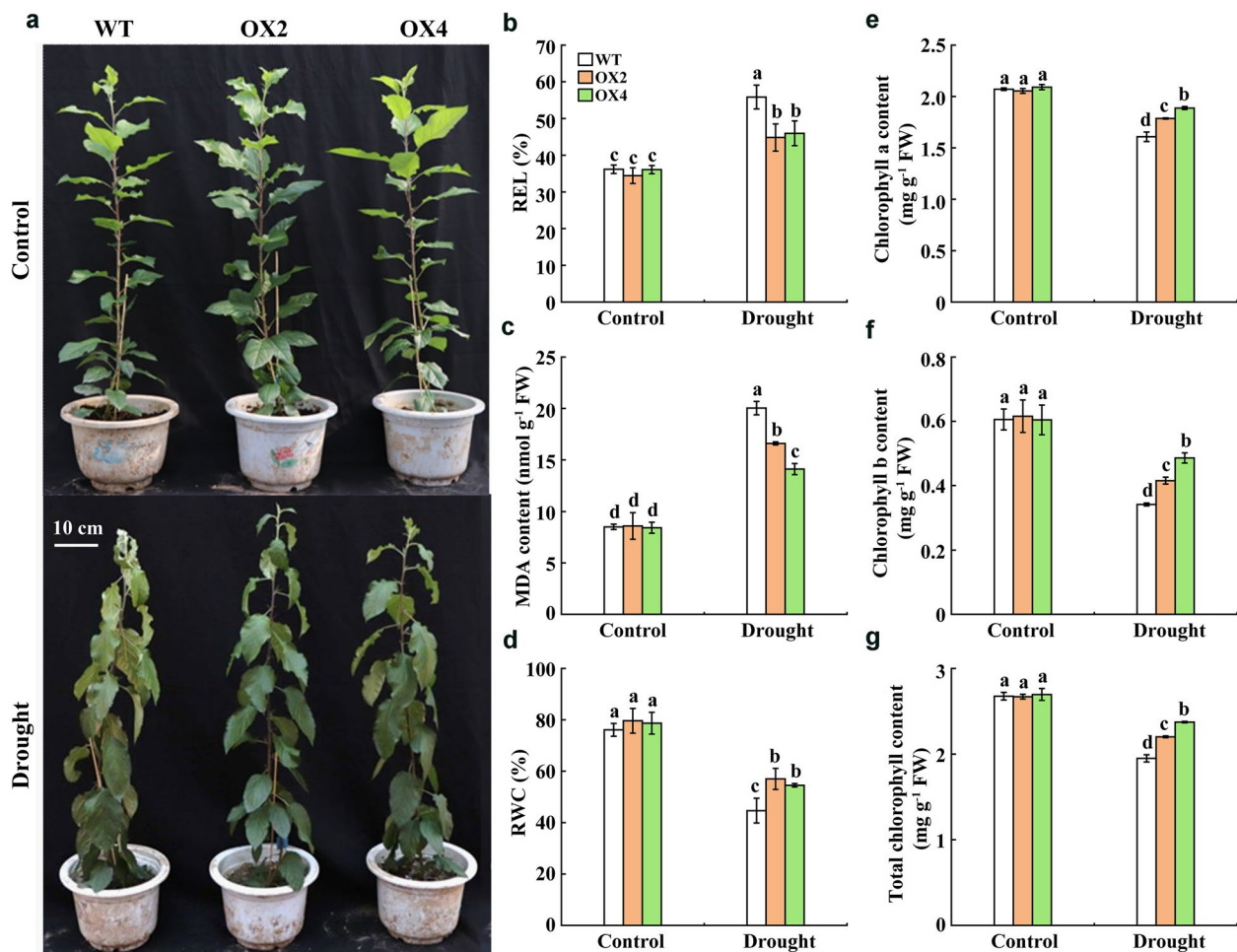


Fig. 3 *MdUGT88F4* overexpression enhances drought tolerance in apple plants. **a** Phenotypic comparison of transgenic lines overexpressing *MdUGT88F4* (OX) and wild type (WT) with and without 9-day drought treatment. **b–g** Relative electrolyte leakage (REL, **b**), malondialdehyde (MDA) content (**c**), relative water content (RWC, **d**), chlorophyll a content (**e**), chlorophyll b content (**f**), and total chlorophyll content (**g**) in the OX and WT plants. Data are presented as mean $\pm$ SE ($n \geq 3$). Different letters indicate that the values are significantly different ($P < 0.05$). OX2/OX4, two transgenic lines overexpressing *MdUGT88F4*

differed between WT and OX2 plants, with 15 phenolic acids significantly higher in OX2 plants (Fig. 6). Among these, most were 2–3 times more abundant in OX2 plants compared to WT, with Prupersin F levels exceeding those in WT by over ninefold. In contrast, isochlorogenic acid C was significantly reduced in OX plants, showing a twofold decrease compared to WT.

These findings suggest that *MdUGT88F4* overexpression enhances the antioxidant capacity of apple plants through upregulation of key antioxidant enzymes and enhanced phenolic acid accumulation, thereby improving drought resistance.

***MdUGT88F4* promotes the accumulation of isosalipurposide in apple plants under drought stress**

MdUGT88F4 was initially identified in the apple genome as the homolog of *MdUGT88F1*, the key enzyme in

phloridzin biosynthesis. However, our *in vitro* analyses revealed that *MdUGT88F4* participates in the biosynthesis of isosalipurposide, not phloridzin (Zhou et al. 2017; Ye et al. 2024). Isosalipurposide, a type of chalcone, is known for its effectiveness in mitigating oxidative injury (Han et al. 2015). Under control conditions, the isosalipurposide content in OX plants was 227 and 107 ng g⁻¹ Fresh Weight (FW), while WT plants contained only 64 ng g⁻¹ FW. Under drought conditions, isosalipurposide content was significantly higher in all plants compared to control conditions, with OX plants showing 2.64 and 1.46 times more isosalipurposide than WT plants under drought and control conditions, respectively (Fig. 7). These findings suggest elevated *MdUGT88F4* expression promotes isosalipurposide accumulation in plants subjected to drought conditions, potentially mitigating oxidative damage caused by drought.

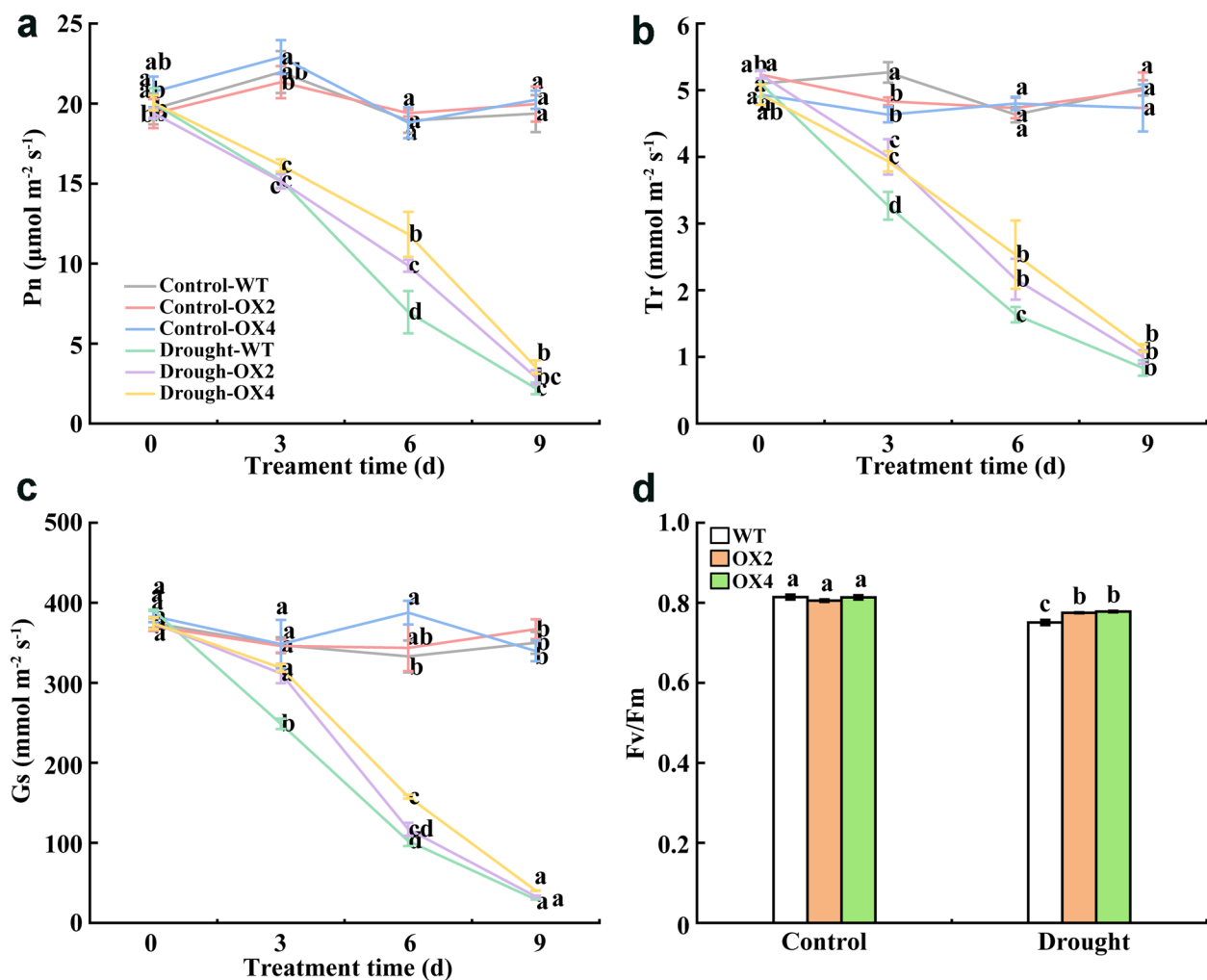


Fig. 4 *MdUGT88F4* overexpression improves photosynthetic capacity under drought stress. **a–d** Net photosynthetic rate (Pn, **a**), transpiration rate (Tr, **b**), stomatal conductance (Gs, **c**), and Fv/Fm ratio (**d**) in the transgenic lines overexpressing *MdUGT88F4* (OX) and wild type (WT). Data are presented as mean $\pm$ SE ($n \geq 3$). Different letters indicate that the values are significantly different ($P < 0.05$). OX2/OX4, two transgenic lines overexpressing *MdUGT88F4*

Greater accumulation of amino acids and their derivatives in transgenic apple plants overexpressing *MdUGT88F4*

Amino acids are crucial osmotic regulators in plants under stress (Hildebrand 2018). Our previous study quantified 54 amino acids and their derivatives in the leaves of WT and OX2 plants using broad-target metabolomics *via* UPLC-MS (Ye et al. 2024). Significant differences in amino acid levels were observed, with glycine and Pro-Asp levels being higher in OX2 plants than in WT plants (Fig. 8a). Additionally, this study analyzed the free amino acid profiles of both WT and OX plants, quantifying 17 distinct amino acids under both control and drought stress conditions (Fig. 8b). The results indicated that some amino acids, such as glycine (Gly), tyrosine (Tyr), valine (Val), and

threonine (Thr), showed minimal change after drought treatment. However, most amino acids, including γ -aminobutyric acid (GABA), aspartic acid (Asp), leucine (Leu), isoleucine (Iso), proline (Pro), serine (Ser), histidine (His), lysine (Lys), and methionine (Met), were more abundant in OX plants than in WT plants (Fig. 8b). Among these, GABA accumulation was the most notably different between OX and WT plants. Under drought conditions, GABA levels in WT plants increased by 2.17-fold compared to control conditions, while OX2 and OX4 transgenic lines exhibited nearly a tenfold increase in GABA levels under drought stress relative to well-watered conditions. These results suggest that *MdUGT88F4* enhances the accumulation of free amino acids in transgenic apple varieties, helping them better tolerate drought stress.

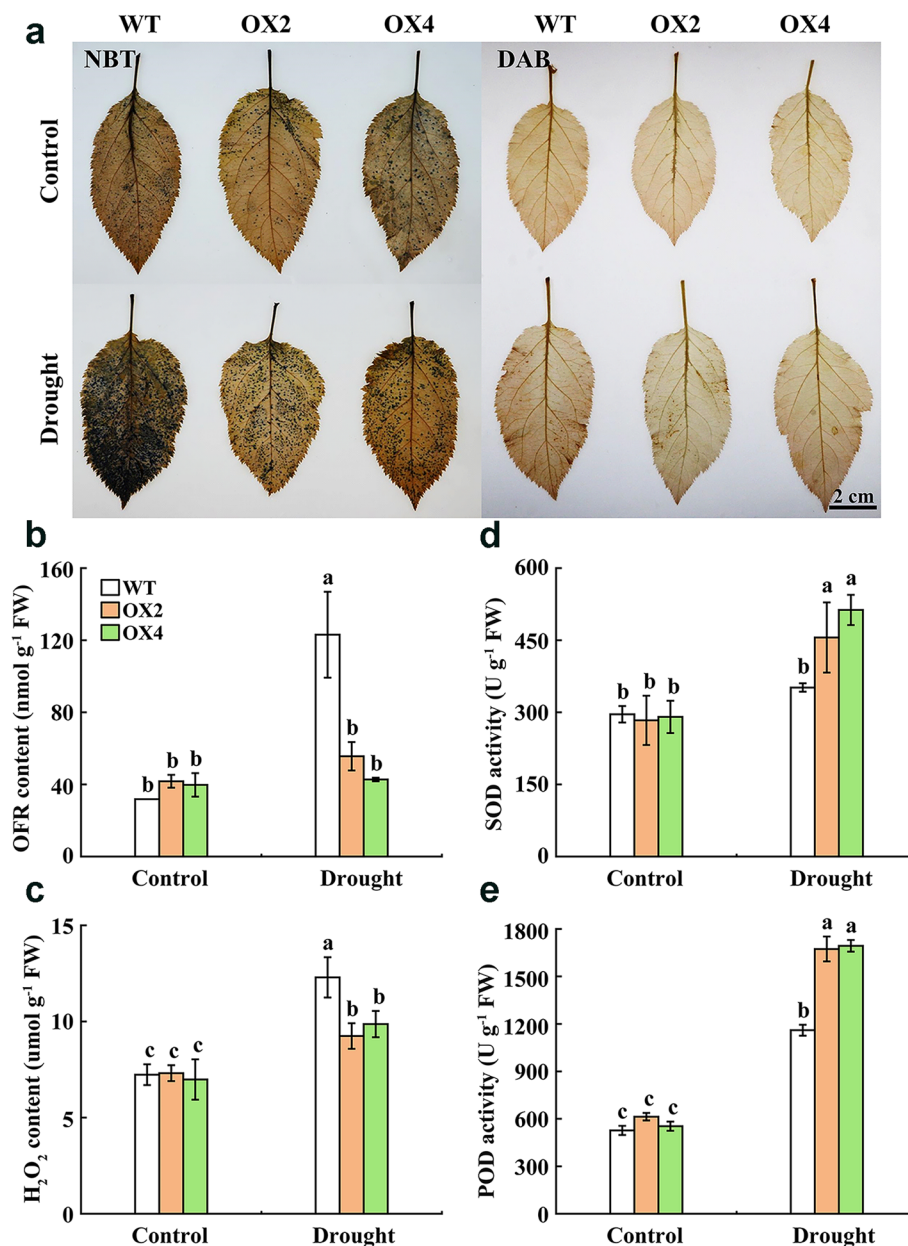


Fig. 5 *MdUGT88F4* overexpression reduces reactive oxygen species (ROS) accumulation under drought stress in apple plants. **a** H_2O_2 and O_2^- accumulation in leaves, revealed by nitro blue tetrazolium (NBT) and 3,3'-diaminobenzidine (DAB) staining, respectively. **b–c** Quantitative measurements of oxidative free radicals (OFR, **b**) and H_2O_2 contents (**c**). **d–e** Superoxide dismutase (SOD, **d**) and peroxidase (POD) activities (**e**). Data are presented as mean $\pm$ SE ($n \geq 3$). Different letters indicate that the values are significantly different ($P < 0.05$). WT, wild type; OX2/OX4, two transgenic lines overexpressing *MdUGT88F4*

RNA-seq reveals differences in global expression profiles between WT and transgenic line

To further investigate the regulatory mechanisms of *MdUGT88F4* under drought conditions, RNA-Seq analysis was performed on WT and OX2 plants following drought treatment. Clustering of DEGs revealed significant differences in expression profiles between OX2 and

WT plants under drought conditions, with the greatest number of DEGs identified in the DT vs. CK comparison group, rather than the OX2 vs. WT group. Specifically, 654, 689, 745, and 194 upregulated DEGs were identified in the WT (DT vs. CK), OX2 (DT vs. CK), CK (WT vs. OX2), and DT (WT vs. OX2) comparison groups, respectively, along with 1,624, 1,184, 176, and 184 downregulated

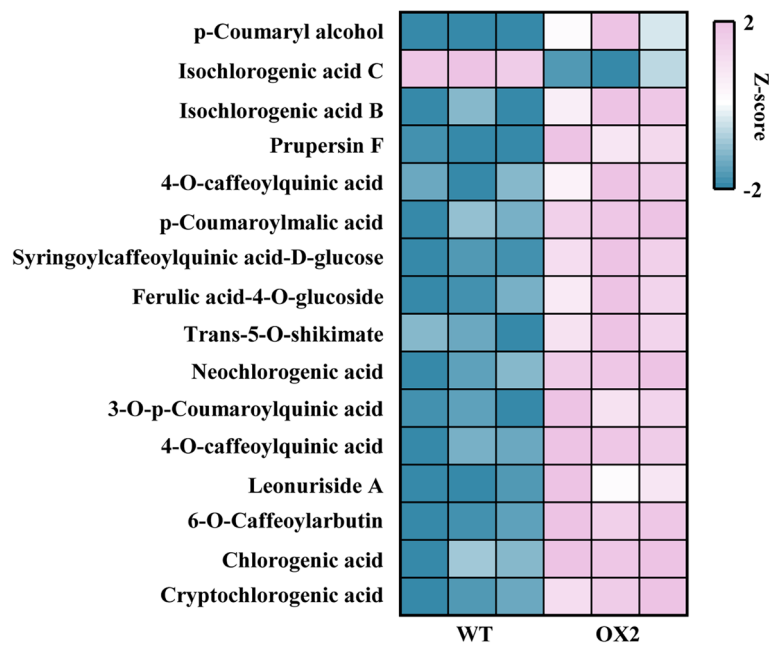


Fig. 6 Heatmap of differential metabolites in the phenolic acids group across different apple plants. Data are normalized using Z-score, ranging from −2 (low) to 2 (high). WT, wild type; OX2, a transgenic line overexpressing *MdUGT88F4*

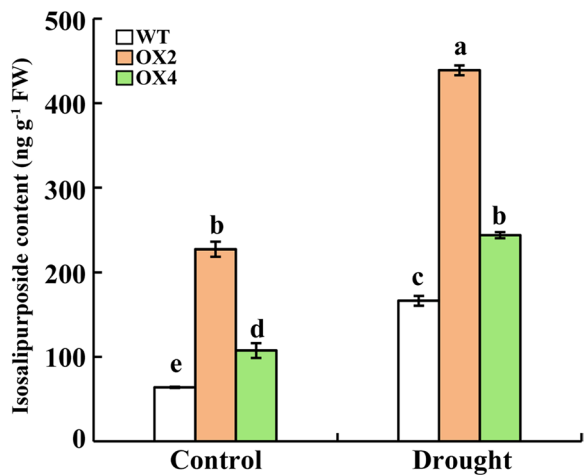


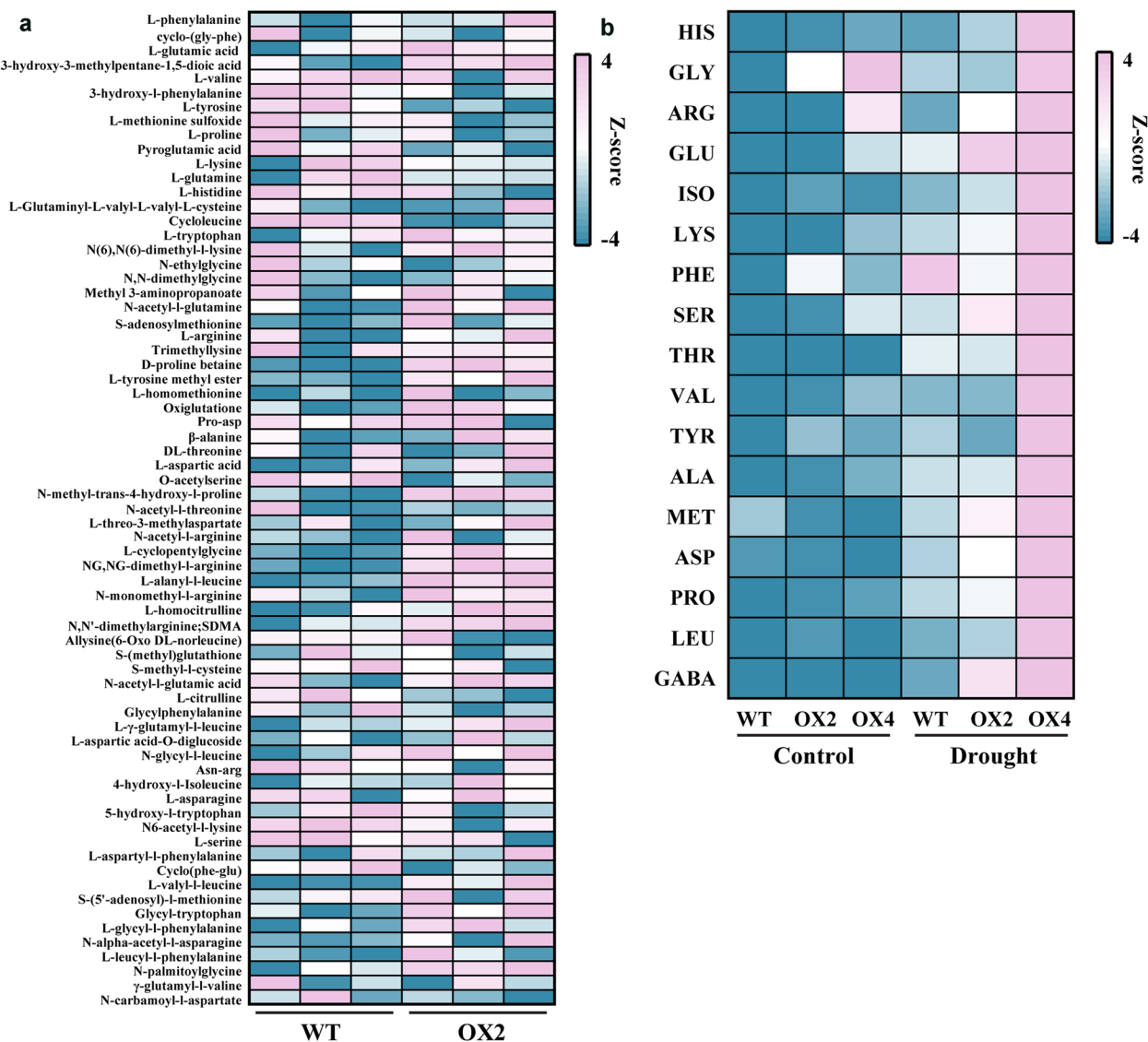
Fig. 7 Accumulation of isosalipurposide under drought stress in different apple plants. Data represent mean ± SE (n ≥ 3). Different letters indicate that the values are significantly different (*P* < 0.05). WT, wild type; OX2/OX4, two transgenic lines overexpressing *MdUGT88F4*

DEGs in these groups (Fig. S1a). Functional enrichment analysis revealed that the DEGs in the WT vs. OX2 comparison group were primarily associated with pathways related to “single-organism cellular processes,” “response to stimulus,” “cellular metabolic reactions,” “metabolic functions of organic substances,” “general metabolic activity,” “single-organism processes,” and “cellular processes.” Among these, “metabolic processes” contained

the highest number of downregulated DEGs in the WT vs. OX2 group after drought treatment (Fig. S1b). Several DEGs that were more highly expressed in OX2 plants compared to WT plants under drought stress are highlighted in Fig. 9. For instance, *MD15G1063000*, encoding branched-chain amino acid aminotransferase, and *MD00G1005700*, involved in minor carbohydrate metabolism and sugar alcohols, were significantly upregulated in OX2 plants after drought treatment. Furthermore, as noted earlier, significant changes in amino acid levels and derivatives were observed in OX2 plants. Table S1 presents all DEGs associated with amino acid metabolism, including *MD02G1188900* (encoding ACT Domain Repeat1), which is involved in amino acid metabolism, and *MD07G1250300* (encoding L-asparaginase), part of the aspartate family, both of which were more highly expressed in OX2 plants compared to WT after drought. These findings suggest that *MdUGT88F4* could improve drought resistance in apple plants by modulating the expression of genes involved in various metabolic processes.

Discussion

Glycosylation, catalyzed by GTs, plays a key role in regulating cellular metabolic homeostasis, allowing glycosylated compounds to participate in metabolic processes and influencing plant tolerance to abiotic stress. In tomato (*Solanum lycopersicum*), the *SlUGT* promoter contains multiple phytohormone-responsive and



stress-related cis-regulatory elements, with the gene contributing to detoxification through interactions with transcription factors (Yu et al. 2022). Recent studies have also shed light on the molecular mechanisms underlying UGT-mediated osmotic stress responses. For example, Wu et al. (2024) conducted the first genome-wide analysis of *UGT* genes in potato (*Solanum tuberosum*), providing a comprehensive characterization of this gene family, examining expression profiles under osmotic stress, and identifying key promoter cis-elements within intronic regions. Similarly, in *Phoebe bournei*, UGTs within the same subfamily exhibit conserved exon–intron

structures, motif compositions, and protein architectures, with significant variation in their expression levels under salt and drought stress conditions (Guan et al. 2024). This study revealed a significant increase in the transcript levels (Fig. 1), suggesting its involvement in drought stress response. To further investigate its role, transgenic apple lines overexpressing *MdUGT88F4* were generated, and these plants displayed enhanced dehydration resistance and drought tolerance. Specifically, the transgenic lines exhibited reduced water loss rates during dehydration and maintained higher RWC under drought conditions compared to WT controls.

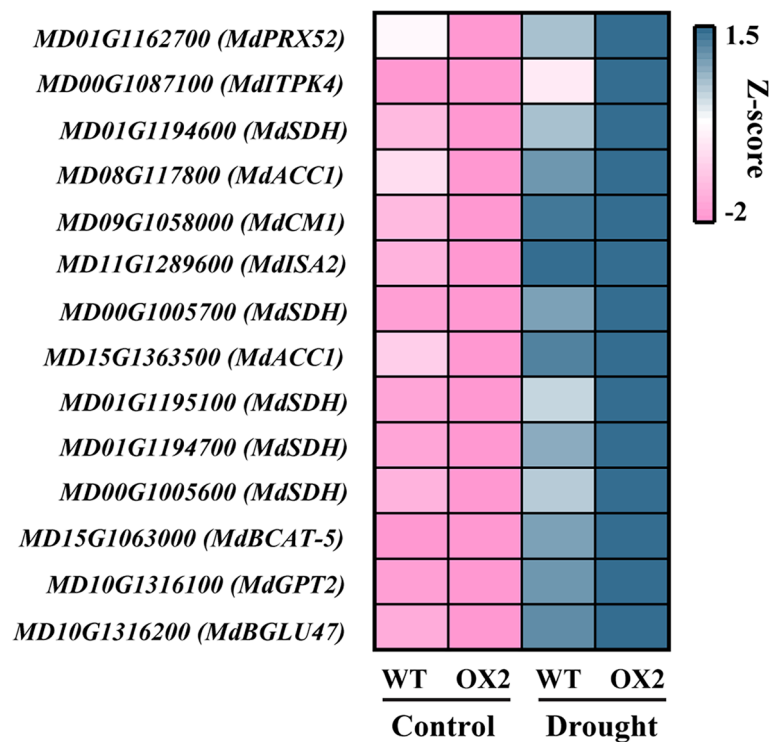


Fig. 9 Heatmap of selected differentially expressed genes (DEGs) related to metabolic pathways in RNA-seq data. Data are normalized using Z-score. WT, wild type; OX2, a transgenic line overexpressing *MdUGT88F4*

During growth, plants subjected to drought stress experience cellular water loss and plasma membrane damage (Gong et al. 2003). A key adaptive strategy for drought resistance is the regulation of stomatal movement. Our observations revealed that under dehydration treatment, WT plants exhibited significantly larger stomatal apertures compared to *MdUGT88F4*-overexpressing (OX) plants, suggesting that *MdUGT88F4* enhances drought tolerance by promoting stomatal closure. Consistent with previous studies (Xing et al. 2016), drought-resistant varieties typically show reduced MDA and ROS accumulation. In our study, OX plants displayed milder wilting symptoms, lower REL, reduced chlorophyll degradation, and decreased MDA levels, alongside higher RWC than WT plants. These results collectively indicate that OX plants exhibit enhanced drought resilience. Photosynthetic efficiency, a reliable indicator of abiotic stress tolerance, can be evaluated through key parameters such as Pn, Tr, and Gs (Duan et al. 2013; Zeng et al. 2024). Additionally, photosystem II (PSII) integrity is often assessed via the Fv/Fm ratio, with a decline indicating photodamage (D'Alessandro and Havaux 2019). Drought-tolerant plants typically maintain higher photosynthetic activity and experience less PSII impairment (Zhang et al. 2023). In line with this, our data show that OX plants experienced smaller declines in photosynthetic performance

and Fv/Fm ratios under drought stress compared to WT plants. Drought stress induces an accumulation of ROS in plant leaves, leading to oxidative damage to membrane lipids, catalase enzymes, and DNA, which compromises membrane integrity and causes cytotoxicity (Parihar et al. 2015). Our results showed that OX plants exhibited weaker NBT and DAB staining intensity compared to WT plants under drought stress, indicating reduced ROS accumulation. Furthermore, both OFR and H₂O₂ levels were significantly lower in OX plants, confirming the attenuation of ROS accumulation. Extensive research has demonstrated that plants combat oxidative stress during drought by upregulating antioxidant systems, including increased activity of antioxidant enzymes and higher accumulation of non-enzymatic antioxidants (Ahmad et al. 2021; Zandalinas et al. 2017). In line with these findings, higher POD and SOD activities were observed in OX plants compared to WT controls under drought conditions. Moreover, drought stress is known to stimulate phenolic acid biosynthesis, which plays a critical role in ROS scavenging (Sarker and Oba 2018; Oksana et al. 2023). For instance, redox-active phenolics such as gallic, protocatechuic, and chlorogenic acids help maintain redox homeostasis under water deficit in rice (Dey and Bhattacharjee 2020). Similarly, drought-tolerant cultivars often exhibit increased synthesis of phenolics,

such as caffeic acid, which enhances stress resilience (Dvojković et al. 2023). In line with these observations, OX2 plants exhibited significantly higher levels of phenolic acids, particularly chlorogenic acid, neochlorogenic acid, and isochlorogenic acid B, compared to WT plants. This enhanced phenolic biosynthesis likely contributed to more efficient ROS detoxification, thereby improving drought tolerance in *MdUGT88F4*-overexpressing plants.

Extensive studies have demonstrated that plants mitigate drought stress by regulating various metabolites, including amino acids, flavonoids, and phenolic acids (Shim et al. 2023; Ma et al. 2014; Turtola et al. 2005). For example, Xu et al. (2021) investigated metabolic protective agents in drought-stressed barley and found that enhanced drought tolerance was linked to increased flavonoid biosynthesis, particularly glycosylated flavonoids. Isosalipurposide, a flavonoid compound, has been shown to be synthesized in vitro by *MdUGT88F4* (Ye et al. 2024). Furthermore, studies suggest that isosalipurposide mitigates oxidative damage by activating the Nrf2 pathway and upregulating its downstream genes (Han et al. 2015). However, its functional role in plant stress responses remains underexplored. Under drought conditions, isosalipurposide accumulation was significantly higher in OX plants compared to WT plants, suggesting that this differential accumulation may contribute to the enhanced drought resistance of OX plants. Proline (Pro), a key osmolyte, stabilizes membrane integrity and maintains osmotic homeostasis under stress (Sharma et al. 2019). Similarly, GABA acts as an osmoregulatory compound, reducing cellular water loss and alleviating dehydration-induced damage (Tang et al. 2020). Under drought stress, WT plants exhibited significantly lower levels of Pro and GABA compared to OX plants, indicating that these metabolic changes likely contribute to the improved drought tolerance of OX plants.

Conclusion

In conclusion, *MdUGT88F4* acts as a promotive factor that enhances drought tolerance in apple plants. Plants overexpressing *MdUGT88F4* exhibited reduced damage and accelerated growth under drought stress. By regulating stomatal movement, transgenic plants lost less water during drought compared to WT plants. *MdUGT88F4* promoted the accumulation of isosalipurposide and phenolic acids, which likely enhanced antioxidative activity. Additionally, it facilitated the accumulation of key amino acids, such as Pro and GABA, which help maintain osmotic balance under drought conditions. RNA-seq analysis further revealed that changes in metabolic processes contributed to the enhanced drought tolerance observed in the transgenic apple plants.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1007/s44281-025-00083-6>.

Supplementary Material 1: Fig. S1 Effect of *MdUGT88F4* on transcription in apple plants under drought stress. a Statistical comparison of differentially expressed genes (DEGs) upregulated and downregulated in various comparison groups. b Enrichment analysis of DEGs in these groups, with the heatmap representing enrichment degree [hypergeometric distribution P value ($-\log_2(P \text{ value})$)]. CK, control treatment; DT, drought treatment; WT, wild type; OX2, one of the two transgenic lines overexpressing *MdUGT88F4*

Supplementary Material 2: Table S1 Fragments Per Kilobase of exon model per Million mapped fragments (FPKM) values of differentially expressed genes (DEGs) involved in amino acid metabolism

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Authors' contributions

FWM and XQG conceived the ideas; YY, YL, XY, LL, XFC, ZSZ and XJH collected and analyzed the data; YY and XQG wrote the manuscript; FWM and XQG revised the manuscript and provided financial support. All authors contributed critically to the drafts and gave final approval for publication.

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Data availability

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests. Prof. Fengwang Ma is a member of the editorial board of *Horticulture Advances* and was not involved in the journal's review or decisions related to this manuscript.

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