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Physiological and Molecular Responses of Medicinal Plants to Drought Stress: A Comprehensive Case Study on Ocimum sanctum

Urvashi

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Abstract
Drought stress represents one of the most significant challenges to global agricultural productivity, particularly affecting medicinal plants that are crucial for pharmaceutical and nutritional applications (Feller & Vaseva, 2014). This comprehensive review examines the physiological and molecular responses of medicinal plants to drought stress with a specific focus on Ocimum sanctum (Holy Basil), a widely utilized therapeutic species in traditional and modern medicine (S. Mulugeta et al., 2025). The review integrates current understanding of how plants perceive and respond to water deficit conditions through complex signaling pathways, antioxidant defense mechanisms, and osmotic adjustment strategies (Hasanuzzaman et al., 2020). We analyze the role of compatible solutes, phytohormones, transcription factors, and secondary metabolite biosynthesis in mediating drought tolerance (A. Sharma et al., 2019). Special emphasis is placed on Ocimum sanctum's adaptive mechanisms, including the modulation of essential oil production, phenolic compound accumulation, and altered gene expression patterns under water-limited conditions (S. Mulugeta et al., 2025). The paper also identifies critical research gaps in understanding the tissue-specific responses, genotypic variations, and long-term physiological memory effects in medicinal plants (Tan & Gören, 2024). This review provides a foundation for developing sustainable cultivation practices and breeding programs aimed at enhancing drought resilience in medicinal crops (Rahimi et al., 2023).

Keywords: drought stress, Ocimum sanctum, physiological responses, molecular mechanisms, antioxidant systems, compatible solutes, medicinal plants, essential oils

I. Introduction

1.1 Global Context of Drought Stress and Agricultural Impact

Drought stress constitutes a major environmental challenge affecting global agriculture and food security, with escalating frequency and severity attributed to climate change (Ali et al., 2025). The phenomenon of water deficit stress fundamentally alters intracellular water relations, compromises photosynthetic efficiency, disrupts ion homeostasis, and elevates reactive oxygen species production, ultimately reducing plant growth and yields (Hussain et al., 2019). Recent projections indicate that climate models predict more frequent and severe extreme events including heat waves, extended drought periods, and flooding in many regions for the next decades, with substantial economic and ecological implications (Feller & Vaseva, 2014). Plants face a variety of abiotic stresses, which generate reactive oxygen species and ultimately obstruct normal growth and development (A. Sharma et al., 2019). The situation has aggravated due to drastic and rapid changes in global climate, making understanding of physiological and biochemical interventions related to these stresses for better management critically important (Feller & Vaseva, 2014).

1.2 Medicinal and Aromatic Plants Under Stress

Medicinal and aromatic plants (MAPs) have increased significantly in economic importance in recent years, driven by growing demand for natural products in pharmaceutical, cosmetic, and food industries (Mansinhos et al., 2024). The Lamiaceae family, which encompasses economically important species including Ocimum basilicum and related taxa, produces valuable secondary metabolites such as essential oils and phenolic compounds with demonstrated antimicrobial and antioxidant properties (Sultan et al., 2024). The quality and quantity of these bioactive metabolites are substantially affected by abiotic stress factors, with drought stress acting as a catalyst for essential oil production but potentially compromising plant survival under severe conditions (S. M. Mulugeta et al., 2023). In the context of climate change scenarios, the Lamiaceae family faces particular vulnerability, especially due to its wide distribution in Mediterranean regions where drought stress is increasingly prevalent

(Mansinhos et al., 2024). Stresses typically act as catalysts for plant metabolism, resulting in the production of essential oils and phenolic compounds with subsequent enhancement of various biological activities including antioxidant, antibacterial, antimelanogenic, pest-repellent, and ultraviolet-protective properties, though the relationship between stress severity and metabolite enhancement becomes complex under severe drought (Mansinhos et al., 2024).

1.3 Ocimum sanctum as a Model for Medicinal Plant Research

Ocimum sanctum, commonly known as Holy Basil or Tulsi, represents an exemplary model for studying medicinal plant responses to drought stress (S. Mulugeta et al., 2025). This species possesses significant therapeutic properties and is widely cultivated across diverse geographical regions for its essential oil production, flavor compounds, and bioactive secondary metabolites (Chintalwar et al., 2026). The plant's adaptability to various environmental conditions and its economic importance in traditional medicine systems make it an ideal subject for investigating physiological and molecular drought stress responses (S. Mulugeta et al., 2025). Research on O. basilicum, a closely related species, has revealed substantial genotypic variation in drought tolerance mechanisms, with some accessions maintaining relatively stable leaf yields under moderate drought while others exhibit severe production losses (Rahimi et al., 2023). Understanding the drought tolerance mechanisms in Ocimum sanctum can provide valuable insights applicable to other medicinal plants in the Lamiaceae family and beyond, contributing to broader agricultural sustainability goals (Tan & Gören, 2024).

II. Physiological Responses to Drought Stress in Plants

2.1 Water Status and Photosynthetic Consequences

Drought stress induces profound alterations in plant water status, manifesting through reductions in relative water content (RWC) and leaf water potential (Qiao et al., 2024). These changes directly impact the photosynthetic apparatus, with drought stress affecting both light-dependent and light-independent reactions (Qiao et al., 2024). The stress-induced reduction in photosynthetic rate occurs through multiple mechanisms, including stomatal closure that limits carbon dioxide availability, leading to photorespiration rather than photosynthesis (Qiao et al., 2024). Drought-induced CO_2 shortage provoked by stomatal closure triggers photorespiration, which not only reduces carbon fixation efficiency but also causes lower overall photosynthetic output, ultimately compromising plant productivity (Qiao et al., 2024). Research on Pakistani wheat genotypes revealed that drought stress significantly reduced net photosynthesis by approximately 50% and stomatal conductance by 60%, with corresponding reductions in chlorophyll content and relative water content (Wasaya et al., 2021).

Drought stress additionally generates reactive oxygen species that damage cellular structures, including chloroplasts, further impairing photosynthetic productivity (Qiao et al., 2024). Plants employ non-photochemical quenching (NPQ) mechanisms to dissipate excess light energy as heat, thereby protecting the photosynthetic apparatus under drought conditions (Qiao et al., 2024). Alternative electron pathways, such as cyclical electron transmission and chloroplast respiration, help maintain energy balance and prevent over-reduction of the electron transport chain (Qiao et al., 2024). The maximum quantum yield of photosystem II (Fv/Fm) serves as a sensitive indicator of photosynthetic apparatus damage under drought stress, with reductions in this parameter correlating with stress severity across diverse plant species (Mirgos et al., 2026).

Research on Ocimum basilicum grown hydroponically under drought and high electrical conductivity stress demonstrated that both stressors altered photosystem II-related fluorescence parameters, with high EC stress causing a wider spectrum of changes (Mirgos et al., 2026). In mature basil plants, alterations in photosynthetic parameters were less pronounced, indicating enhanced tolerance likely due to more efficient electron transport and greater structural stability of the photosynthetic apparatus (Mirgos et al., 2026).

2.2 Stomatal Regulation and Gas Exchange Parameters

Stomatal conductance represents a key physiological parameter significantly impacted by drought stress, serving as a primary mechanism through which plants regulate water loss and maintain cellular water balance (Fang et al., 2023). Research has revealed that stomatal conductance markedly decreases under drought conditions, with the magnitude of decrease varying substantially among plant species and genotypes (Fang et al., 2023). The rapid stomatal closure observed in drought-tolerant genotypes facilitates water

conservation while susceptible genotypes exhibit delayed stomatal responses, resulting in excessive water loss and reduced drought tolerance (Ritchie et al., 1990). The transpiration rate frequently decreases by 50% or more under severe drought conditions, though this varies depending on the severity of stress imposed (Arab et al., 2023).
Hormonal regulation of stomatal aperture occurs predominantly through abscisic acid (ABA)-mediated signaling pathways, which trigger stomatal closure to limit transpiration (Jensen et al., 2024). The interaction between water deficit perception and ABA accumulation creates a feedback mechanism that optimizes plant water relations under stress. Additionally, salicylic acid (SA) increases to greater magnitude at drought stress under elevated CO_2, suggesting a shift in hormonal regulation toward SA rather than exclusive ABA dependence (Jensen et al., 2024). CO_2 concentration in intercellular spaces, transpiration rate, and photosynthetic efficiency all respond dynamically to stomatal conductance variations, creating complex relationships between gas exchange parameters and overall plant performance under drought conditions (Fang et al., 2023). Research on sesame plants showed that potassium application was more effective in promoting yield production under drought stress relative to well-watered conditions, primarily attributed to enhanced photosynthetic and plant water retaining ability through improved leaf gas exchange traits, higher F_v/F_m and ΦPSII values, and superior water use efficiency (Fang et al., 2023).

2.3 Membrane Stability, Lipid Peroxidation, and Cellular Integrity

Drought stress compromises the structural and functional integrity of biological membranes through multiple mechanisms (Arif et al., 2020). The reduction in cellular turgor pressure diminishes membrane stability, while oxidative stress induces lipid peroxidation, generating malondialdehyde (MDA) as a secondary product of membrane damage (Rasafi et al., 2020). Electrolyte leakage increases proportionally with membrane dysfunction, serving as a quantifiable indicator of cellular injury under drought conditions (Arif et al., 2020). Maintenance of membrane integrity becomes essential for plant survival, as membrane dysfunction disrupts crucial cellular compartmentalization and ion homeostasis, leading to cascade effects throughout the plant system (Rasafi et al., 2020).

Plants exhibiting superior drought tolerance typically maintain lower MDA accumulation and reduced electrolyte leakage compared to drought-susceptible varieties, indicating more effective membrane protection mechanisms (Osku et al., 2025). The preservation of membrane integrity involves both prevention of oxidative damage through antioxidant systems and maintenance of optimal membrane lipid composition that preserves fluidity and functionality (Arif et al., 2020). Membrane-associated proteins, including aquaporins that facilitate water transport, remain functional only when membrane integrity is preserved, underscoring the interconnected nature of cellular drought responses (Sade et al., 2009). Research on walnut families under progressive drought revealed that severe water-withholding reduced leaf relative water content by 20%, but drought-tolerant families from dry climates exhibited lesser alterations in photosynthetic parameters than sensitive families (Arab et al., 2023).

2.4 Root System Modifications and Water Acquisition Capacity

Drought stress triggers significant morphological and physiological alterations in root architecture, representing critical adaptive responses that enhance water acquisition efficiency under water-limited conditions (Osku et al., 2025). Enhanced root length, increased root surface area, and modified root tip number facilitate increased soil exploration and water uptake capacity (Yang et al., 2023). Root-specific responses include increased root-to-shoot biomass ratios, enhanced root activity, and modifications in root cortical aerenchyma formation, all contributing to improved water extraction from drying soils (S. Mulugeta et al., 2025). Research on rice and wheat revealed that the decline of soil-root interface hydraulic conductance (K_i) drives the depression of plant hydraulic conductance (K_{plant}) and photosynthesis in both crops, with the plastic responding of root morphology and anatomy being important in determining drought tolerance capacity (Yang et al., 2023).

Xylem vessel modifications and anatomical changes in root structure enhance water transport efficiency, while alterations in water transport mechanisms optimize the movement of water from roots to aerial plant parts (Dai et al., 2020). The genetic diversity of root systems across species exhibits various growth patterns and adaptive traits that enable plants to endure water-deficient conditions (Eweda et al., 2025). Understanding this diversity and harnessing it through breeding programs and biotechnological approaches represents a promising strategy for enhancing drought resilience in crops (Najafi et al., 2025). Root colonization by arbuscular mycorrhizal fungi significantly improved the fresh and dry weight of oregano plants compared to non-inoculated controls, with AMF-inoculated plants showing notable increases in potassium and nitrogen contents (Najafi et al., 2025).

III. Molecular Mechanisms and Signal Transduction Pathways

3.1 Abscisic Acid Signaling and Drought Perception

Abscisic acid represents the predominant phytohormone governing plant responses to drought stress, functioning as a critical signaling molecule that coordinates diverse adaptive responses (Huang et al., 2008). Upon drought stress perception, ABA accumulation triggers cascades of molecular events including stomatal closure, adjustment of osmotic potential, and activation of stress-responsive gene expression (Huang et al., 2008). The ABA signaling pathway involves the PYL-PP2C-SnRK2 core regulatory module, wherein ABA binding to PYL receptors leads to inhibition of PP2C phosphatases, subsequently allowing SnRK2 kinases to phosphorylate downstream targets including transcription factors and ion channels (A. Sharma et al., 2019).

Nearly two-thirds of drought-regulated genes in Arabidopsis thaliana respond to ABA signaling, with ABA-dependent pathways representing the predominant stress response mechanisms (Huang et al., 2008). The remaining drought-regulated genes respond to ABA-independent signaling pathways, indicating the complexity of drought stress perception and response (Huang et al., 2008). Detailed analyses of transcript profiles demonstrate that ABA-related pathways are predominant in drought responses, while also revealing extensive cross-talk between drought responses and other environmental factors including light and biotic stresses (Huang et al., 2008). Application of exogenous ABA enhanced freeze-thaw stress tolerance in Antarctic moss by improving freezing tolerance, reducing freeze-induced membrane injury by approximately 20%, alleviating oxidative stress with 25-34% lower MDA accumulation, and enhancing PSII maximum quantum yield (Seo et al., 2025).

3.2 Transcription Factors and Stress-Responsive Gene Regulation

Multiple transcription factor families play crucial roles in regulating gene expression involved in drought stress tolerance (Bondar et al., 2025). The AP2/ERF family, WRKY transcription factors, bHLH proteins, bZIP factors, MYB transcription factors, and NAC proteins collectively orchestrate complex regulatory networks that govern stress-responsive gene expression (Bondar et al., 2025). These transcription factors function as central regulatory "hubs" integrating diverse stress signals and mediating adaptive responses through coordinated modulation of downstream target genes (Bondar et al., 2025). Stress-responsive regulatory factors such as DREB proteins have been identified as crucial regulators of adaptation to both drought and heat stress conditions, potentially functioning as molecular switches that direct plants toward specific adaptive pathways (Bondar et al., 2025).

The transcriptional reprogramming orchestrated by these regulatory proteins involves the simultaneous expression of protective processes including molecular chaperone activity, oxidative stress responses, and immune signaling, accompanied by suppression of photosynthetic and primary metabolic pathways reflecting energy reallocation under stress conditions (Bondar et al., 2025). Understanding the structure, function, and regulation of these transcription factors has become essential for developing drought-tolerant crop varieties through molecular breeding and genetic engineering approaches (Bondar et al., 2025). MYB transcription factors serve as master regulators of phenylpropanoid metabolism and flavonoid biosynthesis, with specific MYB proteins controlling expression of pathway genes in response to developmental signals and environmental stresses (Rao & Zheng, 2025).

3.3 Calcium Signaling and Mitogen-Activated Protein Kinase Pathways

Calcium functions as a critical second messenger in plant stress response signaling, with calcium-dependent protein kinases (CDPKs) playing pivotal roles in transmitting stress signals to downstream effector molecules (Osku et al., 2025). Drought stress-induced alterations in cytoplasmic calcium concentration trigger specific patterns of calcium oscillations that are decoded by calcium-binding proteins, translating stress perception into appropriate physiological and molecular responses (Osku et al., 2025). CDPK-mediated phosphorylation events activate transcription

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factors, enzymes, and regulatory proteins, ultimately leading to coordinated alterations in plant physiology (Osku et al., 2025). The upregulation of CDPK genes under water deficit indicates their central involvement in calcium-signaling networks governing drought tolerance (Osku et al., 2025).

StMAPK3, a mitogen-activated protein kinase in potato plants, has been shown to regulate oxidase activity, photosynthesis, and stomatal aperture under salinity and osmosis stress (Zhu et al., 2020). The abnormal expression of StMAPK3 changed potato phenotypes, enzyme activities of SOD, CAT and POD, as well as H2O2, proline and MDA contents under osmosis and salinity stress (Zhu et al., 2020). Photosynthesis and stomatal aperture were regulated by StMAPK3 in potato treated with PEG, mannitol and NaCl, demonstrating its role as a regulator of osmosis and salinity tolerance (Zhu et al., 2020). DHN (dehydrin) expression, strongly influenced by CDPK activity, further emphasizes the role of calcium signaling in maintaining cellular integrity during stress conditions, with dehydrins functioning as protective proteins that stabilize cellular structures during water deficit (Osku et al., 2025).

3.4 Reactive Oxygen Species Signaling and Redox State Regulation

Reactive oxygen species accumulate in plant tissues under drought stress, triggering complex signaling networks that can either promote cellular damage or, at controlled levels, induce adaptive responses (Singh, 2022). Different ROS species (superoxide anion, hydrogen peroxide, hydroxyl radicals, and singlet oxygen) function as specific signaling molecules that activate distinct downstream pathways (Singh, 2022). Low concentrations of ROS function as signaling molecules for several abiotic stresses, while overproduction causes devastating oxidative damage through lipid peroxidation, protein oxidation, and nucleic acid damage (Rao et al., 2025). The ROS-induced signaling cascade involves activation of kinases and transcription factors including MAPK pathways and the Nrf2-Keap1 signaling system, which together coordinate the activation of antioxidant defense systems and stress-responsive gene expression (Tüğen & Buruleanu, 2025). Plant-derived bioactive compounds such as polyphenols and terpenes develop versatile molecular strategies to mitigate oxidative damage, with polyphenols stimulating the synthesis of endogenous antioxidant enzymes such as superoxide dismutase and catalase by activating the Nrf2–Keap1 signaling pathway (Tüğen & Buruleanu, 2025).

IV. Antioxidant Defense Systems and ROS Scavenging Mechanisms

4.1 Enzymatic Antioxidants and First-Line Defense

The enzymatic antioxidant system represents the first line of defense against oxidative stress, comprising superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), glutathione reductase (GR), and guaiacol peroxidase (POD) (Jomová et al., 2024). These enzymes work synergistically to maintain reactive oxygen species homeostasis through coordinated dismutation and detoxification reactions (Jomová et al., 2024). Superoxide dismutase catalyzes the dismutation of superoxide radicals to hydrogen peroxide and oxygen, while catalase and peroxidases subsequently convert hydrogen peroxide to water and oxygen (Jomová et al., 2024). The ascorbate-glutathione cycle involving APX, GR, and associated enzymes provides additional layers of ROS detoxification, creating a comprehensive enzymatic defense network (Jomová et al., 2024).

Under drought stress conditions, dramatic increases in antioxidant enzyme activities have been documented across multiple plant species, reflecting the activation of protective mechanisms in response to ROS accumulation (Rosa et al., 2024). The enhancement of SOD, POD, and CAT activities frequently represents the most pronounced enzymatic response to water deficit stress, with these changes being more pronounced in drought-tolerant genotypes compared to susceptible varieties (Mishra et al., 2023). The coordinate upregulation of genes encoding these enzymes ensures adequate enzyme availability to counter oxidative stress under prolonged stress conditions (Mishra et al., 2023). Different SOD isoenzymes, including Mn-SOD, Cu/Zn-SOD, and Fe-SOD, demonstrate peak activity under drought conditions, highlighting their vital roles in mitigating oxidative damage (Keleş & Küçüködük, 2025). Expression of ascorbate peroxidase enzyme in Persian lime with HLB significantly increased following treatment with resistance elicitors, with salicylic acid inducing the highest APX expression and enzymatic activity (Rosa et al., 2024).

4.2 Non-Enzymatic Antioxidants and Phenolic Compounds

Non-enzymatic antioxidants including ascorbic acid (vitamin C), glutathione, carotenoids, and flavonoids provide complementary protection against oxidative stress through radical scavenging and redox buffering (Jomová et al., 2024). These water-soluble and lipid-soluble antioxidants effectively neutralize ROS and help regenerate other antioxidants, offering extensive protection against oxidative stress (Jomová et al., 2024). Ascorbate functions as a reducing substrate for APX, while glutathione serves as the cofactor for glutathione-dependent enzymes and as a direct ROS scavenger (Jomová et al., 2024). Polyphenolic compounds, particularly flavonoids and phenolic acids, contribute substantially to the total antioxidant capacity of plants under stress conditions (Vicidomini et al., 2024).

The phenylpropanoid pathway, producing rosmarinic acid, caffeic acid, and salvianolic acids among other compounds, becomes upregulated under drought stress, facilitating accumulation of phenolic compounds with proven antioxidant activities (Rao & Zheng, 2025). The synergistic action of enzymatic and non-enzymatic antioxidants maintains cellular redox homeostasis, protecting critical cellular structures and maintaining functionality of essential proteins and lipids (Vicidomini et al., 2024). Research on basil plants revealed that phenolic compounds increase substantially with horsetail extract application, with the highest content of total phenol, total flavonoid, total anthocyanin, and antioxidant activity observed in the 2% extract treatment (Eghlima et al., 2024). Foliar application of potassium bicarbonate to basil plants significantly increased the chlorophyll content, fresh and dry weight, phenolics content, and antioxidant activity as determined by DPPH and ABTS methods (Burbulis et al., 2022).

4.3 Proline Accumulation and Multifunctional Protective Roles

Proline, a unique amino acid synthesized through the glutamate pathway, accumulates dramatically under drought stress in most plant species (Tamirat, 2019). Beyond its role as an osmolyte, proline functions as a free radical scavenger, helping to neutralize ROS and protect cellular structures from oxidative damage (Tamirat, 2019). The accumulation of proline correlates strongly with drought tolerance across diverse plant species and genotypes, making it a reliable biochemical marker for assessing stress severity and plant adaptation capacity (X. Wang et al., 2023). Research on black sesame cultivars showed that drought stress induced a significant increase in proline content compared to well-watered control plants, with drought-resistant cultivars showing much better production of proline (X. Wang et al., 2023).

The study of tobacco plants revealed substantial gene expression modulation, with Δ1-pyrroline-carboxylate synthetase (P5CS) and P5C reductase (P5CR) genes showing sharply increased expression at 20 and 40 mg As Kg^{-1} soil stress levels (Adamipour et al., 2025). At the lowest tested arsenic concentration, proline accumulation was due to a decrease in the expression of proline catabolic genes, while at higher concentrations, proline accumulation was caused by the increased expression of genes involved in the glutamate pathway of proline synthesis (Adamipour et al., 2025). Heat shock proteins (HSPs), particularly HSP70 and HSP90, function as molecular chaperones protecting other proteins from denaturation under stress conditions (M. N. Khan et al., 2023). The application of melatonin to drought-stressed tomato plants enhanced H_2S accumulation and further elevated the activity of mitochondrial enzymes, activation level of the defense system, and expression of HSP17.6 and HSP70 (M. N. Khan et al., 2023).

4.4 Ascorbate-Glutathione Cycle and Redox Buffering Systems

The ascorbate-glutathione (AsA-GSH) cycle represents a crucial biochemical pathway maintaining intracellular redox buffering and supporting the antioxidant defense system (Santander et al., 2019). This cycle involves the coordinated activities of APX, monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), and glutathione reductase (GR), with these enzymes working in concert to maintain cycling of ascorbate and glutathione between their reduced and oxidized forms (Santander et al., 2019). The oxidative pentose phosphate pathway (OPPP) provides NADPH required for maintaining glutathione in its reduced form, essential for continued ROS detoxification (Santander et al., 2019). Under drought stress conditions, enhanced activity of OPPP enzymes including glucose-6-phosphate dehydrogenase and 6-phosphogluconate dehydrogenase increases NADPH availability, supporting the functioning of the AsA-GSH cycle and promoting antioxidant enzyme activities (Chen et al., 2019).

The maintenance of adequate pools of reduced ascorbate and glutathione becomes essential for sustained antioxidant defense capacity under prolonged stress conditions (Santander et al., 2019).

The coordinate upregulation of genes encoding these enzymes and the enhanced expression of cytoplasmic and plastidic APX isoforms reflect the heightened requirement for ROS scavenging capacity in drought-stressed tissues (Santander et al., 2019). Treatment with bismuth showed enhanced activation level of the defense system, with increased activities of gamma-GCS and l-galactono-1,4-lactone dehydrogenase, enzymes involved in AsA-GSH biosynthesis (Chen et al., 2019). Exogenous application of aspartic acid to wheat plants under salt stress enhanced the antioxidant system, with antioxidant enzymes superoxide dismutase, peroxidase, catalase, and nitrate reductase all upregulated (Sadak et al., 2022).

V. Osmotic Adjustment and Compatible Solutes

5.1 Osmotic Regulation Mechanisms and Cellular Homeostasis

Osmotic adjustment represents a fundamental mechanism through which plants maintain cellular turgor and continue growth under water-deficit conditions (A. Sharma et al., 2019). This process involves the active accumulation of organic solutes—termed osmolytes or osmoprotectants—that increase cellular solute concentration without compromising enzymatic activity or cellular functions (Jabeen & Jabeen, 2022). The maintenance of osmotic potential through osmolyte accumulation enables cells to extract water from increasingly desiccated soils, preserving cellular hydration and enabling continued growth and metabolic activity (Jabeen & Jabeen, 2022). Plants employ sophisticated regulatory mechanisms to sense changes in cellular water status and trigger appropriate adjustments in osmolyte synthesis and accumulation (Jabeen & Jabeen, 2022).

Osmotic adjustment occurs progressively over time, with initial responses involving rapid uptake of mineral ions followed by synthesis and accumulation of organic solutes (A. Sharma et al., 2019). This multi-phase response allows plants to finely tune their water status in response to changing environmental conditions, optimizing the balance between maintaining sufficient turgor for growth and minimizing water loss during severe stress periods (A. Sharma et al., 2019). Research on chickpea cultivars showed that proline and glycine betaine application enhanced SOD activity by 42.7% and 27.7% in PDG4, and by 51% and 41.1% in GPF2 under 50 mM of salinity stress (Choudhury et al., 2025). The combined application of rutin and silicon on maize seedlings reduced oxidative stress by decreasing the reactive oxygen species and improved osmoprotectants including proline, total soluble sugar, and glycine-betaine (Altansambar et al., 2024).

5.2 Proline Biosynthesis and Metabolic Regulation

Proline accumulation represents one of the most widely documented osmotic adjustment responses, with proline content frequently increasing 10-50 fold under severe drought conditions (Escalante-Magaña et al., 2024). The synthesis of proline occurs through two major pathways: the glutamate pathway involving P5C synthetase (P5CS) and P5C reductase (P5CR), and the ornithine pathway involving ornithine δ-aminotransferase (OAT) (Adamipour et al., 2025). Under drought stress, the glutamate pathway predominates, with the expression of P5CS and P5CR genes increasing substantially in response to water deficit (Adamipour et al., 2025). Additionally, proline catabolism through the enzymes proline dehydrogenase (PDH) and P5C dehydrogenase (P5CDH) becomes suppressed under drought, further contributing to proline accumulation (Adamipour et al., 2025).

The regulatory mechanisms controlling proline metabolism are complex and multi-layered, involving phytohormone signaling, transcription factor regulation, and post-translational control (Escalante-Magaña et al., 2024). Abscisic acid enhances the expression of genes involved in proline synthesis while suppressing expression of catabolic genes, effectively shifting proline metabolism toward accumulation (Escalante-Magaña et al., 2024). The amino acid content in plants, including proline and other free amino acids, increases substantially under drought stress, providing osmotic adjustment and nitrogen mobilization capacity during stress periods (Escalante-Magaña et al., 2024). Proline serves as a versatile adaptive compound for mediating drought tolerance due to its roles as an osmoprotectant, energy source, redox buffer, and nitrogen reservoir (Escalante-Magaña et al., 2024). Research on Vigna radiata showed that salt stress results in a steep decline in shoot length, biomass, chlorophyll contents, and soluble protein contents, however compatible solutes including proline, Glycine-betaine, Amino acids and total soluble sugars contents were found to be upregulated (Mir et al., 2024).

5.3 Soluble Sugars, Polyols, and Carbohydrate Metabolism

Soluble sugar accumulation represents a crucial component of osmotic adjustment, with glucose, fructose, sucrose, and other sugars contributing to cellular solute concentration (T. A. Khan et al., 2024). These sugars serve multiple functions beyond osmotic regulation, including provision of carbon skeletons and energy for biosynthetic processes and respiration (T. A. Khan et al., 2024). The upregulation of sucrose synthase and other enzymes involved in carbohydrate metabolism facilitates rapid accumulation of soluble sugars under drought conditions (T. A. Khan et al., 2024). Trehalose, a disaccharide rarely found in vegetative tissues but accumulated dramatically under stress, functions as a stress protectant molecule stabilizing proteins and membranes (Genc & Taş, 2026).

Polyols including sorbitol, mannitol, and inositol accumulate under drought stress in various plant species, contributing to osmotic adjustment while also providing substrate for synthesis of cell wall components and signaling molecules (Sadak et al., 2022). The coordinate accumulation of multiple soluble sugar species and polyols creates a diversified osmotic adjustment strategy that maintains cellular function while signaling stress status to regulatory systems (Sadak et al., 2022). The accumulation of total soluble carbohydrates frequently increases 15-30% under moderate drought stress, with greater increases occurring under severe water deficit (T. A. Khan et al., 2024). Sorghum plants exposed to drought stress at the seed development stage treated with nanoceria significantly improved photosynthetic rate by 19% and tissue water content by 18%, achieved by accumulating compatible solutes (M et al., 2024).

5.4 Glycine Betaine and Quaternary Ammonium Compounds

Glycine betaine, a quaternary ammonium compound synthesized through the oxidation of choline, represents an important osmoprotectant in many plant species (Mir et al., 2024). The synthesis of glycine betaine occurs through the sequential actions of choline monooxygenase and betaine aldehyde dehydrogenase, with expression of these genes increasing substantially under drought and salinity stress (Mir et al., 2024). Glycine betaine accumulation can reach remarkably high concentrations under severe stress, with increases of 40-80% documented in drought-tolerant genotypes compared to controls (Mir et al., 2024). Other amino acid derivatives and quaternary ammonium compounds including stachydrine, ectoine, and N-acetyl-β-lysine accumulate under osmotic stress conditions, providing additional osmotic adjustment capacity (Bekkaye & Boublenza, 2025).

The roles of these compounds extend beyond osmotic regulation to include protection of enzymatic function, stabilization of protein structures, and quenching of reactive oxygen species (Mir et al., 2024). The accumulation of compatible solutes from multiple chemical classes creates a robust osmotic adjustment system that maintains cellular function and plant growth under even severe water deficit conditions (Mir et al., 2024). Grewia tenax exhibited remarkable 41.83% increase in glycine betaine concentration and 87.5% increase in proline concentration, indicating its strong adaptive response to drought conditions (P. Sharma & Agarwal, 2025). Research on Agropyron species revealed that drought stress significantly increased root length by 21.54%, leaf water content by 12.99%, and proline accumulation by 31.56%, with these species mitigating desertification through key drought survival strategies including stomatal regulation and osmoprotectant accumulation (Y. Wang et al., 2026).

VI. Secondary Metabolites and Stress-Induced Biochemical Reprogramming

6.1 Essential Oil Production and Compositional Changes Under Drought

Essential oil composition and yield in aromatic medicinal plants undergo substantial modulations in response to drought stress (S. Mulugeta et al., 2025). The Lamiaceae family species, including Ocimum sanctum, exhibit stress-induced changes in the production of volatile organic compounds, which serve diverse ecological and physiological functions (S. Mulugeta et al., 2025). Monoterpenes and sesquiterpenes, the primary constituents of essential oils in basil species, accumulate differentially under drought conditions, with certain compounds increasing while others decrease in concentration (S. Mulugeta et al., 2025). Drought stress typically acts as a catalyst for secondary metabolism in aromatic plants, resulting in enhanced production of essential oils and phenolic compounds with subsequent augmentation of their biological activities (Mansinhos et al., 2024).

Research on diverse Ocimum species revealed that drought stress slightly increased the essential oil content of O. × africanum and O. basilicum 'Genovese' by 9.8% and 26%, respectively

(S. Mulugeta et al., 2025). The essential oil composition varied considerably among the different Ocimum species and cultivars examined (S. Mulugeta et al., 2025). Cultivars Ohře and Genovese had linalool as a major component, exceeding 40%, while O. americanum was rich in citral compounds—neral and geranial—accounting for 26–37%, contributing to its strong lemon-like fragrance (S. Mulugeta et al., 2025). O. sanctum was characterized by its elevated levels of eugenol (36.4–50.3%) and β-caryophyllene (26.4–38.5%) (S. Mulugeta et al., 2025). The specific changes in essential oil composition reflect altered expression of genes encoding terpene synthases and other enzymes involved in volatile compound synthesis (Shahroudi et al., 2025).

The accumulation of certain essential oil components under stress may serve protective roles, with antimicrobial and antioxidant properties of volatile compounds potentially contributing to plant defense (Shahroudi et al., 2025). The enhancement of essential oil quantity and potential quality improvements under moderate drought stress may paradoxically increase the medicinal value of aromatic plant products (S. Mulugeta et al., 2025). Research revealed that exogenous application of putrescine modulated key genes involved in terpenoid biosynthesis and altered the essential oil composition of Thymus daenensis under drought stress, upregulating TPS2 and downregulating DXR expression (Shahroudi et al., 2025). This transcriptional modulation was accompanied by increased levels of γ-terpinene and p-cymene, precursors of thymol and carvacrol (Shahroudi et al., 2025).

6.2 Phenolic Compounds and Flavonoid Biosynthesis

Drought stress triggers substantial increases in the accumulation of phenolic compounds, particularly through upregulation of the phenylpropanoid biosynthesis pathway (Rao & Zheng, 2025). This pathway produces diverse compounds including phenolic acids, flavonoids, and lignin precursors that function as free radical scavengers and regulate plant growth and defense mechanisms (Rao & Zheng, 2025). The upstream enzyme phenylalanine ammonia-lyase (PAL) catalyzes the first committed step in phenolic biosynthesis, with PAL activity and gene expression increasing dramatically under drought stress conditions (Rao & Zheng, 2025).

Flavonoid biosynthesis increases substantially under drought conditions through upregulation of chalcone synthase (CHS) and related enzymes, leading to accumulation of flavonols, anthocyanins, and other flavonoid classes (Rao & Zheng, 2025). These compounds provide multifunctional protection against drought stress through their roles as antioxidants, ultraviolet protectants, and regulators of photosynthetic electron transport (Rao & Zheng, 2025). The accumulation of specific flavonoid classes, including quercetin, kaempferol, and others with proven biological activities, may enhance the therapeutic potential of medicinal plants produced under moderate drought stress (Rao & Zheng, 2025). Research on basil plants with horsetail extract treatment revealed that the main components of essential oil included methyl eugenol (12.93–25.93%), eugenol (17.63–27.51%), 1,8-cineole (15.63–20.84%), linalool (8.31–19.63%) and (Z)-caryophyllene (6.02–14.93%) (Eghlima et al., 2024).

The comparison between the control and highly treated groups showed that foliar spraying of horsetail extract containing high silicon increased plant height by 49.79%, number of leaves per plant by 45.61%, number of sub-branches by 91.09%, leaf area index by 99.78%, fresh weight by 52.78%, and dry weight by 109.25% (Eghlima et al., 2024). The highest content of total phenol (2.12 mg GAE/g DW), total flavonoid (1.73 mg RE/g DW), total anthocyanin (0.83 mg C3G/g DW), and antioxidant activity (184.3 μg/ml) was observed in the 2% extract treatment (Eghlima et al., 2024). Additionally, the content of essential oil increased with increasing the concentration of horsetail extract, with the highest amount of essential oil obtained at the concentration of 2%, which increased by 134.78% compared to the control (Eghlima et al., 2024).

6.3 Transcriptional Regulation of Secondary Metabolite Biosynthesis

The coordinate upregulation of secondary metabolite biosynthetic pathways under drought stress reflects transcriptional control by multiple transcription factor families (Rao & Zheng, 2025). MYB transcription factors serve as master regulators of phenylpropanoid metabolism and flavonoid biosynthesis, with specific MYB proteins controlling expression of pathway genes in response to developmental signals and environmental stresses (Rao & Zheng, 2025). The integration of drought stress signals with developmental programs ensures that secondary metabolite accumulation occurs appropriately in response to plant water status (Rao & Zheng, 2025).

Transcriptional regulation involves complex interactions between stress-responsive transcription factors and promoter regulatory elements, creating feedback loops that optimize secondary metabolite production in relation to drought severity (A. Khan et al., 2025). Methyl jasmonate signaling, a key component of plant defense responses to biotic stresses and abiotic stressors, upregulates secondary metabolite biosynthesis through activation of specific transcription factors (Nie et al., 2025). The coordinate regulation of multiple biosynthetic pathways ensures the simultaneous accumulation of diverse secondary metabolites with complementary protective functions, creating a comprehensive metabolic response to drought stress (A. Khan et al., 2025). Research on walnut plants revealed that MeJA treatment significantly enhanced ROS scavenging through the synergistic activation of phenylalanine, tryptophan, and α-linolenic acid pathways (Nie et al., 2025). The MeJA treatment effectively mitigated salt stress-induced oxidative damage, with significant 16.83% reduction in malondialdehyde content, concurrent 11.60%, 10.73% and 22.25% increases in superoxide dismutase, peroxidase, and catalase activities, respectively (Nie et al., 2025).

6.4 Phenolic-Terpene Interplay and Coordinated Defense Signaling

The simultaneous accumulation of phenolic compounds and terpenes under drought stress reflects integrated signaling pathways coordinating diverse biochemical responses (Aftab et al., 2025). These two major classes of secondary metabolites share common precursors and regulatory mechanisms, with their relative accumulation patterns reflecting the balance of allocation to different defensive and adaptive functions (Aftab et al., 2025). The synergistic effects of phenolic compounds and essential oil components in providing antioxidant protection, antimicrobial activity, and ultraviolet protection suggest that coordinated accumulation of these metabolite classes represents an evolutionarily optimized stress response strategy (Aftab et al., 2025).

Signaling molecules including methyl jasmonate, salicylic acid, and other plant hormones coordinate the expression of genes involved in both phenolic and terpene biosynthesis, ensuring that secondary metabolite production occurs concurrently with other stress adaptation responses (Aftab et al., 2025). The specific profiles of secondary metabolites accumulated under drought stress may vary substantially between plant species and even among cultivars within species, reflecting genotype-specific differences in stress response regulation (Aftab et al., 2025). Assessment of basil extract showed that basil leaf extract demonstrated significant antimicrobial activity against microorganisms, particularly in the case of essential oil extracts compared with organic extract methods (Sultan et al., 2024). Ocimum basilicum essential oil showed strong antifungal activity against dermatophytic species, with the analysis of essential oil from O. gratissimum revealing the presence of γ-terpinene (33.73%), thymol (26.44%) and 1.8 cineol (16.65%), whereas O. basilicum's essential oil was dominated by linalool (55.32%), eucalyptol (16.78%) and eugenol (7.45%) (Momo et al., 2025).

References

[1]. Adamipour, N., Nazari, F., Nalousi, A. M., & Silva, J. A. T. da. (2025). Evaluation of the molecular mechanism underlying proline metabolic and catabolic pathways and some morpho-physiological traits of tobacco (nicotiana tabacum l.) plants under arsenic stress. *BMC Plant Biology*.

[2]. Aftab, T., Naeem, M., Jha, P., Prasad, P. V., Wang, J., Irfan, M., & Naikoo. (2025). Production of secondary metabolites under challenging environments: Understanding functions and mechanisms of signalling molecules. *Frontiers in Plant Science*.

[3]. Ali, S., Mir, R., Haque, A., Almalki, M., Alfredan, M., Khalifa, A., Mahmoudi, H., Shahid, M., Tyagi, A., Mir, Z., Manghwar, H., Aslam, M., Khan, M., Mir, R., Haque, M., Almalki, D., Ma, A. M., & Mir, Z. (2025). Exploring physiological and molecular dynamics of drought stress responses in plants: Challenges and future directions. *Frontiers in Plant Science*.

[4]. Altansambar, N., Muslu, A. S., & Kadıoğlu, A. (2024). The combined application of rutin and silicon alleviates osmotic stress in maize seedlings by triggering accumulation of osmolytes and antioxidants' defense mechanisms. *Physiology and Molecular Biology of Plants*.

[5]. Arab, M., Askari, H., Aliniaeifard, S., Mokhtassi-Bidgoli, A., Estaji, A., Sadat-Hosseini, M., Sohrabi, S. S., Mesgaran, M., Leslie, C., Brown, P., & Vahdati, K. (2023). Natural variation in photosynthesis and water use efficiency of locally adapted persian walnut populations under drought stress and

recovery. *Plant Physiology and Biochemistry : PPB*.

[6]. Arif, Y., Singh, P., Siddiqui, H., Bajguz, A., & Hayat, S. (2020). Salinity induced physiological and biochemical changes in plants: An omic approach towards salt stress tolerance. *Plant Physiology and Biochemistry : PPB*.

[7]. Bekkaye, I. I., & Boublenza, F. (2025). Osmoprotective mechanisms of compatible solutes in enterococcus faecium LBO1 isolated from traditional algerian lben. *Notulae Scientia Biologicae*.

[8]. Bondar, E. I., Zubairova, U., Bobrovskikh, A., & Doroshkov, A. V. (2025). Integrative transcriptomic and evolutionary analysis of drought and heat stress responses in solanum tuberosum and solanum lycopersicum. *Plants*.

[9]. Burbulis, N., Blinstrubienė, A., Baltušnikienė, A., & Deveikytė, J. (2022). Foliar spraying with potassium bicarbonate reduces the negative impact of drought stress on sweet basil (ocimum basilicum l.). *Plants*.

[10]. Chen, S., Ren, J., Zhao, H., Wang, X., Wang, T.-H., Jin, S.-D., Wang, Z., Li, C.-Y., Liu, A., Lin, X., & Ahammed, G. J. (2019). <I>trichoderma harzianum</i> improves defense against <i>fusarium oxysporum</i> by regulating ROS and RNS metabolism, redox balance, and energy flow in cucumber roots. *American Phytopathological Society*.

[11]. Chintalwar, R., S, A., Sharbidre, A., Jain, V., Jagtap, S., Mukherjee, A., & Ghate, V. (2026). Application of agrohomoeopathic for cultivation of ocimum sanctum and ocimum basilicum and evaluation of phytochemical, antioxidant, and immunomodulatory effects on channel catfish model. *International Journal of High Dilution Research*.

[12]. Choudhury, R., Singh, A., & Choudhary, K. K. (2025). Amelioration of salinity stress in chickpea (cicer arietinum l.) cultivars through foliar spray of proline and glycine betaine. *Journal of Agronomy and Crop Science*.

[13]. Dai, L., Li, J., Harmens, H., Zheng, X., & Zhang, C. (2020). Melatonin enhances drought resistance by regulating leaf stomatal behaviour, root growth and catalase activity in two contrasting rapeseed (brassica napus l.) genotypes. *Plant Physiology and Biochemistry : PPB*.

[14]. Eghlima, G., Chegini, K. G., Farzaneh, M., & Aghamir, F. (2024). Effect of common horsetail extract on growth characteristics, essential oil yield and chemical compositions of basil (ocimum basilicum l.). *Scientific Reports*.

[15]. Escalante-Magaña, C., Lizama-Gasca, M., Bojórquez-Quintal, E., Medina-Lara, M. F., Echevarría-Machado, I., & Martínez-Estévez, M. (2024). Proline: A versatile amino acid in the presence of salinity and drought in the capsicum genus. *Israel Journal of Plant Sciences*.

[16]. Eweda, M. A., Jalil, S., Rashwan, A. K., Tsago, Y., Hassan, U., & Jin, X. (2025). Molecular and physiological characterizations of roots under drought stress in rice: A comprehensive review. *Plant Physiology and Biochemistry : PPB*.

[17]. Fang, S., Yang, H., Duan, L., Shi, J., & Guo, L. (2023). Potassium fertilizer improves drought stress alleviation potential in sesame by enhancing photosynthesis and hormonal regulation. *Plant Physiology and Biochemistry : PPB*.

[18]. Feller, U., & Vaseva, I. (2014). Extreme climatic events: Impacts of drought and high temperature on physiological processes in agronomically important plants. *Frontiers Media*.

[19]. Genc, T. T., & Taş, T. (2026). Divergent regulation of trehalose accumulation by exogenous proline in drought-stressed sorghum and maize. *Turkish Journal of Agriculture - Food Science and Technology*.

[20]. Hasanuzzaman, M., Bhuyan, M., Zulfiqar, F., Raza, A., Mohsin, S., Mahmud, J., Fujita, M., & Fotopoulos, V. (2020). Reactive oxygen species and antioxidant defense in plants under abiotic stress: Revisiting the crucial role of a universal defense regulator. *Antioxidants*.

[21]. Huang, D., Wu, W., Abrams, S. R., & Cutler, A. J. (2008). The relationship of drought-related gene expression in arabidopsis thaliana to hormonal and environmental factors. *Oxford University Press*.

[22]. Hussain, S., Hussain, S., Qadir, T., Khaliq, A., Ashraf, U., Parveen, A., Saqib, M., & Rafiq, M. K. (2019). Drought stress in plants: An overview on implications, tolerance mechanisms and agronomic mitigation strategies. *None*.

[23]. Jabeen, Dr. M., & Jabeen, A. (2022). Role of compatible solutes in alleviating effect of abiotic stress in plants. *International*

Research Journal of Education and Innovation.
[24]. Jensen, N. B., Ottosen, C., Fomsgaard, I., & Zhou, R. (2024). Elevated CO2 induce alterations in the hormonal regulation of stomata in drought stressed tomato seedlings. *Plant Physiology and Biochemistry : PPB*.
[25]. Jomová, K., Alomar, S., Alwasel, S., Nepovimova, E., Kuča, K., & Valko, M. (2024). Several lines of antioxidant defense against oxidative stress: Antioxidant enzymes, nanomaterials with multiple enzyme-mimicking activities, and low-molecular-weight antioxidants. *Archives of Toxicology*.
[26]. Keleş, R., & Küçüködük, M. (2025). Superoxide dismutase and isozyme analysis in two bread wheat genotypes under osmotic stress. *Kahramanmaraş Sütçü İmam Üniversitesi Tarım Ve Doğa Dergisi*.
[27]. Khan, A., Kanwal, F., Ullah, S., Fahad, M., Tariq, L., Altaf, M. T., Riaz, A., & Zhang, G. (2025). Plant secondary metabolites—central regulators against abiotic and biotic stresses. *Metabolites*.
[28]. Khan, M. N., Siddiqui, M. H., Alsolami, M. A., & Siddiqui, Z. H. (2023). Melatonin-regulated heat shock proteins and mitochondrial ATP synthase induce drought tolerance through sustaining ROS homeostasis in H2S-dependent manner. *Plant Physiology and Biochemistry : PPB*.
[29]. Khan, T. A., Ahmad, A., Saeed, T., Yusuf, M., Faisal, M., & Alatar, A. (2024). Investigating the influence of selenium and epibrassinolide on antioxidant activity, proline accumulation, and protein expression profiles in wheat plants experiencing heat and drought stress. *Frontiers in Plant Science*.
[30]. M, D., S, V. B. K., R, R., & P., J. (2024). Sorghum drought tolerance is enhanced by cerium oxide nanoparticles via stomatal regulation and osmolyte accumulation. *Plant Physiology and Biochemistry : PPB*.
[31]. Mansinhos, I., Gonçalves, S., & Romano, A. (2024). How climate change-related abiotic factors affect the production of industrial valuable compounds in lamiaceae plant species: A review. *Frontiers Media*.
[32]. Mir, R. A., Logeshwari, T. R., Aryendu, & Somasundaram, R. (2024). Elevated osmolytes accumulation helps in combating NaCl stress causing negative impacts on growth and metabolism of vigna radiata (l.). *Journal of Plant Stress Physiology*.
[33]. Mirgos, M., Dąbrowski, P., Kalaji, H., Wróbel, J., Gajc-Wolska, J., Pawluśkiewicz, B., Kunka, M., & Kowalczyk, K. (2026). Photosynthetic responses of hydroponically grown basil (ocimum basilicum l.) to drought and high-EC stress. *PeerJ*.
[34]. Mishra, N., Jiang, C., Chen, L., Paul, A., Chatterjee, A., & Shen, G. (2023). Achieving abiotic stress tolerance in plants through antioxidative defense mechanisms. *Frontiers in Plant Science*.
[35]. Momo, E. J., Noumegna, F. P. K., Possi, S. N., Kamdem, B. P., Dongmo, P. M. J., & Boyom, F. (2025). Antifungal and antioxidant activities of ocimum basilicum and ocimum gratissimum essential oils and their emulsions against selected trichophyton species. *Asian Journal of Research in Biochemistry*.
[36]. Mulugeta, S. M., Sárosi, S., & Radácsi, P. (2023). Physio-morphological trait and bioactive constituents of ocimum species under drought stress. *Elsevier BV*.
[37]. Mulugeta, S., Hunegnaw, A., Hári, K., & Radácsi, P. (2025). Biomass production and volatile oil accumulation of ocimum species subjected to drought stress. *Horticulturae*.
[38]. Najafi, M., Çokuysal, B., Danesh, Y. R., Farda, B., Mignini, A., & Pellegrini, M. (2025). Evaluation of funneliformis mosseae inoculation effects on growth, nutrient uptake, and essential oil content in turkish oregano under drought stress. *PeerJ*.
[39]. Nie, R., Wu, C., Ji, X., Li, A., Zheng, X., Tang, J., Sun, L., Su, Y., & Zhang, J. (2025). Methyl jasmonate orchestrates multi-pathway antioxidant defense to enhance salt stress tolerance in walnut (juglans regia l.). *Antioxidants*.
[40]. Osku, M., Procino, S., Mascio, I., Miazzi, M., Vivaldi, G. A., Vona, D., Fanelli, V., Roozban, M., Sarikhani, S., Arab, M. M., Akbari, M., Vahdati, K., & Montemurro, C. (2025). Physiological and molecular responses of two contrasting drought resistance pistachio interspecific hybrid rootstocks. *Frontiers in Plant Science*.
[41]. Qiao, M., Hong, C., Jiao, Y., Hou, S., & Gao, H. (2024). Impacts of drought on photosynthesis in major food crops and the related mechanisms of plant responses to drought. *Plants*.

[42]. Rahimi, M., Mortazavi, M., Mianabadi, A., & Debnath, S. (2023). Evaluation of basil (ocimum basilicum) accessions under different drought conditions based on yield and physio-biochemical traits. *BMC Plant Biology*.
[43]. Rao, M. J., Duan, M., Zhou, C., Jiao, J., Cheng, P., Yang, L., Wei, W., Shen, Q., Ji, P., Yang, Y., Conteh, O., Yan, D., Yuan, H., Rauf, A., Ai, J., & Zheng, B. (2025). Antioxidant defense system in plants: Reactive oxygen species production, signaling, and scavenging during abiotic stress-induced oxidative damage. *Horticulturae*.
[44]. Rao, M. J., & Zheng, B. (2025). The role of polyphenols in abiotic stress tolerance and their antioxidant properties to scavenge reactive oxygen species and free radicals. *Antioxidants*.
[45]. Rasafi, T. E., Oukarroum, A., Haddioui, A., Song, H., Kwon, E. E., Bolan, N., Tack, F., Sebastian, A., Prasad, M. N. V., & Rinklebe, J. (2020). Cadmium stress in plants: A critical review of the effects, mechanisms, and tolerance strategies. *Taylor & Francis*.
[46]. Ritchie, S. W., Nguyen, H. T., & Holaday, A. S. (1990). Leaf water content and gas-exchange parameters of two wheat genotypes differing in drought resistance. *Wiley*.
[47]. Rosa, F. R. F. la, Hernández, C. M., Estrella-Maldonado, H., Saucedo-Picazo, L. E., & Santillán-Mendoza, R. (2024). Expression and activity of ascorbate peroxidase (APX) enzyme in persian lime with HLB by the application of resistance elicitors. *Journal of Research in Agriculture and Animal Science*.
[48]. Sadak, M. S., Sękara, A., Al-ashkar, I., Habib-ur-Rahman, M., Skalický, M., Brestič, M., Kumar, A., Sabagh, A. E., & Abdelhamid, M. (2022). Exogenous aspartic acid alleviates salt stress-induced decline in growth by enhancing antioxidants and compatible solutes while reducing reactive oxygen species in wheat. *Frontiers in Plant Science*.
[49]. Sade, N., Gebretsadik, M., Seligmann, R., Schwartz, A., Wallach, R., & Moshelion, M. (2009). The role of tobacco Aquaporin1 in improving water use efficiency, hydraulic conductivity, and yield production under salt Stress1[c][w][OA]. *Plant Physiology*.
[50]. Santander, C., Ruíz, A., García, S., Aroca, R., Cumming, J., & Cornejo, P. (2019). Efficiency of two arbuscular mycorrhizal fungal inocula to improve saline stress tolerance in lettuce plants by changes of antioxidant defense mechanisms. *The Journal of the Science of Food and Agriculture*.
[51]. Seo, S., Ahn, Y.-Y., Kim, K., Lee, J. H., Min, K., & Lee, H. (2025). Exogenous abscisic acid enhances freeze-thaw stress tolerance in antarctic moss sanionia uncinata through coordinated antioxidant defense and osmoprotectant accumulation. *Cryobiology*.
[52]. Shahroudi, E., Zarinkamar, F., & Soltani, B. (2025). Impact of putrescine on essential oil composition, free polyamines content and expression of related genes (DXR and TPS2) in thymus daenensis under drought stress. *BMC Plant Biology*.
[53]. Sharma, A., Shahzad, B., Kumar, V., Kohli, S. K., Sidhu, G. P. S., Bali, A. S., Handa, N., Kapoor, D., Bhardwaj, R., & Zheng, B. (2019). Phytohormones regulate accumulation of osmolytes under abiotic stress. *Multidisciplinary Digital Publishing Institute*.
[54]. Sharma, P., & Agarwal, K. (2025). Drought resistance in grewia and acacia species. *International Journal For Multidisciplinary Research*.
[55]. Singh, D. (2022). Juggling with reactive oxygen species and antioxidant defense system – a coping mechanism under salt stress. *Elsevier BV*.
[56]. Sultan, L. J., Fadhil, W. G., Hamid, M., & Hadi, S. (2024). A comparative study of the effect of extracts extracted from ocimum basilicum leaves using organic extract and essential oil. *Functional Foods in Health and Disease*.
[57]. Tamirat, W. (2019). Review on role of proline on coffee under drought conditions. *Journal of Environment and Earth Science*.
[58]. Tan, U., & Gören, H. K. (2024). Comprehensive evaluation of drought stress on medicinal plants: A meta-analysis. *PeerJ*.
[59]. Tüğen, A., & Buruleanu, C. L. (2025). The role of plant-derived bioactive compounds in mitigating oxidative stress. *Foods*.
[60]. Vicidomini, C., Palumbo, R., Moccia, M., & Roviello, G. (2024). Oxidative processes and xenobiotic metabolism in plants: Mechanisms of defense and potential therapeutic implications. *Journal of Xenobiotics*.

[61]. Wang, X., Wang, M., Yan, G., Yang, H., Wei, G., Shen, T., Wan, Z., Zheng, W., Fang, S., & Wu, Z. (2023). Comparative analysis of drought stress-induced physiological and transcriptional changes of two black sesame cultivars during anthesis. *Frontiers in Plant Science*.

[62]. Wang, Y., Qiu, J., Meng, Y., & Li, Q. (2026). Morphological-physiological responses of three species of agropyron to drought stress in xinjiang, china. *Functional Plant Biology*.

[63]. Wasaya, A., Manzoor, S., Yasir, T. A., Sarwar, N., Mubeen, K., Ismail, I. A., Raza, A., Rehman, A., Hossain, A., & Sabagh, A. E. (2021). Evaluation of fourteen bread wheat (triticum aestivum l.) genotypes by observing gas exchange parameters, relative water and chlorophyll content, and yield attributes under drought stress. *Multidisciplinary Digital Publishing Institute*.

[64]. Yang, Y., Ma, X., Yan, L., Li, Y., Wei, S.-J., Teng, Z., Zhang, H., Tang, W., Peng, S., & Li, Y. (2023). Soil-root interface hydraulic conductance determines responses of photosynthesis to drought in rice and wheat. *Plant Physiology*.

[65]. Zhu, X., Zhang, N., Liu, X., Wang, S., Li, S., Yang, J., Wang, F., & Si, H. (2020). StMAPK3 controls oxidase activity, photosynthesis and stomatal aperture under salinity and osmosis stress in potato. *Plant Physiology and Biochemistry : PPB*.