INTERNATIONAL JOURNAL OF APPLIED AND EXPERIMENTAL BIOLOGY
(ISSN PRINT: 2790-6523; ISSN ONLINE: 2790-6531)
2024, Vol. 3, NO. 2, 159-175
doi: 10.56612/ijaaeb.v1i1.92
https://eminentscientists.com/

Plant tolerance to drought stress: Complexity and mechanism across physiological, molecular and biochemical scales

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Abstract
Drought stress limits crop yield globally and is growing as a result of climate change. Water deficit of soil frequently reduces crop growth and yield regardless of developmental stages and nature of genotypes. There are a variety of mechanisms involved in plants in response to drought stress and they trigger the plant drought tolerance strategies. Plants subjected to drought undergo a sequence of physiological, biochemical, and molecular mechanisms to combat the effects of drought, just like plants exposed to other environmental stressors. Using various methods, researchers are currently attempting to understand the intricate operation of the drought stress response in plants. During particular crucial stages such as seed germination, and formation of seedlings, flowering, and grains, plants are particularly vulnerable to drought stress. Through the activation of tolerance mechanisms, plants successfully mitigate the impacts of drought stress during vegetative development stages. However, drought stress during the generative phase might result in yield losses that are irreversible. The present review highlights the tolerance mechanisms in plants and the functioning of physiological, molecular, and biochemical processes involved in plants' resistance to water deficit as well as how various crops react to drying conditions at various developmental points.

ARTICLE TYPE
Review Article (RA)

SECTION
Plant Biology (PB)

HANDLING EDITOR
Ashraf, M. (CE)

ARTICLE HISTORY
Received: 15 Oct, 2023
Accepted: 14 Feb, 2024
Published: 04 Jul, 2024

KEYWORDS
Abiotic stresses;
Crop yield;
Germination;
Plant growth;
Tolerance mechanisms

Introduction

There are numerous factors such as biotic and abiotic, that limit plant growth and development (Yohannes et al., 2020). The direct or indirect effects of climatic change are one of the abiotic factors that directly or indirectly affect crop yield (Billah et al., 2021; El Haddad et al., 2022). Water is an important

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TO CITE THIS ARTICLE: Batool, A., Yue, D.X., Xiao, Y.L., Li, S.S., Duan, H.X., Haq, Z., Ahmed, K., Zhao, L., Zhu, L., Xiong, Y.C. (2024). Effects of plant growth-promoting rhizobacteria on uptake and utilization of phosphorus and root architecture in apple seedlings under water limited regimes. *International Journal of Applied and Experimental Biology* 3(2): 159-175.

factor to enhance the crop growth and productivity and it is essential for all living organisms including plants. Various metabolic activities and photosynthesis mechanisms require water (Oo et al., 2020). Additionally, to maintain their growing performance, maximum amount of water is required by the plants (Tátrai et al., 2016). A physiological form of water deprivation known as drought occurs when there is inadequate soil moisture available to plants, which negatively impacts their metabolism (Kumar et al., 2018). Plants combat the detrimental effects of drought using a sophisticated set of interlinked processes (Pamungkas et al., 2022). Tolerating the detrimental consequences of a stress is made easier by physiological and metabolic changes that come from interaction of these systems (Hossain et al., 2021).

The intricate networks that regulate the plant's stress response systems are influenced by both environmental and genetic variables. The intricate tolerance mechanism cannot be controlled or understood using traditional approaches (Sinclair, 2011). In this regard, omic technologies show a promise for enhancing the ability of several biotechnological techniques to tolerate drought stress (Hossain et al., 2021). The goal of these investigations is to identify prospective areas and genes for stress resilience across the genome (Billah et al., 2021). Numerous investigations using techniques like quantitative trait loci (QTL) analysis, transcriptome analysis, and genome-wide association study (GWAS) have been made on well-designed functional genes implicated against stress response in crop species (Cormier et al., 2014; Swamy et al., 2018; Gahlaut et al., 2019; Ballesta et al., 2020). By using various techniques such as gene silencing, transgenic strategies, genome engineering, i.e., CRISPR/Cas9 techniques, and recognized marked genes help increase stress tolerance strategies (Billah et al., 2021; Hossain et al., 2021).

There are numerous mechanisms generated in plants to produce defense against drought conditions. These plant responses include physiological, morphological and biochemical (Haworth, et al., 2013). Production/accumulation of antioxidants, chlorophyll, proline, hormones and secondary metabolites are considered as biochemical responses. Stomatal closure, osmotic adjustment, photosynthesis, leaf water content, transpiration and water transport are physiological responses of plants to drought stress (Conesa et al., 2016). Reduction in leaf area and leaf number, and incline in root length, early microbial development, and leaf aging are morphological responses by plants under drought. Enhancement in the generation of transcription factor genes is one of the biological processes that works here (Anjum et al., 2011; Ammar et al., 2015). The plant's stress response and coping strategies under drying conditions are also dependent on the stage of growth (Nezhadahmadi et al., 2013). Plants might vary in their sensitivity to drought stress depending on where they are in their growth cycle. During the vegetative developmental cycle, if a plant is exposed to drought, it shows the abnormalities in leaf water content, turgor pressure, leaf coloring, stomatal movement, leaf vitality, respiration, and photosynthesis, thereby causing reduced growth (Queiroz et al., 2019). These reactions might motivate the plant to cut down on the length of its vegetative phase and hasten through the generative stage (Pamungkas et al., 2022). Decline in blooming rate, seed setting, fertilization, and plant productivity are carried out by exposure under drying conditions during the generative phase of development stage (Mahla et al., 2017; Akram et al., 2018). A wide range of crops, including sorghum (Sanjari et al., 2021; Sarshad et al., 2021), maize (Goodarzian Ghahfarokhi et al., 2015; Hammad et al., 2017), wheat (Mahla et al., 2017; Jin et al., 2018; Kulczycki et al., 2022), rice (Akram et al., 2018; Yang et al., 2019), mung bean (Prakash et al., 2017; Bangar et al., 2019; Jincy et al., 2021), soybean (Dong et al., 2019; Felisberto et al., 2022), and lentil (El Haddad et al., 2022), have been studied for their responses to drought stress. The plant growth cycle is crucial for controlling its response to stress, and it depends on drought duration and its intensity (Çakir, 2004).

This review focuses on drought stress tolerance mechanisms and interplay of different plant responses such as molecular, physiological and biochemical, in order to better understand how plants respond to drying environment, particularly during critical stages of plant development.

Signaling from drying environment and molecular regulation

Numerous physiological and biochemical activities, including translocation, respiration, water relations, ion uptake, photosynthesis, stomatal closure, nutrient and sugar metabolisms, phytohormones and, antioxidant system, are negatively affected by drought stress (Wang et al., 2021). The plant responds to drying environment by undergoing biochemical and physiological changes caused by the activation of multiple genes with various roles (Impa et al; 2019; Tovignan et al., 2020). Two major categories are used to study the molecular pathways involved in drought resistance. Signal transduction components, such as protein kinases, transcriptional regulators, and abscisic acid receptors, come first. Another category is an array of functional factors, which includes specific proteins that regulate metabolic process, osmotic control, synthesis of proteins and their modification, and accumulation and transport of ROS (Razi and Muneer, 2021; Wang et al., 2021).

Cell wall disruption causes activation of protein molecules due to activation of stress signals. Water deficit triggers various signaling pathways in plants that include a myriad of biomolecules and enzymes such as molecular chaperones, enzymes, TFs (transcription factors) and various other metabolites (Song et al., 2013). There are a number of genes identified in different plants so far that show variation in expression under water deficit (Joshi et al., 2016; Rasheed et al., 2016; Hu et al., 2022). These genes have many cellular signaling and response roles, including transcriptional control (Wei et al., 2009; Bashir et al., 2021). Transcriptional factors include gene families such as WRKY, DREB, bHLH, bZIP, MYC, NAC, and MYB, as well as protein kinases MAPK (mitogen-activated protein kinases) and CDPK (calcium-dependent protein kinases) (Lata et al., 2015; Fàbregas et al., 2020). In numerous plant species, TF genes connected to stress have been found (Kumar et al., 2018). To detect and react to drought stress, plants use ABA-independent and ABA-dependent signaling pathways (Kim, 2014). In gene promoter regions, during signal transduction, ABA-independent TFs work as molecular switches that straightly regulate the associated gene expression due to cis-elements interaction (Franco-Zorrilla et al., 2014; Villano, 2020) and this is based on the unique characteristics of the DNA binding sites (Jin et al., 2014; Joshi et al., 2016). In this context, TF genes are consequently involved in particular gene expressions (Franco-Zorrilla et al., 2014; Anbazhagan et al., 2015; Rao and Chaitanya, 2016; Islam et al., 2022).

An incline in the production of ROS (reactive oxygen species) is another stress signaling mechanism. The signaling of ROS is linked with increase in ABA and Ca^{2+} production in plants under water deficit conditions (Kumari, et al., 2021). More accumulation and production of reactive oxygen species in different plant cells and tissues are involved in stress signaling (Kaur and Asthir, 2017), as well as protective molecules like polyols, sugars, and amino acids, i.e., proline (osmolytes), ABA and HSPs (heat shock proteins) take part effectively in drought tolerance (Hasanuzzaman, 2020). Stress signaling causes the plant cell's genes to be expressed in the form of proteins. Synthesized proteins control antioxidant generation, cell membrane protection, transcriptional regulation, starting or ending of physiological processes among other biochemical, physiological, and morphological functions (Nakashima et al., 2014).

Biochemical responses of plants to drought stress

A combination of numerous stress-sensitive systems results in a complicated series of events known as drought resistance (Ahmad et al., 2015). Environmental factors that are dry and semi-dry encourage the production of reactive oxygen species in plants and result in oxidation harm to plant cells. The beginning of various responses induced by stress signals are physiological, biochemical, morphological and molecular (Saeidnejad and Rajaei, 2015; Sharma et al., 2021; Zou et al., 2021). When production of ROS rises under drought stress, ABA is generated, which is an essential part of stress signaling (Sah et al., 2016). By generating catalase (CAT) and superoxide dismutase (SOD), it can control gene expression for biological reactions (Guan et al., 2000).

Numerous physiological and metabolic functions, including antioxidant protection system and photosynthesis in plants, can be harmed by high amounts of ROS generation (Zou et al., 2021). The two main defense mechanisms that give plants the ability to withstand water stress circumstances are the antioxidant system and osmotic control. Enzymatic antioxidants include superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), glutathione reductase (GR), ascorbate peroxidase (APX), and glutathione peroxidase (GPX), while non-enzymatic ones include phenolic substances such ascorbic acid, vitamins, carotenoids, and phenols (Hossain et al., 2013).

In the presence of ROS, SOD serves as the main agent for plant defense mechanism. ROS are detoxified by APX and CAT, which also stop the ROS from building-up in cells and tissues (Cruz De Carvalho, 2008). However, phenolic substances like flavonoids and tannins, which are non-enzymatic antioxidants, are important in the detoxification of ROS and in reducing the consequences of oxidative stress (Kumar et al., 2020). In order for plants to survive in stressful environments, natural antioxidants bind to and neutralize free radicals (Most and Papenbrock, 2015; Fujita and Hasanuzzaman, 2022). The combined action of non-enzymatic and enzymatic antioxidants forms the basis of the antioxidant defense system, which offers a competent method for reducing the toxic elements brought about by reactive oxygen species. In response to drought stress, plants store soluble substances including glycine-betaine, proline, fructose, glucose, inositol, mannitol, isoleucine, valine, etc. in their cytoplasm. Under typical circumstances, these metabolites do not prevent metabolic processes from taking place. However, during stress conditions, the metabolites function as osmoprotectants to control the plant's osmotic adjustment, preserve molecular stability and water flow, and stop the buildup of free ion radicals that are associated with the stress (Padmavathi and Rao, 2013; Rao and Chaitanya, 2016; Ozturk et al., 2021). Proline is a crucial amino acid among osmoprotectants that has excellent antioxidant capabilities, and it aids in cell death prevention (Bhardwaj and Yadav, 2012; Oguz et al., 2022). Many scientists believe that proline accumulation due to a stress serves as the biochemical indicator for choosing resistant cultivars

(Mwadzingeni et al., 2016). Another such osmoprotectant, glycine betaine carries out indirect and direct interactions with large molecules, and it protects against the unfolding and denaturation of proteins (Giri, 2011; He et al., 2020). Likewise, mannitol, one of the potential osmolytes, may increase the activities of plant enzymatic antioxidants. For example, in wheat shoots and roots, exogenous mannitol treatment boosted catalase and ascorbate peroxidase activity (Adrees et al., 2015). Another significant osmolyte abundantly present in plants is sucrose. It aids in increasing anthocyanins, which scavenge ROS and are crucial in lessening their impact (Zhang et al., 2020). Thus, plants contain a multitude of osmolytes that play a significant role in safeguarding the functionalities of key metabolites.

Plants' physiological responses and drought stress resistance mechanisms

Reduction/disruption in a number of key processes such as plant cell growth, leaf water content, turgor pressure, bio-chemical substances buildup, performance of roots, activity of photosynthesis, and metabolic performance, is the distinctive effect of drought stress (Tarafdar et al., 2022). Molecular, biochemical, and physiological systems control how plants react to drying conditions (**Figure 1**). Short-term and long-term reactions make up plant physiological response to drought stress (Tardieu et al., 2018). Water deficit has a negative long-lasting effects on plants in a number of ways, including altered maturation dates (early productive maturity), yield losses, and disruption in physiological cycles in the leaves and roots (Demidchik, 2018). Alterations in stomatal responses, changes in potential of water across tissues, root movements for nutrient and water uptake, biochemical composition and turgor pressure, are among the short-term responses to drought in plants (Batool et al., 2018). For the purpose of environmental adaptation, plants can transfer both negative and positive signals between their roots and branches (Roblero et al., 2020).

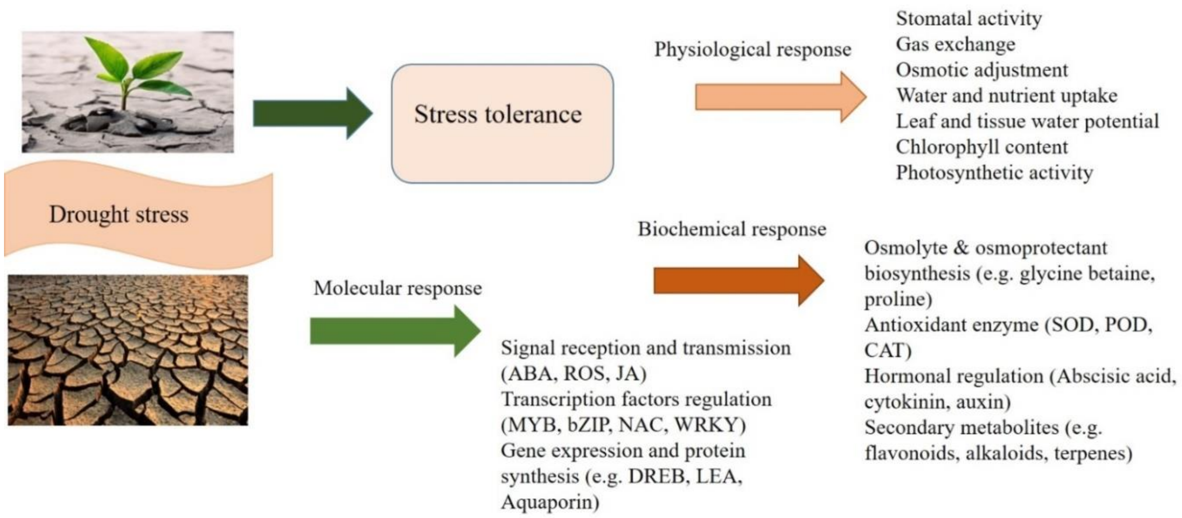

Figure 1. Interplay of physiological, biochemical and molecular responses. ABA, abscisic acid; ROS, reactive oxygen species; JA, jasmonic acid; MYB, myeloblastosis viral oncogene homolog transcription factors; bZIP, Basic leucine zipper; NAC, The NAC (NAM-ATAF1/2-CUC2) family is a group of plant-specific transcription factors that have vital roles in the growth and development of plants; WRKY, WRKY transcription factors; DREB, dehydration-responsive element-binding protein; LEA, Late embryogenesis-abundant; SOD, Superoxide dismutase; POD, Peroxidase ; CAT, Catalase

The signals sent from the roots to the shoots under drying conditions can have an effect on the shoots; as a result, several physiological processes engaged therein may cause the plant's vital activities to decline (Bashir et al., 2021). Numerous substances, including as strigolactone (SL), jasmonic acid (JA), auxins, cytokinins, ethylene, proline, and gibberellins operate as signaling molecules under a variety of drying conditions and are responsible for controlling different biochemical and physiological mechanisms (Schachtman and Goodger, 2008; Mittler and Blumwald, 2015; Rameau et al., 2019; Razi and Muneer, 2021). A plant hormone called strigolactone (SL) (Yamada and Umehara, 2015) impacts physiological procedures such as shoot branching, leaf senescence and root elongation. Additionally, SL functions as a signaling molecule for the tolerance to water deficit conditions (Visentin et al., 2016; Min et al., 2019). The key regulators in the plant response to drought conditions is the enhanced amount of gene expression of SL biosynthesis during water deficit (Wang et al., 2020).

A biochemical process alters cellular ROS, which impacts a variety of physiological and metabolic processes in the plant. In stress adaptation, some ROS also function as signaling molecules (Foyer and Noctor, 2005; Jaspers and Kangasjärvi, 2010). In addition, when the roots sense a lack of water in the soil, they produce stress-related hormones and osmoprotectants, which they then transmit to the shoot via the transpiration stream (Schachtman and Goodger, 2008). In leaf tissues, these chemicals build up and start molecular, biochemical, and physiological activities. According to O'Guz et al. (2022) leaf tissues were physiologically more impacted by drought stress as compared to roots, and they also showed substantially more gene expression.

Reduced stomatal transpiration is the initial physiological reaction by plants due to the effect of water deficit conditions (Hartmann et al., 2013). Stomatal closure and decrease in water loss by plants is a physiological reaction by plants under water deficit conditions (Chaves et al., 2009; Murata and Mori, 2013). The stomatal closure, on the other hand, affects biochemical and physiological procedures, such as a decrease in chlorophyll quantity, leaf water content, gas exchange, chloroplast fragmentation, photosynthesis, and ion exchange between shoot and root, thereby reducing morphological leaf expansion (Bray, 2002; Mumm et al., 2011; Rollins et al., 2013; Potopová et al., 2016; Fahad et al., 2017). All of these physiological processes and events consequently had a direct or indirect impact on photosynthetic activity (Zhang, 2007; Sharma et al., 2019; Muhammad et al., 2021). Movement of water and gas and movement in leaf via stomata is regulated by plants. The usage of CO_2, being crucial for photosynthesis, is prevented when stomata close as a result of dryness (Sevanto, 2014). Low photosynthetic activity is a direct result of the plant's reduced CO_2 uptake (Flexas et al., 2004).

The ability of plants to absorb nutrients from soil through their roots, and transfer them to their upper sections of the plant is further constrained by decreased transpiration brought about by the closure of stomata in water-scarce conditions (**Figure 2**) (Kheradmand et al., 2014; Hammad et al., 2017). The nutritional concentration of plant tissues and ion balance are dramatically reduced as a result of this circumstance (Kheradmand et al., 2014; Ahanger et al., 2016). The interruption of gas, water, mineral and nutrient movement in tissues of plants has a negative impact on several processes (Bhargava and Sawant, 2013; Ying et al., 2013; Rivas et al., 2016). Another crucial physiological characteristic is relative water content (RWC), which influences plant water relations, transpiration rate, stomatal resistance, and leaf water potential (Hartmann et al., 2013). Relative water content is regarded as a sign of the water state of a plant, which controls metabolic activities in tissues. Transpiration and root uptake cause water loss which results in the formation of RWC (Nayyar and Gupta, 2006; Nezhadahmadi et al., 2013; Georgii et al., 2017). Turgor pressure is intimately linked to stomatal closure and the cell development; leaf water potential is crucial for plant life and photosynthesis (Sun et al., 2013; Alghabari et al., 2015). The ability to tolerate mild to severe water stress depends on balancing leaf water potential (Nikinmaa et al., 2013).

The most crucial physiological mechanism directly influencing plant growth and development, and crop productivity in green plants is photosynthesis (Ashraf and Harris, 2013). Cellular organelles called chloroplasts are crucial for photosynthesis. Chloroplasts offer resistance to numerous abiotic challenges, such as drought, with the aid of various metabolites produced during the process of photosynthesis, and in metabolic processes there are important proteins that govern these processes (Sun et al., 2009). Chlorophyll synthesis is negatively impacted by drought-induced chloroplast structural deterioration (Ashraf and Harris, 2013). For photosynthesis, the primary chloroplast constituent is chlorophyll, and the amount of chlorophyll in an organism has a favorable correlation with the rate of photosynthesis. It has been stated that oxidative stress typically manifests itself as a decrease in chlorophyll content under water deficit conditions (Faisal et al., 2019). Chlorophyll breakdown and pigment photo-oxidation cause the reduction in chlorophyll content caused by water deficit (Nezhadahmadi et al., 2013). The authors further stated that environmental stresses may cause concentrations of photosynthetic pigments like chlorophyll to decrease, which could subsequently impede the generation of photosynthetic activities.

Plant's management under drought stress

To improve plant adaptability to various abiotic stresses due to climate changes, several significant agronomic methods have been developed over time (Raza et al., 2019). In order to prevent this, choosing the right tillage strategy, fertilization, and irrigation schedules based on the plants' developmental stages, are crucial (Karavidas et al., 2022). Under water deficit, plants experience yield declines. Other significant management tactics to increase crop productivity include crop rotation, sowing timing, sowing to stubble, sowing frequency, choosing short life cycle plant varieties, using biofertilizers, and selecting genotypes having short life span (Marcinkowski and Piniewski, 2018; Deligios et al., 2019; Abebe et al., 2020; Chojnacka et al., 2020). Plants have developed numerous strategies to tolerate water drying conditions in addition to the techniques and procedures created by farmers and scientists.

The impact of drought on a plant depends on the kind of a stress it is experiencing and at which stage of growth cycle it is (Cooper et al., 2006). Low-level and short-term drought stress, and chronic and extreme drought stress, both have different effects on plants. The way a plant reacts to drought stress depends on its severity and timing. Escape, avoidance, and tolerance are the three mechanisms under which the plant's stress reactions can be categorized (**Figure 2**).

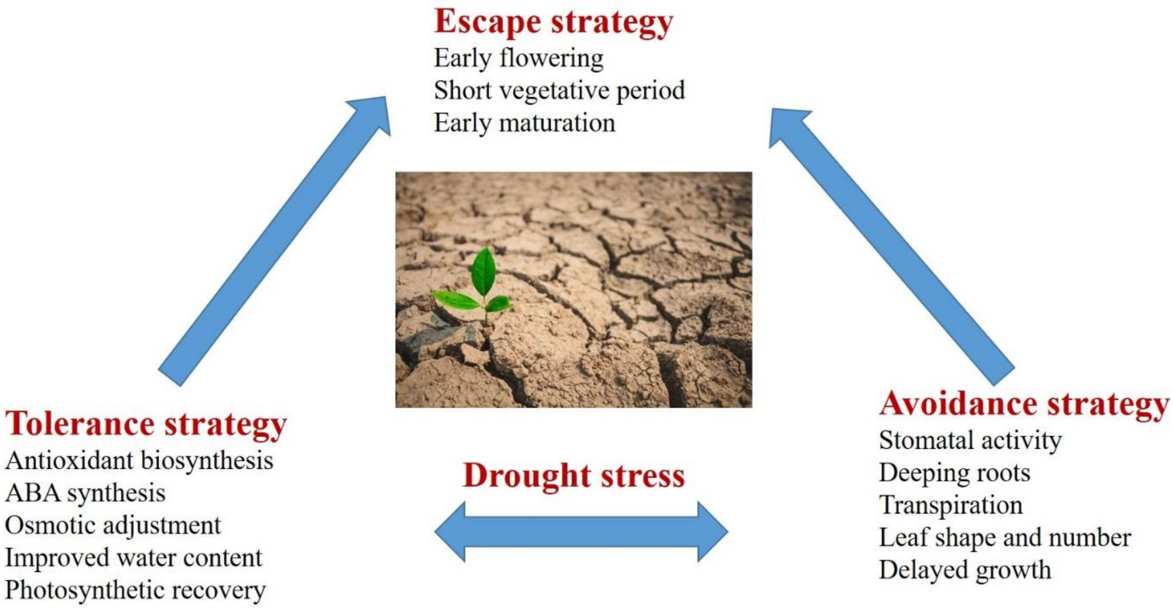

Figure 2. Management of plants by developing and adopting different strategies under drought stress

Plants can shift their roots deeper to access water, close their stomata, roll their leaves, and use more effectively the water they have (Nezhadahmadi et al., 2013). The vegetative cycle is finished quickly to avoid drought. Plants swiftly leave the generative stage. Early flowering and seed germination result from this circumstance (Turyagyenda et al., 2013). Multiple stress tolerance systems that are active within the plant cause these reactions to happen.

Effect of drought stress on various plant growth stages

Water stress affects a variety of processes that further influence different growth and development mechanisms in plants. The culmination of these processes is yield. Depending on different crop varieties, severity and length of water deficit, and other factors, different plants respond differently to drought (Shao et al., 2009; Anjum et al., 2011).

Cell division, cell proliferation, and cell differentiation establish growth. Cell development is severely constrained by low turgor pressure (Jaleel et al., 2009). Drought impairs the mitotic process, which in turn inhibits cell growth and development (Hussain et al., 2008). As a result, one of the physiological processes that is most sensitive to dryness is cell growth. Cell growth is said to react and can be negatively impacted by modest drought stress (Alves and Setter, 2004). Cell death could happen if the drought stress persists and becomes more severe. Due to this circumstance, the metabolism is disturbed, which impedes a variety of key physiological functions (Apel and Hirt, 2004).

From germination to harvest, plants may be subjected to water deficit over a long period of time. In order to direct development of seedlings, germination, shoot and root growth, flower initiation, tillering, fertilization, pollination, quality and seed output (Jaleel et al., 2007), drought stress plays a significant role. Throughout all phases of growth, plants are vulnerable to drying conditions (Pratap et al., 2020). The vegetative development stages constitute the development and growth stages of the plant's, including germination, formation of seedlings, and stage of tillering. The plant generative growth stage consists of fertilization, flowering, time of grain filling and formation of seed. Generative and vegetative plant growth stages might be affected by drought in diverse ways (Shi et al., 2010; Anjum et al., 2011; Veselá et al., 2022). During these crucial developmental stages, researchers focused much on observing the impacts of water deficit on crop quality and output (Nezhadahmadi et al., 2013; Ahmed et al., 2022).

Drought-induced stress during the vegetative stage

The beginning of vegetative growth occurs with seed germination. Inside the seed, a complex set of physiological and biochemical processes trigger the embryo to grow. After absorbing water, seeds soon undergo metabolic modifications. How much water is ingested and absorbed depends on how much water is present in the environment and how much is the absorbing capacity of the seed (Harris et al., 2001). For seeds to absorb enough water at the absorption stage to reactivate the processes of metabolism and promote embryonic axis growth, germination must be successful. A reasonable time period is required to modify seed's osmotic potential while it is under drought stress (Abreha et al., 2022). As a result, the process of absorption is delayed (Queiroz et al., 2019). Poor seedling formation takes place when seed germination cannot achieve necessary level of hydration, so resultantly the germination phase is prolonged (Liu et al., 2015). Early indicators of drought stress include reduced germination rate and less development in seedlings (Harris et al., 2001). Plant establishment per unit area is decreased as a result of the negative effects of water deficit conditions experienced at early plant growth phases (Okçu et al., 2005; Kaya et al., 2006; Queiroz et al., 2019). Numerous studies (Tawfik, 2008; Chaniago, 2017; Ali et al., 2018; Li et al., 2019; Gano et al., 2021) have documented the harmful effects of water deficit on physiological processes at the early stages of development, including root and shoot length, coleoptile length and germination. The success of seedling production and seed germination and emergence in soil are significantly influenced by the length of the coleoptile; this has significant effects on shoot elongation and root growth at later growth stages (Rana et al., 2017; Queiroz et al., 2019; Abreha et al., 2022).

Vigorous seedlings having more developed root systems can be able to absorb water from deep soil and this trait is very common in varieties that display lengthy and broad development of root for resistance to water deficit conditions (Fadoul et al., 2018). The plant develops this trait as one of its defenses against drought stress. In addition, root traits such as the quantity, size, depth, angle, full length, dispersion, and plant biomass during vegetative growth phase are strongly associated with drought resistance (Lopes and Reynolds, 2010; Wang and Han, 2022).

Drought-resistant plant types have excellent water usage efficiency physiologically. Less transpiration rate and less water consumption enable them to produce better energy and photosynthetic activity (Abbate et al., 2004; Monclus et al., 2006). A phytohormone, abscisic acid, is linked in controlling use of water by straightly controlling perspiration and opening of stomata (Mega et al., 2019). As a result of reduced transpiration, greater photosynthetic activity, and improved water usage efficiency, plant development is positively impacted.

When under water stress, plants can limit leaf elongation by maintaining a level between water supplied from plant roots and water level in their tissues (Rucker et al., 1995). Some negative consequences of water deficit at the vegetative phase include a decrease in leaf number, leaf size, and leaf senescence incline (Munné-Bosch et al., 2004; Rizza et al., 2004; Zhang et al., 2006; Shao et al., 2008). Leaf rolling is a significant physiological response to water stress, and it can significantly lower down the rate of transpiration in plants (Wang et al., 2021). By showing such kind of actions, plants try to minimize loss of water. However, reduced gas assimilation and, leaf chlorophyll, and compromised biochemical and physiological balance, for example leaf relative water content, may harm photosynthetic activities (Fu and Huang, 2001; Anjum et al., 2011; Anjum et al., 2016; Sehgal et al., 2018).

The ability of plants to absorb essential minerals and nutrients from the soil is greatly impacted by drought. Drought-related decrease in soil water content has a negative impact on the water content of plant cells and tissues (Manickavelu et al., 2006; Jabran et al., 2017). Water also plays a significant role in the soil's ability to dissolve the nutrients required for plant growth and development. There are issues with the uptake of these nutrients as a result of the decrease in root assimilation (Selvakumar et al., 2012; Nasim et al., 2016; Awais et al., 2017). Reduced production of dry biomass, fresh biomass, shorter initial internodes, delayed tillering, unexpected plant losses and early maturity, are all consequences of water deficit during the vegetative period in plants (Zlatev et al., 2012). According to Semerci et al. (2017), less turgor pressure, which causes the plant to grow stuntedly under water deficit, causes a considerable decrease in overall plant growth, such as shoot length, leaf number and plant biomass.

The effects of drought stress on relative water content, plant biomass, number of siblings, and yield productivity (grain output) are generally observed during the vegetative growth period. Additionally, under drought stress conditions, there were substantial and positive relationships found between yield and physio-biochemical traits such as concentration of proline, activities of CAT and POD, RWC, and total chlorophyll content (Panda et al., 2016). Drying conditions caused a significantly reduced plant height, number of days to blooming, yield per plant and number of seeds in mung bean (Hossain and Fujita, 2010). In the same crop, water deficit conditions caused a significant reduction in MSI (membrane stability index), RWC, leaf proline, plant height, leaf area, and yield production (Bangar et al., 2019).

Although most of the physio-biochemical and morphological attributes differ in terms of regulation at different growth stages, it is pertinent to ensure that up to what level they differ in different crops and how far they can act as potential indicators for appraising drought tolerance in a specific crop.

Drought stress effects on plants during the generative stage

Yield is impacted by water deficit in plants during the developmental and vegetative growth stages.

However, fertilization and grain output are more severely impacted by exposure of plants to water deficit conditions during the plant generative period. Plant generative time is shorter than the vegetative stage. As a result, it provides more time to plants to adapt to drying conditions by enhancing physiological processes (de Souza et al., 2015). Moreover, the pressures experienced by plants in the generative phase may have irreparable effects (Sehgal et al., 2018). Critical times for yield losses include when plants are pollinating, fertilizing, forming and filling grains in generative stage (Sarshad et al., 2021).

After the vegetative period is over, a plant enters its flowering phase, where significant changes take place. Drought has an effect at the start of these stages and then their total duration of these important developmental plant growth stages. When there is a moderate drought, plants often shorten the interval between the onset of blossoming and blooming in an effort to avoid it. However, this time window might be prolonged if there is a severe drought (Prasad et al., 2008).

Arid conditions slow down development, because less photosynthesis occurs, causing reduction in yield, grain filling, and flower production (Flexas et al., 2004). Sterility is frequently brought about by drought during blossoming. The inadequate minerals and nutrients flow to the growing generative plant parts is one of the major reasons of sterility (Yadav et al., 2004; Murtaza et al., 2016). On the other side, anthesis (flower bud blossoming and death) is brought about by drought stress. Due to plants' propensity to flee stressful situations, the reproductive phase is shortened by anthesis (Basu et al., 2019). Drying environment can considerably impact the flowering and pod-filling phase (Ranawake et al., 2012).

According to Vadez et al. (2011), enhancement in water use efficiency and transpiration rate, the two physiological processes, at pre-blooming stage, enhance the tolerance in plants against water deficit conditions. Water storage requirement in plants at the grain filling stage required by the plant is ensured by physiological adaptations like efficient water usage at the vegetative phase, limited movement of stomata, and sustained turgor pressure equilibrium (Lopez et al., 2017). Additionally, higher photosynthetic activities caused by high chlorophyll concentration have a favorable impact on flowering and reproductive times (Rama Reddy et al., 2014). On the other hand, during the flowering season, plants are more vulnerable to drought stress (Zahedi et al., 2011). Stress due to drought delays the stage of flower formation and can have negative effects on seed formation, cluster development and fertilization processes (Ndlovu et al., 2021). As a result, drying environment during anthesis causes a significant and permanent impact on crop productivity (Yang et al., 2019).

Water deficit during the generative phase imposes a considerable effect on grain quality and productivity by lowering the size of seed, quantity, and plant weight (Sehgal et al., 2018; Sarshad et al., 2021). The inactivation of carbohydrate metabolism, energy synthesis, and production of starch and sucrose due to interruptions in photosynthetic mechanism causes a significant suppression in grain filling (Nasim et al., 2016; Mahla et al., 2017). For example, yield related components including grain quantity, grain order, grain yield per plant, 1000 grain weight, harvest index and biological yield, were found to be significantly decreased in maize as a result of drought stress throughout the fertilization and cob formation stages (Anjum et al., 2011). According to Cakir (2004), water stress during the time of cob development results in a 40% yield loss in maize. However, Rizza et al. (2004) reported that anthesis in wheat during drought at the reproductive growth stage resulted in a 72% reduction in grain yield. The brief seed-filling time is important adaptive strategy which plants develop to combat water deficit. By shortening the duration of seed filling period and smaller seeds due to drought stress, lead to reductions in seed yield (Pervez et al., 2009). According to Felisberto et al. (2022), the yield of soybeans is critically dependent on the amount of water available during the grain-filling stage.

Future Research Endeavors for Achieving Enhanced Agricultural Sustainability

Avoiding loss in yield because of abiotic stressors in agronomic perspective is essential to meet the rising global population's demand for food. Understanding plant response mechanisms to a stress is a requirement for enhancing plant stress tolerance. In order to increase tolerance to an abiotic stress, innovative and biotechnological strategies are crucial (Hossain et al., 2021). To develop plant stress tolerance, researchers employ a variety of omic strategies (Billah et al., 2021).

Due to their extensive genetic diversity, native populations are valuable assets and can be employed in selection of plant genotypes resistant to water deficit (Lopes et al., 2015; Karavidas et al., 2022). Particularly, plant characteristics related to agronomy of regional plant populations have been used in developing water deficit-tolerant cultivars, while resilience of these cultivars to drying environment is of dire need. Because regulation of several such growth characteristics, i.e., spike number, plant height, harvest index, grain weight, grain yield, and TKW (thousand kernel weight), can affect the production of field crops (Sabella et al., 2020).

Researchers have recently concentrated on developing innovative, ecologically-friendly methods to stop yield losses in plants. For example, the utilization of agro-industrial wastes, bio-stimulants and biofertilizers, as compost is crucial for agricultural sustainability under abiotic stress conditions and in changing climatic conditions (Ait-El-Mokhtar et al., 2019; Meddich et al., 2019; Boutasknit et al., 2020).

The majority of research projects to improve stress tolerance concentrate on particular plant development stages. Plant responses, however, differ depending on the developmental phases. Various mechanisms in plants under stress conditions during different growth phases need to be studied. Such methods must be validated by field tests and integrated into agronomy. The arguments will also be significantly supported by conducting field trials in various settings and weather situations.

Conclusion

It is apparent that due to changes in climate worldwide, water deficit would continue to be considered as the main factor limiting yield of crops as it is today and will do in the future. Stress due to drought impacts plant growth and productivity. Under drought, plant adaptive responses are surely influenced by the duration, timing, severity, and stress pace. However, under natural circumstances, drought is a challenging problem to manage. Cultivar development having higher ability to tolerate stresses must take into account how plants react to a stress at various phases of growth. The interaction of molecular, biochemical, physiological, and morphological systems results in the stress response of plants. These mechanisms are all too intricate to be looked at separately. New strategies might be developed by concentrating on the variations in these systems' activation and regulation during critical plant development stages. In this review, we attempted to provide an explanation for how the plant body reacts to drought stress throughout crucial vegetative and generative times. Therefore, figuring out how drought affects the crucial stages of growth would direct innovative findings that must be done to avoid loss in crop productivity.

Acknowledgement

All authors contributed equally to the manuscript.

Author(s), Editor(s) and Publisher's declarations

Supplementary material

No supplementary material is included with this manuscript.

Conflict of interest

The authors declare no conflict of interest.

Source of funding

The current work was supported by Key Research and Development Program of Gansu Province (20YF8WA083), National Natural Science Foundation of China (32161143012), and Fundamental Research Funds for the Central Universities (lzujbky- 2022-kb05).

Contribution of authors

Conceptualization and designing of the review: AB, DXY, YLX, LZ. Preparation of initial draft: SSL, HXD, ZUH, KA. Proof reading and approval of the final version: LZ, YCX.

Ethical approval

This study does not involve human/animal subjects, and thus no ethical approval is needed.

Handling of bio-hazardous materials

Since this a review article, so it does not involve any experimentation or use of any types of materials or chemicals

Availability of primary data and materials

As per editorial policy, experimental materials, primary data, or software codes are not submitted to the publisher. These are available with the corresponding author and/or with other author(s) as declared by the corresponding author of this manuscript.

Authors' consent

All authors contributed in designing and writing the entire review article. All contributors have critically read this manuscript and agreed for publishing in IJAaEB.

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Declaration of Generative AI and AI-assisted technologies in the writing process

It is declared that we the authors did not use any AI tools or AI-assisted services in the preparation, analysis, or creation of this manuscript submitted for publication in the International Journal of Applied and Experimental Biology (IJAaEB).

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