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\*CORRESPONDENCE Lizhi Long Ionglizhi@tricaas.com Yuanzhi Shi Shiyuanzhi@caas.cn

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## Exogenous strigolactones modulate antioxidant metabolism via *CsD27* to enhance drought tolerance in tea plants

Jingyue Shen<sup>1,2</sup>, Manni Tong<sup>1</sup>, Qingyun Yuan<sup>1</sup>, Lizhi Long<sup>1\*</sup> and Yuanzhi Shi<sup>1\*</sup>

<sup>1</sup>Key Laboratory of Tea Biology and Resource Utilization of Tea, Tea Research Institute, Chinese Academy of Agricultural Sciences, Hangzhou, China, <sup>2</sup>Graduate School of Chinese Academy of Agriculture Science, Beijing, China

Drought stress adversely affects the growth, yield, and quality of tea plants (*Camellia sinensis* L.). Although strigolactones (SLs) are known to mediate drought adaptation in plants, their regulatory mechanisms in tea plants remain elusive. In this study, we demonstrated that exogenous SL application alleviated drought-induced symptoms by photosynthetic adaptation and mitigating the damage of cell membrane. Moreover, exogenous SL enhanced antioxidant response through regulating catechins metabolism in drought-sensitive cv. 'Huangjinya'. Notably, we identified *CsD27* as a key SL-biosynthetic gene, whose expression level was negatively correlated with malondialdehyde (MDA), mechanistically linking its function in drought tolerance in tea plants. Overexpression of *CsD27* enhanced the drought tolerance of transgenic *Arabidopsis* with decreased MDA content and increased survival rate under drought stress. These findings elucidate a dual SL-mediated mechanism that simultaneously enhances stress tolerance and preserves tea quality, which provide a potential target for molecular breeding in perennial crops.

KEYWORDS

strigolactones, drought stress, tea plant, CsD27, catechin

## **1** Introduction

Tea plant (*Camellia sinensis* L.), a perennial crop of significant economic importance, produces the world's second most consumed non-alcoholic beverage. This commercially important species is extensively cultivated across more than 50 countries spanning five continents (Ahmed et al., 2019). However, due to its hygrophilous nature and the spatial heterogeneity of water resources in major tea-growing regions, tea plants face increasing exposure to drought stress. In fact, drought has emerged as one of the predominant abiotic constraints on global tea production (Lv et al., 2021; Yang et al., 2024), causing reduced

shoot elongation, leaf chlorosis, and progressive wilting that ultimately lead to substantial yield reduction (Liu, 2015). Furthermore, the compounding effects of severe drought extend beyond physiological damage to fundamentally alter tea's biochemical fingerprint, triggering metabolic reprogramming that reduces key quality-determining metabolites such as catechins, caffeine, theanine, and certain free amino acids (Wang, 2016; Zhang et al., 2020a). These challenges are exacerbated by climate change-induced weather extremes, which intensify drought frequency and severity in tea-growing areas.

Strigolactones (SLs), a class of terpenoid lactone phytohormones, play multifaceted roles in plant growth and stress adaptation (Nomura et al., 2024). Initially, SLs were identified as germination stimulants for Striga seeds when isolated from root exudates of cotton (Cook et al., 1966) and a rhizosphere signaling molecule for promoting symbiotic establishment with mycorrhizal fungi (Akiyama et al., 2005). Recent advances have revealed their involvement in shoot branching (Snowden et al., 2005; Umehara et al., 2008), mesocotyl elongation (Hu et al., 2010; Zheng et al., 2020), root development (Kapulnik et al., 2011; Marzec and Melzer, 2018), leaf senescence (Snowden et al., 2005; Yan et al., 2007; Yamada and Umehara, 2015) and stress response, including nutrient deficiency (Santoro et al., 2021; Marro et al., 2022; Gu et al., 2023), drought stress (Min et al., 2019; Xu et al., 2023; Li et al., 2024), extreme temperature (Omoarelojie et al., 2020, 2021; Zhang et al., 2020b), salt stress (Kong et al., 2017) and heavy metal stress (Tai et al., 2017; Qiu et al., 2021; Chen et al., 2022). For instance, application of GR24 could maintain photosynthetic efficiency and reduce biomass loss under drought stress in rapeseed (Wan et al., 2020), and upregulating antioxidant enzyme activities to mitigate oxidative damage (Li, 2018; Cheng, 2019; Wang et al., 2021; Xu et al., 2023).

The SL biosynthetic pathway initiates with all-trans- $\beta$ -carotene conversion to 9-cis- $\beta$ -carotene by DWARF27 (D27), followed by sequential cleavage via CAROTENOID CLEAVAGE DIOXYGENASE7 (CCD7/D17) and CCD8/D10 to produce carlactone (CL), a conserved precursor shared by all SLs. The CL is further diversified into various SLs when transported from the plastid to the cytoplasm, possibly depending on plant species. These SL biosynthesis genes exhibit complex regulatory mechanisms in response to drought stress. Aboveground, drought stress significantly induced the expression of *D27* in rice (Haider et al., 2018) and *FaD27* in tall fescue (Zhuang et al., 2017), while upregulated the expression of *SlCCD7* and *SlCCD8* in tomato (Visentin et al., 2016). These differential responses suggest complex regulatory networks influenced by drought intensity, treatment methods, and species-specific adaptations.

In this study, we investigate SL-mediated drought tolerance mechanisms in tea plants through: i) Physiological characterization of GR24-treated plants under drought stress in hydroponics; ii) Comparative analysis of four cultivars with varying drought tolerance in pot experiments; iii) Overexpression of *CsD27* in Arabidopsis to validate SL function. Our findings demonstrated that SL application alleviated drought-induced physiological damage and revealed a positive correlation between *CsD27*  expression levels and drought tolerance across cultivars. These results provided valuable insights into SL-mediated drought resistance mechanisms while establishing a foundation for improving tea quality and yield stability under waterlimited conditions.

## 2 Methods and materials

### 2.1 Plant materials and treatments

Annual tea plant cuttings (*Camellia sinensis* L. cv. 'Longjing43') were pre-cultured hydroponically in a growth chamber (16 h light/8 h dark cycle, 25°C/23°C, and 50% humidity). The nutrient solution containing 15% PEG-6000 was used to simulate drought stress. Plants exposed to PEG were treated with 0, 5, 10 and 30  $\mu$ M GR24 via foliar spray every 48 hours, ensuring complete coverage but not dripping. One bud and one leaf of tea plant were harvested after 1 day (24 h)with the first treatment for subsequent experiment. After 8 days of treatment, the shoots of tea plants were collected for physiological indicator determination.

Two-year-old seedlings of Camellia sinensis L.cv. Shancha NO.1 (SC), Huangjinya (HJY), Longjin43 (LJ43) and Zijuan (ZJ) were grown in the greenhouse of Tea Research Institute of the Chinese Academy of Agricultural Sciences. Tea seedlings with consistent growth were selected and randomly divided into three groups: (1) Control group (CK), no stress and no GR24 treatment; (2) Drought stress group (DS), no watering was applied during the treatment period.; (3) GR24 treatment group (SL), drought treatment with 10 µM GR24 spray application. The CK and DS groups were sprayed with a 3% acetone solution, while the SL group was sprayed with a 10 µM GR24 solution. All treatments were uniformly watered and sprayed with the corresponding solutions, designated as Day 0. Subsequently, the solutions were sprayed every 2 days (48 h) for a total of 10 days. Following 10 days of water deprivation, the shoots were harvested, immediately flash-frozen in liquid nitrogen, and stored at -80°C for subsequent analyses.

Wild-type *Arabidopsis thaliana* (Columbia-0 ecotype, Col-0) and three independent *CsD27*-overexpressing T3 generation homozygous lines (*OE5-9, OE9-2, OE12-1*) were selected and used for further experiments. For the germination assays, the seeds were sown on 1/2MS medium with and without 200 mM mannitol (control). For the drought stress treatment, the 3-weeks-old seedlings of transgenic lines and WT were grown on soil for one week with or without watering (CK treatment and DS treatment, respectively).

## 2.2 Chlorophyll $\alpha$ fluorescence

The OJIP curves of tea plant were measured at 1, 2, 4, 6 and 8 d after exposure to drought stress and foliar application of GR24 with various concentrations. Chlorophyll  $\alpha$  fluorescence was measured after a 30-minute dark treatment using FluorPen FP110 portable fluorometer (Photon Systems Instruments, Czech Republic).

Formulae and explanation of the fluorescence parameter used in this study are provided in Supplementary Table 1.

## 2.3 Determination of malondialdehyde (MDA) and lipid peroxidation

Fresh leaves were rinsed with deionized water to remove surface contaminants and gently blotted dry with tissues. For each treatment group, six leaves were punched by hole puncher (0.5 cm diameter). The leaf discs were transferred into 50 mL conical tubes containing 15 mL of deionized water. The tubes were shaken (200 rpm) for 1 h to measure the conductivity of the solution, recorded as EC1. Subsequently, samples were boiled for 30 min at 100 °C. Followed by cooling to room temperature, the solution was measured and the results were recorded as EC2. The fresh samples were pulverized in liquid nitrogen, and 0.1 g of each samples was accurately weighed to determined the production rate of MDA and  $H_2O_2$  by using the detection kits (Suzhou Comin Biotechnology Co., Ltd, Suzhou, China).

### 2.4 Total RNA isolation and qRT-PCR assay

Total RNA was extracted using the RNA prep Pure Plant kit (TIANGEN biotech CO., Ltd, Beijing, China) and 2  $\mu$ g of total RNA was used for first-strand cDNA synthesis by the PrimeScript<sup>TM</sup> RT Reagent Kit (TaKaRa, Dalian). Subsequently, quantitative PCR was performed using SYBR<sup>®</sup> Premix Ex Taq<sup>TM</sup> (TaKaRa, Dalian). Transcript levels were normalized to GAPDH, and the calculation of relative transcript abundance using the 2<sup>- $\Delta\Delta$ Ct</sup> method. For each treatment, three biological replicates were used to analyze the expression of each gene.

## 2.5 Subcellular localization

The CDS of *CsD27* (excluding the termination codon) were PCR-amplified and cloned into the pBWA(V)HS-GFP fusion vector. The recombinant constructs were introduced into *A. tumefaciens* through electroporation, followed by transient transformation of *N. benthamiana* leaf epidermis using syringe infiltration. An empty vector control (35S:GFP) was co-infiltrated under identical conditions. At 2 days post-infiltration, transformed leaf sections were excised and mounted on glass slides to detect the subcellular localization of the CsD27 protein using a confocal laserscanning microscope (Nikon C2-ER).

## 2.6 Determination of catechins

The samples were lyophilized with FreeZone freeze dryer (LABCONCO, America) for 4 days and ground with a RETSCH MM400 grinder (Duesseldorf, Germany). To analyze catechin concentrations, 0.1000g of each freeze-dried samples was used to

extract following a high-performance liquid chromatography (HPLC) -based method as previously described in detail (Tong et al., 2023).

## **3** Result

# 3.1 Effects of exogenous GR24 on physiological indexes of tea plant under drought stress

#### 3.1.1 Photosynthetic performance

OJIP original kinetics were analyzed in CK, DS, and GR24treated tea plants (5  $\mu$ M, 10  $\mu$ M, 30  $\mu$ M) on day 8, to characterize drought-induced photosynthetic damage, revealing treatmentdependent divergence in fluorescence transients (Figure 1A). Compared to CK, drought stress significantly reduced the fluorescence curve and caused the J-step to approach F<sub>p</sub>, leading to the disappearance of the IP phase of the OJIP curve. However, the application of GR24 alleviated the negative effect of drought stress, as indicated by the increase in the fluorescence yield of OJIP curve.

For detailed analysis, fluorescence curves were doublenormalized between  $F_o$  and  $F_m$  to derive relative variable fluorescence (V<sub>t</sub>) and  $\Delta V_t$  at a logarithmic time scale (Figures 1C, D). Upon drought stress, tea plants showed a positive  $\Delta V_t$  amplitude with a distinct J peak, indicating significant impairment of the early stages of electron transfer. As the concentration increased from 0 to 30  $\mu$ M, the amplitude was gradually decreased and eventually became negative, indicating alleviation of drought-induced impairment in photosynthetic performance.

To obtain further insights into the OJIP curve, additional normalizations and corresponding curve subtractions were performed to gain the L-band and K peak features, reflecting the OK and OJ phases respectively (Figures 1G-J). Drought treatment increased both the L-band and the K peak, while GR24 treatments, especially at 10 and 30  $\mu$ M, reduced these drought-induced increases, demonstrating the positive role of GR24 in improving energetic connectivity and preserving activity of oxygen-releasing complex (OEC) centers under drought stress. The alterations in M<sub>o</sub> and V<sub>j</sub> further corroborated these findings (Figure 1B). Notably, the K peak of plants treated with 5  $\mu$ M GR24 under drought stress exceeded that observed in DS treatment, suggesting potential concentration-dependent effects.

Under stress-free conditions,  $F_v/F_m$  values in plants typically range from 0.7 to 0.8 (Maxwell and Johnson, 2000), but decline when subjected to environmental stress. Here, we monitored  $F_v/F_m$ , as a critical indicator of PSII maximum quantum efficiency, after 1, 2, 4, 6 and 8 days(d) of drought stress treatment. The  $F_v/F_m$  values of the second leaf of shoot decreased with the prolonged duration of drought stress, however, the application of exogenous GR24 significantly mitigated the damage of photosynthetic apparatus from drought stress (Figures 1E, F). Among them, the  $F_v/F_m$ values of GR24 at 10  $\mu$ M and 30  $\mu$ M concentrations increased by 118.1% and 158.1%. respectively, compared to DS treatment (Figure 1F). Taken together, exogenous GR24 effectively mitigates drought-induced damage on photosynthesis of tea plants.



photochemical efficiency of PSII; **(B)** The value of  $M_0$ ,  $V_j$  and  $V_i$  in each treatment on day 8; **(C)** OJIP curve on day 8 normalized by  $F_0$  and  $F_m$  as  $V_t = (F_t - F_0)/(F_m - F_0)$ ; **(D)**  $\Delta V_t = V_{t(treatment)} - V_{t(control)}$ ; **(E)** Trend analysis of Fv/Fm after 8 days of treatment with 15% PEG-6000; **(F)** The value of Fv/Fm on day 8; **(G)** OJIP curve on day 8 normalized by  $F_0$  and  $F_k$  as  $W_{OK} = (F_t - F_0)/(F_K - F_0)$ ; **(H)**  $\Delta W_{OK} = W_{OK}$  (treatment)  $- W_{OK}$  (control; **(I)** OJIP curve on day 8 normalized by  $F_0$  and  $F_k$  as  $W_{OK} = (F_t - F_0)/(F_K - F_0)$ ; **(H)**  $\Delta W_{OK} = W_{OK}$  (treatment)  $- W_{OK}$  (control; **(I)** OJIP curve on day 8 normalized by  $F_0$  and  $F_J$  as  $W_{OJ} = (F_t - F_0)/(F_J - F_0)$ ; **(J)**  $\Delta W_{OJ} = W_{OJ}$  (treatment)  $- W_{OJ}$  (control). In **(B, F)**, the values are means  $\pm$  SD (n > 3), and one-way ANOVA was performed for the statistical analysis. Different letters represent significant differences between treatments (P < 0.05). CK, control with no stress; DS, drought stress treatment, 5  $\mu$ M -30  $\mu$ M, drought stress treatment with various concentrations of GR24 applied.

### 3.1.2 Cell membrane damage

Water deficit typically damages the integrity of the cell membrane and lipid peroxidation (Su et al., 2025), as demonstrated by a substantial increase in the levels of relative electrical conductivity (REC) and malondialdehyde (MDA) content. We measured the physiological indicators of each treatment after 8 days of treatment. Compared to CK, the REC and MDA content under drought stress increased significantly by 139.43% and 81.93%, respectively (Figures 2A, B). Conversely, all the treatments with different concentrations of GR24 under drought

stress, particularly those with 10  $\mu$ M and 30  $\mu$ M, mitigated these increases, showing significant reductions of 39.76% and 57.70% in REC, and 19.26% and 9.39% in MDA content, respectively, compared to DS treatment. These physiological results are consistent with the trend observed in chlorophyll fluorescence, further providing evidence for the positive regulation of GR24 on drought tolerance of tea plants.

 $H_2O_2$  serves as a critical intracellular signaling molecule in plants. Moderate accumulation of reactive oxygen species (ROS) acts as a prerequisite for triggering plant adaptive mechanisms in response to abiotic stress, while excessive ROS accumulation induces oxidative damage, leading to physiological and metabolic disorders that impair plant growth. Drought stress significantly increased  $H_2O_2$  accumulation, reaching approximately 1.3-fold of CK group (Figure 2C). However, the effect of exogenous GR24 on  $H_2O_2$  accumulation differed from that observed for REC and MDA contents. It was observed that the  $H_2O_2$ level was significantly reduced by 26.99% in tea plants treated with 5  $\mu$ M GR24, but increased by 16.35% and 50.72% in 10  $\mu$ M and 30  $\mu$ M treatments, respectively.

## 3.2 The effects of GR24 on different tea plant cultivars under drought stress

To further investigate the relationship between SL and drought tolerance in tea plants, we examined the phenotypic characteristics of four cultivars and measured the MDA content of four cultivars after 10 days drought stress and GR24 treatments (Figure 3, Supplementary Figure 1), revealing different levels of stress response. SC and LJ43 exhibited milder wilting and lower MDA content, while ZJ showed moderate wilting and MDA levels. In contrast, HJY suffered the most severe damage from drought stress, characterized by burning symptoms appearing on wilted shoots and the highest MDA content.

To confirm the impact of SL on tea catechins, the main flavonoid antioxidants, we measured the catechin components in the shoots of drought-insensitive cultivar LJ43 and droughtsensitive cultivar HJY under drought stress (Figure 4). Generally, epigallocatechin gallate (EGCG) was the most abundant catechin, followed by epigallocatechin (EGC). In the drought-insensitive cultivar which showed no visible symptoms of drought stress, there were no significant differences in catechin components across the three treatments. However, HJY showed a significantly decrease in both total catechin and individual catechin components. Consistent with the phenotypic observations and MDA content, the application of GR24 alleviated drought-induced damage and promoted catechin accumulation, indicating that SL positively influenced tea quality under drought stress.

## 3.3 CsD27 was significantly correlated to drought tolerance

D27 has been confirmed to be involved in the plant response to abiotic stress across multiple species. Previous studies have shown that the drought resistance of D27 knockout mutants is significantly reduced, while overexpressing lines exhibit the opposite result (Haider et al., 2018). Given the central role of SL in drought response based on the above observation, we identified 8 CsD27, the key SL biosynthesis genes, from tea plant genome of Camellia sinensis L.cv. Shuchazao (Supplementary Figure 2). Specifically, the member (CSS0025398.1) was regulated in Camellia sinensis L.cv. Tieguanyin by long-term drought stress as revealed in previous database (unpublished). Additionally, we measured the expression levels of CsD27 across four tea plant cultivars. While CsD27 exhibited higher expression levels in SC and LJ43 (droughttolerant cultivars), its expression was significantly reduced in both HJY and ZJ (drought-sensitive cultivars) (Figure 5B). Correlation analysis showed a significant and negative correlation between expression of CsD27 and MDA content, indicating that cultivars with higher expression levels exhibited higher drought tolerance (Figure 5C). Therefore, we cloned the CsD27 gene (CSS0025398.1) and performed a multiple sequence alignment, followed by the construction of a phylogenetic tree (Figures 5A, D). The results demonstrated that CsD27 shared conserved regions with D27 proteins from other species, and exhibited the highest similarity to SlD27 and GmD27.



FIGURE 2

GR24 promoted the drought tolerance of tea plants grown in hydroponics. (A) Determination of relative electrical conductivity (REC); (B) Determination of malondialdehyde (MDA); (C) Determination of H<sub>2</sub>O<sub>2</sub>. In (A–C), values are means  $\pm$  SD (n > 3), and one-way ANOVA was used to assess statistical differences, where different letters indicate significant differences between treatments (*P* < 0.05). CK, control with no stress; DS, drought stress treatment, 5  $\mu$ M -30  $\mu$ M, drought stress treatment with various concentrations of GR24 applied.



#### FIGURE 3

The phenotypic observation of four cultivars after 10 days of drought and GR24 treatment. CK, control with no stress; DS, drought stress treatment; SL, drought stress treatment with 10  $\mu$ M GR24 applied, scale bar = 10 cm.

## 3.4 Subcellular localization of CsD27

In order to identify the subcellular localization of CsD27 protein, the 35S:CsD27-GFP plasmid was introduced into tobacco

leaves. The results showed that strong GFP fluorescence of the 35S: CsD27-GFP fusion protein was predominantly observed in the chloroplast, indicating that CsD27 is mainly localized in the chloroplast, consistent with the predicted localization (Figure 5E).



## 3.5 Expression patterns of CsD27 in tea plant

To investigate the tissue-specific expression pattern of *CsD27*, total RNA from various tea plant tissues including root, stem, mature leaves, the first leaf of shoot and bud were extracted and used for qPCR (Figure 5F). The results showed that the expression level of *CsD27* was higher in mature leaves than other tissues, while exhibited extremely low expression levels in both buds and stems.

Meanwhile, *CsD27* was differentially expressed under stress and hormone treatment. The expression of *CsD27* after 24 hours of DS treatment slightly decreased compared to CK in LJ43. Under GR24 treatment, the expression of *CsD27* transcript was effectively upregulated, with a 2.2-fold increase at 5  $\mu$ M, a maximum induction of 2.4-fold at 10  $\mu$ M, and an increase of approximately 1.7-fold at 30  $\mu$ M (Figure 5G). These results implied that *CsD27* might be a crucial gene in response to drought, and the regulation networks were probably related to GR24 concentration.

## 3.6 Overexpression of CsD27 increased the drought tolerance of *Arabidopsis thaliana*

To further investigate its function in drought stress tolerance, we developed three transgenic *Arabidopsis* lines with *CsD27* overexpression (*OE5-9*, *OE9-2*, *OE12-1*). The result indicated that the expression levels of *CsD27* were significantly higher in the transgenic lines than in the wild-type (WT) (Figure 6A, Supplementary Figure 3).

Seeds of each genotype were planted on 1/2 Murashige and Skoog (MS) media containing 0 or 200 mM mannitol to assess the seed germination rates under osmotic stress. Although germination and cotyledon greening rates were comparable between WT and transgenic lines under 200 mM mannitol treatment, the transgenic lines exhibited larger cotyledon areas and enhanced growth performance compared to WT seedlings under osmotic stress conditions (Figures 6C, D). Additionally, we selected three-weekold seedlings of each genotype to expose to one week of drought



control (c) and drought stress (S) treatments; (D) Amino acid sequence analysis of *CsD27* and other *D27* genes from other species; (E) Subcellular localization of CsD27 protein through transient expression in tobacco leaf epidermis, scale bar =  $20 \ \mu m$ ; (F) Expression levels of *CsD27* in different tea plant tissues; (G) Expression analysis of *CsD27* after 1 day(24 h) treatment. CK, control with no stress; DS, drought stress treatment, 5  $\mu$ M -30  $\mu$ M, drought stress treatment with various concentrations of GR24 applied. In (A, F, G), one-way ANOVA was used for statistical analysis, where different letters indicate significant differences between treatments (*P* < 0.05), and and \*\* indicates extremely significant differences between treatments and cultivars (*P* < 0.01). The values are means + SD (n > 3).

stress to investigate the role of CsD27 in drought response of *Arabidopsis*. Compared to WT, the majority of overexpression line seedlings retained green coloration and exhibited better growth under drought stress, as evidenced by less severe wilting phenotype and significantly higher fresh weight (Figures 6E, F). Similarly, the MDA result was demonstrated that OE5-9, OE9-2 and OE12-1 exhibited significant reduction of drought-induced damage, which was consistent with the phenotypic observation (Figure 6B). After 3 days of re-watering, the OE5-9, OE9-2 and OE12-1 seedlings exhibited superior recovery, whereas WT seedlings showed only 25% survival rates (Figure 6C). These results indicated that CsD27 enhanced the drought tolerance of *Arabidopsis*.

## 4 Discussion

Drought stress has emerged as a critical constraint to agricultural productivity worldwide, which has caused billions of economic losses over the past decade (Gupta et al., 2020). The intensification of drought events due to climate change scenarios necessitates the development of drought-resistant crop varieties capable of maintaining photosynthetic efficiency under water-deficit conditions. Our study demonstrated that exogenous application of SL analog GR24 effectively mitigated drought-induced photosynthetic impairment and modulated antioxidant metabolism in tea plants, providing new insights into phytohormone-mediated stress adaptation mechanisms.

## 4.1 Photosynthetic apparatus protection by GR24

Water deficit induces multilevel photosynthetic dysfunction, manifested through stomatal closure, structural disorganization of thylakoid membranes, disruption of photosynthetic pigments, and degradation of photosynthetic proteins (Vanlerberghe et al., 2016; Razi and Muneer, 2021). The  $\Delta V_t$  in tea plant revealed that drought



wild-type and transgenic plants under osmotic stress(200mM Mannitol), scale bar = 1 cm; (**E**, **F**) The fresh weight measurement and phenotypic observation of wild-type and transgenic plants after 7 days without watering, scale bar = 5 cm. In (**A**, **E**, **G**), one-way ANOVA was performed for the statistical analysis, where different letters represent significant differences (P < 0.05), and \*\* indicates extremely significant differences between treatments and cultivars (P < 0.01). In (**B**), two-way ANOVA was used for the statistical analysis, where different letters represent significant differences (P < 0.05). In (**A**-**C**, **E**), values are means  $\pm$  SD (n > 3). CK, control with no stress; DS, drought stress treatment.

stress induced the emergence of a distinct phase in the OJIP kinetic curve, the J peak (Figure 1D) caused by the accumulation of  $Q_A^-$  in PSII reaction centers (RCs), indicating that drought stress disrupted the electron flow beyond  $Q_A$  (Guo et al., 2020; Tsimilli-Michael, 2020; Jiang et al., 2025). A significant increase in  $M_o$  and  $V_j$  under drought stress further corroborated this result (Figure 1B). Whereas, the GR24-treatments efficiently improved the probability of PSII photosynthetic electron transport, thereby conferring protection against drought in the acceptor-side of PSII. Moreover, this effect became more pronounced with increasing GR24 concentrations. The L-band analysis revealed a positive L-band under drought stress, indicating reduced energetic connectivity and system stability (Antunović Dunić et al., 2023). Conversely, GR24 treatment

enhanced PSII unit connectivity (Figures 1G, H), implying optimized excitation energy distribution (Yusuf et al., 2010).

Significantly, we identified a drought-induced K-band appearance at 150  $\mu$ s (Figures 1I, J), indicative of OEC dysfunction (Strasser et al., 2004). Tea plants with 10  $\mu$ M and 30  $\mu$ M GR24 had negative K-band, indeed improving the fraction of the active OEC centers. However, the K-band of 5  $\mu$ M treatment exceeded that of DS treatment. This phenomenon may be caused by SL-induced stomatal closure via ABA-dependent/independent ways, which exacerbated CO<sub>2</sub> limitation and thereby amplified oxidative stress on the PSII donor side (Cui, 2017; Korek and Marzec, 2023; Zhang et al., 2024). In addition, the results demonstrated that drought stress caused a decline in  $F_v/F_m$ , while

exogenous application of SL mitigated this reduction, indicating enhanced PSII functionality and alleviation of photoinhibition. This findings align with previous reports in wheat (Wei, 2021), grapevine (Min et al., 2019) and *purpureum* (Li et al., 2022), suggesting conserved SL functions across plant taxa.

## 4.2 Oxidative stress modulation and membrane protection

The plant cell membrane plays a vital role in maintaining normal metabolic activities. Our results demonstrated that drought-induced redox imbalance triggered substantial membrane damage in both hydroponic and pot experiments (Figures 2, 3, Supplementary Figure 1), consistent with the findings in grapevine (Wang et al., 2021) and soybean (Xie et al., 2024). GR24 treatment attenuated damage to cell integrity and oxidative stress with significant reduction in REC and MDA content, which might be attributed to ROS-scavenging capacity through both expression and activities of antioxidant enzymes (Wang et al., 2021; Xie et al., 2024). Intriguingly, we observed a concentration-dependent dichotomy in H<sub>2</sub>O<sub>2</sub> regulation (Figure 2C), whereby low-dose GR24 suppressed H<sub>2</sub>O<sub>2</sub> accumulation, while high-dose treatment potentiated ROS signaling. This dual functionality mirrors the hormetic effect of phytohormone signaling, where low-dose GR24 attenuates acute oxidative damage by limiting ROS accumulation, thereby maintaining membrane integrity. In contrast, elevated H<sub>2</sub>O<sub>2</sub> levels under high-dose GR24 may reflect an adaptive signaling phase, potentially involving ABA-mediated activation of respiratory burst oxidase homologs (RBOHs) (Rodrigues and Shan, 2022). Moreover, the possibility that SLs directly promote ROS production through ABA-independent pathways cannot be excluded (Lv et al., 2018; Wei, 2021). These dual roles of GR24 highlight its complex involvement in redox regulation and drought adaptation, necessitating complementary analyses of antioxidant system activity and ABA biosynthesis profiles.

### 4.3 CsD27 in drought resistance regulation

D27 is involved in abiotic stress resistance. For example, overexpression of D27 could decrease drought tolerance in transgenic rice (Haider et al., 2018). A correlation analysis was made to investigate the relationship between *CsD27* and drought tolerance. We found that the cultivars with higher expression levels exhibited better drought tolerance compared to those with lower expression. In *Arabidopsis*, SL-deficient mutants which have a 70–75% reduction in SL content exhibited a hypersensitivity to drought, and they could be rescued when sprayed with SL to almost the same level of WT plants (Ha et al., 2014). Both of these results implicated the involvement of SL as a positive regulator in abiotic stress responses.

Phylogenetic analysis showed that CsD27 had the closest relationship with SlD27 and GmD27 (Figure 5A). It was reported that GmD27 could reduce the accumulation of ROS in an ABA– dependent manner (Han et al., 2025), providing phylogenetic evidence for CsD27's putative role in drought adaptation. To verify this hypothesis, we generated CsD27-overexpressing *Arabidopsis* lines (*OE5-9*, *OE9–2 and OE12-1*). It was found that the transgenic plants with overexpression of CsD27 had enhanced osmotic resistance for the better growth, lower MDA content and higher survival rate under stress (Figure 6). This might contribute to the crucial role for D27 in determining ABA and SL content (Haider et al., 2018). Future investigations should prioritize expanding genetic diversity across tea cultivars to systematically characterize the functional association between CsD27 allelic variation and drought resistance phenotypes.

## 4.4 Secondary metabolism and tea quality preservation

Catechins are the main flavonoid antioxidants in tea plants, functioning primarily by donating hydrogen atoms and electrons to scavenge ROS (Lv et al., 2021). In the drought-sensitive cultivar HJY, both the total catechins and individual catechin levels declined under drought stress, whereas the drought-insensitive cultivar LJ43 maintained catechin content, particularly the key antioxidants epigallocatechin gallate (EGCG) and epigallocatechin (EGC). Such cultivar-specific response might align with PAL-mediated phenylpropanoid flux redirection under mild drought stress (Chakraborty et al., 2002). Additionally, GR24 application enhanced both total and individual catechin accumulation under drought conditions, suggesting that SL contribute to improved nonenzymatic antioxidant capacity, consistent with the results in crab apple (Xu et al., 2023). Notably, we observed that the expression of CsD27 was significantly negatively correlated with epicatechin (EC). This correlation may reflect complex SL-mediated effects on isomerization processes and branch-point regulation within the catechin biosynthesis pathway. Future studies are warranted to elucidate the precise role of SL in catechin metabolism and to explore strategies for optimizing catechin synthesis and accumulation through modulation of SL signaling. Moreover, the results also indicated that SLs application under drought stress contributed to tea quality. By preserving catechin levels, SLs not only directly enhanced the catechin accumulation, but also facilitated the production of downstream quality-related metabolites. Since oxidative catechin are inherently unstable, they might be further oxidized to facilitate theaflavins (TFs) and thearubigins (TRs), which are critical for taste, liquor color, and aroma quality of black tea (Lv et al., 2021). However, more evidence and experiments are needed to delineate SL-regulated biosynthetic nodes in catechin metabolism, potentially enabling targeted metabolic engineering.

## 5 Conclusion

In summary, this study elucidates that the application of exogenous SL confers drought resilience of tea plants through photosynthetic

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maintenance, ROS scavenging via catechin accumulation, and mitigating oxidative membrane damage. Meanwhile, the transcript of CsD27 was correlated with drought tolerance and its overexpression Arabidopsis lines enhanced drought adaptation, achieving more than 88% survival rates versus 25% in wild-type controls, alongside preserved membrane integrity (MDA reduced by 59.99%, 61.70% and 54.71% respectively) and biomass (2.82, 1.91 and 2.08-fold higher fresh weight) under drought conditions. Our findings redefined strigolactones as metabolic coordinators that synchronize drought resilience with quality retention in tea plants, establishing an actionable framework for next-generation plant growth regulators. Furthermore, we functionally validated CsD27 as a molecular determinant of SL-mediated drought adaptation and identified its variants as precision breeding targets, enabling molecular markerassisted development of elite drought-insensitive cultivars without compromising catechin biosynthesis.

## Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding authors.

## Author contributions

JS: Writing – original draft, Investigation, Data curation, Conceptualization, Formal Analysis. MT: Writing – original draft, Investigation. QY: Investigation, Writing – original draft. LL: Writing – review & editing. YS: Writing – review & editing.

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## Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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## Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpls.2025.1601094/ full#supplementary-material

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