

Morphometric, Physiological, and Proteomic Insights into Drought Stress Mitigation in Big Leaf Mahogany: The Role of Defense Hormones JA and SA in Enhancing Stress Resilience

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Morphometric, Physiological, and Proteomic Insights into Drought Stress Mitigation in Big Leaf Mahogany: The Role of Defense Hormones JA and SA in Enhancing Stress Resilience

Abstract

Drought stress is a major abiotic constraint affecting growth and productivity in tropical forestry species such as *Swietenia macrophylla* (mahogany). This study investigates the morphometric, physiological, biochemical, and proteomic responses of mahogany seedlings to drought and evaluates the ameliorative potential of two defense hormones—Jasmonic Acid (JA) and Salicylic Acid (SA). Seedlings were subjected to three phases: pre-drought (well-watered), drought (25% field capacity), and recovery (rehydration with foliar application of 0.6 mM JA or 0.8 mM SA). Drought stress significantly reduced photosynthetic rate (P_n), stomatal conductance (G_s), transpiration rate (T_r), pigment content, and relative water content (RWC), while enhancing proline and superoxide dismutase accumulation and altering protein expression profiles. Exogenous hormone application mitigated these effects, with JA showing superior efficacy in restoring growth traits, physiological function, and pigment levels compared to SA. Proteomic analysis revealed drought-induced downregulation of photosynthetic and metabolic proteins such as RuBisCO and DAHP synthase, along with upregulation of stress-responsive proteins including Heat Shock Protein 90 (HSP90) and sulfiredoxin. Hormonal treatments reversed these patterns, promoting the accumulation of proteins associated with photosynthesis and stress defense. Gene Ontology (GO) enrichment highlighted the involvement of photosynthetic processes, metabolic reprogramming, and reactive oxygen species (ROS) scavenging in drought adaptation. Overall, the findings demonstrate that JA and SA play complementary roles in alleviating drought stress, with JA being more effective, and provide valuable insights for enhancing stress resilience in tropical tree species through targeted hormonal interventions.

Key Words- Abiotic Stress, Drought, Defense hormones, Proteomic analysis, Jasmonic acid and *Swietenia macrophylla*

1. Introduction

As climate change exerts growing pressure on ecosystems worldwide, the resilience of forest species under abiotic stress has emerged as a focal point in plant science and forestry research. Among the myriads of tropical hardwoods, *Swietenia macrophylla* King, commonly known as big-leaf mahogany stands out not only for its exceptional timber quality but also for its ecological significance in neotropical rainforests. However, this iconic species now faces an escalating threat from prolonged droughts and erratic precipitation patterns, which undermine its growth, productivity, and survival (Trugman *et al.*, 2018; Schwarz *et al.*, 2020). In the face of such environmental adversity, understanding the intrinsic mechanisms that underpin drought tolerance in mahogany is no longer a scientific curiosity, but a conservation imperative.

Abiotic stresses, intensified by climate change such as drought, heat, and salinity—pose significant threats to plant health, productivity, and ecological balance, particularly in tropical forestry species (Eckardt *et al.*, 2022). Nevertheless, trees demonstrate remarkable adaptive potential through intrinsic physiological and biochemical mechanisms, including stomatal regulation, osmoregulation, and metabolic adjustments, which collectively mitigate stress-induced damage (Zhang *et al.*, 2023; Muhammad *et al.*, 2024). Understanding these mechanisms is crucial for advancing tree improvement programs focused on enhancing resilience and productivity under adverse environmental conditions (Tanaka *et al.*, 2023). Among these stresses, drought remains one of the most

severe constraints, impairing photosynthetic efficiency, disrupting plant water balance, and reducing carbon assimilation, potentially leading to mortality under prolonged conditions (Mitchell *et al.*, 2014). While drought-induced depletion of non-structural carbohydrate (NSC) reserves has been associated with mortality in many temperate species, tropical angiosperms often exhibit divergent and species-specific responses, underscoring the complexity of drought adaptation strategies (Mitchell *et al.*, 2014). In this context, *Swietenia macrophylla* stands out due to its pronounced morphological plasticity, physiological adaptability, and biochemical flexibility, making it a valuable model for elucidating the survival strategies of tropical trees under water-deficit conditions (Wu *et al.*, 2023; Robinson *et al.*, 2023).

Plant defense hormones, particularly JA and SA, play a central role in orchestrating complex stress signaling networks that enhance tolerance to abiotic stresses such as drought, salinity, and heat (Vos *et al.*, 2015). These defense hormones function as key regulators of adaptive responses, activating antioxidant defenses, modulating gene expression, and maintaining cellular homeostasis during and after stress exposure (Adams *et al.*, 2013; Anderegge & Callaway, 2012; Grams *et al.*, 2021). JA levels typically increase under abiotic stress conditions, triggering the expression of biosynthetic and stress-responsive genes while enhancing the activities of crucial antioxidant enzymes like superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX). These enzymes collectively mitigate oxidative damage caused by reactive oxygen species (ROS), thereby sustaining physiological balance (Ali and Baek, 2020; Wang *et al.*, 2021). Similarly, SA contributes to stress resilience by regulating ROS dynamics, modulating stress-responsive gene networks, and interacting with other signaling pathways, further reinforcing its multifaceted role in abiotic stress mitigation (Yang *et al.*, 2023). The interplay between JA and SA becomes especially critical under drought conditions, where their synergistic effects finely tune key physiological processes such as stomatal regulation, osmotic adjustment, and ROS scavenging, enabling plants to better withstand and recover from stress episodes.

In recent years, advancements in proteomic technologies have significantly deepened our understanding of how plants like *Swietenia macrophylla* respond and adapt to abiotic stress at the molecular level. Proteomics particularly through high-resolution techniques such as liquid chromatography-tandem mass spectrometry (LC-MS/MS) and MALDI-TOF MS has revolutionized stress biology by enabling the comprehensive profiling of protein expression patterns under drought, salinity, and hormone treatment conditions (Schnabel *et al.*, 2021; Dey *et al.*, 2022; Machado *et al.*, 2023). These approaches have uncovered a diverse array of stress-responsive proteins involved in key physiological processes such as photosynthesis, energy metabolism, water-use efficiency, and cellular protection. Functional genomic insights derived from proteomics have also revealed how complex signaling pathways—especially those mediated by defense hormones like JA and SA govern biosynthesis, post-translational modifications, and downstream responses critical for cellular resilience (Stroud *et al.*, 2022; Shoaib *et al.*, 2024). Notably, proteins such as Rubisco, heat shock proteins (HSPs), and various metabolic enzymes have emerged as central players in maintaining homeostasis and promoting stress tolerance (Ahmad *et al.*, 2016). The integration of proteomics with transcriptomic and metabolomic data further enhances our ability to dissect plant stress responses, providing a powerful framework for the development of targeted breeding and genetic engineering strategies aimed at improving stress resilience in tropical forestry species.

By integrating morphometric, physiological, and proteomic analyses, this study provides a holistic view of how *Swietenia macrophylla* orchestrates its defense repertoire under water-deficit conditions. It further underscores the potential of JA and SA as

bioactive tools for enhancing drought tolerance, with implications extending beyond individual tree performance to broader forestry practices, restoration programs, and climate-resilient silviculture. In essence, the findings of this research pave the way for strategic interventions that may reinforce the ecological stability and economic viability of *Swietenia macrophylla*, ensuring its continuity in an increasingly water-limited world. As climate pressures intensify, such integrative studies will be key to safeguarding not only a keystone timber species but also the intricate forest systems it supports.

2. Materials and methods

Plant material, drought treatments and defense hormones applications

The present study was conducted between July 2023 and September 2024 at the College of Forestry, Kerala Agricultural University, Vellanikkara, Kerala, India, located at 10°54.132' N latitude and 76°27.451' E longitude. Six-month-old *Swietenia macrophylla* seedlings were obtained from the High-tech Forest Nursery of the same institute. The experiment was laid out in a Completely Randomized Design (CRD) with three treatment groups, each comprising five replications with five seedlings per replication, resulting in a total of 25 seedlings per treatment. The treatment groups consisted of a control (no hormone application), a foliar application of 0.6 mM Jasmonic Acid (JA), and a foliar application of 0.8 mM Salicylic Acid (SA) (Karthik *et al.*, 2024). The experiment comprised three stages: normal condition/ Pre-drought (seedlings irrigated to field capacity), drought condition (seedlings subjected to 25% field capacity), and recovery condition (rehydration with foliar application of JA or SA). Drought stress was induced by gradually reducing soil moisture from 80% to 25% field capacity (FC) over seven days. Soil moisture was monitored every two days using a TDR moisture meter, with gravimetric validation. To maintain 25% FC, measured water amounts were added every three days, while control seedlings remained at 80% FC. The regain stage was considered as the recovery phase, assessed 30 days after hormone treatment. Morphological, physiological, and biochemical parameters were measured at all three stages, and leaf samples from each stage were collected for proteomic analysis. Protein extraction was performed using three biological replicates, while photosynthetic and physiological parameters were evaluated in five biological replicates.

Morphometric parameters

Morphological parameters including seedling height (cm), collar diameter (mm) and number of leaves were recorded at the pre-drought, drought, and recovery stages. Additionally, shoot length (cm), shoot biomass (g), root attributes, epicormic shoot production, and total biomass (g) were assessed during the recovery phase, 30 days after hormone treatment.

Physiological parameters

Gas Parameters

Physiological changes in *Swietenia macrophylla* seedlings were assessed by measuring gas exchange parameters, including net photosynthetic rate (Pn), stomatal conductance (Gs), and transpiration rate (Tr). These measurements were conducted using a Li-6400 portable photosynthesis system between 9:00 a.m. and 11:00 a.m. The measurement conditions included a CO₂ concentration of 450 µmol·mol⁻¹, a light intensity of 1,000 µmol·m⁻²·s⁻¹, and a gas flow rate of 500 µmol·s⁻¹.

Pigment Parameters

Chlorophyll a, chlorophyll b, carotenoids, and total chlorophyll contents were determined following the method of Hiscox and Israelstam (1979). Fresh leaf samples (0.1 g) were cut into small pieces and incubated in 7 mL of dimethyl sulfoxide (DMSO) in the dark for 24 hours. Absorbance readings were taken at 645 nm (A645), 663 nm (A663), and 652 nm (A652) using a Thermo Orion AquaMate 7000 Visible Spectrophotometer. Pigment concentrations were calculated using standard formulas and expressed in mg·g⁻¹ FW.

$$\text{Chlorophyll a (mg g}^{-1}\text{)} = [12.7 (A663) - 2.69 (A645)] \times V / 1000 \times W$$

$$\text{Chlorophyll b (mg g}^{-1}\text{)} = [22.9 (A645) - 4.68 (A663)] \times V / 1000 \times W$$

$$\text{Carotenoid (mg g}^{-1}\text{)} = [7.6 (A480) - 1.49 (A510)] \times V / 1000 \times W$$

$$\text{Total chlorophyll (mg g}^{-1}\text{)} = [A652 \times 1000 \times V] / 34.5 \times 1000 \times W$$

where V = volume of the extract (mL) and W = weight of the fresh leaf (g).

Relative Water Content (RWC)

Relative water content was determined using the method of Schonfeld *et al.* (1988). Fresh leaf samples were collected, and their fresh weight (FW) was recorded. Samples were soaked in distilled water for 24 hours at room temperature to measure their turgid weight (TW) and then dried in an oven at 70°C for 72 hours to record their dry weight (DW). RWC was calculated using the formula:

$$\text{RWC (\%)} = [(FW - DW) / (TW - DW)] \times 100.$$

where FW = Fresh weight, DW = Dry weight, and TW = Turgid weight

Biochemical parameters

Proline Content

Proline content was estimated following the method described by Bates *et al.* (1973). Fresh leaf tissue (0.2 g) was homogenized in 3% Sulpho-salicylic acid, and the homogenate was centrifuged at 6,000 rpm for 5 minutes. The supernatant (1 mL) was mixed with 1.5 mL of glacial acetic acid and 2 mL of ninhydrin solution, then incubated at 100°C for 30 minutes. After cooling, the reaction mixture was extracted with 4 mL of toluene. The absorbance of the organic phase was measured at 520 nm using a spectrophotometer. Later proline was estimated by obtaining standard curve developed using L-proline as standard.

SOD activity

Superoxide dismutase (SOD) activity was estimated following the method of Giannopolitis and Ries (1977). Approximately 0.5 g of fresh leaf tissue was homogenized in 5 mL of ice-cold 50 mM phosphate buffer (pH 7.8) containing 1% (w/v) polyvinylpyrrolidone (PVP). The homogenate was centrifuged at 15,000 rpm for 15 minutes at 4°C, and the supernatant was collected as the enzyme extract. The reaction mixture (3 mL total volume) consisted of 2.6 mL of 50 mM phosphate buffer (pH 7.8), 0.1 mL of 13 mM methionine, 0.1 mL of 75 µM nitro blue tetrazolium (NBT), 0.1 mL of 100 µM EDTA, 0.05 mL of 2 µM riboflavin, and 0.05 mL of enzyme extract. The tubes were illuminated under fluorescent light (approximately 30 µmol m⁻² s⁻¹) for 15 minutes to initiate the reaction. A control tube without enzyme extract was kept in the dark to correct for non-enzymatic background. After illumination, the absorbance was measured at 560 nm using a UV-Vis spectrophotometer. One unit (U) of SOD activity was defined as the amount of enzyme required to cause 50% inhibition of NBT photoreduction under assay conditions. The activity was expressed as units per milligram of protein (U/mg protein).

CSI and MSI

Chlorophyll Stability Index (CSI) was determined following the method of Murthy and Majumdar (1962). Fresh leaves (0.1 g) were cut and placed in two test tubes containing 20 mL distilled water. One tube served as the control, while the other was incubated at 55°C for 30 minutes. After cooling, both samples were transferred to new tubes, and 7 mL of dimethyl sulfoxide (DMSO) was added. Samples were kept at room temperature overnight, and the volume was adjusted to 10 mL with DMSO. Absorbance was recorded at 652 nm using a visible spectrophotometer (Thermo Orion AquaMate 7000 Vis). CSI (%) was calculated as:

$$\text{CSI (\%)} = [\text{Total chlorophyll of treatment} / \text{Total chlorophyll of control}] \times 100$$

Membrane Stability Index (MSI) was determined following the method of Sairam (1994). Fresh leaf samples (100 mg) were placed in two test tubes containing 10 mL distilled water. One set was incubated at 35°C for 30 minutes (C1), and the other at 100°C for 15 minutes (C2). After cooling, leaf discs were removed, and the electrical conductivity of both samples was measured using a conductivity meter. MSI was calculated as:

$$\text{MSI (\%)} = [1 - \text{C1} / \text{C2}] \times 100$$

Protein extraction and SDS PAGE

Proteins were extracted using the Trichloroacetic acid (TCA)-acetone method (Niu *et al.*, 2018), and their concentration was determined using the Bradford assay (Balion, 1996). Frozen leaf samples were homogenized with polyvinyl polypyrrolidone (10% of sample weight) in liquid nitrogen and mixed with 10% TCA-acetone. After centrifugation at 5,000 rpm for 20 minutes at 4°C, the supernatant was discarded. The pellet was washed with 80% methanol containing 0.1 M ammonium acetate, centrifuged, and resuspended in 80% acetone. Following additional centrifugation and air-drying, the pellet was resuspended in a 1:1 phenol (pH 7.9)/SDS buffer solution. After centrifugation (5000 rpm for 20 minutes), protein precipitation was induced using methanol containing 0.1 M ammonium acetate. The protein pellet was washed with 100% methanol and 80% acetone, dissolved in re-suspension buffer, and processed for analysis.

SDS-PAGE was performed following procedures reported by Singh *et al.*, (1991). Focused IPG strips were equilibrated sequentially: first in buffer I (20% glycerol, 0.375 M Tris-HCl pH 8.8, 6 M urea, 2% SDS, 130 mM DTT), then in buffer II (same composition, but with 135 mM iodoacetamide replacing DTT). Separation was done using 12% polyacrylamide gels (20 cm × 18 cm, 1.5 mm thickness) in a PROTEAN II xi system (Bio-Rad) at 200 V for 7.5 hours. Gels were stained overnight with 0.1% Coomassie Brilliant Blue G-250, destained, and stored in 5% acetic acid at 4°C.

In-gel digestion

Protein spots excised from preparative gels underwent in-gel digestion with trypsin, following three key steps: reduction/alkylation, trypsin digestion, and peptide extraction. Differentially expressed protein spots were excised, washed three times with double-distilled water, and destained with 25 mM NH₄HCO₃ for Coomassie Brilliant Blue (CBB) G-250-stained spots. The protein spots were then dehydrated with 50% (v/v) acetonitrile (ACN) in 25 mM NH₄HCO₃, reduced with 10 mM dithiothreitol (DTT) in 50 mM NH₄HCO₃ for 1 hour at 56 °C, and alkylated with 55 mM iodoacetamide in 50 mM NH₄HCO₃ for 1 hour at 25 °C. Samples were dried twice using 100% ACN and digested overnight at 37 °C with sequencing-grade modified trypsin in 50 mM NH₄HCO₃. Peptides were extracted by washing the gel pieces twice with 0.1% trifluoroacetic acid (TFA) in 67% ACN, and the extracts were pooled and lyophilized. The lyophilized tryptic peptides were dissolved in 0.1% TFA, desalted using C18 Ziptips, mixed with 5 mg/mL α-cyano-4-

hydroxycinnamic acid in 0.1% TFA and 50% ACN, and spotted onto MALDI target plates for further analysis.

MALDI-TOF MS analysis and database searching

Peptide mass spectra were obtained using an Auto Flex II MALDI TOF/TOF mass spectrometer (Bruker Daltonics) equipped with a pulsed N₂ laser ($\lambda = 337$ nm, 50 Hz). Data analysis was performed using Flex Analysis v2.4 and the MASCOT search engine v2.2. Proteins were identified using the following parameters: database (MSDB, NCBI nr, Swissprot), taxonomy (green plants, Viridiplantae), enzyme (trypsin), peptide mass tolerance (≤ 100 ppm), and maximum missed cleavages (1). Protein identification was considered valid based on a minimum of five matched peptides, a molecular weight search (MOWSE) score above the threshold, and sequence coverage percentage. False Discovery Rates (FDR) were assessed using decoy database searches, with a 0% FDR threshold.

GO, PPI and fold change analysis

Identified proteins were subjected to Gene Ontology (GO) enrichment using ShinyGO v0.75. GO terms were categorized under biological processes, molecular functions, and cellular components to elucidate the functional roles of proteins under different treatments. To further explore functional interactions, protein-protein interaction (PPI) analysis was performed using the STRING database (version 11.5), which integrates both physical and functional protein associations. A high-confidence interaction score was applied to filter significant interactions, and network visualization helped identify major hubs and interaction clusters. For additional refinement, protein annotations were cross-referenced with the Gene Ontology (GO) database (www.geneontology.org) emphasizing biological processes associated with stress response. Fold change (FC) analysis was conducted to determine differential protein expression. Proteins were classified as upregulated if $\log_2(\text{FC}) > 0.6$ and downregulated if $\log_2(\text{FC}) < -0.6$, with a statistical significance threshold of $P < 0.05$. These differentially expressed proteins were prioritized for functional enrichment and network analysis.

Statistical Analysis

Morphological, physiological, and biochemical parameters were analyzed using one-way Analysis of Variance (ANOVA) in R software (v4.3.1). When significant differences between treatments were obtained, mean values were compared using Least Significant Difference (LSD) test at $p < 0.05$. A 5% significance level was applied for hypothesis testing.

3. Results

Morphometric parameters

The morphometric analysis of *Swietenia macrophylla* seedlings under normal, drought, and recovery conditions demonstrated distinct trends across treatments (Tables 1 and 2). Under drought stress, *S. macrophylla* seedlings exhibited typical symptoms, including wilting, yellowing, curling, and leaf abscission, leading to a marked reduction in vitality (Fig. 01). In contrast, seedlings under normal conditions displayed healthy growth. However, no significant differences were observed during the normal and drought stage, as uniform drought conditions were induced at 25% field capacity. Under normal and drought conditions, plant height remained comparable across control, SA (0.8 mM), and JA (0.6 mM)-treated seedlings, with values ranging from 85.55 to 88.05 cm. However, during the recovery phase, JA-treated seedlings exhibited the tallest height (96.73 cm), followed by SA (90.60 cm) and control (88.25 cm). Similarly, leaf count

remained stable under drought but increased during recovery, with JA-treated seedlings producing 24 leaves, followed by SA (20) and control (16), reflecting a hormone-induced enhancement in foliar development. Collar diameter showed consistent values under stress, but improved post-recovery, with JA registering 9.989 mm, SA 9.471 mm, and control 9.130 mm.

Significant improvements in root and shoot parameters were observed after the 30 days of post hormone treatments. JA-treated seedlings recorded the highest shoot fresh weight (38.58 g), shoot dry weight (27.83 g), and shoot length (79.67 cm), outperforming both SA (30.05 g, 19.77 g, 69.56 cm) and control (22.07 g, 14.91 g, 62.11 cm), respectively. JA also induced the greatest number of epicormic shoots (6.9), while SA and control produced 2.9 and 1.8, respectively, indicating a strong regenerative response.

SA-treated seedlings had the highest root dry weight (8.34 g), followed by JA (7.12 g) and control (4.75 g). Root fresh weight ranged from 10.30 g (control) to 13.25 g (SA), and root length varied from 17.00 cm to 19.33 cm across treatments. With regard to total biomass accumulation, JA-treated seedlings recorded the highest value (33.13 g), followed by SA-treated (25.89 g) and control seedlings (20.25 g). Root-to-shoot ratios remained relatively stable across treatments (0.245–0.275), suggesting balanced biomass allocation under hormone influence. Overall, the phenotype morphometric findings underscore the superior recovery performance of seedlings treated with 0.6 mM JA, followed by 0.8 mM SA, particularly evident 30 days after stress withdrawal.

Physiological parameters

Physiological parameters varied significantly across treatment groups during drought stress and recovery phases. The net photosynthetic rate (Pn), transpiration rate (Tr), stomatal conductance (Gs), relative water content (RWC), and pigment levels declined under drought stress (Fig. 2). Under normal irrigation, Pn was $3.574 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, decreasing by 43.6% to $2.016 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ during drought stress. Upon recovery, JA treatment (0.6 mM) improved Pn by 48.0% to $2.98 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, while SA treatment (0.8 mM) enhanced it by 33.3% to $2.686 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. Gs and Tr also decreased significantly under drought conditions, with Gs dropping to $0.006 \text{ mol m}^{-2} \text{ s}^{-1}$ and Tr to $0.540 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$, compared to their normal values of $0.091 \text{ mol m}^{-2} \text{ s}^{-1}$ and $1.063 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$, respectively. During recovery, SA restored Gs to $0.091 \text{ mol m}^{-2} \text{ s}^{-1}$, while JA enhanced Tr by 123.3%, reaching $1.206 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$. RWC decreased from 74.77% under normal conditions to 52.25% during drought stress. After recovery, untreated plants showed a RWC of 56.08%, whereas SA and JA treatments increased it to 62.67% and 70.14%, respectively.

Pigment levels, including chlorophyll-a (Chl-a) and chlorophyll-b (Chl-b), showed significant recovery with hormonal treatments. Drought stress reduced Chl-a from 1.846 mg/g to 1.263 mg/g and Chl-b from 1.401 mg/g to 0.873 mg/g. Following recovery, JA treatment increased Chl-a to 1.979 mg/g and Chl-b to 1.235 mg/g, while SA treatment enhanced Chl-a to 1.549 mg/g and Chl-b to 1.100 mg/g. Carotenoid content also decreased from 1.257 mg/g under normal conditions to 0.795 mg/g during drought stress, recovering to 1.320 mg/g with SA and 1.080 mg/g with JA.

Biochemical parameters

Biochemical responses to drought stress were evident through variations in proline content, superoxide dismutase (SOD) activity, chloroform stability index (CSI), and membrane stability index (MSI) (Fig. 3). Proline accumulation, a key osmoprotectant and marker of stress, increased from $1.878 \mu\text{g/g}$ under normal conditions to $3.857 \mu\text{g/g}$ during

drought. Recovery treatments effectively reduced proline levels to 1.180 µg/g with JA and 1.903 µg/g with SA, indicating stress alleviation. Similarly, SOD activity, a crucial enzymatic antioxidant that scavenges superoxide radicals, showed a significant rise under drought stress. Under normal conditions, SOD activity was relatively low 29.4 U/mg protein in control, 28.2 U/mg protein in SA, and 30.5 U/mg protein in JA. It sharply increased during drought, reaching 88.1 U/mg in control, 87.3 U/mg in SA, and 89.2 U/mg in JA. Upon recovery, activity declined to 74.8 U/mg protein in control, while JA and SA treatments showed reduced levels of 38.7 and 53.1 U/mg protein, respectively. CSI also decreased under drought conditions, dropping to 49.2% compared to 66.3% under normal conditions. During recovery, JA restored CSI to 69.5%, while SA further enhanced it to 72.0%. MSI followed a similar trend, declining to 52.1% under drought from a normal value of 63.2%, and upon recovery, increasing to 68.5% with JA and 61.5% with SA. These findings indicate that both JA and SA effectively mitigate physiological and biochemical stress, with JA showing superior recovery.

PCA and correlation analysis

Principal component analysis was conducted to identify key traits contributing to seedling recovery following stress, with defense hormone treatments of JA and SA. The first two principal components (PC1 and PC2) together accounted for 100% of the total variation, with PC1 alone explaining 80.2% and PC2 explaining 19.8%. As shown in the PCA biplot (Fig. 4), PC1 was heavily influenced by growth-promoting and physiological parameters. Traits such as number of leaves, shoot length, seedling height, collar diameter, shoot fresh weight, shoot dry weight, relative water content, membrane stability index, chlorophyll a, total chlorophyll, photosynthetic rate, and total biomass showed strong positive loadings on PC1. These traits were closely associated with the JA (0.6 mM) treatment, which occupied the far-right quadrant of the biplot indicating its strong influence on these traits and overall seedling vigor during the recovery phase.

Conversely, proline, superoxide dismutase, and root-to-shoot ratio showed negative loadings on PC1, aligning more with the control group, suggesting higher stress levels or lack of growth stimulation in untreated seedlings. PC2, contributing 19.8% of variation, was primarily influenced by root biomass and biochemical traits, with strong negative loadings for root fresh weight, root dry weight, carotenoids, transpiration rate, and chlorophyll b. These parameters were closely associated with the SA (0.8 mM) treatment, which was positioned in the lower part of the biplot, suggesting its influence on root-related traits and stress pigment accumulation. Notably, the control group clustered in the top left quadrant, distanced from most growth and physiological parameters, indicating poor performance during the regain phase.

A strong and consistent pattern emerged from the correlation analysis (Table 3), revealing that specific morphological, physiological, and biochemical traits are critically associated with enhanced drought stress tolerance and post-stress recovery in *Swietenia macrophylla* seedlings. Among the treatments, JA was most effective in improving recovery, followed by SA, while seedlings without hormone treatment exhibited poor recovery. In morphological traits, shoot length showed a significant positive correlation with number of leaves and shoot number along with shoot fresh weight and dry weight, suggesting that vigorous shoot development is associated with enhanced vegetative resilience. Root traits also contributed significantly, with a strong correlation between root fresh weight and dry weight, indicating that robust root systems play a pivotal role in recovery from drought stress. Physiologically, the photosynthetic rate was highly and positively correlated with relative water content, chlorophyll pigments and carotenoids, implying that water retention and pigment stability are essential for maintaining

photosynthetic efficiency during drought. Notably, RWC also showed strong positive associations with total chlorophyll, carotenoids, and membrane stability index (MSI), highlighting its central role in sustaining cellular function under stress. On the other hand, photosynthetic rate showed a strong negative correlation with proline and SOD activity, indicating that plants experiencing greater oxidative stress had suppressed photosynthesis. Biochemically, proline content exhibited a strong positive correlation with SOD activity, confirming its role as a key osmoprotectant and antioxidant in stress response. Chlorophyll a also correlated positively with number of leaves and extended shoot length, reinforcing the link between pigment retention and vegetative growth. Among the treatments, JA-treated seedlings consistently showed higher values for these key traits, followed by SA, suggesting a superior role of JA in activating stress tolerance pathways.

Proteomic analysis

Comparative proteomic analysis revealed significant variations in protein expression across normal, stress, and recovery conditions. Proteins were extracted using the TCA-acetone method, visualized via SDS-PAGE, and analyzed through Peptide Mass Fingerprinting (PMF) and MALDI-TOF MS (Table 4). Under normal conditions, balanced protein expression was observed, with prominent bands at 50 kDa, 37 kDa, and 25 kDa. Drought stress significantly reduced protein expression, particularly at lower molecular weights, suggesting membrane damage and decreased photosynthetic activity. Recovery without hormone treatment showed partial restoration of protein expression. However, SA treatment significantly enhanced the expression of defense-related proteins, particularly at 50 and 37 kDa size (Fig. 5). JA treatment facilitated the most substantial recovery, with high expression of structural and defense-related proteins (~50 kDa). Key proteins identified included heat shock protein 90 (HSP90), DAHP synthase, and ribulose biphosphate carboxylase (RuBISCO), which play critical role in photosynthesis and defense. SA treatment significantly increased the expression of RuBISCO, guanine nucleotide-binding protein alpha-1, and PGDH1, enhancing metabolic recovery and defense. JA treatment elevated the expression of stress-responsive proteins, such as RuBISCO, HSP90, and allene oxide synthase, indicating its role in adaptive stress responses.

Drought stress induced the expression of defense-related proteins like Heat shock protein 90 (HSP90), sulfiredoxin, and DAHP synthase, alongside metabolic proteins like ribulose biphosphate carboxylase (RuBISCO), which supported photosynthesis. During recovery without hormone treatment, protein levels are partially restored, with guanine nucleotide-binding protein alpha-1 remaining prominent. The application of SA significantly boosted the defense response during drought recovery, increasing the expression of PGDH1, RuBISCO, and guanine nucleotide-binding protein alpha-1, enhancing defense and photosynthesis. JA treatment during recovery also contributed to stress adaptation, with elevated expression of proteins such as RuBISCO, guanine nucleotide-binding protein alpha-1, Heat stress transcription factor 4A, DAHP synthase, and Allene oxide synthase. Total protein concentrations during recovery were highest with SA treatment, underscoring its superior role in enhancing metabolic and defense-related proteins. The application of SA significantly boosted the defense response during drought recovery, increasing the expression of PGDH1, RuBISCO, and guanine nucleotide-binding protein alpha-1, enhancing defense and photosynthesis.

JA treatment during recovery also contributed to stress adaptation, with elevated expression of proteins such as RuBISCO, guanine nucleotide-binding protein alpha-1, Heat stress transcription factor 4A, DAHP synthase, and Allene oxide synthase. The differential

expression of identified proteins based on concentration is summarised in Fig. 6. Total protein concentrations during recovery were highest with SA treatment, underscoring its superior role in enhancing metabolic and defense-related proteins. The protein concentration(mg/g) variation between the treatment at different conditions is summarised in Fig. 9.

Biological functions of identified proteins

Functional annotation of identified proteins revealed distinct shifts in functional priorities under drought stress and recovery conditions. Under normal conditions, protein functions were predominantly associated with photosynthesis (28%) and metabolism (27%), supported by defense mechanisms (18%) and secondary metabolite production (9%) to maintain a balanced physiological state (Fig. 7). During drought stress, there was a marked shift toward defense mechanisms (38%), accompanied by reductions in photosynthesis (25%) and metabolism (12%), reflecting the prioritization of protective responses to mitigate stress-induced damage. Recovery without hormonal treatment showed a moderate return to normal functional states, with photosynthesis (29%) and metabolism (27%) regaining prominence. However, defense (14%) and secondary metabolite production (14%) remained elevated, indicating partial adaptation and recovery. In seedlings treated with SA during recovery, photosynthesis accounted for 28% of protein functions, while defense and metabolism were equally prioritized at 18%, and hormonal signaling accounted for 9%, suggesting a stable recuperation pattern. Conversely, JA treatment exhibited a more balanced response, with photosynthesis (22%) and metabolism (22%) on par, defense (21%) slightly lower, and secondary metabolites (14%) and hormonal signalling (7%) present. This pattern suggests that JA treatment modulates multiple functional pathways, contributing to a well-rounded stress recovery mechanism.

Both SA and JA treatments highlighted the critical role of hormonal signalling in recovery processes (Fig. 7). SA treatment primarily supported energy production and stress adaptation, whereas JA treatment effectively enhanced both growth and stress resilience. These results underscore the importance of employing defense hormones to optimize recovery and functional stability in drought-stressed *Swietenia macrophylla* seedlings.

Fold change analysis of identified proteins

Fold change analysis revealed significant alterations in protein abundance under drought and hormone-treated conditions in *Swietenia macrophylla* seedlings (Table 5). A total of 16 differentially abundant proteins were identified, predominantly involved in defense, photosynthesis, metabolism, and gene expression, with subcellular localization primarily in the chloroplasts, ER, and plasma membrane. Under drought stress, key photosynthetic proteins like RUBP and Cytochrome b6-f complex subunit were down-regulated, while stress-responsive proteins such as DAHP synthase, AOS3, and HSP were up-regulated, reflecting a typical stress-induced metabolic shift. Following regain control, partial recovery was observed in proteins like SAP, ChlaP, and GKP, though many photosynthetic and metabolic proteins remained suppressed. SA treatment enhanced the expression of several defense and regulatory proteins (Zinc finger CCCH domain, Protein MEI2-like 7), indicating its role in boosting gene expression and signalling during recovery. In contrast, JA treatment showed a more robust response, with up-regulation of proteins involved in photosynthesis (RUBP), defense (AOS3, FDH1), and gene regulation, suggesting JA's superior role in stress recovery and proteome reprogramming. Overall, hormonal treatments particularly JA modulated protein abundance more effectively than

re-watering alone, enhancing stress resilience and recovery in *Swietenia macrophylla* seedlings.

Protein-Protein Interaction (PPI) Network Analysis

To further explore the functional associations and cooperative behaviour among differentially expressed proteins under drought and hormone treatments, a protein-protein interaction (PPI) network was constructed using the STRING database (Fig. 8). The interaction map centered around the Ribulose biphosphate carboxylase small chain 2 (Ris2) protein, a crucial component of the photosynthetic apparatus, which showed multiple direct and indirect interactions with several proteins involved in chloroplast function and stress response. The network revealed a dense interaction cluster comprising proteins such as petA, petN, B4FSD8_MAIZE, C4JAJ6_MAIZE, and several uncharacterized chloroplast-localized proteins. These interactions indicate that Ris2 serves as a central hub coordinating photosynthetic regulation and stress mitigation pathways. Notably, interactions with A0A1D6P793 and A0A1D6KJM8 suggest possible co-regulation with light-harvesting complex proteins and carbon metabolism enzymes.

Furthermore, several proteins, including A0A1D6LEW9 and A0A1D6EF84, were linked through co-expression and predicted functional associations, pointing to their involvement in maintaining chloroplast integrity and energy transduction under stress. The presence of G-protein-coupled receptor (GPCR)-like signaling proteins in the network reinforces the influence of hormonal signalling particularly under JA and SA treatments on protein interaction dynamics. The interaction map also indicated that JA treatment enhanced the complexity and number of protein connections within the photosynthesis-related cluster, suggesting that JA possibly promotes the formation of multi-protein complexes to stabilize photosynthetic efficiency during drought stress. In contrast, SA treatment showed fewer central hub interactions but included proteins related to redox regulation and cytosolic signalling, reflecting its role in intracellular stress buffering. Overall, the PPI network analysis highlights the tightly knit collaboration of stress-responsive proteins, particularly within chloroplast compartments, and underscores the role of defense hormones in modulating protein networks that sustain photosynthetic and metabolic stability under drought conditions.

Gene Ontology (GO) Enrichment Analysis

Gene Ontology (GO) enrichment analysis ($p < 0.05$) of differentially expressed proteins revealed significant biological insights into the stress-responsive functions modulated by JA and SA treatments under drought conditions in *Swietenia macrophylla*. The GO terms were classified into three major domains: Biological Process (BP), Molecular Function (MF), and Cellular Component (CC), each revealing specific hormone-induced functional responses (Fig. 10).

Within the Biological Process domain, significant enrichment was observed for terms related to photosynthesis, aromatic amino acid biosynthetic and metabolic processes, and responses to various stimuli, including light, radiation, and pheromones (Fig. 10A). These processes were predominantly upregulated in JA-treated seedlings, followed by SA treatments. Notably, photosynthesis-related proteins exhibited higher expression under JA, indicating the hormone's potential to sustain photosynthetic activity during drought. Enrichment of aromatic amino acid metabolism, a key pathway for phenolic compound biosynthesis, was also more prominent in JA treatments. Furthermore, JA significantly enhanced expression of genes involved in stimulus responses and light perception, suggesting an amplified hormonal regulation of stress perception pathways. The G protein-coupled receptor signaling pathway, important for

hormonal signal transduction, was also enriched under JA treatment, indicating its role in strengthening the drought signaling network.

In the Molecular Function category, proteins associated with ion binding, particularly those involved in metal ion interactions (e.g., magnesium, iron, manganese), were upregulated, especially under JA treatment (Fig. 10B). These functions are critical for maintaining enzymatic activities related to photosynthesis and oxidative stress management. Carboxy-lyase activity and 3-deoxy-7-phosphoheptulonate synthase activity, which are involved in carbon fixation and the shikimate pathway respectively, showed higher expression in JA-treated seedlings. The enrichment of 3-deoxy-7-phosphoheptulonate synthase, a key enzyme in secondary metabolite biosynthesis, points toward JA's role in enhancing the production of precursor compounds for SA and other phenolics. GPCR activity was also enriched under JA treatment, highlighting hormone-mediated signal amplification during stress.

In terms of the Cellular Component domain, the majority of the differentially expressed proteins were localized to the chloroplast, thylakoid membrane, plasto-globule, and cytoplasm. Proteins associated with the chloroplast and thylakoid membranes were predominantly upregulated under JA treatment, suggesting hormonal protection of the photosynthetic machinery (Fig. 10C). Thylakoid membrane-related proteins, which are involved in light harvesting and energy transfer, were notably enriched in JA-treated seedlings, indicating a potential role of JA in maintaining photosynthetic efficiency under drought. Additionally, proteins associated with plastoglobules, which are involved in lipid metabolism and antioxidant function, were enriched under both JA and SA treatments. In contrast, SA-treated seedlings showed greater enrichment of cytoplasmic proteins, many of which were involved in protein folding, ROS detoxification, and intracellular signaling, suggesting SA's role in maintaining cellular homeostasis under drought stress.

Overall, the GO enrichment results clearly demonstrate that JA exerted a more comprehensive influence on stress-responsive processes compared to SA. JA predominantly enhanced biological processes related to photosynthesis and secondary metabolism, stimulated enzymatic and cofactor-binding functions, and supported structural and functional maintenance of chloroplast-associated components. SA, on the other hand, contributed significantly to cytoplasmic protein regulation and intracellular detoxification mechanisms. These findings indicate that both hormones play coordinated yet distinct roles in mediating drought tolerance in *Swietenia macrophylla* through the modulation of specific functional gene categories.

4. Discussion

Water deficit remains one of the major environmental challenges limiting the productivity of tropical plantation species in Peninsular India, where rain-fed agroforestry and plantation forestry systems predominate. In this context, understanding drought resilience mechanisms—particularly those mediated by defense hormones is critical for improving growth and stress adaptation in economically valuable tree species such as *Swietenia macrophylla*. Plants employ a range of physiological, biochemical, and molecular responses to counteract drought stress, but these responses are often species-specific. This study contributes novel insights by examining the morphometric, physiological, and proteomic responses of *Swietenia macrophylla* seedlings to drought stress and the mitigating roles of exogenously applied JA and SA.

Morphometric insights

Our findings confirm that drought stress, simulated by maintaining soil at 25% field capacity, significantly disrupts plant homeostasis, leading to visible symptoms such as wilting, yellowing, leaf curling, and abscission. These stress symptoms, observed uniformly across all treatments, underscore the inherent sensitivity of *S. macrophylla* to water deficit, corroborating previous reports by Horta *et al.*, (2014) Zhou *et al.*, (2018) and Bhattacharya (2021). Interestingly, despite clear signs of physiological stress, morphometric traits such as plant height, collar diameter, and leaf number did not significantly differ across treatments during the drought phase. This suggests either a threshold effect in early stress response or a latency in the morphological manifestation of stress, as also reported by Li *et al.*, (2023) and Longo *et al.*, 2018. The most compelling differences emerged during the 30-day post-stress recovery period, wherein hormone-treated seedlings especially those treated with JA, exhibited enhanced growth and biomass accumulation. JA-treated seedlings recorded significant improvements in height (96.73 cm), collar diameter (9.989 mm), leaf number (24), and shoot biomass, compared to SA-treated and control seedlings (Table 1). The stimulation of epicormic shoots in JA-treated plants further indicates reactivation of dormant meristems and axillary bud development, underscoring JA's role in structural regeneration and growth reprogramming. These findings align with previous studies in herbaceous species such as wheat, where JA was found to improve drought adaptability through enhanced photosynthetic performance, antioxidant activity, and stomatal regulation (Saxena *et al.*, 2019).

In contrast, SA-treated seedlings exhibited pronounced improvements in root development, showing the highest root fresh and dry biomass among treatments. Although aboveground growth metrics were relatively modest, SA appears to support drought recovery by enhancing root system architecture, thereby facilitating better water uptake and root function restoration (Table 2). This observation aligns with reports by Hayat *et al.*, (2013), who emphasized SA's role in modulating root development and oxidative stress responses. Root length under SA treatment was comparable to that under JA, indicating its contribution to effective soil exploration and moisture acquisition. Total biomass accumulation peaked in JA-treated seedlings (33.13 g), reflecting a coordinated enhancement in both shoot and root compartments. Notably, the root-to-shoot ratio remained relatively consistent across treatments (0.245–0.275), suggesting that exogenous hormone application promoted balanced biomass allocation without altering growth equilibrium, a key trait for maintaining functional stability during and after drought. These findings illustrate that JA and SA confer drought resilience through distinct yet complementary mechanisms, JA by promoting shoot regeneration and accelerated recovery, and SA by reinforcing root structure and sustaining water uptake. The significant morphological gains observed during the recovery phase highlight the critical role of hormone timing and duration in shaping drought recovery outcomes. Moreover, the differential effects of JA and SA reflect their unique signalling pathways, with JA often linked to rapid growth responses, while SA contributes to sustained resilience and stress buffering. These results are consistent with broader research indicating the efficacy of JA and SA in improving drought tolerance across various plant systems (Raza *et al.*, 2020; Wang *et al.*, 2021). However, the efficacy of these hormones is often dose- and species-dependent (Hayat *et al.*, 2013), and the promising results observed in *Swietenia macrophylla* suggest their potential for integration into drought mitigation strategies within tropical forestry (Liu *et al.*, 2023; Chen *et al.*, 2020).

Physiological insights

From a physiological standpoint, drought stress significantly impaired key plant functions, including photosynthetic rate (P_n), stomatal conductance (G_s), transpiration

rate (Tr), relative water content (RWC), and pigment composition (Fig. 02). Net photosynthetic rate declined by 43.6%, from $3.574 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ under normal conditions to $2.016 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ during drought, aligning with Bhattacharya (2021), who reported similar reductions in CO_2 assimilation in tropical species under water deficit. The simultaneous suppression of Gs (from 0.0189 to $0.0067 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$) and Tr (from 1.950 to $0.872 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$) highlights a characteristic drought-induced stomatal closure, an immediate defense strategy to reduce transpiration, though it limits CO_2 uptake and hampers photosynthetic efficiency a trade-off well-documented by Ghassemi-Golezani & Farhangi-Abriz (2021). RWC, an indicator of plant water status, also declined significantly under stress, dropping from 74.77% to 52.25%. Pigment levels were similarly affected: Chl-a decreased from 1.846 to 1.263 mg/g, Chl-b from 1.401 to 0.873 mg/g, and carotenoids from 1.347 to 0.968 mg/g. These reductions reflect impaired photosynthetic machinery and oxidative stress, corroborated by reports from Tatar *et al.*, (2015) and Todorova *et al.*, (2022).

Upon rewatering, the influence of hormonal priming became evident. JA at 0.6 mM resulted in a 48.0% increase in Pn (to $2.984 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), while SA at 0.8 mM improved Pn by 33.3% (to $2.688 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), underscoring JA's stronger efficacy in restoring photosynthetic function. JA-treated seedlings also exhibited a 123.3% increase in Tr (from 0.861 to $1.924 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$), suggesting improved root water uptake and enhanced stomatal regulation. SA treatment, on the other hand, effectively restored Gs to near-normal levels ($0.0182 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$), promoting better water-use efficiency. RWC recovered to 70.14% and 62.67% in JA- and SA-treated seedlings, respectively, demonstrating the effectiveness of hormonal treatment in restoring cellular hydration and osmotic balance. These improvements are consistent with findings by Pflug *et al.* (2018) and Luo *et al.* (2020), who emphasized hormone-mediated recovery of hydric equilibrium following abiotic stress. Recovery of chlorophyll content was also more pronounced in JA-treated plants, where Chl-a and Chl-b levels were restored to 1.979 and 1.235 mg/g, respectively, surpassing pre-stress values indicating either enhanced biosynthesis or reduced degradation of photosynthetic pigments. SA also facilitated moderate pigment recovery, with Chl-a and Chl-b levels at 1.691 and 1.095 mg/g, respectively. Notably, carotenoid content was higher in SA-treated seedlings (1.320 mg/g) compared to JA-treated ones (1.080 mg/g), suggesting SA's potential role in enhancing antioxidant protection during recovery, as also noted by Todorova *et al.*, (2021).

The observed differential recovery trends among physiological parameters indicate that recovery from drought is a dynamic, multi-phase process regulated by complex hormonal interactions. The faster rebound of Pn compared to Gs, for example, may lead to altered intrinsic water-use efficiency, a pattern highlighted by Raubenheimer *et al.*, (2023) and Sánchez-Gómez & Aranda, 2024. Such disparities underscore the need to assess not only the magnitude of recovery but also the timing and coordination among physiological processes. These findings reinforce the conclusions of earlier studies (Ávila *et al.*, 2011; Chen *et al.*, 2016; Sun *et al.*, 2018) that hormonal treatments can significantly aid in the repair of drought-induced damage, particularly in tropical species with high water sensitivity. The integrated recovery of Pn, Tr, Gs, RWC, and pigments illustrates that JA and SA effectively facilitate the physiological restoration of seedlings post-drought, with JA demonstrating a more pronounced influence on water relations and photosynthetic components. Thus, the results collectively illustrate a multi-dimensional view of how drought stress and recovery influence plant physiology, emphasizing not only the physiological decline but also the potential for recovery through careful management of hormonal treatments. This insight can guide further investigations aimed at augmenting drought tolerance in vulnerable crops through targeted hormone

applications or the development of stress-resistant genotypes (Zhang *et al.*, 2018; Bisaga *et al.*, 2017). The results indicate that understanding the regulatory mechanisms of hormonal responses during stress and recovery phases is vital for improving yield and sustainability in forestry practices, particularly in the face of increasing climate volatility (Evans & Al-Hamdani, 2015; Song *et al.*, 2017).

Biochemical insights

The biochemical responses of plants under drought stress provide critical insights into their adaptive capacity and resilience mechanisms. A substantial increase in proline content from 1.878 µg/g under normal conditions to 3.857 µg/g during drought highlights its role as a key osmoprotectant and biochemical stress marker (Fig. 03). Proline accumulation is a well-documented adaptive strategy to mitigate cellular dehydration, stabilize subcellular structures, and maintain osmotic balance, as supported by previous studies (Muzammil *et al.*, 2018; Jurkonienė *et al.*, 2023). Following hormone application, proline levels declined to 1.180 µg/g with JA (JA) and 1.903 µg/g with SA (SA), demonstrating the efficacy of these treatments in alleviating drought stress and facilitating recovery (Chapman *et al.*, 2022; Jurkonienė *et al.*, 2023). Jurkonienė *et al.*, (2023) further confirmed that proline plays a central role not only in drought resistance but also in the post-stress recovery of plants. Similarly, the activity of Superoxide Dismutase (SOD), a vital component of the plant antioxidant defense mechanism, showed a marked elevation under drought stress—from 29.4 U/mg protein in control plants to 88.1 U/mg during drought. This increase suggests an upregulation of ROS-scavenging activity to counteract oxidative stress induced by drought (Marsita & Arumingtyas, 2014; Abid *et al.*, 2018). During the recovery phase, SOD activity decreased to 74.8 U/mg in untreated control seedlings, while hormone-treated plants exhibited further reductions—38.7 U/mg with JA and 53.1 U/mg with SA. These trends suggest that hormonal treatments not only reduce the oxidative burden but also promote enzymatic homeostasis during recovery (Shrestha *et al.*, 2022).

Indicators of membrane stability, such as the Chloroform Stability Index (CSI) and Membrane Stability Index (MSI), also reflect the plant's physiological state during stress and recovery. CSI declined from 66.3% to 49.2% under drought conditions, pointing to compromised photosynthetic membranes and stress-induced lipid peroxidation (Sohail *et al.*, 2022). However, CSI values were restored to 69.5% and 72.0% with JA and SA, respectively, indicating that these hormones aid in membrane repair and stabilization (Meena *et al.*, 2017; Jurkonienė *et al.*, 2023). MSI followed a comparable pattern, decreasing from 63.2% to 52.1% during drought, but rebounding to 68.5% (JA) and 61.5% (SA) post-treatment, further supporting their protective role in mitigating oxidative membrane damage (Shrestha *et al.*, 2022; Dien *et al.*, 2019). Collectively, these biochemical alterations underscore the oxidative and osmotic challenges plants face during drought, marked by proline accumulation and enhanced antioxidant enzyme activity (Liu *et al.*, 2019; Kishor & Sreenivasulu, 2013). Beyond its osmoprotective function, proline is implicated in stress signal transduction, influencing downstream pathways involved in cellular protection and recovery (Jurkonienė *et al.*, 2023). JA and SA treatments effectively modulated these stress-responsive markers, facilitating recovery and underscoring their potential as biostimulants for improving drought resilience in forestry and agriculture (La *et al.*, 2020). While the exact dynamics of ROS in these stress-recovery pathways require further exploration, current findings affirm that controlling oxidative stress and maintaining cellular homeostasis are pivotal for drought adaptation. Proline metabolism, antioxidant enzyme regulation, and membrane integrity, when coordinated through targeted hormonal treatments, present promising avenues for enhancing plant stress tolerance (Renzetti *et al.*, 2024; Nasrin *et al.*, 2020). The

coordinated biochemical responses involving proline accumulation, enhanced SOD activity, and stabilized membrane indices (CSI and MSI) illustrate the adaptive strategies employed by plants under drought conditions. Hormonal interventions with JA and SA significantly improved post-stress recovery, highlighting their utility in mitigating drought-induced damage. These findings advocate for the strategic use of defense hormones to bolster plant resilience and ensure sustainable productivity under water-limited conditions.

PCA and correlation analysis

The principal component analysis (PCA) underscored the influential role of growth-promoting and physiological parameters in the recovery of *Swietenia macrophylla* seedlings from drought stress (Fig. 04). PC1, which explained nearly 80% of the variation, was strongly associated with traits such as shoot length, number of leaves, collar diameter, and biomass—all of which aligned with JA treatment, highlighting its central role in enhancing post-stress vigor (Chen *et al.*, 2016). These traits serve as reliable indicators of recovery efficiency and stress resilience.

Negative loadings on PC1, such as proline content and superoxide dismutase (SOD) activity, were more evident in control seedlings, reflecting higher stress levels in untreated plants (Chai *et al.*, 2010; Parvin *et al.*, 2019). This inverse relationship indicates that oxidative stress and osmotic imbalance may hinder recovery when hormonal support is absent. PC2 highlighted root-associated and biochemical traits. Notably, SA-treated seedlings were positioned in this dimension, suggesting that SA contributed more to root development than shoot recovery (Shi *et al.*, 2016). Though beneficial, SA's influence appeared less comprehensive than that of JA regarding whole-plant recovery under drought.

Correlation analysis reinforced these observations (Table 3), showing strong positive associations between shoot traits (length, fresh weight, dry weight) and the number of leaves, pointing to foliar development as a key component of drought resilience (Fujimoto *et al.*, 2024). Furthermore, significant correlations among chlorophyll content, relative water content, and photosynthetic rate revealed their pivotal role in facilitating recovery, particularly in JA-treated plants (Schneider *et al.*, 2019; Cano *et al.*, 2014). Together, the PCA and correlation analyses provide a robust framework to understand the physiological and morphological responses of *Swietenia macrophylla* to defense hormone treatments. This insight can inform the strategic application of phytohormones in tropical forestry for improving seedling resilience to abiotic stress (Lawas *et al.*, 2019).

Proteomic insights

JA and SA are well-established defense hormones that play pivotal roles in orchestrating plant responses to biotic and abiotic stresses. Proteomic studies have significantly advanced our understanding of how these hormones modulate protein expression to facilitate stress adaptation and recovery. SA and JA regulate a wide array of stress-responsive proteins (Fig. 5), enabling plants to fine-tune defense responses based on the nature and severity of environmental stimuli (Qu *et al.*, 2023; Vos *et al.*, 2015; Nye *et al.*, 2023).

Under normal conditions, protein expression remains relatively stable, with prominent bands observed at various molecular weights. However, drought stress induces a marked decline in total protein levels, especially in low-molecular-weight proteins, indicating membrane damage and disrupted cellular homeostasis (Venegas-Molina, 2020; Bockhaven *et al.*, 2015; Schroeder *et al.*, 2019). Recovery without hormonal

application partially restores protein expression, yet the application of SA and JA significantly enhances this response, underscoring their protective and restorative capacities. SA treatment notably upregulates defense-related proteins such as ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO), which is central to photosynthetic carbon fixation and energy metabolism. Additionally, SA enhances the expression of heat shock protein 90 (HSP90), which contributes to cellular repair and stabilization under stress (Schroeder *et al.*, 2019; Venegas-Molina, 2020). These findings illustrate SA's dual role in both defense and metabolic restoration. JA application, in contrast, induces the expression of proteins associated with structural defense and secondary metabolism, including HSP90 and allene oxide synthase key components in jasmonate biosynthesis and signal transduction (Vos *et al.*, 2015; Xie *et al.*, 2022; Wang *et al.*, 2021). JA not only supports recovery from abiotic stress but also modulates primary metabolic pathways and transcriptional regulation of defense genes (Vleesschauwer *et al.*, 2016; Wang *et al.*, 2021). The dynamic interaction between SA and JA pathways both synergistic and antagonistic—is critical for optimizing the plant's defense machinery. SA primarily mediates resistance against biotrophic pathogens through systemic acquired resistance, while JA is essential for countering necrotrophs and herbivores via induced systemic resistance (Robert-Seilanianantz *et al.*, 2011; Birkenbihl & Somssich, 2011; Falconieri *et al.*, 2022).

Crosstalk between these hormones enables precise tailoring of defense responses, with proteomic data revealing distinct expression profiles depending on the hormonal treatment applied (Argueso *et al.*, 2012; Liu *et al.*, 2015). Importantly, co-application of SA and JA has been shown to elicit a broader spectrum of defense-related proteins, leading to a more comprehensive and robust stress response (Venegas-Molina, 2020; Peng *et al.*, 2021). The upregulation of key proteins like RuBisCO and HSP90 under combined hormonal treatments highlights the capacity of these compounds to reinforce both immediate defense and long-term resilience mechanisms (Bockhaven *et al.*, 2015; Nye *et al.*, 2023; Xie *et al.*, 2022). Proteomic insights also offer an evolutionary perspective, revealing how plants adaptively utilize hormonal signaling to regulate protein turnover, stabilize stress-responsive proteins, and maintain cellular function during recovery. Fold changes in protein expression and total protein content underscore the strategic role of SA and JA in fine-tuning plant immunity (Aerts *et al.*, 2022; Schroeder *et al.*, 2019). In conclusion, SA and JA serve as central regulators in the proteomic landscape of stress response, enabling plants to maintain homeostasis, trigger defense mechanisms, and recover from stress-induced damage. Comparative proteomic studies offer valuable insights into these hormonal effects and present promising avenues for enhancing crop resilience and sustainability in agriculture, especially under climate-induced stress scenarios (Torrens-Spence *et al.*, 2019; Peng *et al.*, 2021; Vos *et al.*, 2015).

Protein-protein interaction

The protein-protein interaction (PPI) network in *Swietenia macrophylla* seedlings under drought and hormonal treatments highlighted Ribulose bisphosphate carboxylase small chain 2 (Ris2) as a central hub linking photosynthesis and stress responses (Fig.8). Key chloroplast-localized proteins, such as petA and petN, clustered around Ris2, reinforcing the role of chloroplast coordination in stress tolerance (Ling & Jarvis, 2015). JA treatment enhanced PPI network complexity, particularly among photosynthetic proteins, supporting its role in stabilizing chloroplast function during drought (Sham *et al.*, 2019; Ling & Jarvis, 2016). In contrast, SA triggered distinct interaction pathways focused on redox signaling and cytosolic regulation (Zheng & Zhao, 2013; Argueso *et al.*, 2012). Additionally, the emergence of GPCR-like proteins in the network reveals intricate hormonal crosstalk, notably between JA and SA, in modulating stress-adaptive responses

(Barda & Levy, 2021; Vos *et al.*, 2015). These dynamic interactions underpin a coordinated system that integrates hormonal signaling with metabolic resilience, offering insights into stress mitigation strategies through targeted hormone application (Tian *et al.*, 2019; Holzmeister *et al.*, 2011; Ramundo *et al.*, 2020; Huang *et al.*, 2021).

Gene Ontology (GO) Enrichment Analysis

Gene Ontology (GO) enrichment analysis provides a valuable framework to interpret the biological significance of differentially expressed proteins in *Swietenia macrophylla*, especially under drought stress modulated by phytohormones such as JA and SA (Fig. 10). The analysis underscores how exogenous application of JA and SA leads to marked modulation of various cellular processes, revealing distinct yet complementary mechanisms that these hormones employ to confer drought resilience.

In the Biological Process (BP) category, proteins related to photosynthesis, aromatic amino acid biosynthesis, and environmental stimulus response were significantly enriched under JA treatment. The upregulation of photosynthesis-associated pathways suggests that JA plays a crucial role in maintaining photosynthetic efficiency under drought conditions (Li *et al.*, 2021). Proteins involved in chlorophyll biosynthesis and light-dependent reactions were prominent, indicating that JA enhances the photosynthetic apparatus to support energy demands during stress. Additionally, JA-treated seedlings showed modulation of aromatic amino acid metabolic processes precursors to phenolic compounds that are essential for defense and antioxidant activities. This aligns with findings that JA facilitates metabolic reprogramming toward the production of protective secondary metabolites during abiotic stress (Akhoundnejad & Baran, 2023; Omid *et al.*, 2022). In contrast, SA treatment was associated with the enrichment of stress-related cytoplasmic proteins, including those involved in detoxification and redox regulation. These proteins are central to maintaining cellular homeostasis during oxidative stress, highlighting SA's function in intracellular stabilization and stress signal processing (Zafar *et al.*, 2021; Xie *et al.*, 2022). The dichotomy in enriched processes suggests that while JA primarily augments energy production and metabolic adaptability, SA focuses on fortifying cellular defense and detox pathways.

The Molecular Function (MF) domain analysis revealed significant upregulation of ion-binding proteins and enzymes under JA treatment. These include metal-ion dependent enzymes such as carboxy-lyases and 3-deoxy-7-phosphoheptulonate synthase—key players in carbon fixation and shikimate pathway activity. The enrichment of these enzymatic functions highlights JA's role in supporting redox balance, enzymatic activity, and biosynthesis of vital secondary metabolites (Li *et al.*, 2021). In SA-treated seedlings, the enrichment of proteins involved in reactive oxygen species (ROS) detoxification—such as peroxidases and thioredoxins—points to an emphasis on mitigating oxidative damage, a well-established function of SA during abiotic stress (Liu *et al.*, 2015; Zafar *et al.*, 2021). These findings support prior reports suggesting that SA enhances drought tolerance by modulating antioxidative defense systems and promoting cellular redox homeostasis (Omid *et al.*, 2022; Venegas-Molina, 2020).

Within the Cellular Component (CC) category, a large number of differentially expressed proteins were localized to chloroplasts, especially in JA-treated seedlings. This chloroplast-centric enrichment—particularly in the thylakoid membrane—emphasizes JA's role in maintaining photosystem integrity and promoting energy capture under drought stress (Sun *et al.*, 2018; Akhoundnejad & Baran, 2023). Proteins involved in light-harvesting complex stabilization and electron transport were significantly represented,

underlining the hormone's role in sustaining efficient photosynthetic machinery during water-limiting conditions. In contrast, SA treatment led to higher enrichment of cytoplasmic proteins related to protein folding, detoxification, and intracellular trafficking. These adaptations likely support critical metabolic adjustments under drought, emphasizing SA's protective function at the cellular level (Xie *et al.*, 2022; Omid *et al.*, 2022; Venegas-Molina, 2020). This suggests that while JA's effects are concentrated in energy-producing organelles, SA's influence permeates cellular machinery critical for maintaining biochemical equilibrium under stress.

Conclusion

This investigation provides comprehensive insights into the defense hormones mediated physiological, biochemical, and proteomic responses of *Swietenia macrophylla* seedlings under drought stress and subsequent recovery. All measured morphometric, physiological and biochemical parameters were significantly affected by drought, disrupting photosynthesis, water balance, and protein expression. However, the application of defense hormones JA and SA mitigated these effects by enhancing recovery mechanisms. Among the two, JA (0.6mM) demonstrated superior efficacy by improving photosynthetic performance, reducing oxidative damage, and enhancing protein recovery. Proteomic analysis identified key drought-responsive proteins such as RuBisCO and HSP90, which play pivotal roles in photosynthesis and stress defense. Notably, drought conditions induced proteins associated with reactive oxygen species (ROS) scavenging, while JA treatment promoted chlorophyll biosynthesis and stimulated photochemical reactions and electron transport, thereby supporting photosynthetic recovery. Gene Ontology (GO) analysis revealed that photosynthesis, metabolic regulation, and ROS detoxification are central adaptive responses. This study underscores the potential of JA and SA as effective tools to enhance drought resilience in *S. macrophylla*, contributing to the development of climate-resilient forestry practices. Furthermore, the application of defense hormones in nursery settings offers a promising strategy to improve seedling vigor and drought tolerance during early establishment phases. Integrating such treatments into reforestation and plantation forestry practices can enhance survival rates and growth performance under water-limited conditions. Future research should aim to validate these findings through integrative multi-omics approaches and field-level trials to extend their applicability across diverse environmental scenarios.

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Figures

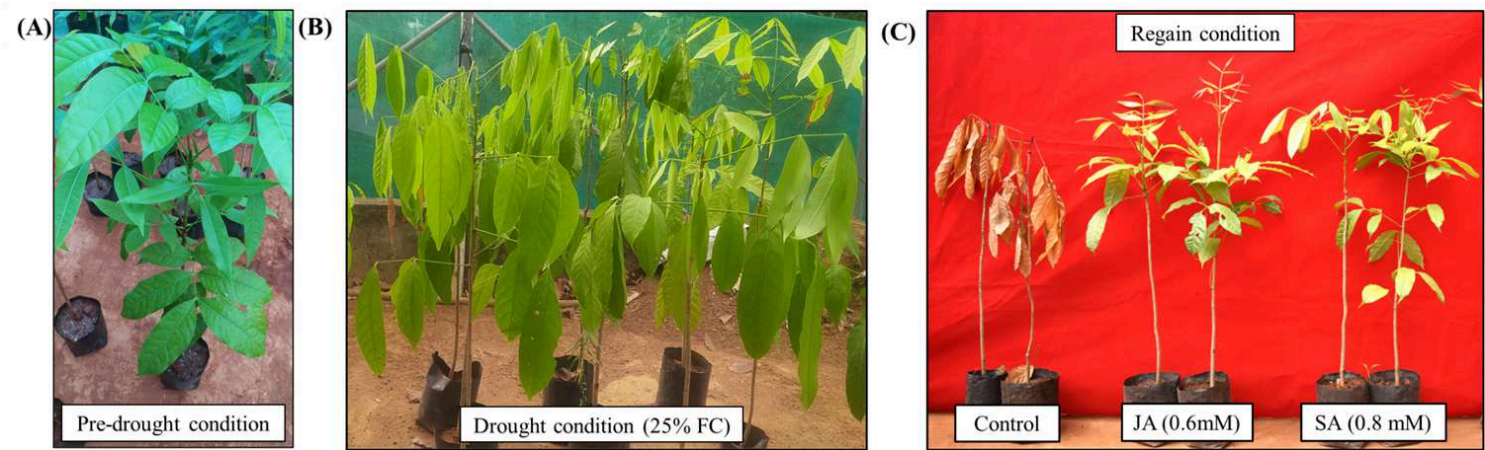


Figure 1

Visual representation of *Swietenia macrophylla* seedlings under (A) Pre-drought condition, (B) Drought condition (25% FC), and (C) Recovery stage under different treatments: Control, SA (0.8 mM), and JA (0.6 mM).

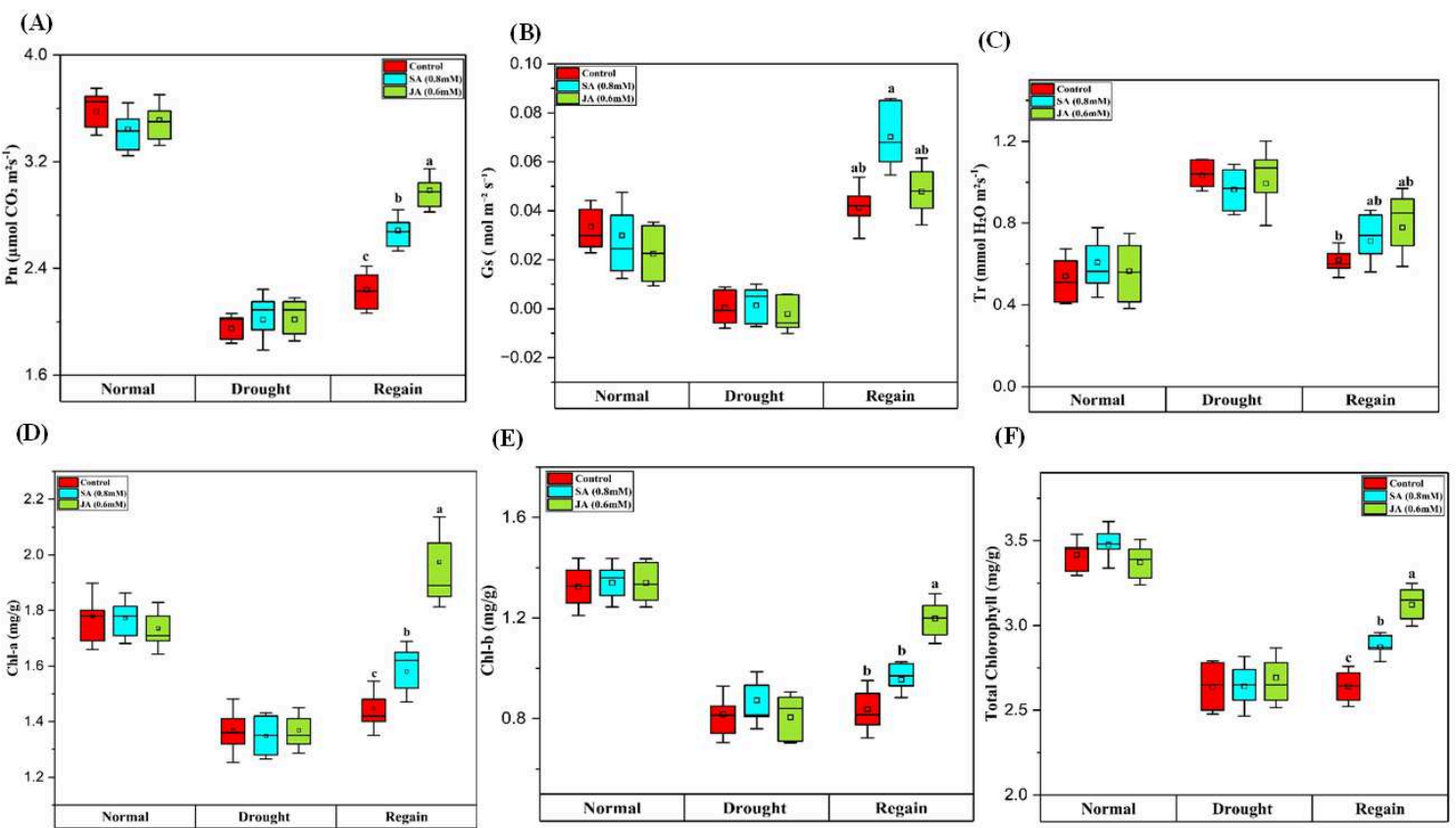


Figure 2

Physiological changes in defense hormone-mediated drought response in *Swietenia macrophylla* seedlings. (A) Net photosynthetic rate (Pn), (B). Stomatal conductance (Gs), (C) Transpiration rate (D) Chlorophyll a, (E) Chlorophyll b and (F). Total Chlorophyll content. The data were analyzed by one-way ANOVA combined with LSD test. Bars followed by the different letters are significantly different by LSD test at $P < 0.05$ ($\pm$ SE, $n = 25$)

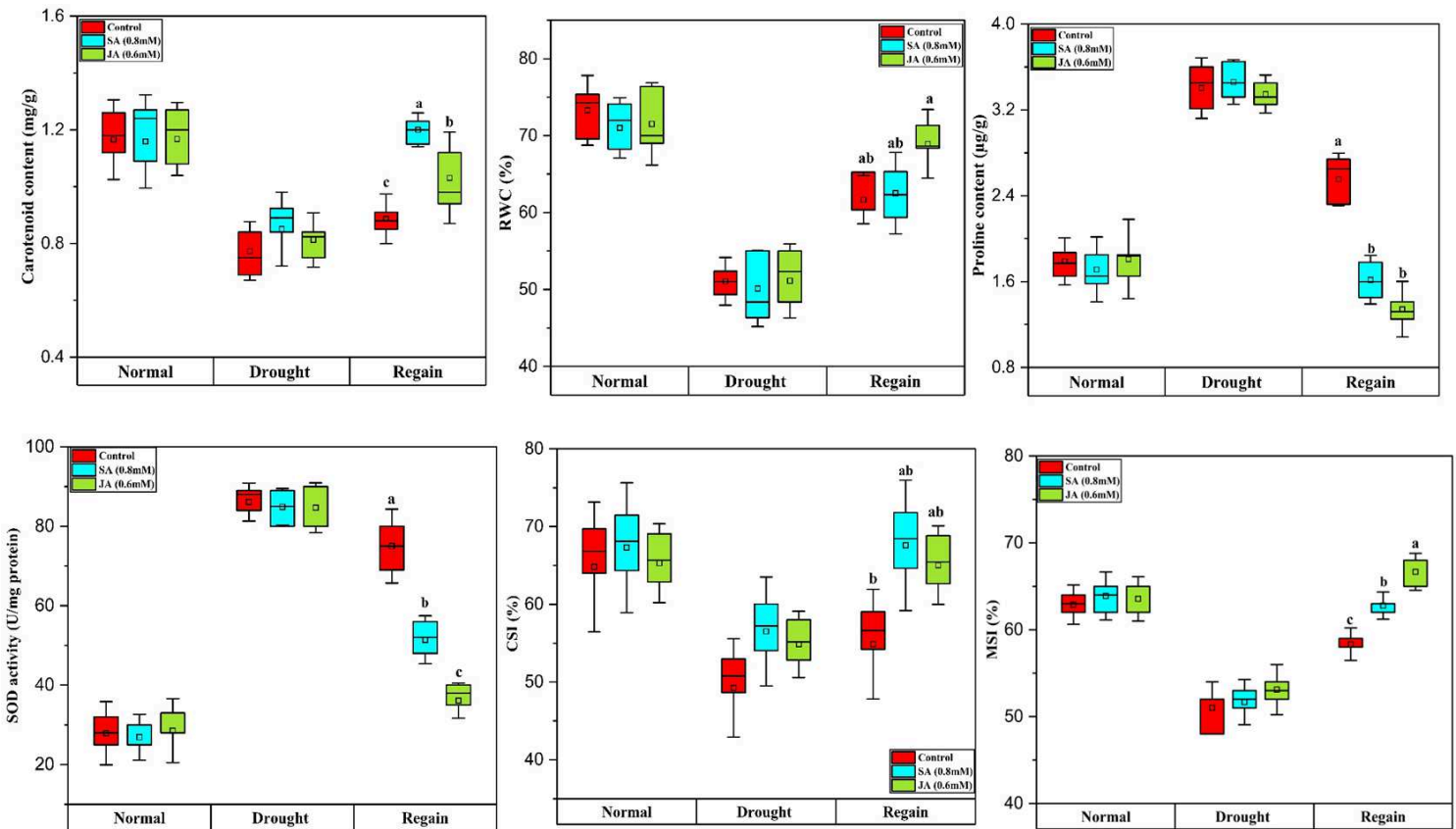


Figure 3

Physiological and biochemical changes in defense hormone-mediated drought response in *Swietenia macrophylla* seedlings. (G) Carotenoid content, (H). Relative water content (RWC), (I) Proline content, (J) Superoxide dismutase (SOD), (K) Chlorophyll Stability Index (CSI), (L) Membrane Stability Index (MSI) The data were analyzed by one-way ANOVA combined with LSD test. Bars followed by the different letters are significantly different by LSD test at $P < 0.05$ ($\pm$ SE, $n = 25$)

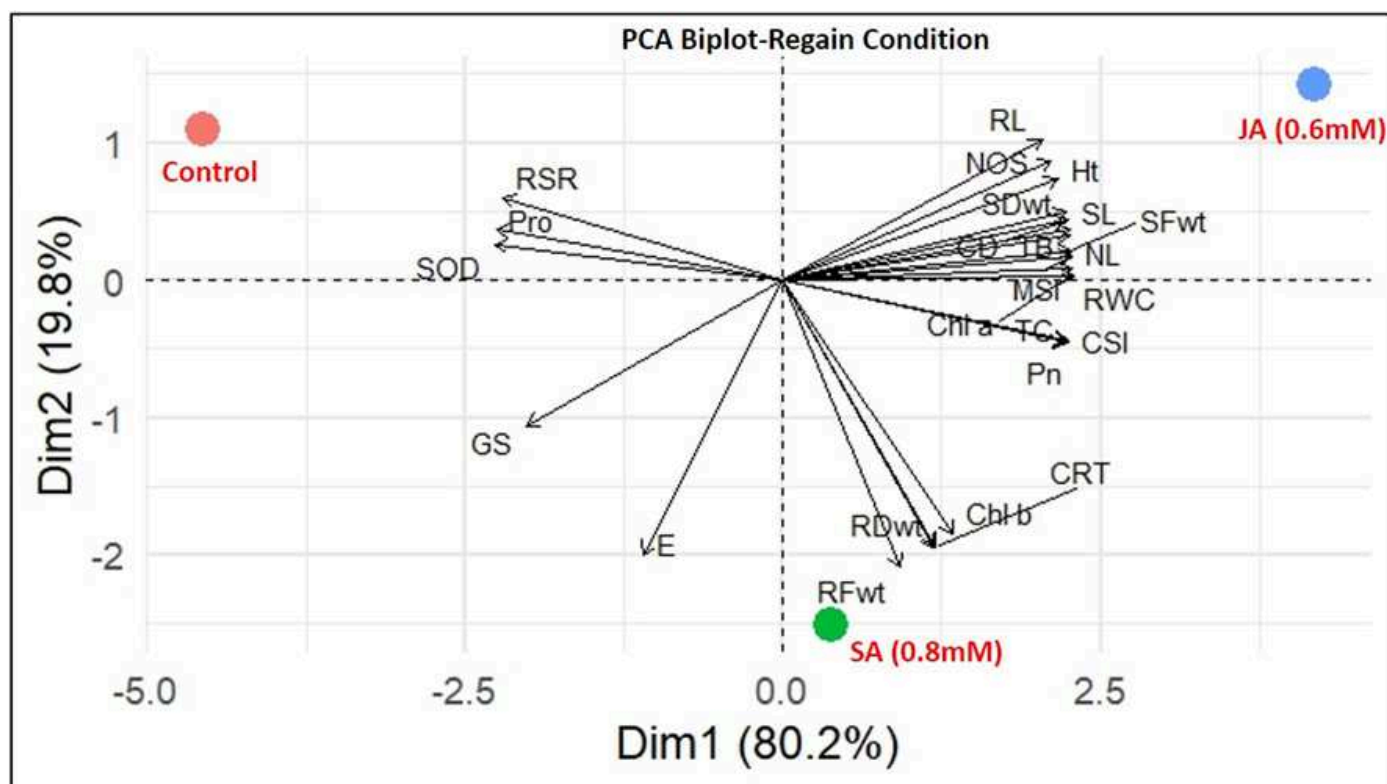


Fig4. PCA biplot depicting the distribution of different morphometric, physiological and biochemical parameters during the recovery phase of drought response in *Swietenia macrophylla* seedlings.

Figure 4

PCA biplot depicting the distribution of different morphometric, physiological and biochemical parameters during the recovery phase of drought response in *Swietenia macrophylla* seedlings.

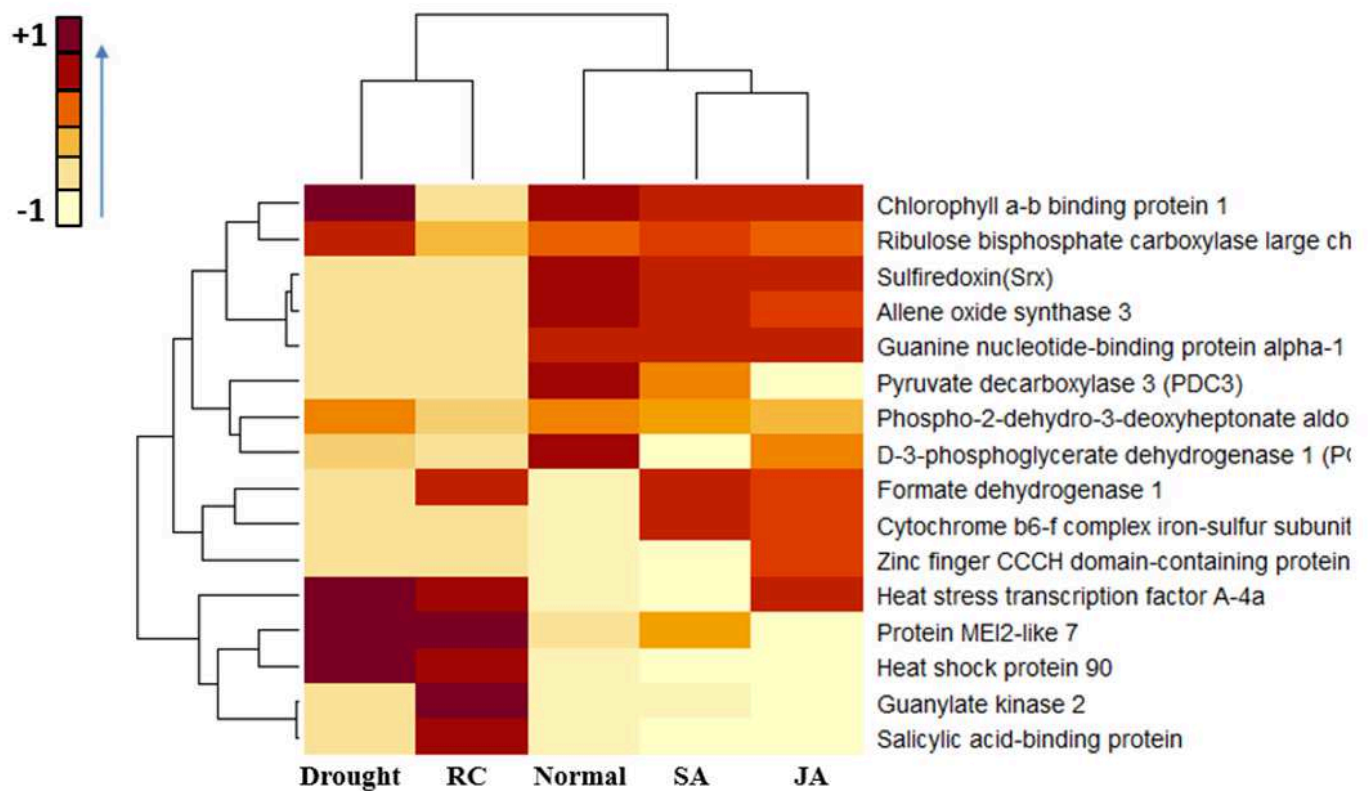


Figure 6

Clustered heatmap depicting the differential expression of proteins under various drought stress conditions. "Normal" represents the pre-drought condition, "Drought" indicates the drought stress condition, "RC" refers to recovery without hormone treatment, "SA" denotes recovery with Salicylic Acid (0.8mM) treatment, and "JA" signifies recovery with Jasmonic Acid (0.6mM) treatment.

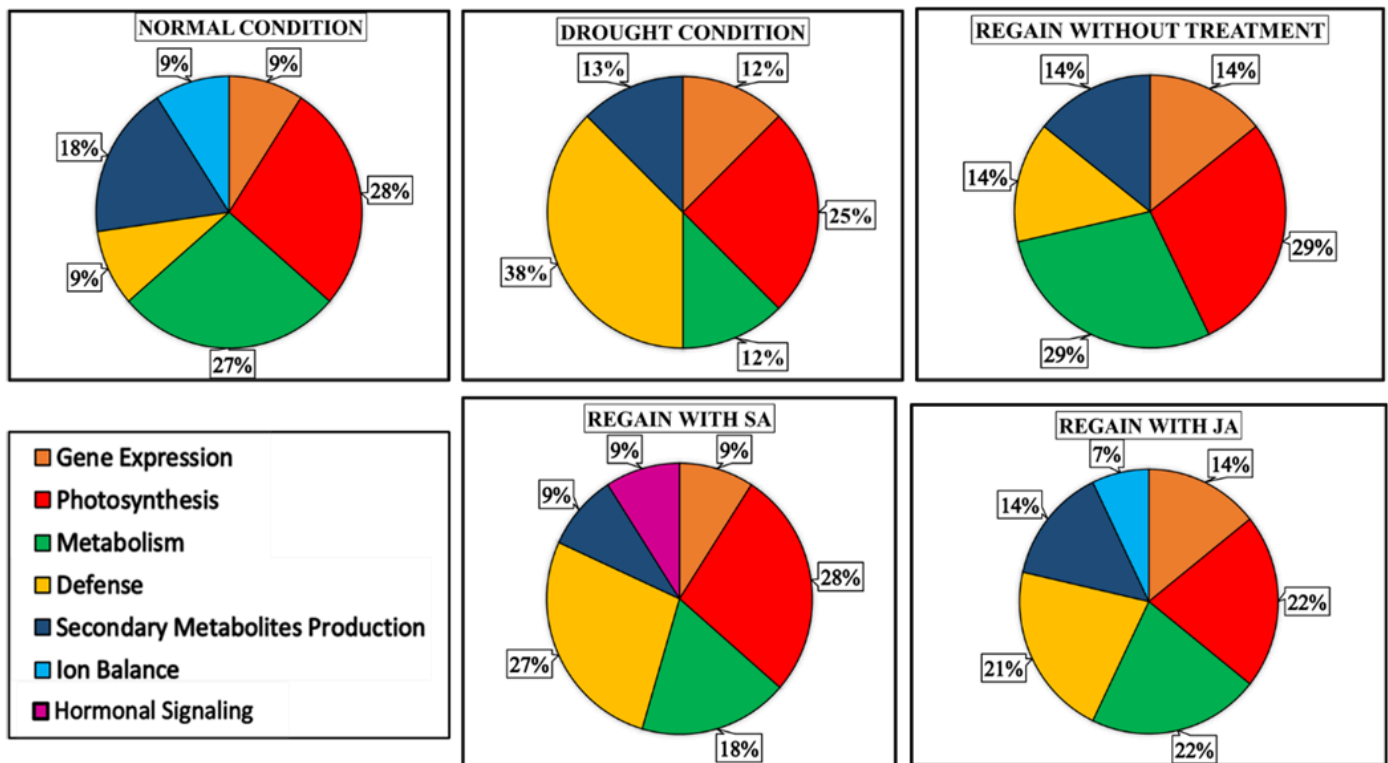


Fig 04. Functional annotation of differentially expressed proteins for different conditions under drought stress

Figure 7

Functional annotation of differentially expressed proteins for different conditions under drought stress

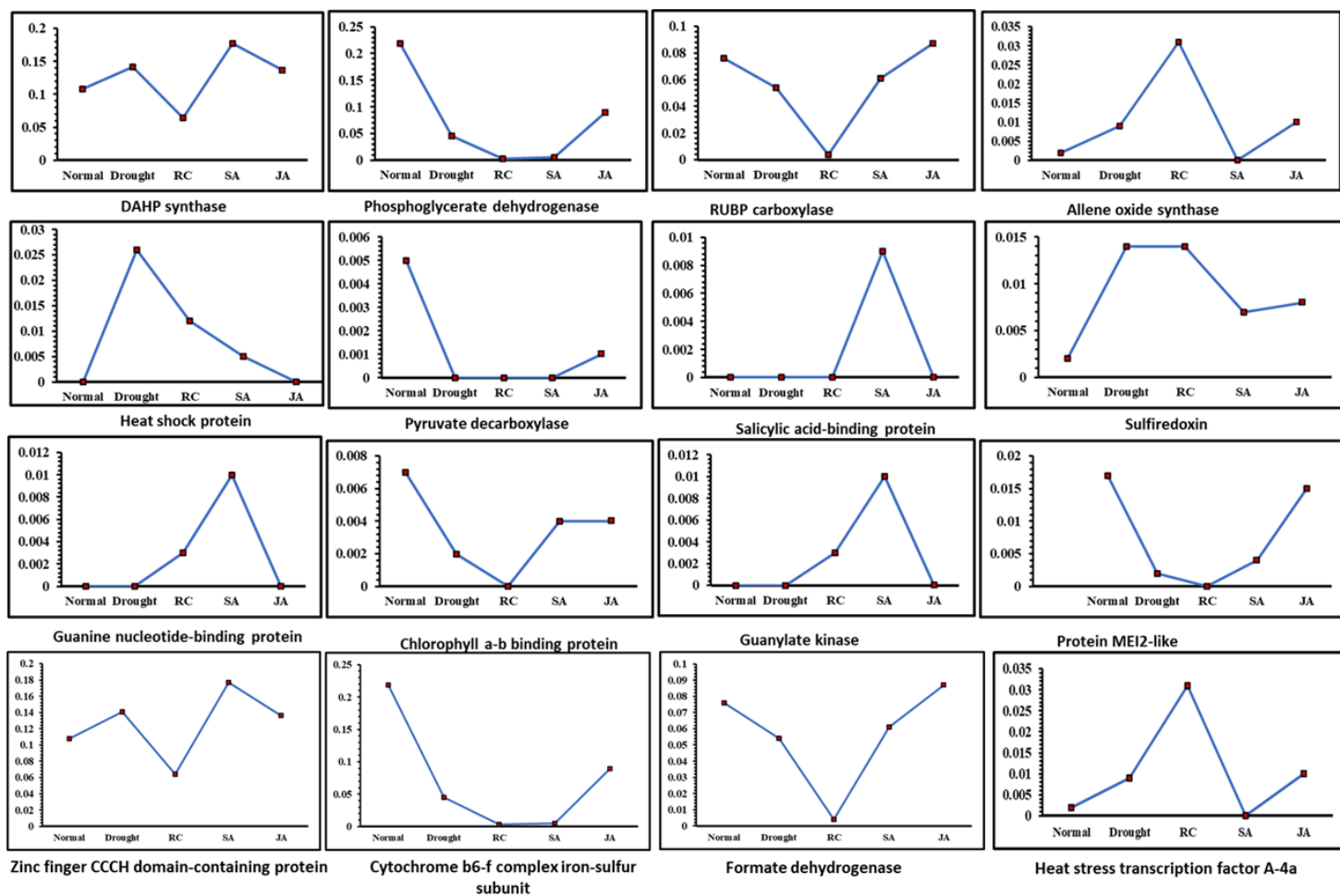


Figure 9

Protein concentration(mg/g) changes during different stress conditions in *Swietenia macrophylla* seedlings. "Normal" represents the pre-drought condition, "Drought" indicates the drought stress condition, "RC" refers to recovery without hormone treatment, "SA" denotes recovery with Salicylic Acid (0.8mM) treatment, and "JA" signifies recovery with Jasmonic Acid (0.6mM) treatment.