

DROUGHT STRESS AND THEIR ADAPTATIONS IN PLANTS

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Drought is one of the most important environmental constraints limiting plant growth, development and productivity. It occurs when water availability in the soil and atmosphere becomes insufficient to meet the water requirements of plants, resulting in a negative water balance and progressive tissue dehydration. The effects of drought are expressed at morphological, physiological, biochemical and molecular levels and depend on the intensity, duration and timing of stress as well as on plant species and genotype. Plants have evolved several adaptive mechanisms to withstand drought, broadly classified as drought escape, drought avoidance and drought tolerance. Drought escape involves completion of the life cycle before severe water deficit develops, whereas drought avoidance maintains plant water status through improved water uptake and reduced water loss. Drought tolerance enables plants to survive cellular dehydration through osmotic adjustment, maintenance of membrane integrity, accumulation of compatible solutes, antioxidant defense and stress-responsive gene expression. Drought commonly reduces root and shoot growth, biomass accumulation, leaf area, chlorophyll content, photosynthesis, stomatal conductance and transpiration. In contrast, tolerant plants may maintain higher relative water content, photosynthetic activity, water-use efficiency, osmolyte accumulation and antioxidant enzyme activities under stress. Understanding these mechanisms is essential for identifying physiological and biochemical traits that can be used in breeding drought-resilient crops.

Keywords: *drought stress, water deficit, drought avoidance, drought escape, drought tolerance, osmotic adjustment, proline, antioxidants, photosynthesis, water-use efficiency.*

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**1. INTRODUCTION**

Drought stress is a major abiotic stress that adversely affects plant growth, development and agricultural productivity. In simple terms, drought may be described as a prolonged period of inadequate rainfall; from an agricultural perspective, however, it is more appropriately considered an inadequate supply and distribution of water, including precipitation and soil-water storage, during the crop life cycle that prevents the expression of its genetic yield potential [1,2]. Because plants depend on a continuous supply of water for cell expansion, photosynthesis, nutrient transport and metabolic activity, reductions in water availability can have profound effects on almost every aspect of plant function [2,3].

Plant water deficit develops when water loss through transpiration exceeds water uptake by the root system. Water uptake is influenced by soil moisture, soil aeration, root distribution, rooting depth and hydraulic conductance, whereas transpiration is controlled by solar radiation, temperature, atmospheric humidity, wind, leaf characteristics and stomatal aperture [2,4]. Consequently, water stress is a dynamic phenomenon whose intensity may change according to environmental conditions and developmental stage.

Drought stress is particularly important in agriculture because crop productivity is determined not simply by the ability of plants to survive water deficit, but by their capacity to maintain growth and yield during and after stress. Plant responses to drought are therefore complex and involve coordinated changes in morphology, physiology, metabolism, cellular structure, gene expression and hormonal signaling [3,5]. Plants have evolved mechanisms that allow them to escape drought, avoid dehydration or tolerate low tissue water status [5,6].

2. MAJOR STRATEGIES OF PLANT ADAPTATION TO DROUGHT

Plant responses to drought are traditionally grouped into three major strategies: drought escape, drought avoidance and drought tolerance [5,6]. These mechanisms are not mutually exclusive, and a particular genotype may employ several of them simultaneously.

2.1 Drought escape

Drought escape is the ability of a plant to complete its vegetative and reproductive development before the onset of severe water deficit. This strategy is particularly advantageous in environments where the growing season is short and terminal drought is predictable [5,6]. Early flowering and early maturity allow plants to complete grain or seed formation while adequate soil moisture is still available.

Development of short-duration crop varieties is therefore an important strategy for drought-prone environments. However, shortening crop duration can reduce yield under favorable conditions because yield is often associated with the duration of photosynthetic activity and biomass accumulation. Consequently, breeding for drought escape requires an appropriate balance between early maturity and yield potential [2,5].

2.2 Drought avoidance

Drought avoidance refers to the ability of a plant to maintain relatively high tissue water content despite declining soil-water availability. This can be achieved by reducing water loss, increasing water uptake, or combining both mechanisms [5,6].

Plants reduce water loss through stomatal closure, reduced leaf area, leaf rolling or folding, changes in leaf orientation, increased wax deposition, development of trichomes and shedding of older leaves. These modifications reduce transpiration and radiation load on the plant [5,7]. Stomatal closure is one of the earliest responses to declining water availability and is strongly associated with abscisic acid (ABA) signaling originating from dehydrating roots and leaves [8].

Water uptake can be improved through deeper and more extensive root systems, greater root length density, improved root hydraulic conductance and development of roots into moist soil layers. Deep and dense root systems are particularly valuable in deep soils because they allow plants to extract water from lower soil horizons after surface soil moisture has declined [5,6].

2.3 Drought tolerance

Drought tolerance is the capacity of plants to maintain cellular function and survive despite low tissue water content. It involves cellular and biochemical mechanisms that protect membranes, proteins, enzymes and other cellular components from dehydration-induced injury [5,9].

Important components of drought tolerance include osmotic adjustment, accumulation of compatible solutes, maintenance of membrane integrity, synthesis of protective proteins, antioxidant defense, regulation of gene expression and metabolic adjustment [9,10]. Unlike drought avoidance, which attempts to maintain tissue hydration, drought tolerance allows plants to continue functioning even when tissue water status is substantially reduced.

3. EFFECTS OF DROUGHT STRESS ON PLANT GROWTH

Drought stress strongly affects plant growth because cell expansion is highly dependent on water availability and cellular turgor. Cell division, expansion and differentiation are affected when water deficit reduces cell turgor and alters cell-wall extensibility [2,11]. Growth inhibition may occur before major reductions in photosynthesis, making growth one of the earliest visible responses to water limitation [2,12].

3.1 Root and shoot growth

Roots are particularly important in drought adaptation because they are responsible for soil-water acquisition and also act as sites for sensing changes in soil moisture. Drought can modify root length, depth, density, branching pattern and hydraulic conductance [5,13].

Under moderate drought, some plants increase root growth or allocate proportionally more assimilates to roots, allowing them to explore deeper and wetter soil layers. In contrast, severe drought can inhibit both root and shoot growth. Deep and extensive root systems can delay dehydration by maintaining water uptake as the upper soil layers become dry [5,13]. Shoot growth is generally more strongly inhibited than root growth under moderate water deficit. Consequently, drought often increases the root-to-shoot ratio. Such increased allocation to roots can be regarded as an adaptive response because

it increases the capacity for water acquisition while reducing the transpiring shoot surface [5,14]. However, the response is species- and genotype-dependent, and severe drought may eventually suppress root growth as well.

3.2 Biomass accumulation

Water deficit commonly decreases fresh and dry biomass because of reduced cell expansion, leaf development, photosynthesis and canopy formation [2,12]. The magnitude of biomass reduction depends on drought severity, duration and the developmental stage at which stress occurs.

Maintenance of dry matter under drought is an important characteristic of tolerant genotypes. Genotypes that maintain greater biomass under water deficit generally have better water relations, photosynthetic activity and metabolic adjustment than sensitive genotypes [2,5]. Therefore, biomass retention can be used as one of the phenotypic indicators of drought tolerance.

3.3 Leaf area

Leaf expansion is among the most drought-sensitive growth processes. Reduced leaf expansion decreases the transpiring surface and thereby contributes to water conservation [2,5]. Although reduction in leaf area limits photosynthetic surface and therefore potentially reduces carbon gain, it can also be advantageous under severe drought by decreasing transpirational water loss.

Leaf rolling, folding and changes in leaf orientation are additional mechanisms that reduce radiation interception and leaf temperature. These responses are particularly important in cereals and legumes exposed to declining soil moisture [5,7].

4. PLANT WATER RELATIONS UNDER DROUGHT

Plant water status is commonly described using water potential and relative water content (RWC). Water potential reflects the energetic status of water in plant tissues, whereas RWC provides an estimate of tissue hydration relative to the fully hydrated state [15]. Drought generally decreases leaf water potential and RWC. The magnitude of these changes varies among species and genotypes and depends on stress severity and duration [2,5]. Drought-tolerant genotypes often maintain higher RWC than susceptible genotypes because of more efficient water uptake, reduced transpiration and/or osmotic adjustment. Maintenance of tissue hydration is important because adequate water status is required for cell expansion, stomatal regulation, photosynthesis and enzymatic activity. Consequently, RWC has frequently been used as a physiological indicator of drought resistance [5,15].

5. PHOTOSYNTHETIC RESPONSES TO DROUGHT

Photosynthesis is highly sensitive to water deficit. Drought reduces photosynthesis through both stomatal and non-stomatal mechanisms [2,16]. During mild drought, stomatal closure is generally one of the earliest responses. Closure reduces the diffusion of carbon dioxide into the leaf and simultaneously limits water loss. As drought becomes more severe or prolonged, non-stomatal limitations become increasingly important. These may include impairment of chlorophyll and photosystem activity, reduced Rubisco activity, impaired ATP synthesis, decreased electron transport and reduced regeneration of ribulose-1,5-bisphosphate [2,16].

5.1 Net photosynthetic rate

Net photosynthetic rate generally declines as drought intensity increases. Reduced photosynthesis is initially associated mainly with stomatal limitation, whereas prolonged or severe stress can cause metabolic and photochemical damage [2,16]. Genotypes that maintain higher photosynthetic rates under water deficit are often better able to sustain growth and yield.

5.2 Stomatal conductance

Stomatal conductance decreases during drought as stomata close to restrict transpirational water loss. This response is regulated by both hydraulic and chemical signals, particularly ABA [8]. Although stomatal closure conserves water, it simultaneously restricts carbon dioxide entry and therefore may decrease photosynthesis. Thus, stomatal regulation represents an important trade-off between water conservation and carbon assimilation. Drought-tolerant plants frequently exhibit more effective stomatal regulation, allowing them to balance water conservation with sufficient photosynthetic activity [2,5].

5.3 Interacellular CO₂ concentration

The response of intercellular CO₂ concentration (C_i) to drought is variable. A decrease in C_i often indicates that stomatal closure is the dominant limitation to photosynthesis, whereas an increase in C_i may indicate impaired carbon fixation or

other non-stomatal limitations [2,16]. Therefore, C_i , when interpreted together with stomatal conductance and photosynthetic rate, can provide useful information about the mechanism responsible for drought-induced photosynthetic inhibition.

5.4 Transpiration and water-use efficiency

Transpiration generally declines under drought because of stomatal closure and reduced leaf area. Water-use efficiency (WUE), broadly defined as biomass or carbon gain relative to water consumption, is an important trait under water-limited conditions [2,17]. Higher WUE may arise from reduced unnecessary water loss, improved photosynthetic performance or greater biomass production per unit of water consumed. However, extremely strong reductions in transpiration may also restrict carbon assimilation. Therefore, an optimal rather than maximal reduction in water loss is desirable for crop productivity.

6. CHLOROPHYLL AND PHOTOSYNTHETIC PIGMENTS

Chlorophylls are essential for light harvesting and photosynthetic energy conversion. Drought stress can decrease chlorophyll a, chlorophyll b and total chlorophyll content and can alter the chlorophyll a/b ratio [2,16]. Chlorophyll degradation may result from impaired biosynthesis, oxidative damage to pigments and chloroplast structures, and reduced metabolic activity. Severe drought can damage thylakoid membranes and photosynthetic reaction centers, thereby reducing photosynthetic efficiency [16]. The maintenance of chlorophyll under drought is often associated with greater tolerance because it indicates better preservation of the photosynthetic apparatus. Chlorophyll stability index has consequently been used as a screening parameter for identifying drought-tolerant genotypes [18].

7. OSMOTIC ADJUSTMENT AND OSMOPROTECTANTS

One of the most important mechanisms of drought tolerance is **osmotic adjustment**, in which plants accumulate solutes to lower cellular osmotic potential and maintain water uptake and turgor under declining water availability [9,10]. Compatible solutes can accumulate to high concentrations without disrupting normal cellular metabolism. Major osmoprotectants include soluble sugars, sugar alcohols, proline, glycine betaine and other amino acids and metabolites [9,19].

7.1 Soluble sugars

Drought commonly causes changes in carbohydrate metabolism. Soluble sugars may accumulate because of starch degradation, altered carbon partitioning and reduced export from leaves [19]. Sugars can contribute to osmotic adjustment, stabilize membranes and proteins, and provide carbon for recovery after stress. In contrast, starch content often decreases during drought because carbon assimilation is reduced and starch may be mobilized to maintain soluble sugar pools [19].

7.2 Proline

Proline is one of the most extensively studied drought-responsive metabolites in plants. Its accumulation under water deficit is widespread and is associated with osmotic adjustment, stabilization of proteins and membranes, protection against oxidative damage and regulation of cellular redox balance [19,20].

Proline can be synthesized mainly through pathways involving glutamate and ornithine. Under drought, increased synthesis and reduced degradation contribute to its accumulation. Following recovery, accumulated proline can be metabolized and may contribute to energy and nitrogen metabolism [20]. Although high proline accumulation is frequently associated with drought tolerance, it should not be regarded as an independent or universal indicator of tolerance. In severely damaged tissues, proline accumulation may also reflect stress injury and metabolic disruption. Therefore, proline should preferably be evaluated together with physiological and biochemical indicators of plant performance [20].

7.3 Glycine betaine

Glycine betaine is another important compatible solute in plants. It contributes to osmotic adjustment and can stabilize proteins, membranes and photosynthetic structures under stress [19]. However, the capacity to accumulate glycine betaine differs considerably among plant species; some crops accumulate substantial amounts, whereas others possess limited endogenous synthesis.

8. NITROGEN METABOLISM UNDER DROUGHT

Nitrogen is an essential constituent of amino acids, proteins, nucleic acids, chlorophyll and numerous enzymes. Drought stress can substantially alter nitrogen uptake, assimilation and redistribution [2]. Protein synthesis is generally reduced during severe water deficit, while protein degradation may increase. Enhanced proteolysis can release amino acids that contribute to osmotic adjustment and nitrogen remobilization. Drought-tolerant genotypes may maintain higher protein content because of better protection of the protein-synthesizing machinery and lower rates of protein degradation.

Nitrate reductase, a key enzyme in nitrate assimilation, is frequently inhibited by drought. This reduction may result from decreased nitrate availability, altered protein synthesis, reduced photosynthetic carbon supply and direct metabolic effects of water deficit [2]. Glutamine synthetase and glutamate synthase are also important because they assimilate ammonium released during photorespiration and protein degradation. The interaction between nitrogen metabolism and drought tolerance is particularly important in legumes because nitrogen fixation and nitrogen assimilation are closely associated with plant water status. Maintenance of nitrogen metabolism may therefore contribute to sustained growth under drought.

9. OXIDATIVE STRESS AND ANTIOXIDANT DEFENSE

Drought stress disturbs cellular metabolism and can increase the production of reactive oxygen species (ROS), including superoxide radicals, hydrogen peroxide, hydroxyl radicals and singlet oxygen [21]. At controlled concentrations, ROS can function as signaling molecules; excessive accumulation, however, causes oxidative damage to lipids, proteins, pigments and nucleic acids [21,22].

Plants protect themselves through coordinated enzymatic and non-enzymatic antioxidant systems. Important antioxidant enzymes include superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), peroxidases, glutathione reductase (GR) and glutathione peroxidase. Important non-enzymatic antioxidants include ascorbate, glutathione, carotenoids, tocopherols and phenolic compounds [21,22].

9.1 Superoxide dismutase

SOD is the first major enzymatic defense against superoxide radicals. It converts superoxide into hydrogen peroxide, which is subsequently removed by CAT, APX and other peroxidases [21]. In many drought-tolerant plants, SOD activity increases under water deficit, helping to prevent excessive accumulation of superoxide radicals. However, the response is not universal and may depend on species, genotype, stress intensity and duration.

9.2 Catalase

Catalase converts hydrogen peroxide into water and oxygen and is particularly important in peroxisomes, where hydrogen peroxide is generated during photorespiration and other oxidative processes [21]. Increased CAT activity can contribute to the detoxification of hydrogen peroxide during drought.

9.3 Peroxidases and ascorbate peroxidase

Peroxidases participate in hydrogen peroxide removal and may also contribute to cell-wall modification and defense signaling. APX is an important component of the ascorbate-glutathione cycle and efficiently removes hydrogen peroxide using ascorbate as an electron donor [21,22].

9.4 Glutathione reductase

Glutathione reductase maintains the cellular pool of reduced glutathione by converting oxidized glutathione to its reduced form. This is important for maintaining redox balance and supporting hydrogen peroxide detoxification through the ascorbate-glutathione pathway [21].

10. LIPID PEROXIDATION AND MEMBRANE STABILITY

Cell membranes are major targets of drought-induced oxidative damage. Excess ROS can attack polyunsaturated fatty acids, causing lipid peroxidation and formation of secondary products such as malondialdehyde (MDA) [21,22]. Increased MDA is therefore commonly used as an indicator of oxidative membrane damage. Drought-tolerant plants generally maintain lower levels of lipid peroxidation because of more effective antioxidant protection and better membrane stabilization [21].

Cell membrane stability (CMS) is another useful indicator of drought tolerance. Membranes that remain stable under water deficit show lower electrolyte leakage, whereas greater leakage indicates increased membrane permeability and cellular injury. Maintenance of membrane integrity is therefore an important component of drought tolerance [5,18].

11. MOLECULAR AND HORMONAL RESPONSES

Drought stress activates complex signaling pathways involving phytohormones, reactive oxygen species, calcium signaling, protein kinases and stress-responsive transcription factors. Among the hormones, ABA has a central role in drought signaling because it promotes stomatal closure and regulates the expression of many drought-responsive genes [8,23].

Stress-induced changes in gene expression result in the synthesis of proteins involved in protection, signaling, metabolism and repair. Stress-responsive proteins include late embryogenesis abundant (LEA) proteins, dehydrins, molecular chaperones, antioxidant enzymes and proteins involved in osmolyte metabolism [23]. The perception of water deficit therefore initiates a signaling network rather than a single response. Signals generated in roots can influence shoot behavior through hydraulic and hormonal pathways, while leaves can also perceive declining water status and activate local and systemic responses [8,23].

12. INTEGRATED NATURE OF DROUGHT ADAPTATION

Drought adaptation is not controlled by a single physiological or biochemical characteristic. Rather, tolerance results from the interaction of multiple mechanisms operating at different organizational levels. At the morphological level, important traits include deep and extensive roots, reduced leaf area, leaf rolling, altered root-to-shoot ratio and early maturity. At the physiological level, maintenance of RWC, water potential, photosynthesis, stomatal regulation and WUE are important. At the biochemical level, osmolyte accumulation, maintenance of proteins and pigments, and enhanced antioxidant activity contribute to stress tolerance. At the molecular level, stress-responsive genes, transcription factors and hormonal signaling coordinate these responses [5,9,23].

The effectiveness of any individual mechanism depends on the environment. For example, early maturity may be beneficial in regions with predictable terminal drought but may reduce yield under favorable conditions. Similarly, stomatal closure conserves water but restricts carbon dioxide uptake and can reduce photosynthesis. Osmotic adjustment maintains turgor but requires metabolic energy and resources. Thus, successful drought adaptation involves an appropriate balance among water conservation, carbon assimilation, growth and reproduction [2,5].

13. PHYSIOLOGICAL AND BIOCHEMICAL INDICATORS OF DROUGHT TOLERANCE

Several traits can be used to screen crop genotypes for drought tolerance. These include:

- root depth, root length and root density;
- root-to-shoot ratio;
- plant height and relative growth rate;
- fresh and dry biomass;
- leaf area;
- relative water content;
- leaf water potential;
- chlorophyll content and chlorophyll stability index;
- net photosynthetic rate;
- stomatal conductance and transpiration;
- intercellular CO₂ concentration;
- water-use efficiency;
- soluble sugars;
- proline and other osmolytes;
- total protein and nitrogen;
- antioxidant enzymes such as SOD, CAT, APX and GR;
- lipid peroxidation and MDA content; and
- cell membrane stability/electrolyte leakage [5,18,23].

No single parameter is sufficient to characterize drought tolerance. A combination of morphological, physiological and biochemical traits provides a more reliable assessment because drought responses are highly dependent on genotype, developmental stage, stress intensity and duration [5,23].

14. IMPLICATIONS FOR CROP IMPROVEMENT

The ultimate objective of drought research in agriculture is not merely to ensure plant survival but to maintain economically important yield under water-limited conditions. This distinction is important because mechanisms that enhance survival may sometimes reduce productivity.

Breeding programs can exploit traits such as deep rooting, improved WUE, maintenance of RWC, chlorophyll stability, sustained photosynthesis, osmotic adjustment and efficient antioxidant defense. Physiological screening can complement conventional yield-based selection by identifying mechanisms responsible for drought adaptation [5,23].

Molecular approaches have further increased the potential for improving drought resistance. Identification of drought-responsive genes, transcription factors and signaling pathways can support marker-assisted breeding and other molecular approaches. Nevertheless, drought tolerance is a complex quantitative trait controlled by many genes and strongly influenced by the environment. Therefore, successful crop improvement requires integration of physiological, biochemical, genetic and agronomic approaches [23].

15. CONCLUSION

Drought stress is a complex environmental constraint that affects virtually every stage of plant growth and development. Water deficit reduces cell expansion, root and shoot growth, biomass production, leaf area, water status, chlorophyll content and photosynthetic activity. Prolonged drought also disrupts nitrogen metabolism, increases oxidative stress and damages cellular membranes.

Plants have evolved diverse mechanisms to cope with these adverse effects. Drought escape allows plants to complete their life cycle before severe water deficit occurs, drought avoidance maintains tissue hydration by improving water uptake and limiting water loss, and drought tolerance enables cellular functions to continue despite dehydration. Osmotic adjustment through accumulation of proline, soluble sugars and other compatible solutes, together with efficient antioxidant systems, membrane protection and stress-responsive gene expression, forms an important component of drought tolerance.

The literature indicates that drought resistance is a complex and integrated trait rather than a response controlled by a single mechanism. Therefore, the identification of genotypes that combine efficient water acquisition, controlled water loss, sustained photosynthesis, osmotic adjustment, antioxidant protection and stable growth is essential for developing drought-resilient crops. Such integrated knowledge provides an important scientific basis for physiological screening, breeding and selection of crop varieties capable of maintaining productivity under increasingly water-limited environments.

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