

Plant Adaptations to Drought Stress: Morphological, Physiological, and Biochemical Responses

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Abstract

Drought stress is one of the major abiotic constraints affecting plant growth, development, productivity and survival. Water deficiency disrupts cellular water relations and subsequently influences plant morphology, physiology, metabolism and molecular regulation. Plants respond to drought through a combination of adaptive mechanisms rather than through a single tolerance trait. Morphological responses include modification of root architecture, reduction in leaf area, leaf rolling, changes in shoot growth and altered biomass allocation. Physiological responses involve stomatal regulation, reduction in transpiration, maintenance of cellular water status, osmotic adjustment, changes in photosynthesis and improvement of water-use efficiency. At the biochemical level, drought induces accumulation of compatible solutes, activation of antioxidant defence, changes in secondary metabolism and regulation of phytohormones and stress-responsive proteins. These responses are coordinated through signalling networks involving abscisic acid, reactive oxygen species, calcium and other signalling molecules. Recent research also highlights the importance of root–shoot communication, plant–microbiome interactions, genomic and proteomic regulation, and the capacity of plants to recover after rewatering. This review synthesizes the major morphological, physiological and biochemical adaptations of plants to drought stress and discusses their integration, influencing factors, current research gaps and future directions.

Keywords: Drought stress, plant adaptation, morphology, physiology, biochemical responses, osmotic adjustment, antioxidant defence, drought tolerance

INTRODUCTION

Water availability is fundamental for plant growth because it supports cell expansion, photosynthesis, nutrient transport, metabolic reactions and maintenance of cellular turgor. A reduction in available water, therefore, affects several interconnected processes within the plant. Drought stress occurs when water availability becomes insufficient to meet the physiological requirements of a plant for a particular period. It is considered one of the major environmental constraints limiting agricultural productivity and plant performance [1, 2].

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The effects of drought are not restricted to a single level of plant organization. Water deficit can modify root and shoot growth, leaf development, photosynthesis, stomatal conductance, water relations, nutrient uptake, membrane stability and cellular metabolism. A meta-analysis of 1,301 paired observations from 84 studies showed that water stress generally decreases plant growth and photosynthesis while increasing reactive oxygen species (ROS), membrane permeability and antioxidant activity [3]. The severity of these effects depends on drought intensity, duration, plant genotype, developmental stage and environmental conditions.

Plants have evolved different strategies to cope with water limitation. These strategies are commonly described as drought escape, drought avoidance and drought tolerance. Drought avoidance involves maintaining favourable tissue water status through mechanisms, such as deeper rooting and stomatal regulation, whereas drought tolerance allows cellular functions to continue despite reduced water availability. Morphological, physiological and biochemical mechanisms often operate simultaneously and interact with one another [1, 4].

At the morphological level, plants may reduce leaf expansion, alter root-to-shoot allocation, modify root architecture and develop anatomical characteristics that reduce water loss. Such changes help plants maintain water balance under limited moisture availability [5]. At the physiological level, stomatal closure, reduction in transpiration, osmotic adjustment and modifications in photosynthetic activity contribute to water conservation and maintenance of cellular function [2, 6].

Drought also produces biochemical disturbances, particularly through excessive generation of ROS. Plants respond by increasing enzymatic and non-enzymatic antioxidant systems, accumulating compatible solutes and modifying primary and secondary metabolism. Antioxidant enzymes, such as superoxide dismutase, catalase, and peroxidases, together with compounds such as ascorbate, glutathione, carotenoids and phenolics, contribute to protection against oxidative damage [7, 8].

Recent research has expanded the understanding of drought adaptation beyond individual physiological traits. Genomic and proteomic studies demonstrate that drought responses involve extensive changes in gene expression, protein abundance, hormone signalling and metabolic pathways [9]. Root-to-shoot signalling, particularly involving abscisic acid (ABA), ROS and calcium signalling, contributes to rapid coordination of drought responses throughout the plant [10, 11].

Furthermore, drought adaptation is increasingly being considered in relation to plant–microbiome interactions. Root exudates and microbial communities can influence plant water relations, nutrient acquisition and stress signalling, suggesting that the root–soil–microbiome interface represents an important component of drought resilience [12]. Recent research also emphasizes that drought response should not be considered independently from recovery because the ability to resume physiological activity after rewatering influences long-term plant performance [13].

Therefore, understanding drought adaptation requires an integrated consideration of morphological, physiological and biochemical responses. This review discusses these responses, their coordination, factors influencing drought tolerance, current research gaps and future research directions (Figure 1).

DROUGHT STRESS IN PLANTS

Definition and Characteristics

Drought stress represents a condition in which water availability becomes insufficient to maintain normal plant physiological activity. It may develop gradually through prolonged reduction in soil moisture or occur rapidly under conditions such as flash drought. The resulting decline in plant water status affects cell expansion, stomatal behaviour, photosynthesis, nutrient transport and metabolism [1, 4].

The response to drought is dynamic rather than uniform. Mild water limitation may initially produce reversible changes, such as stomatal closure and reduced leaf expansion, whereas prolonged or severe drought can cause membrane damage, oxidative stress, inhibition of photosynthesis and extensive growth reduction [6]. The intensity and duration of stress, therefore, influence the magnitude and nature of plant responses.

Drought responses can broadly be classified into three strategies: escape, avoidance and tolerance. Escape involves completing the life cycle before severe water limitation occurs. Avoidance maintains tissue hydration through mechanisms such as root development and reduction of water loss. Tolerance involves maintaining cellular functions despite declining tissue water potential [4].

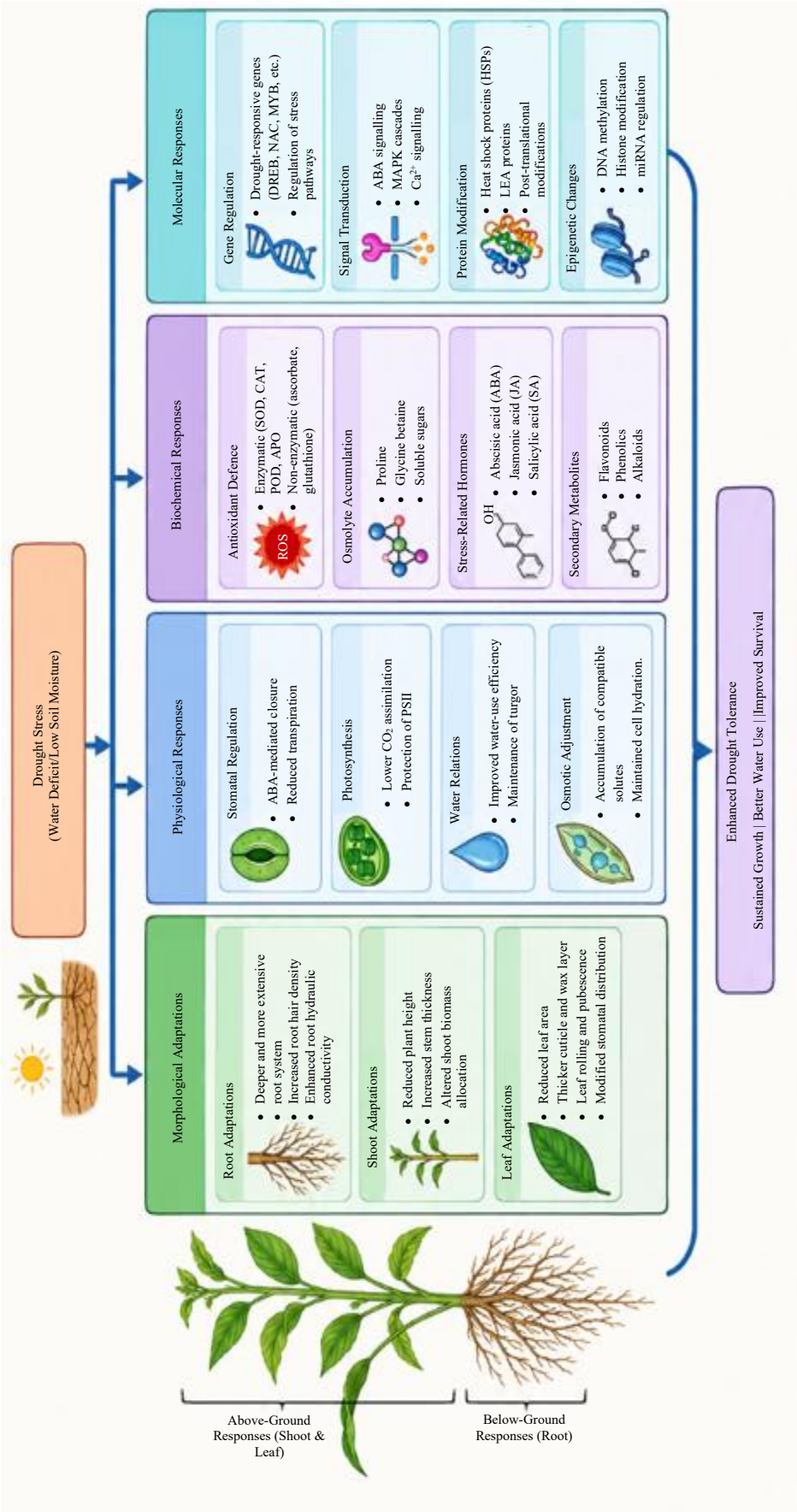


Figure 1. Overview of plant responses to drought stress. Drought stress triggers a cascade of morphological, physiological, biochemical and molecular adaptations that work together to enhance plant drought tolerance.

Causes and Occurrence

Drought may result from insufficient precipitation, high evaporative demand, increased temperature, soil water limitation and irregular rainfall. Climate change can increase the frequency and intensity of water-deficit events in many regions, creating additional challenges for agricultural systems [14, 15].

The impact of drought depends not only on rainfall but also on soil properties, atmospheric demand, root distribution, temperature, relative humidity and plant characteristics. Consequently, two plants experiencing similar rainfall conditions may experience different levels of physiological water stress.

Drought can occur during different stages of plant development. Stress during germination, vegetative growth, flowering or reproductive development may produce different effects. The timing of water limitation is, therefore, an important determinant of drought-induced damage and yield reduction [2, 16].

Effects of Water Deficit on Plants

Water deficit initially reduces cell turgor and restricts cell expansion. Continued drought can reduce leaf area, shoot growth and biomass production. Root growth may either be promoted relative to shoot growth or become inhibited depending on stress intensity and plant genotype [1, 5].

Photosynthesis is commonly affected because stomatal closure restricts carbon dioxide entry into leaves. Under more severe stress, non-stomatal limitations may also occur because of damage to photosynthetic pigments, chloroplast structure and metabolic processes [3, 16].

Water limitation can also disturb nutrient acquisition and transport, alter membrane stability and increase ROS production. Plants consequently activate antioxidant defence, osmotic adjustment and other protective mechanisms to limit cellular injury [7, 8].

The major effects of drought stress on plant growth, water relations, photosynthesis and cellular metabolism are summarised in Table 1

Table 1. Major effects of drought stress on plants.

Plant process/trait	Effect of drought stress	Major mechanism/response	Consequence for the plant	Supporting references
<i>Cellular water status</i>	Decrease in water potential and turgor	Water loss exceeds water uptake; osmotic adjustment may occur	Reduced cell expansion and growth	[1, 6]
<i>Root growth</i>	Changes in root elongation, branching and root: shoot ratio	Increased soil exploration under moderate drought; inhibition under severe drought	Altered capacity for water acquisition	[5, 17]
<i>Shoot growth</i>	Reduced shoot elongation and biomass accumulation	Reduced cell expansion and carbon assimilation	Lower plant growth	[1, 2]
<i>Leaf development</i>	Reduced leaf expansion and leaf area; leaf rolling may occur	Reduced cell expansion and water-conservation responses	Reduced transpiring surface	[1, 5]
<i>Stomatal conductance</i>	Stomatal closure	ABA-, ROS- and Ca ²⁺ -mediated signalling	Reduced transpiration but restricted CO ₂ entry	[6, 10]
<i>Photosynthesis</i>	Decline in photosynthetic rate	Stomatal limitation followed by possible non-stomatal limitations	Reduced carbon assimilation and growth	[3, 6]
<i>Transpiration</i>	Decrease in water loss	Stomatal closure and leaf structural changes	Improved short-term water conservation	[2, 15]
<i>Water-use efficiency</i>	May increase under moderate drought	Greater control of water loss relative to carbon gain	More efficient use of available water	[15]

<i>Osmotic adjustment</i>	Accumulation of compatible solutes	Increased synthesis/retention of proline, sugars and other osmolytes	Maintenance of cellular turgor and protection of macromolecules	[6, 18]
<i>Reactive oxygen species</i>	Increased ROS generation	Disturbance of photosynthetic and respiratory metabolism	Signalling at controlled levels; oxidative damage when excessive	[3, 7]
<i>Antioxidant defence</i>	Increased activity of antioxidant systems	Activation of SOD, CAT, APX, peroxidases and non-enzymatic antioxidants	Protection against oxidative damage	[7, 8]
<i>Phytohormones</i>	Changes in ABA and other hormone pathways	Stress-induced hormonal signalling and cross-talk	Regulation of stomata, growth and stress responses	[10]
<i>Secondary metabolism</i>	Changes in phenolics, flavonoids and other metabolites	Reprogramming of secondary metabolic pathways	Antioxidant protection and stress signalling	[6]
<i>Gene and protein expression</i>	Activation/repression of drought-responsive genes and proteins	Transcriptional, post-transcriptional and proteomic regulation	Adjustment of metabolism and stress tolerance	[9, 19]
<i>Recovery after rewetting</i>	Restoration may be rapid, partial or delayed	Re-establishment of water relations, photosynthesis and metabolism	Determines resilience following drought	[13]

MORPHOLOGICAL ADAPTATIONS TO DROUGHT STRESS

Morphological adaptations represent some of the most visible responses of plants to water limitation. They include changes in root architecture, shoot growth, leaf size, leaf orientation, biomass allocation and anatomical characteristics. These modifications generally contribute to water conservation or improvement of water acquisition.

Root Adaptations

Roots constitute the primary interface between plants and soil water. Under moderate drought, some plants increase root elongation or develop deeper and more extensive root systems, allowing access to water stored in deeper soil layers. Changes in lateral root development and root branching can also modify soil exploration.

Recent research emphasizes that roots act not only as water-absorbing organs but also as important drought-sensing and signalling organs. Root-derived hydraulic and hormonal signals contribute to shoot responses during soil drying [17]. Root-to-shoot signalling involving ABA and peptide signals also contributes to coordination of drought responses [10].

However, severe drought may inhibit root growth and reduce root metabolic activity. Therefore, the response of roots depends on stress severity, developmental stage and genotype.

Shoot Growth and Biomass Allocation

Shoot growth is often more strongly inhibited than root growth during moderate drought. Reduction in shoot elongation and leaf expansion decreases the transpirational surface and can conserve water. Changes in root-to-shoot biomass allocation may consequently improve the plant's capacity to acquire water relative to its water demand [1, 5].

Leaf Area and Leaf Rolling

Reduction in leaf area is a common drought response because smaller leaf surfaces reduce transpiration. Leaf rolling and changes in leaf orientation can further reduce radiation exposure and evaporative water loss. Such responses are particularly important when drought coincides with high temperature and atmospheric demand.

In crops, such as rice, drought may reduce leaf expansion, tillering and biomass while inducing early developmental changes and other mechanisms associated with water conservation [16].

Anatomical Adaptations

Drought can induce anatomical changes in leaves, stems and roots. Increased tissue thickness, modifications of epidermal characteristics, changes in stomatal traits, development of protective tissues and changes in vascular characteristics may influence water retention and transport.

Zahedi et al. (2025) [5] emphasized that anatomical and morphological characteristics can contribute to maintaining plant water status by reducing water loss and improving water acquisition. Such characteristics include changes in leaf thickness, cuticular properties, stomatal features, root structure and vascular tissues.

Integration of Morphological Responses

Morphological adaptations do not operate independently. Root development influences water acquisition, while leaf characteristics influence water loss. The balance between these processes determines whole-plant water status.

Thus, drought-adaptive morphology can be understood as a coordinated adjustment of water acquisition, water conservation and carbon gain rather than as individual traits [5, 15]. Morphological and anatomical adaptations of plants to drought stress is given in Table 2.

Table 2. Morphological and anatomical adaptations of plants to drought stress.

Morphological/ anatomical trait	Typical drought-induced response	Adaptive significance
<i>Root length/depth</i>	Development of deeper or more extensive roots under moderate drought	Improves access to water in deeper soil layers.
<i>Lateral roots</i>	Changes in lateral root formation and distribution	Enhances exploration of available soil moisture.
<i>Root hairs</i>	Increased root-hair development in some species	Increases effective root–soil contact.
<i>Root:shoot ratio</i>	Often increased because shoot growth is more strongly restricted	Allocates relatively more biomass to water acquisition.
<i>Shoot growth</i>	Reduced height, internode elongation and shoot biomass	Decreases water demand and transpirational load.
<i>Leaf area</i>	Reduction in leaf expansion and total leaf area	Reduces transpiration and water loss.
<i>Leaf rolling</i>	Increased rolling or folding of leaves	Reduces exposed surface and evaporative water loss.
<i>Leaf orientation</i>	Changes in leaf angle/orientation	Can reduce radiation load and transpiration.
<i>Leaf thickness</i>	Increased thickness in some drought-adapted plants	May improve water storage and reduce dehydration.
<i>Cuticle/wax layer</i>	Increased deposition or modification of cuticular waxes	Restricts non-stomatal water loss.
<i>Stomatal traits</i>	Changes in stomatal density, size and distribution	Regulates gas exchange and water loss.
<i>Leaf surface structures</i>	Increased pubescence/trichome development in some species	Reduces radiation and boundary-layer water loss.
<i>Vascular tissues</i>	Modification of xylem/vascular characteristics	Supports water transport while reducing hydraulic risk.
<i>Biomass allocation</i>	Greater relative allocation to roots under some drought conditions	Improves water acquisition relative to shoot demand.

PHYSIOLOGICAL RESPONSES AND ADAPTATIONS TO DROUGHT STRESS

Plant Water Status

Maintenance of tissue hydration is a major physiological objective during drought. Water deficit decreases leaf water potential and cellular turgor, leading to changes in growth and physiological activity. Plants respond through water conservation, osmotic adjustment and changes in root water acquisition [6].

Stomatal Regulation

Stomata play a central role in controlling the balance between carbon dioxide uptake and water loss. During drought, stomatal closure reduces transpiration and helps conserve water but simultaneously restricts carbon dioxide entry and may reduce photosynthetic carbon assimilation [2].

ABA is one of the major signals involved in drought-induced stomatal closure. ABA interacts with ROS and Ca²⁺ signalling pathways to regulate guard-cell ion transport and stomatal movement [11].

Photosynthesis and Gas Exchange

Drought commonly reduces photosynthetic rate through both stomatal and non-stomatal mechanisms. Initial reductions are frequently associated with stomatal limitation, whereas prolonged or severe stress can impair photosynthetic pigments, chloroplast function, electron transport and carbon metabolism [3, 6].

The reduction in photosynthesis also decreases carbon availability for growth. Consequently, plants must balance carbon assimilation with water conservation.

Osmotic Adjustment

Osmotic adjustment involves accumulation of solutes that help maintain cellular turgor as water availability declines. Compatible solutes – such as proline, soluble sugars, and certain amino acids – can contribute to maintenance of cellular water relations and protection of macromolecules.

Blum (2017) [18] demonstrated the importance of osmotic adjustment as an adaptive mechanism under drought and reported a positive relationship between osmotic adjustment and yield under drought across diverse crops. Therefore, osmotic adjustment represents an important physiological mechanism linking cellular water relations with plant productivity.

Water-Use Efficiency

Plants may improve water-use efficiency by maintaining carbon assimilation while reducing unnecessary water loss. Stomatal regulation, changes in root architecture and alterations in leaf characteristics can contribute to improved water-use efficiency [15].

However, extremely strong stomatal closure may conserve water at the expense of carbon fixation. Thus, drought adaptation involves a balance between water conservation and photosynthetic productivity.

Recovery After Rewatering

Drought response should not be evaluated only during stress. Plants differ considerably in their ability to recover after water becomes available again. Recovery involves restoration of stomatal function, photosynthesis, cellular metabolism and growth.

Wang and Xu (2026) [13] highlighted drought recovery and rewatering as important but comparatively understudied components of plant drought responses. The speed and completeness of recovery may, therefore, represent important indicators of plant resilience.

BIOCHEMICAL RESPONSES AND ADAPTATIONS TO DROUGHT STRESS

Osmoprotectants

Drought commonly stimulates the accumulation of compatible solutes such as proline, soluble sugars, amino acids, and other osmolytes. These compounds contribute to osmotic adjustment and may protect proteins, membranes and other cellular structures during dehydration [6, 18].

Reactive Oxygen Species

Water deficit disrupts normal cellular metabolism and can increase the generation of ROS. Important ROS include superoxide radicals, hydrogen peroxide and hydroxyl radicals. At controlled concentrations, ROS can function as signalling molecules, whereas excessive accumulation can cause oxidative damage to lipids, proteins and nucleic acids [3, 7].

Antioxidant Defence

Plants possess enzymatic and non-enzymatic antioxidant systems to maintain redox balance. Major enzymatic antioxidants include superoxide dismutase, catalase, ascorbate peroxidase and other peroxidases. Non-enzymatic components include ascorbate, glutathione, carotenoids, tocopherols and phenolic compounds.

The antioxidant system helps prevent excessive oxidative damage and contributes to drought tolerance [7]. Recent work continues to emphasize the coordinated action of enzymatic and non-enzymatic antioxidant systems under drought [8].

Secondary Metabolites

Drought may alter the synthesis of phenolics, flavonoids and other secondary metabolites. These compounds may contribute to antioxidant protection and other aspects of stress adaptation. Changes in secondary metabolism can, therefore, complement primary physiological mechanisms.

Phytohormones

Phytohormones regulate many aspects of drought adaptation. ABA is particularly important in stomatal regulation and drought signalling, while other hormones, including auxins, cytokinins, ethylene, jasmonates and salicylic acid, participate in growth regulation and stress responses.

Genomic and proteomic studies demonstrate that drought modifies hormone-related pathways together with transcription factors, signalling proteins and metabolic processes [9].

Stress-Responsive Proteins and Molecular Regulation

Drought activates genes encoding transcription factors, signalling proteins, enzymes and stress-responsive proteins. Molecular responses can alter osmolyte production, antioxidant defence, membrane protection, photosynthesis and hormonal regulation [4].

Genomic and proteomic approaches have consequently become important for identifying mechanisms and candidate genes associated with drought tolerance [9].

Coordination of Biochemical Responses

Biochemical responses are interconnected. ROS can function in signalling, ABA can regulate stomatal responses, osmolytes can support water relations, and antioxidant systems can control oxidative damage.

Therefore, biochemical drought tolerance results from coordinated regulation rather than accumulation of one protective compound (Figure 2). Physiological and biochemical responses of plants to drought stress is given in Table 3.

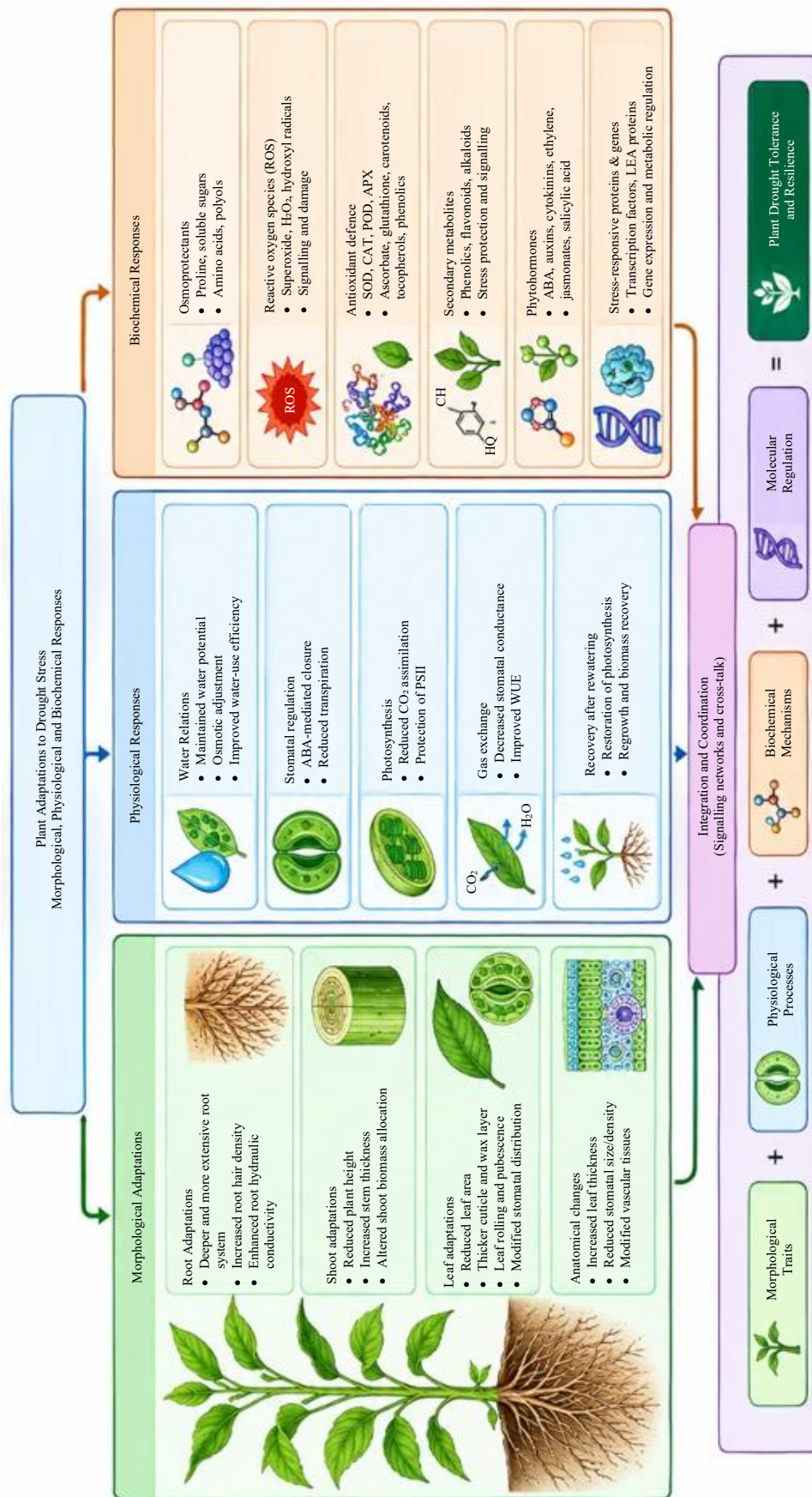


Figure 2. Morphological, physiological and biochemical adaptations of plants to drought stress. These responses are coordinated through signalling networks to enhance water conservation, maintain cellular functions and improve plant survival.

Table 3. Physiological and biochemical responses of plants to drought stress.

Response category	Drought-induced response	Major mechanism	Adaptive significance	Key references
<i>Plant water status</i>	Decrease in leaf water potential and relative water content	Reduced soil–water availability and water uptake	Triggers water-conservation responses.	[1, 6]
<i>Stomatal regulation</i>	Stomatal closure	ABA, ROS and Ca ²⁺ signalling	Reduces transpirational water loss.	[6, 11]
<i>Transpiration</i>	Reduced transpiration	Stomatal closure and reduced leaf area	Conserves water.	[2, 15]
<i>Photosynthesis</i>	Reduced photosynthetic rate	Reduced CO ₂ availability and, under severe stress, metabolic/photosynthetic impairment	Conserves resources but may restrict carbon gain.	[3, 6]
<i>Water-use efficiency</i>	Often improved under moderate drought	Greater regulation of water loss relative to carbon assimilation	Enhances efficient use of limited water.	[15]
<i>Osmotic adjustment</i>	Accumulation of compatible solutes	Increased proline, soluble sugars and other osmolytes	Maintains cell turgor and hydration.	[6, 18]
<i>ROS production</i>	Increased ROS generation	Disturbance of photosynthetic and respiratory metabolism	ROS act in signalling; excessive ROS cause oxidative damage.	[3, 7]
<i>Antioxidant enzymes</i>	Increased SOD, CAT, APX and peroxidase activity	Activation of antioxidant defence	Detoxifies excess ROS.	[7, 8]
<i>Non-enzymatic antioxidants</i>	Increased or altered ascorbate, glutathione, carotenoids and phenolics	Enhanced redox protection	Protects membranes and cellular components.	[7, 8]
<i>Secondary metabolites</i>	Altered phenolic and flavonoid metabolism	Activation of secondary metabolic pathways	Antioxidant protection and stress signalling.	[6]
<i>Phytohormones</i>	Increased ABA and changes in other hormones	Hormonal signalling and cross-talk	Coordinates stomatal behaviour, growth and stress responses.	[11]
<i>Stress-responsive proteins</i>	Altered abundance of protective proteins and enzymes	Stress-responsive gene and protein regulation	Protects cellular structures and maintains metabolism.	[9, 19]
<i>Gene regulation</i>	Activation of drought-responsive genes and transcription factors	ABA-dependent and ABA-independent signalling pathways	Reprograms metabolism and stress defence.	[9, 19]
<i>Root–microbiome response</i>	Changes in root-associated microbial interactions	Altered root exudates and microbial functions	May improve nutrient acquisition and stress resilience.	[12]
<i>Recovery after rewetting</i>	Restoration of photosynthesis, water relations and growth	Rehydration and reversal/reorganisation of stress responses	Determines post-drought resilience.	[13]

INTEGRATION OF MORPHOLOGICAL, PHYSIOLOGICAL AND BIOCHEMICAL ADAPTATIONS

Plant drought tolerance cannot be adequately explained by a single morphological, physiological or biochemical trait. Instead, plants employ interconnected mechanisms that operate at different levels of organization.

Root development may increase water acquisition, while reduced leaf area and stomatal closure decrease water loss. At the same time, osmotic adjustment maintains cellular turgor and antioxidant systems protect cellular components from oxidative damage. These responses are coordinated through hormonal and molecular signalling networks [1, 6].

Root-to-shoot communication represents an important component of this integration. Soil drying is sensed by roots, and hydraulic, hormonal and chemical signals influence shoot responses. ABA, peptides, ROS and Ca²⁺ are involved in long-distance and local signalling processes [10, 11].

At the whole-plant level, drought adaptation involves a trade-off between growth and survival. Reduction in growth can decrease water demand and protect plants during severe stress, whereas maintaining photosynthetic activity and growth may be advantageous when water limitation is moderate. The balance, therefore, changes according to drought intensity, duration and developmental stage.

Recent reviews emphasize the need to integrate morphological, physiological, biochemical and molecular traits rather than treating them as independent mechanisms (Figure 3) [13, 15].

FACTORS AFFECTING DROUGHT TOLERANCE

Plant Species and Genotype

Drought responses vary substantially among species and genotypes. Differences in root architecture, stomatal behaviour, osmotic adjustment, antioxidant capacity and molecular regulation can contribute to variation in drought tolerance [1].

Developmental Stage

The response to drought depends on developmental stage. Water limitation during germination, vegetative growth, flowering or reproductive development can produce different effects on plant performance and yield [16].

Severity, Duration and Timing of Stress

Mild, moderate and severe drought do not produce identical physiological responses. Similarly, short-term and prolonged drought may activate different mechanisms. The meta-analysis of [3] demonstrated that the magnitude of several physiological and oxidative responses is influenced by stress intensity and duration.

Soil and Atmospheric Conditions

Soil texture, water-holding capacity, temperature, relative humidity and atmospheric vapour–pressure deficit influence the rate at which plants experience water limitation. Consequently, drought responses observed under controlled experimental conditions may differ from those under field conditions.

Root Characteristics

Root depth, density, branching and hydraulic properties influence access to soil water. Root characteristics are, therefore, important determinants of drought avoidance and resilience [17].

Plant–Microbiome Interactions

The root-associated microbiome can influence drought responses through nutrient acquisition, hormonal regulation, root development, metabolite exchange and stress signalling. Plant root exudates can also modify microbial community composition under drought [12].

Combined Stresses

In natural environments, drought frequently occurs together with heat, salinity or nutrient limitation. Responses to combined stresses may differ from responses to drought alone. Therefore, future drought studies should increasingly incorporate realistic environmental combinations.

CURRENT RESEARCH GAPS AND FUTURE PERSPECTIVES

Despite substantial progress, several gaps remain in understanding plant drought adaptation.

First, many studies continue to investigate individual traits independently. Greater integration of morphology, physiology, biochemistry, molecular biology and ecology is required to understand whole-plant drought resilience.

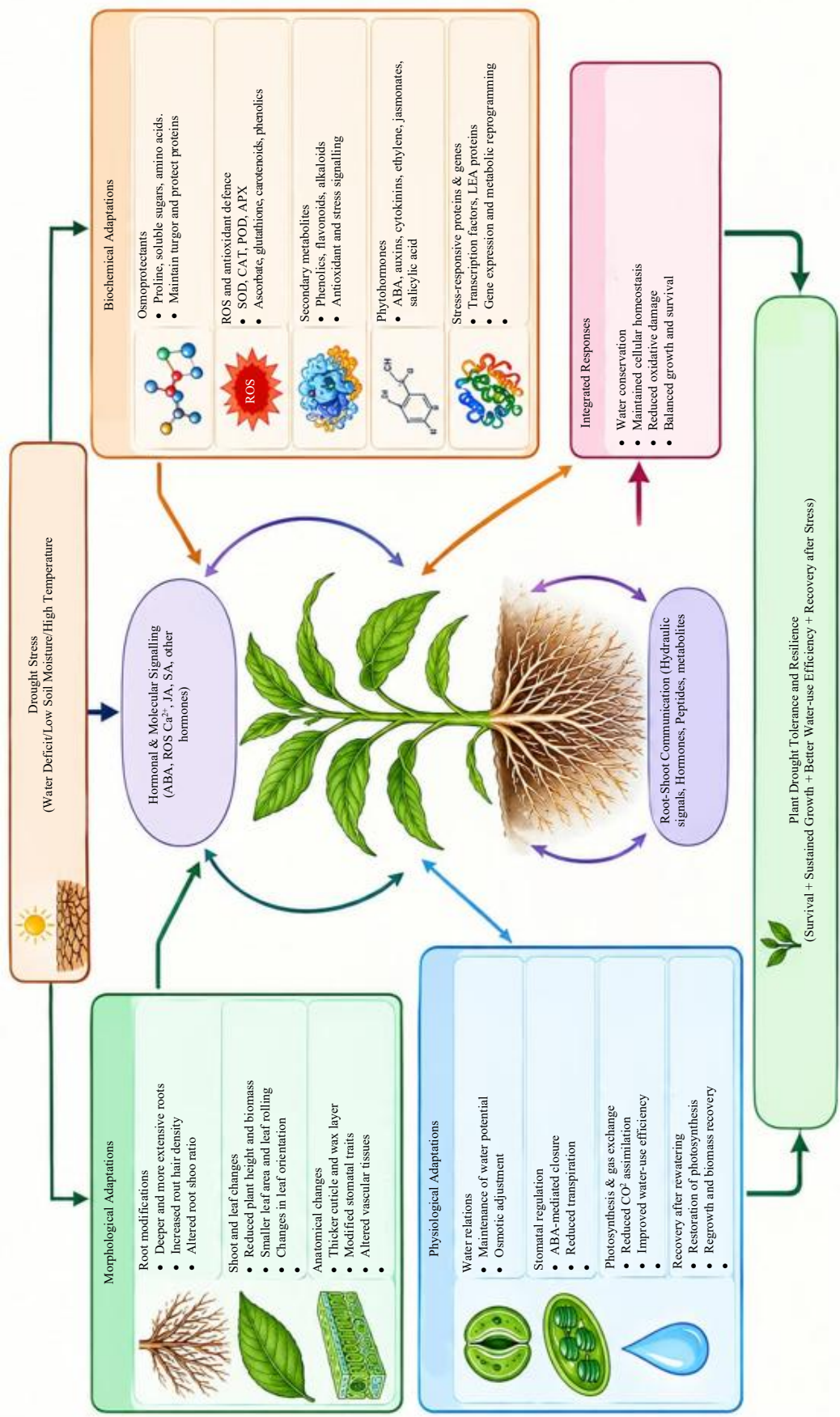


Figure 3. Integrated mechanism of plant drought tolerance. Morphological, physiological and biochemical adaptations are coordinated through hormonal and molecular signalling networks, root-shoot communication and integrated responses to ensure plant survival and resilience under drought stress.

Second, controlled experiments may not fully reproduce field conditions. Future studies should, therefore, include realistic fluctuations in soil moisture, temperature, atmospheric demand and combined stresses [15].

Third, drought recovery remains less studied than drought response itself. Evaluating plant performance during both stress and recovery will provide a better assessment of resilience [13].

Fourth, roots require greater attention. Recent work emphasizes their importance as water-acquiring structures, drought sensors and signalling organs [17].

Fifth, plant–microbiome interactions represent an expanding research area. Understanding how root exudates influence microbial communities and how microbial metabolites influence plant drought responses may contribute to new strategies for improving resilience [12].

Sixth, genomic, transcriptomic, proteomic and metabolomic approaches can help identify regulatory networks associated with drought adaptation. Integration of these approaches with physiological phenotyping may improve the identification of useful drought–tolerance traits [9].

Finally, future research should give greater attention to translating laboratory findings into field-level applications. Breeding, genome editing, microbial technologies, irrigation management and precision agriculture may need to be combined rather than considered as isolated approaches [4, 20].

CONCLUSION

Drought stress induces a complex and highly coordinated series of responses in plants. Morphological adaptations – such as changes in root architecture, leaf area, shoot growth, and anatomical characteristics – influence water acquisition and conservation. Physiological mechanisms including stomatal regulation, osmotic adjustment, photosynthetic regulation and water-use efficiency help maintain plant water balance. Biochemical mechanisms, particularly osmolyte accumulation, antioxidant defence and hormonal signalling, protect cells from dehydration and oxidative damage.

These mechanisms are interconnected through root-to-shoot communication and molecular signalling involving ABA, ROS, Ca²⁺ and other regulatory components. Recent research further demonstrates the importance of root traits, plant–microbiome interactions, genomic and proteomic regulation and recovery after rewetting.

Therefore, drought tolerance should be regarded as an integrated property resulting from the coordinated functioning of morphological, physiological, biochemical and molecular mechanisms. Future research should move towards multi-level approaches conducted under realistic environmental conditions and should evaluate not only survival during drought but also the capacity of plants to recover and maintain productivity after stress.

REFERENCES

1. Anjum SA, Xie XY, Wang LC, Saleem MF, Man C, Lei W. Morphological, physiological and biochemical responses of plants to drought stress. *Afr J Agric Res*. 2011;6(9):2026–2032. doi: [10.5897/AJAR10.027](https://doi.org/10.5897/AJAR10.027).
2. Wach D, Skowron P. An overview of plant responses to the drought stress at morphological, physiological and biochemical levels. *Pol J Agron*. 2022 Sep 30;(50):25–34. doi: [10.26114/pja.iung.435.2022.04](https://doi.org/10.26114/pja.iung.435.2022.04).
3. Sun Y, Wang C, Chen HYH, Ruan H. Response of plants to water stress: A Meta-Analysis. *Front Plant Sci*. 2020;11:978. doi: [10.3389/fpls.2020.00978](https://doi.org/10.3389/fpls.2020.00978).
4. Bashir SS, Hussain A, Hussain SJ, Wani OA, Zahid Nabi S, Dar NA, et al. Plant drought stress tolerance: Understanding its physiological, biochemical and molecular mechanisms. *Biotechnol Biotechnol Equip*. 2021;35(1):1912–1925.

5. Zahedi SM, Karimi M, Venditti A, Zahra N, Siddique KH, Farooq M. Plant adaptation to drought stress: The role of anatomical and morphological characteristics in maintaining the water status. *J Soil Sci Plant Nutr.* 2025;25(1):409–427.
6. Haghpanah M, Hashemipetroudi S, Arzani A, Araniti F. Drought tolerance in plants: Physiological and molecular responses. *Plants (Basel).* 2024;13(21):2962.
7. Laxa M, Liebthal M, Telman W, Chibani K, Dietz KJ. The role of the plant antioxidant system in drought tolerance. *Antioxidants (Basel).* 2019;8(4):94.
8. Chinmayi S, Yadav M, Nandhan NS, Barot M, Saikrishna M. Enzymatic and nonenzymatic antioxidant defense in plants under drought stress. In: *Role of Antioxidants in Mitigating Plant Stress.* Academic Press; 2025 Jan 1. p. 75–85. doi: [10.1016/B978-0-443-26799-4.00016-5](https://doi.org/10.1016/B978-0-443-26799-4.00016-5).
9. Singh PK, Indoliya Y, Agrawal L, Awasthi S, Deebea F, Dwivedi S, et al. Genomic and proteomic responses to drought stress and biotechnological interventions for enhanced drought tolerance in plants. *Curr Plant Biol.* 2022 Jan 1;29:100239. doi: [10.1016/j.cpb.2022.100239](https://doi.org/10.1016/j.cpb.2022.100239).
10. Takahashi F, Kuromori T, Urano K, Yamaguchi-Shinozaki K, Shinozaki K. Drought stress responses and resistance in plants: From Cellular Responses to Long-Distance Intercellular Communication. *Front Plant Sci.* 2020;11:556972. doi: [10.3389/fpls.2020.556972](https://doi.org/10.3389/fpls.2020.556972).
11. Liu H, Song S, Zhang H, Li Y, Niu L, Zhang J, et al. Signaling transduction of ABA, ROS, and Ca²⁺ in plant stomatal closure in response to drought. *Int J Mol Sci.* 2022;23(23):14824.
12. Pantigoso HA, Ossowicki A, Stringlis IA, Carrión VJ. Hub metabolites at the root–microbiome interface: Unlocking plant drought resilience. *Trends Plant Sci.* 2025;30(9):1046–1059.
13. Wang J, Xu Z. Plant response to and recovery from drought. *Curr Biol.* 2026;36(8):R362.
14. Cotrina Cabello GG, Ruiz Rodriguez A, Husnain Gondal A, Areche FO, Flores DD, Astete JA, et al. Plant adaptability to climate change and drought stress for crop growth and production. *CABI Rev.* 2023 Jan 18;2023.
15. Franco-Navarro JD, Padilla YG, Álvarez S, Calatayud Á, Colmenero-Flores JM, Gómez-Bellot MJ, et al. Advancements in water-saving strategies and crop adaptation to drought: A comprehensive review. *Physiol Plant.* 2025;177(4):e70332. doi: [10.1111/ppl.70332](https://doi.org/10.1111/ppl.70332).
16. Bhandari U, Gajurel A, Khadka B, Thapa I, Chand I, Bhatta D, et al. Morpho-physiological and biochemical response of rice (*Oryza sativa* L.) to drought stress: A Review. *Heliyon.* 2023;9(3):e13744. doi: [10.1016/j.heliyon.2023.e13744](https://doi.org/10.1016/j.heliyon.2023.e13744).
17. Marik D, Sadhukhan A. Unearthing the hidden organ: Vital role of the root in drought tolerance of plants. *Plant Mol Biol.* 2025;115(6):119.
18. Blum A. Osmotic adjustment is a prime drought stress adaptive engine in support of plant production. *Plant Cell Environ.* 2017;40(1):4–10.
19. Wang X, Li X, Zhao W, Hou X, Dong S. Current views of drought research: Experimental methods, adaptation mechanisms and regulatory strategies. *Front Plant Sci.* 2024;15:1371895. doi: [10.3389/fpls.2024.1371895](https://doi.org/10.3389/fpls.2024.1371895).
20. Dubey A, Kumar A, Malla MA, Chowdhary K, Singh G, Ravikanth G, et al. Approaches for the amelioration of adverse effects of drought stress on crop plants. *Front Biosci (Landmark Ed).* 2021;26(10):928–947. doi: [10.52586/4998](https://doi.org/10.52586/4998).