**REVIEW**

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# Drought Stress in Plants: Effects and Tolerance

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Water is the catalyst of life and plays a profound role in plant physiological processes ranging from photosynthesis to intermolecular interactions through a hydrophobic bond. Because of the alterations due to changing environmental conditions, the plants are continuously exposed to a lack of optimum water availability, leading to impaired growth and disturbance in water transport and uptake. Drought is a prominent environmental factor that triggers various plant processes from morphological, physiological, biochemical, and molecular. Plants portray an array of drought tolerance mechanisms; these responses differ based on the type of plant species and may involve the functions of various stress genes. Reduction in plant growth and productivity due to stomatal closure affects photosynthetic efficiency, altering membrane integrity and several enzymes involved in adenosine triphosphate synthesis. Plants exhibit a range of drought tolerance mechanisms and undergo several phenological, morphological, physiological, biochemical, and molecular adaptations at the cellular, subcellular and whole plant levels. Also, drought stress induces the production of reactive oxygen species at the cellular level and is strongly protected by the increase in the enzymatic and non-enzymatic antioxidative system. This chapter/ review provides a glimpse of the effects and tolerance strategies adapted by the plant under drought stress.

*Key words:  Abiotic stress, drought, phytohormone, reactive oxygen species, antioxidants*

By 2050, it is hypothesized that the world's population will overdo 9.7 billion, and over 65% will solely rely on agriculture (Castañeda *et al*., 2016). Consequently, food supply and also nation's financial system will be influenced mainly by agronomy. On the other hand, agronomic practices combat hurdles such as inadequate irrigation systems, scarcity of good trait seeds, the excessive course of chemical pesticides and fertilizers leading to unsuitable soils, and soil erosions (Dev 2012). Besides the above constraints, plants both in the natural and agricultural environment are exposed to a wide array of biotic (insects, bacteria, viruses, fungi) and abiotic (temperature, water, salinity, chilling, freezing) stresses, which will affect their growth and development, thereby hampering crop productivity (Seki *et al*., 2003), in extreme cases, leads to the death of the plant. Due to changing climatic conditions, water scarcity is one of the most severe threats to food security for the rapidly increasing population (Farooq *et al*., 2009a). As a result, a 30% downfall in global crop production is estimated by 2025 compared to current productivity as per World economic forum Q2 (Hasanuzzaman *et al*., 2013).

From an agricultural point of view, alterations in rainfall, light and temperature are the factors to induce water deficit in plants. Also, a shortfall in meteorological drought coupled with an increased evapotranspiration rate leads to a lack of optimum soil moisture required for plant's average growth and development, leading to agricultural drought (Mishra and Cherkauer 2010 Manivannan *et al*., 2008). As a result, plant growth, yield, water relations, membrane integrity, pigment composition, and photosynthetic efficiency is drastically affected by drought (Praba *et al*., 2009). The water content's downturn characterizes the leaf water potential, causing stomatal closure, thereby decreasing cell growth and elongation (Anjum *et al*., 2011a). Lowered water content affects the entire physiological and biochemical mechanisms such as ion uptake and its translocation, photosynthesis, respiration, and nutrient metabolism, thus reducing plant growth (Farooq *et al*., 2009a) and causing the death of the plant (Jaleel *et al*., 2008). Hence, the production of drought-tolerant crop

plants may help meet the food demands. On the other hand, several drought-tolerant traits are used to assess the plant tolerance to drought stress, such as root-leaf traits, the ability for osmotic adjustment, water potential, synthesis of abscisic acid and cell membrane stability (Ha *et al*., 2012). In addition, several molecular mechanisms, including signal transduction, also help the plant in response to drought stress (Nishiyama *et al*., 2013; Osakabe *et al*., 2014). It is of utmost significance to comprehend the effects of drought on plant's morphological, anatomical, physiological and biochemical adaptations to cope with changing climatic challenges. This review is an overview of plant responses and tolerance mechanisms to drought stress and suggests some management strategies and possibilities to cope with drought effects, especially regarding field crops.

## DAMAGING EFFECTS OF DROUGHT STRESS

Plants being sessile need to respond and adapt to various unfavourable environmental conditions. Under normal conditions, there is an irreversible increase in size, weight or volume, which comprises cell division, elongation and differentiation, causing plant growth and establishing an optimum crop stand, which is crucial for producing maximum yield (Farooq *et al*., 2012). Global climatic change is the leading cause of the increase in temperatures and atmospheric $CO_2$ levels, increasing the rate of soil water evaporation, thereby altering the rainfall patterns, ultimately triggering drought stress worldwide (Dai 2011; Mishra and Singh 2011), exposing the plants to water stress. The severity of the stress depends entirely on the intensity, duration of stress, onset time, soil physicochemical conditions and the degree of plant susceptibility. The imbalance in water absorption and water loss rate is mainly due to lower soil water potential than plant roots, primarily due to the atmospheric conditions causing continuous water deficit by transpiration or evaporation (Mafakheri *et al*., 2010). Hence, meteorological drought is followed by agricultural drought (Dai 2011). However, in specific conditions, there is ample soil water content, but various edaphic factors, such as low soil temperatures, salinity, and flooding, decrease the water uptake by roots. Subsequently, inducing water stress in plants defined as

pseudo-drought or physiological drought wherein altered atmospheric conditions are not the decisive factors (Arbona *et al*., 2013; Lisar *et al*., 2012).

Drought, a multidimensional stress factor, affects plants from morphological, physiological, and biochemical levels and is apparent at all plant growth phenological phases (Korgaonker and Bhandari 2021; Anjum *et al*., 2011a). Under severe water deficit, plants exhibit a loss in leaf turgor, making it flaccid, leading to chlorosis and premature senescence (Akhtar and Nazir 2013; Sapeta *et al*., 2013). A few uncommon water deficit symptoms include irregular stunted growth, necrosis, cracks in twigs or bark, thinning of shrub and tree canopy, and extreme situations causing plant death (Arbona *et al*., 2013; Sapeta *et al*., 2013). During the early drought, germination and establishment are affected mainly due to reduced water uptake during the imbibition phase, seed germination, eased energy supply, distorted enzymatic activities and downregulated energy supply from photosynthesis (Okcu *et al*., 2005; Taiz and Zeiger 2010; Bhargava and Sawant 2013; Ding *et al*., 2013). Plant growth is reduced when soil water availability is restrained, wherein shoot development is more stunted than root growth (Anithakumari *et al*., 2012). Avramova *et al*. (2015) observed that water deficit reduces leaf expansion and photosynthesis due to impaired cell mitosis, elongation, proliferation, and differentiation (Potopová *et al*., 2016).

The chief response to drought stress is stomatal closure that disrupts leaf gas exchange, phloem loading, assimilate translocation and dry matter partitioning causing a severe deterioration in plant traits (Farooq *et al*., 2009b; Akram 2011). The drought stress also reduced leaf area due to loss of turgor, cut short the number of leaves, and suppressed leaf expansion and tillering (Farooq *et al*., 2010; Kramer and Boyer 1995; Nooden, 1988). All these constituents lowered the accumulation of dry matter and grain yield.

Drought is also associated to alterations in several aspects of morphological and anatomical features, such as the leaf anatomy, crop phenology and its ultrastructure (Hirt and Shinozaki 2003; Rao *et al*., 2006). It is also reported that the early plant development from the vegetative to reproductive phase is suppressed due to limited water supply (Desclaux and Roumet 1996), leading to a substantial decrease in economic yield in the flowering stage (Hussain *et al*., 2008). An elaborative account of various effects of drought stress concerning their responses and adaptational aspects is conferred below.

## ADAPTATIONS: PLANT RESPONSES TO DROUGHT STRESS

Plants undergo several phenological, morphological, physiological, biochemical, and molecular adaptations to cope with stress at the cellular, subcellular, and whole plant levels.

## MORPHOLOGICAL RESPONSE

Plant resistance to stress conditions is divided into two primary strategies: stress avoidance and stress tolerance (Bhargava and Sawant 2013; Khan *et al*., 2011; Nezhadahmadi *et al*., 2013). These plant responses to withstand drought stress can range from molecular to entire plant level by escape, avoidance and tolerance, which is further explained:

**Drought Escape:** The drought escape shortens the life cycle or grows seasonally and allows the plants to reproduce in the presence of water (Akhtar and Nazir 2013; Bray 2007). A plant's life cycle mainly depends on the individual's genotype and environmental conditions. The synchrony of the plant phenological growth and development with soil moisture availability helps the plant escape drought conditions. A shortened life cycle can lead to drought escape as the plant matures and flowers early, although the yield is negatively affected (Akhtar and Nazir 2013; Farooq *et al*., 2009b).

**Drought Avoidance:** The principal objective used by the plant is to maintain higher water potential by reducing loss of water and preserving the water uptake by developing an extensive and prolific rooting system (Dai 2011; Farooq *et al*., 2009b), enabling the plant to absorb water from a considerable soil depth and far away distance from the plant. The xeromorphic trait such as hairy leaves and thick cuticle layers will assist the plant in maintaining high tissue water potential, but producing such xeromorphic structures consumes high energy and leads to decreased yield. Consequently, plants which use this strategy to uphold an optimum

water potential are generally small because of their adaptation to harsh environments (Khan *et al*., 2011; Lisar *et al*., 2012; Farooq *et al*., 2009b).

**Drought Tolerance:** The plants that adapt tolerance strategy restrict the number of leaves and leaf area in response to drought stress and thus decrease the yield (Akhtar and Nazir 2013; Bray 2007). Also, these plants show some xeromorphic characteristics, such as the presence of trichomes on the adaxial and abaxial surface of leaves, thereby reducing the leaf temperature and minimizing the loss of water by creating a layer of resistance to the movement of water away from the leaf surface (Lisar *et al*., 2012; Farooq *et al*., 2009d, Bray 2007). The root growth rate, size, density and proliferation are the key features of a plant's response to drought stress. However, other mechanisms involved in plant tolerance are the accumulation of compatible solutes, osmotic adjustments, activation of antioxidant systems, modifications in metabolic pathways, increased plant biomass, and stomatal closure (Bray 2007).

## PHYSIOLOGICAL RESPONSE

Inadequate water availability alters crop growth and throughput due to declined water status and turgor. The drought-tolerant plants maintain their metabolic activities at low tissue water potential by adapting effective strategies such as osmotic adjustments, antioxidant defence system and changes in concentration of phytohormones (Kiani *et al*., 2007; Hussain *et al*., 2009). The increased accumulation of organic and inorganic solutes under stress aids in lowering water potential without decreasing actual water contents and is defined as osmotic adjustment or osmoregulation (Serraj and Sinclair 2002) and is one of the dynamic routes in plant adaptation to drought stress, minimizing the effects of drought-induced damage (Blum 2005). Osmo-protectants are compatible solutes with low molecular weight, are highly soluble and non-toxic even at higher concentrations, and confer protection to plants under oxidative damage by stabilizing membranes and maintaining primary structures of enzymes and proteins (Farooq *et al*., 2008). Compatible solutes involve soluble sugars such as fructans, sucrose, sugar alcohols, amino acids that include proline, aspartic acid, glutamic acid,

glycine betaine (GB), organic acids, trehalose, cyclitols such as mannitol and pinitol (Kiani *et al*., 2007; Kaur and Asthir 2015). Synthesis of osmotic compounds helps maintain leaf turgor, improves stomatal conductance for efficient carbon dioxide intake (Kiani *et al*., 2007), and promotes the root's ability for water uptake (Chimenti *et al*., 2006). As a result, an upsurge in water influx, turgor, and cell wall elasticity is obtained to maintain the physiological activity at an average pace helping the plant to attain growth from the vegetative stage until the reproductive stage during the drought phase (Kramer and Boyer 1995; Ludlow and Muchow 1990; Subbarao *et al*., 2000).

The synthesis of proline, a crucial compatible solute at low water potential in plants, is combined with enhanced biosynthesis and ceasing oxidation in mitochondria (Zhu 2002). Proline is seen to accumulate in bacteria, algae and animals to lower water potential, exposed to dehydration stress having a physiological role in stabilizing macromolecules (proteins), maintaining membrane integrity and quenching reactive oxygen species (Perez-Perez *et al*., 2009; Wahid and Close, 2007; Verbruggen and Hermans 2008; Verslues and Sharma 2010; Kaur and Asthir 2015). During post-drought, proline also serves as energy for carbon and nitrogen source (Szabados and Savouré 2009). Transgenic plants, resistant to osmotic stress, accumulate proline due to overexpression of the pyrroline-5-carboxylase synthase (P5CS) gene (Khan *et al*., 2015). Glycinebetaine (N, N, N-trimethyl glycine), an amphoteric quaternary amine, is yet another widely studied compatible solute in plants, animals and bacteria (Wahid *et al*., 2007). Glycinebetaine is critical in strengthening plant growth under various abiotic stresses by participating in the signal transduction pathway. Further, it safeguards the plant cells either by depositing hydration shells or by directly interacting with the macromolecules, thereby preventing them from unfolding and denaturation (Giri 2011; Quan *et al*., 2004; Subbarao *et al*., 2000). According to findings by Nuccio *et al*. (2015), Trehalose, a non-reducing glucose disaccharide, plays a significant role in plant growth and development by effectively preserving the biological structures and stabilizing enzymes, proteins and lipid

bilayer rather than adjusting the water potential under desiccation stress (Goddijn *et al*., 1997; Wingler, 2002; Lee *et al*., 2003). It is reported that the expression of heterologous genes from some eukaryotic species, such as Escherichia coli and Saccharomyces cerevisiae leads to trehalose synthesis and develops tolerance to drought stress in various species of plants (Iordachescu and Imai 2008). Li *et al*. (2011) observed that the overexpression of multiple isoforms of trehalose- 6-phosphate synthase aids in boosting drought tolerance in rice. Akram *et al*. (2016) emphasized the enhanced expression of SOD and POX in radish due to trehalose synthesis under drought stress. Turner *et al*. (2001) highlighted the maintenance of high tissue water potential by synthesizing abscisic acid and the generation of dehydrins that may confer protection to the plant against drought injuries.

## BIOCHEMICAL RESPONSE

The first biochemical response of plants on exposure to any environmental stress that causes a shift from normal ecological conditions such as drought leads to the generation of reactive oxygen species (ROS), also known as oxidative burst, thereby acting as a secondary messenger to induce successive defense responses in plants (Apel and Hirt 2004). ROS radicals such as superoxide radical ($O_2^-$), hydroxyl radical (OH.), hydrogen peroxide ($H_2O_2$), alkoxy radicals (RO), and singlet oxygen causes oxidative stress in plant cell compartments such as chloroplasts, mitochondria, peroxisomes. On the other hand, under normal metabolism, ROS is formed as a natural byproduct having an essential role in cell signalling. However, ROS being highly reactive, denatures the structure and function of macromolecules such as nucleic acid, oxidation of amino acids, protein, and photosynthetic pigments, and boosts up malondialdehyde (MDA) content, which is a crucial marker for oxidative damage (Labudda and Safiul 2014; Osakabe *et al*., 2014; Farooq *et al*., 2009c; Nezhadahmadi *et al*., 2013, Moller *et al*., 2007). Thus, to deal with continuous oxidative bursts under stress, plants have an internal protective enzymatic and non-enzymatic cleanup system, which is enough to deflect injuries, ensuring normal functioning of the plant cell (Horváth *et al*., 2007). The non-enzymatic

antioxidants are low molecular mass, water and lipid-soluble compounds such as glutathione, ascorbic acid, carotenoids, and α-tocopherol. The enzymatic ROS scavenging defense system includes superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), and ascorbate peroxidase (APX), and glutathione reductase (GR) (Apel and Hirt 2004; Lisar *et al*., 2012; Hasegawa *et al*., 2000). During the oxidative burst the non-enzymatic defense system upholds the integrity of the photosynthetic membrane, whereas the enzymatic system may scavenge ROS directly, being the most effective mechanism (Farooq *et al*., 2008). According to the preceding literature, an upregulated antioxidant activity was noticed under water deficit conditions (Chugh *et al*., 2011; Chakraborty and Pradhan 2012; Marok *et al*., 2013). Marok *et al*. (2013) observed higher activity of CAT and SOD in drought-tolerant barley genotypes on exposure to drought compared to its drought-sensitive genotype. Carotenoids and other non-enzymatic compounds form vital components of the plant's antioxidant defense system (Havaux, 1998; Wahid 2007), scavenging singlet oxygen and lipid peroxy radicals inhibiting superoxide generation and lipid peroxidation under dehydrative forces (Deltoro *et al*., 1998). Ascorbate peroxidase is a crucial antioxidant enzyme in plants, whereas the fundamental role of preserving the glutathione pool is carried out by glutathione reductase under stress (Orvar and Ellis 1997; Pastori *et al*., 2000). Superoxide radicals with a half-life of less than one second are rapidly dismutased into $H_2O_2$ by SOD, a moderate stable product eliminated by catalase and peroxidase (Apel and Hirt 2004; Farooq *et al*., 2009b). SOD, a metalloenzyme, is clubbed up as the main line of defense against generating free superoxide radicals under drought conditions. Thus, increased superoxide dismutase activity confers tolerance against oxidative stress (Pan *et al*., 2006).

## MOLECULAR MECHANISMS

Plants exposed to drought undergo several adaptive mechanisms at molecular levels that include signal transduction resulting in the expression of drought-responsive genes and adaptation to drought to curb the water balance (Nishiyama *et al*., 2013;

Osakabe *et al*., 2014; Kaur and Asthir 2017). Sensing stress and activation of defense and acclimation pathways are associated with complex signalling events involving ABA, Ca2+ and calcium-regulated proteins, ROS, phosphoglycerol, diacylglycerols, and signal transduction pathways (Kovtun *et al*., 2000; Kaur and Asthir 2017). These ROS, calcium, and phytohormones are the chemical indicators involved in inducing stress tolerance via transduction cascade and activating genomic reprogramming (Joyce *et al*., 2003). Recent research shows that drought-responsive genes primarily encode proteins involved in transcriptional regulation (mitogen-activated protein kinase cascades, protein phosphatases and cross-talk between diverse transcription factors), signalling cascades and functional proteins that aid the protection to cellular membranes, late embryogenesis abundant (LEA) proteins, antioxidants, proteins related to water uptake such as aquaporins and sugar transporters (Chen *et al*., 2002; Nakashima *et al*., 2014).

Aquaporins are present in the plasma membrane, and vacuoles are a group of crucial intrinsic membrane proteins that assist the passive water exchange across the membranes; their structural analysis reveals the familiar mechanism of protein-mediated water movement (Tyerman *et al*., 2002). These can potentiate a 10 to 20-fold upsurge in water permeability by regulating the hydraulic conductivity of the membranes (Maurel and Chrispeels 2001). Aquaporin activity is significantly controlled by phosphorylation (Johansson *et al*., 1998), calcium and pH (Tournaire- Roux *et al*., 2003). The function of aquaporins is expressed primarily in roots, where they mediate soil water uptake controlled by transcellular water transport (Javot and Maurel 2002).

Production of ABA is triggered in roots under water deficit and transported to shoot, causing restricted growth due to stomatal closure (Mittler and Blumwald 2015). Horváth *et al*. (2014) indicated that ABA compartmentalization and expanse of ABA reaching the stomata are influenced by xylem/apoplastic pH. Underwater deficit condition, xylem/apoplast pH being alkaline results in alkaline ABA trapping; that is, there is a decline in ABA exclusion from xylem and leaf apoplast to symplast, due to which added ABA on reaching guard cells, enables stomatal aperture modulation in response to various stress factors (Shatil- Cohen *et al*., 2011). It was also observed by Le Gall *et al*. (2015) in drought-stressed plants that translocation of sugars through xylem exerts a significant impact on the sensitivity of stomata to ABA.

Many dehydration-responsive element-binding genes are involved in signalling pathways in response to drought and other abiotic stresses (Agarwal *et al*., 2006). The dehydration-responsive element/C-repeat (DRE/CRT) cis-acting element and its DNA-binding protein constitute a significant transcription system modulating ABA-independent gene expression in response to drought and includes dehydration-responsive element-binding proteins (DREB)/C-repeat binding factors (CBF) family of proteins. DREB2 subclass of DREB/CBF family proteins is expressed under drought to articulate genes involved in stress tolerance (Seki *et al*., 2003). Also, an early warning response mechanism exists in plant roots to activate the hydrogen pump ATPase protein (H+-ATPase) on the plasma membrane of root hairs before a substantial decline in plant RWC. The activation further triggers amplified biosynthesis of leaf proline and GB, the key osmolytes that maintain the water budget of plants (Gong *et al*., 2010). Poly Amines (PA) have been associated with the drought response of plants via signalling and are also involved in playing a role in other stresses (Bae *et al*., 2008). In addition, upregulation and downregulation of various gene transcripts and stress protein accumulation are crucial, and stress-driven forces, secondary stress signals, and plant response to injury may trigger gene expression (Kavar *et al*., 2008).

## IMPROVING DROUGHT TOLERANCE AND MANAGEMENT STRATEGY

The cultivation of drought-tolerant crops is one of the options to meet the needs of the escalating world population. The production of transgenic plants is one of the well-known approaches for tolerance as a wide range of genes in the plant genome has opened up excellent prospects for crop improvement (Lisar *et al*., 2012; Xoconostle-Cazares *et al*., 2010). On the other hand, the generation of transgenic plants cannot be

entirely operative for producing drought-tolerant crop plants as it requires detailed and expensive protocol, and the success rate is primarily low (Nezhadahmadi *et al*., 2013; Nakashima *et al*., 2014). In the traditional breeding method, two plant individuals with desirable traits are selected and crossed to exchange genetic material; therefore, the offspring result from a new genetic combination (Khan *et al*., 2011; Nezhadahmadi *et al*., 2013). Some crucial traits used in plant breeding include water use efficiency, hydraulic conductance, osmotic and elastic adjustments, and variation in leaf area (Bhargava and Sawant 2013; Farooq *et al*., 2009b; Ding *et al*., 2013). Genetic data can improve plant breeding efficiency by using suitable tags for the target gene, known as polymorphisms, based on the naturally present sequence in DNA (Xoconostle-Cazares *et al*., 2010). The unique approaches are employed to distinguish linked markers, including restriction fragment length polymorphisms (RFLPs), sequence characteristic amplified regions (SCARs), random amplified polymorphic DNA (RAPDs), simple sequence repeats (SSRs), amplified fragment length polymorphism (AFLPs), and others (Khan *et al*., 2013; Xoconostle-Cazares *et al*., 2010).

Plant breeding methods have a massive potential to fasten the production of drought-tolerant plants, which helps in drought management. However, there are various strategies for managing drought in agricultural fields at different levels, such as irrigation at low soil moisture during germination and crop stand establishment, mulch to maintain the soil moisture level, eliminating attacks by insects and herbivores, appropriate planting practices, native plant individual based on the edaphic conditions, and plant inoculation by symbiotic microorganisms such as AM fungi (Nezhadahmadi *et al*., 2013; Khan *et al*., 2011; Farooq *et al*., 2009b).

Foliar application of assorted PGRs and osmoprotectants can also enhance the drought tolerance of crop plants. The exogenous application of plant hormones and osmoprotectants such as gibberellins (GA3), cytokinin (Ck), abscisic acid (ABA), proline, glycine betaine (GB), brassinolide, polyamine (PA), and salicylic acid (SA) has been recognized to ameliorate stress effects, with high osmotic adjustment to maintain turgor and antioxidants accumulation to detoxify ROS to preserve the stability of membrane structures, enzymes, and other macromolecules (Manivannan *et al*., 2008; Farooq *et al*., 2009b, c; Yuan *et al*., 2010; Alcázar *et al*., 2010; Anjum *et al*., 2011b). Salicylic acid is a secondary metabolite that promotes plant drought tolerance by regulating several physiological processes through signalling (Senaratna *et al*., 2000; Singh and Usha 2003). The foliar application of methyl salicylic acid in water-stressed plants promotes leaf senescence, which contributes to nutrient remobilization, profiting the rest of the plant from the accumulated nutrients of the leaf from its life span (Abreu and Munne-Bosch 2008). Also, exogenously applied glycine betaine involved in osmoregulation acts as an osmoprotectant to protect membranes and enzymes from oxidative stress under drought stress (Ma *et al*., 2006).

## CONCLUSION

Under the impact of ongoing global climate change intensifying greenhouse gas emissions, drought onset, frequency, and severity have been foreseen to increase shortly, affecting plant growth, development, and metabolism. The low rainfall, salinity, high temperature, and high light intensity are some of the main causal factors of the drought. Drought as a multidimensional stress factor negatively affects a plant at the molecular level up to the whole plant level. The plant has adopted strategies by shortening its life cycle and yield penalty to withstand drought. Also, the plants respond to drought by maintaining metabolic activities at low tissue water potential. Plants show physiological adaptation to dehydration tolerance by osmotic adjustments such as increased accumulation of proline, glycine betaine, sugars, inducing antioxidant activities (enzymatic and non-enzymatic systems) by scavenging ROS, maintaining cell membrane stability, expression of aquaporins, and altered growth regulators are vital mechanisms of drought tolerance. To curtail the effects of water stress, plants exhibit various signaling pathways and respond by upregulating antioxidant activity, accumulation of osmolytes and changing the growth pattern by producing chaperones and stress

proteins. The production of drought-tolerant transgenic plants by combining traditional breeding methods and gene manipulation is helpful to curtail the adverse effects of drought on plants. Also, several other strategies in agricultural fields for drought management on multiple levels can be effective.

## CONFLICTS OF INTEREST

The authors declare that they have no potential conflicts of interest.

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