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DROUGHT STRESS AND ADAPTATIONS STRATEGIES IN PLANTS - A REVIEW

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SUMMARY

Plant growth and productivity are significantly impacted by a variety of biotic and abiotic stress factors. Among these, water deficit stress-whether temporary or permanent-has a greater impact on the growth and performance of cultivated plants than most other environmental factors. Water stress is a major issue in agriculture, and the ability of crops to endure such stress is of immense economic value. Drought, as a complex physical-chemical process, adversely affects nearly every aspect of plant metabolism. As a result, it is crucial to understand how crops adapt at morphological, physiological, biochemical, and molecular levels under water deficit conditions. This review aims to provide an overview of research on the mechanisms of drought tolerance in plants.

Key words: Drought stress, antioxidants, enzymes, molecular changes

Plant growth and productivity is adversely affected by various biotic and abiotic stress factors. Water deficit stress, permanent or temporary, limits the growth and the performance of cultivated plants more than any other environmental factors do (Filippou *et al.*, 2011). Water stress is the major problem in agriculture and the ability to withstand such stress is of immense economic importance. Drought is also a complex physical-chemical process, in which many biological macromolecules and small molecules are involved. Drought stress negatively affects almost all aspects of plant metabolism, inducing a number of changes at the morphological, physiological, biochemical and metabolic levels in all plant organs (Qayyum *et al.*, 2012).

MECHANISM OF DROUGHT TOLERANCE

Drought tolerance is a complex trait influenced by several physiological attributes, enabling plants to produce economic yields with minimal water loss under water-deficit conditions. In genetic terms, drought tolerance mechanisms are categorized into four groups: avoidance, tolerance, escape, and recovery (Bhushan *et al.,* 2007). These mechanisms are interconnected, with no clear boundaries between them.

Drought escape refers to a plant's ability to complete its life cycle before significant water deficits occur. This is achieved through early-maturing varieties or early sowing. Chickpea plants, for example, can escape terminal drought by rapid growth, early flowering, and maturation (Toker *et al.*, 2007).

Drought avoidance involves maintaining relatively high tissue water potential during water stress by enhancing water uptake and reducing loss. Key traits for drought avoidance in chickpeas include a larger/deeper root system and smaller leaf area (Saxena, 2003). Other mechanisms include increased hydraulic conductance, reduced stomatal and lenticular conductance, leaf movements (folding/rolling), and phenological plasticity (Mitra, 2001).

Drought tolerance is the ability of cells to function at low leaf water content. It involves osmotic adjustment, which includes solute accumulation, increased cell elasticity, and stabilizing proteins (Mitra,2001). Membrane stability is maintained by reducing solute leakage, and compatible solutes like proline, glycine betaine, and trehalose help preserve cell water content and protect proteins from degradation under stress (Gupta and Kaur, 2005).

EFFECT OF DROUGHT STRESS ON MORPHOLOGICAL CHARACTERISTICS

Growth is an important tool for assessing crop productivity in various crops. Various internal and external factors influence growth besides its genetic make-up (Li and Wang, 2003) and is one of the most drought-sensitive physiological processes due to the reduction of turgor pressure. Low turgor pressure greatly suppresses cell expansion and cell growth. Water loss beyond the turgor loss point (P=0), therefore, results in a negative pressure potential (tension). Upon severe water loss from the cells, membrane disintegration and abolition of metabolic processes occur (Beck *et al.,* 2007).

Root System: Root systems play a crucial role in water acquisition and root characteristics such as root length, density, and the numbers of thick roots are vital during early growth, enabling plants to exploit shallow soil water before it is lost to evaporation (Kumar *et al.,* 2012). A prolific root system is essential for drought adaptation, helping maintain osmotic pressure and supporting longer-duration varieties (Shao *et al.,*2008). Different plant species and varieties show significant variability in root production (Liu *et al.,*2005), though the effect of drought stress on root growth remains debated.Under limited water, root and shoot dry matter reduces but the root-to-shoot ratio typically increases, as roots are less affected by low water availability compared to shoots (Kumar *et al.,* 2012). Roots also trigger a signaling cascade to shoots via xylem, influencing stomatal closure as an adaptation to drought stress. Genotypic variation in rooting depth and water extraction ability affects seed yield by improving water acquisition and transpiration efficiency (Kashiwagi *et al.,* 2006). Drought stress reduces lateral root growth; though primary roots remain relatively unaffected. Despite the importance of root traits, breeding programs for improving these characteristics are limited due to insufficient knowledge on their genetics (Saxena, 2003).

Stem Length and Leaf Area: It has been established that drought stress is a very important limiting factor at the initial phase of plant growth and establishment. Impaired mitosis, cell elongation and expansion resulted in reduced plant height, leaf area and crop growth under drought (Hussain *et al.,* 2008). Continuous water deficit resulted in fewer and smaller leaves, which have smaller and more compact cell. Leaf area plasticity is important to maintain the control of water use in crops. Leaf area expansion depends on leaf turgor, temperature and assimilates supply for growth which is affected by drought (Anjum *et al.,* 2011). Water deficit stress mostly reduced the leaf area in many species of plants. Leaf area was affected adversely in both main shoot and tillers and is ascribed to suppression of leaf expansion through reduction in photosynthesis. Water stress can hinder the initiation and development of tillers, leading to a reduction in their numbers and the reduction in plant height was associated with a decline in the cell enlargement and more leaf senescence under water stress (Khaeim *et al.,* 2022).

Fresh and Dry Weight: Greater plant fresh and dry weights under water limited conditions are desirable characters. A common adverse effect of water stress on crop plants is the reduction in fresh and dry biomass production (Farooq *et al.,* 2009). Plant productivity under drought stress is strongly related to the processes of dry matter partitioning. A decrease in total dry matter may be due to the considerable decrease in plant growth, photosynthesis and canopy structure, as indicated by leaf senescence during water stress. A moderate stress tolerance was noticed based on relative shoot growth studies under stress conditions like drought in transgenic plants by dry weight production. In the number of species the remobilization of pre-anthesis stored reserves of C and N can be an important assimilate source for seed filling, particularly, when plants are subjected to water deficit (Kage *et al.,* 2004).

Yield Parameters: Grain yield is the result of the expression and association of several plant growth components. Effect of drought on yield depends upon severity, duration and timing of stress as well as responses of plants after stress removal, and interaction between stress and other factors (Jaleel *et al.,* 2009). Drought stress inhibited the dry matter production largely through its inhibitory effects on leaf expansion, leaf development and consequently reduced light interception. Thereby, disrupting leaf gas exchange properties which not only limited the size of the source and sink tissues but the phloem loading, assimilate translocation and dry matter partitioning also gets impaired with reduction in activities of sucrose and starch synthesis enzymes. Moreover, loss in grain yield might be the reduction in assimilate flux to the developing ear below some threshold level necessary to sustain optimal grain growth (Farooq *et al.,* 2009). Decrease in water potential and higher ABA accumulation in the reproductive structure of plants subjected to drought may also contribute to the loss of fruit or seed set. ABA accumulation in reproductive organs during early development inhibits cell division and subsequent abortion or failure to set seed. Post-anthesis drought stress was detrimental to grain yield regardless of the stress severity (Gebeyehu *et al.,* 2010).

EFFECT OF DROUGHT ON PIGMENT COMPOSITION

Chlorophyll is one of the major chloroplast components for photosynthesis, and relative chlorophyll content has a positive relationship with photosynthetic rate. The decrease in chlorophyll content under drought stress has been considered a typical symptom of oxidative stress and may be the result of pigment photo-oxidation and chlorophyll degradation. Photosynthetic pigments are important to plants mainly for harvesting light and production of reducing powers. The limitation of photosynthesis under drought through metabolic impairment is more complex phenomenon than stomatal limitation and mainly it is through reduced photosynthetic pigment contents. Both the chlorophyll 'a' and 'b' are prone to soil drying (Farooq *et al.,* 2009).

ROS CHEMISTRY

Under normal and stressed conditions, ROS are produced in chloroplasts, mitochondria, peroxisomes, plasma membranes, the endoplasmic reticulum, and the cell wall. In the presence of light, chloroplasts and peroxisomes are the primary ROS generators, whereas in the absence of light, the mitochondrion is the primary ROS generator (Choudhury *et al.,* 2013). Under extreme stress, the rate of ROS production exceeds the capacity of the cellular defence system to scavenge them, resulting in cellular damage. ROS consists of H_2O_2, O^{2-} and free radicals, such as $^1O_2$, $O_2{}^{2-}$, O_2H, OH^-, RO etc., which are toxic to the metabolism of plants, directly influencing all macromolecules in the cell, including DNA (del-Rio, 2015). Nitric oxide has a strong cross-talk relationship with other radicals such as H_2O_2, resulting in the induction of stress tolerance in response to a variety of abiotic stimuli such as water and salinity (Qiao *et al.,* 2014). ROS connect important signalling pathways for plant growth, development, and phytohormone action (Baxter *et al.,* 2014).ROS can cause peroxidation of polyunsaturated fatty acids, variety of direct and indirect protein modifications as well (Yamauchi *et al.,* 2008).

ROS SCAVENGING ANTIOXIDANT DEFENCE SYSTEM IN PLANTS

Plants have a complex antioxidative defence system that comprises both non-enzymatic and enzymatic components to eliminate ROS. To prevent oxidative injury, higher plants increase their level of endogenous antioxidant defence.Superoxide Dismutase (SOD), Catalase (CAT), Peroxidase (POX), and Polyphenol oxidase (PPO) are the enzymes localised in the various subcellular compartments and constituting the antioxidant machinery (Sharma *et al.,* 2010).

Superoxide Dismutase **(SOD)** catalyse the dismutation of O^{2-} into H_2O_2. SOD has been suggested to play an important role in plant stress tolerance, and it is the first line of defence against the deleterious effects of elevated ROS levels. It eliminates superoxide, thereby reducing the likelihood of hydroxyl radical formation via a metal-catalyzed Haber-Weiss-type reaction. The reaction is 10,000 times more rapid than spontaneous transformation (Boguszewska *et al.,* 2010). SOD enzyme activity increases in stressed plants, indicating that it increases plant tolerance to environmental stresses. Therefore, it could be used as an indirect selection index in early stages to distinguish resistant genotypes to drought stress (Saed-Moucheshi *et al.,*2021).

Catalases (CATs) are heme-containing tetrameric enzymes that catalyse the reduction of H_2O_2 to O_2 and H_2O. They are predominantly found in peroxisomes, but new research indicates that this enzyme is also present in chloroplasts, mitochondria, and cytoplasm. Catalases are divided into three classes: catalases, which are most abundant in photosynthetic tissues and mediate dismutation of H_2O_2 produced during photorespiration; catalases, which are frequently found in vascular tissues and may play a role in lignification; and catalases, which are abundant in seeds and young plants and are involved in the removal of excess H_2O_2 generated during the glyoxylate cycle, in glyoxisomes (Mushtaq *et al.,* 2020).

Peroxidases (POXs) are heme-containing enzymes and a family of H_2O_2-scavenging isoenzymes (Fagerstedt *et al.,*2010). As electron donors for catalysis, guiacol and pyrogallol are utilised. The POX enzyme neutralizesperoxy and other types of oxygen radicals. POX excretion, on the other hand, can generate reactive oxygen species (ROS), which have an active signal transduction role in stomatal closure and cell elongation (Kawano, 2003).

Polyphenol oxidase (PPOs) is a class of Cu-containing enzymes that catalyse the oxidation of multiple phenols to o-quinones. In turn, o-quinones are highly reactive molecules that can undergo non-enzymatic secondary reactions to form melanins and cross-linked polymers with protein functional groups (Taranto *et al.,* 2017).PPO is the primary enzyme responsible for the oxidation of stress-induced phenolic compounds.

Non- enzymatic antioxidants

The non-enzymatic antioxidants form the other half of the antioxidant machinery, comprising of, carotenoids, phenolics, flavonoids, and proline. They not only protect different components from damage, but also play a vital role in plant growth and development by tweaking cellular process like mitosis, cell elongation, senescence and cell death (De Pinto and De Gara, 2004).

Phenolic substances: Plants produce three main types of secondary metabolites: phenolics, terpenes, and nitrogen/sulfur-containing compounds. Phenolic constituents are structurally diverse secondary metabolites, such as flavonoids, tannins, hydroxycinnamate esters, and lignin that have both antioxidant and anti-nutritive properties (Zainab *et al.,* 2013). Phenolics act as defensive constituents and play a crucial role in the host plant's resistance mechanism against various insects and pests.Phenols play diverse roles in stressed plants, including neutralization of reactive oxygen species (ROS) and cell wall lignification (Kovalikova *et al.,* 2019). Flavonoids are divided into four structural classes: flavonols, flavones, isoflavones, and anthocyanins. Flavonoids have multiple functions, including pigmentation in flowers and fruits and defense against plant pests and pathogens. They also play a role in scavenging $^1O_2$ and mitigating the damage caused to the chloroplastic membrane's outer envelope (Fini *et al.,* 2022). The introduction of a second hydroxyl group at the ortho or para position of mono-substituted phenols increases the antioxidant efficiency by a significant extent. Hydroxylation at three consecutive positions particularly in the 3-, 4-, and 5- positions of a phenolic acid compound confers the highest antioxidant activity. Various factors such as climatic conditions, growth stage and genetic make-up influence the total phenolic content of plant (Sakurai*et al.,* 2022).

Sugars: Carbohydrates serve as a source of energy and also act as signaling molecules in the regulation of metabolic pathways under normal and stressed conditions (Gupta and Kaur, 2005). Sucrose and hexoses both play dual functions in gene regulation as examplified by the upregulation of growth-related genes and downregulation of stress-related genes (Rosa *et al.,* 2009).When different abiotic stresses affect plant functionality, alterations in photosynthesis and carbon partitioning are common features that take place at organ level as well as in whole plant. Sugar signalling pathways interact with stress pathways creating into a complex network to modulate metabolic plant responses. Accumulation of simple sugars such as glucose and fructose following an increase in the invertase activity in the leaves of drought challenged plants had been reported (Gonzalez *et al.,* 2009). Oligosaccharides such as raffinose and galactinol were among the sugars synthesized in response to drought and seem to function as osmoprotectants rather than providing osmotic adjustment (Rosa *et al.,* 2009).

***Proline*:** Proline is the only proteogenic amino acid that contains a secondary amine group. Proline's unique characteristics, such as redox buffering, energy transfer, and antioxidant properties, make it more prevalent in stressed plants. It is regarded as a potent antioxidant because it is utilized across kingdoms as a non-enzymatic antioxidant to combat the damaging impacts of various ROS members. In response to stress, proline accumulates in significant quantities in plants (Verbruggen and Hermans, 2008). According to Sharma and Dietz (2009), proline accumulated predominantly in response to abiotic stress (drought, salinity, and heavy metal) and to a lesser extent in response to biotic stress (pest/pathogen).

***Carotenoids*:** Carotenoids are a class of metabolites that are crucial for plant survival in water-deficient environments. The production and regulation of carotenoids are highly dependent on the plant species as well as the duration and severity of drought stress. They serve as antioxidants against various ROS forms and assist the plant in activating its antioxidant defense system. Carotenoids acts as an antioxidant against singlet oxygen ($^1O_2$) generated by triplet chlorophylls either through direct quenching of triplet chlorophyll or through the de-epoxidation reaction (Uarrota *et al.,* 2018), therefore, carotenoids strengthen the rigidity of the thylakoid and cell membrane. In addition, they are the precursors of numerous phytohormones, such as abscissic acid and strigolactones. Carotenoids eliminate excess energy and prevent photosystem II from becoming overexcited (Uarrota *et al.,* 2018).

***DPPH*:** A tissue's antioxidant potential can also be determined by its ability to scavenge (DPPH) radicals and reduce ferric ions. The DPPH method employs a radical nitrogen molecule known as 2,2-

diphenyl-1-picrihydrazyl. This technique is based on the hydrogen capture mechanism by DPPH from the antioxidant itself. The anomalous electron of the nitrogen atom in DPPH is reduced by obtaining a hydrogen atom from antioxidants and converting it to the equivalent hydrazine (Castro-Lopez *et al.,* 2019). DPPH can receive an electron or hydrogen radical to become a stable, diamagnetic molecule; however, it can only be oxidized with great difficulty and then irreversibly.

FRAP**:** The efficacy of antioxidant compounds to reduce iron (III)-tripyrydyl-triazine to iron (II)-tripyrydyltriazine was used to evaluate the FRAP method (Widyastuti, 2010). The FRAP assay is promoted as an innovative method for measuring "antioxidant power." When ferric to ferrous ion reduction occurs at a low pH, a colorful ferrous-tripyridyltriazine complex is generated. Kumar *et al.,* (2016) reported various radical scavenging activities of fractionated foxtail millet protein hydrolysate.

Total reducing power: The reductive capability of a compound may act as a remarkable indicator of its antioxidant potential (Jayanthi *et al.,* 2021). Methanolic extracts of rhizomes of A. calamus showed higher reductive ability which was effective for neutralizing the free radical (Manju *et al.,* 2013). The reducing power activity is due to the presence of reductones (phenolics) (Nanda, 2014).

OH Radical scavenging activity**:** Hydroxyl radical is the most reactive oxygen centered species and causes severe damage to adjacent biomolecule. Hydroxyl radical scavenging activity was estimated by generating the hydroxyl radicals using ascorbic acid–iron EDTA. The hydroxyl radicals were formed by the oxidation reaction with the dimethyl sulphoxide (DMSO) to yield formaldehyde, which provides a convenient method to detect hydroxyl radicals by treatment with Nash reagent (Pavithra and Vadivukkarasi, 2015).

NITROGEN METABOLISM ENZYMES

Many studies have shown the close relationship of nitrogen (N) metabolism with the drought stress in plants. For plant growth and for its normal development, nitrogen is an essential macro-nutrient element required. Nitrogen, in theform of nitrate (NO_3^-), is absorbed by plant roots mainly and it is transported to leaves for its assimilation. The nitrate reductase (NR) reduces the nitrate (NO_3^-) to nitrite (NO_2^-) in the cytoplasm. In choloroplast, nitrite is transformed into ammonia (NH_4^+) by nitrite reductase (NiR)(Du *et al.,* 2020). Ammonia (NH_4^+) is then converted to glutamate and glutamine, by the enzymes glutamine synthetase (GS), glutamate synthetase (GOGAT) and glutamate dehydrogenase pathways. Since, in the nitrogen metabolism in plants, the accumulation of NO_2^- and NH_4^+ is considered to be toxic to the plant cells. Therefore, sustained activities of enzymes, NR, NiR, GS and GOGAT are very much crucial in the process of nitrogen assimilation to maintain plant growth and development. However, drought stress conditions usually lower down the activities of NR and NiR enzymes that result in NO_3^- accumulation. The activities of GS and GOGAT are also associated with the response to drought stress, and they are frequently regarded as significant metabolic indicators of drought tolerance (Nagy *et al.,* 2013).

Nitrogen assimilation products: These not only acting as the important energy sources but they are also involved in the signaling mechanisms and play crucial roles in plant growth and development. Under drought stress, the accumulation and synthesis of compatible solutes (amino acids and soluble sugars) and ions (NO_3^-) are regarded to be the primary contributors to osmotic adjustment in plants (Zahoor *et al.,* 2017). In addition, prior research has demonstrated that nitrogen assimilation products, such as NO_3^-, NH_4^+, and proline, can regulate the selective absorption and transport of ions in plants and play a crucial role in maintaining the dynamic balance of physiological metabolism in plants under abiotic stress (Cui *et al.,*2019).

Drought significantly decreased root NO_3^-N content, but increased leaf NO_3^-N. The variation in NO_3^-N accumulation in leaves and roots followed the trends of NO_3^-N absorption rate and assimilation in roots. Leaf NO_3^-N plays a crucial function in regulating stomatal closure by affecting the depolarization of guard cells (Du *et al.,* 2020). The decrease in leaf NR activity may be associated with a decrease in photosynthesis due to stomatal closure, thereby, inhibiting plant growth. Additionally, reduced NR activity in drought-stressed plants is predominantly attributable to an increase in NO_3^-content. It was confirmed that the residual energy produced by the photosynthetic apparatus could be utilized in the reduction of leaf NO_3^-N. Consequently, the elevated leaf NO_3^-N and decreased NR activity indicated that NO_3^- reduction and assimilation had significantly decreased (Sperandio *et al.,* 2020). In accordance to Sakthivelu *et* *al.*,(2009), this phenomenon was ineffective in preventing ROS accumulation caused by drought stress.

GENE EXPRESSION CHANGES UNDER DROUGHT STRESS

During periods of drought, plants undergo significant physiological changes and activate numerous genes to adapt to the challenging conditions (Yang *et al.*, 2021). Drought, being a severe environmental stressor, is a major global constraint on plant productivity. It stands as one of the most detrimental issues in agriculture. The adaptation of plants to drought often involves an increase in reactive oxygen species (ROS) and in addition to ROS production, adverse conditions such as drought are associated with the accumulation of methylglyoxal (MG). High levels of MG can be detrimental to cells, inhibiting cell proliferation and causing various adverse effects, including increased protein degradation and inactivation of antioxidant defenses (Hasanuzzaman *et al.*, 2020). Due to the highly cytotoxic nature of MG, its concentrations need strict regulation. The glyoxalase system, consisting of glyoxalase I (Gly I) and glyoxalase II (Gly II) enzymes, is primarily responsible for detoxifying MG in plants (Hasanuzzaman *et al.*, 2020). Overexpression of glyoxalase enzymes in plants has been found to limit the increase in ROS and MG levels under stress conditions by maintaining glutathione (GSH) homeostasis and antioxidant enzyme levels. These enzymes play a crucial role in regulating environmental stress in plants; with studies showing that upregulation of Gly I enhance plant stress tolerance.Coordinated induction and modulation of antioxidant and glyoxalase pathway enzymes are essential for significant tolerance to oxidative stress, highlighting the detoxification of both ROS and MG as a strategy for abiotic stress tolerance (Al Mahmud, 2019).

Sucrose synthase, a cytoplasmic enzyme, degrades sucrose and provide carbon for respiration and sugar metabolism for synthesis of cell wall polysaccharides and starch. This enzyme has been ascribed a central function in the determination of sink strength in both storage and developing vegetative tissues. The extent, path, and site of sucrose metabolism are highly responsive to both internal and external environmental signals and which can, in turn, alter development and stress acclimation in plants (Jeandet *et al.*, 2022). Two SuS genes from *Arabidopsis thaliana* were found to be differentially up-regulated in leaves exposed to environmental stresses (Xu *et al.*, 2015). The differential stress responsive regulation of these genes in leaves might represent part of a general cellular response to the allocation of carbohydrates during acclimation processes (Xu *et al.*, 2015).

Rubisco catalyses the carboxylation of ribulose-1, 5-bisphosphate (RuBP), forming two molecules of 3- phosphoglycerate (3-PGA);these are used to form triosephosphates using ATP and NADPH. Under stress conditions the effects of drought stress on Rubisco vary depending on the plant species and intensity of stress; some studies reported a dramatic reduction in Rubisco activity while others showed little or no inhibition of the enzyme (Chatterjee *et al.*,2017). Stay green is a term used to describe plants that retain their green color and photosynthetic activity for an extended period, even under stress conditions. The genes responsible for this trait can vary among different plant species. These genes are typically associated with chlorophyll degradation and senescence regulation. In some cases, the expression of “stay green” genes may be downregulated under drought stress to conserve resources and energy (Zada *et al.*, 2022).

CONCLUSION

In conclusion, drought stress in plants is becoming an increasingly critical concern due to the intensifying effects of climate change. With rising temperatures and unpredictable rainfall patterns, drought conditions are expected to worsen in many regions, severely affecting agricultural productivity and food security. Plants respond to drought stress by initiating various physiological, biochemical, and molecular mechanisms, including stomatal closure, production of protective molecules, and activation of stress-related genes. Drought stress tolerance varies from species to species and even within species. Therefore, advances in plant breeding and genetic engineering are essential for developing drought-resistant varieties by understanding the biochemical and molecular responses to drought for the holistic perception of plant resistance mechanisms.

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