Effects of Drought Stress in Plants: An overview

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Abstract

Water scarcity acts as a major limitation to plant productivity. Each year, agriculture suffers considerable losses because of severe droughts, greatly reducing crop yields. Drought stress disrupts plant physiology, leading to declined productivity. This stress causes diverse physiological and molecular alterations in plants, facilitating their adjustment to challenging environmental circumstances. However, it also brings about detrimental effects like oxidative damage and cell death. To address these challenges, it is essential to understand how drought impacts plant development. This review seeks to delve into the causes and consequences of drought-induced stress on plants, aiming to mitigate its adverse effects.

Key words: Drought stress, Photosynthesis, ROS, Proline

Introduction

Drought is indeed a significant abiotic stressor that greatly impacts crop productivity worldwide. Plants respond to water scarcity with various physiological and developmental adaptations. However, unravelling the intricate biochemical and molecular mechanisms involved in drought stress perception, signalling, and tolerance remains a significant challenge in the field of biology (Valliyodan, et al., 2006). One of the first responses is accumulation of proline in the cytoplasm (Chegah, et al., 2013). Harmful effects like salinity, heat and attack of pathogens followed by drought (Ahluwalia, et al., 2021). Plant growth is affected by water deficit stress in many ways based on duration and severity of scarcity and stage of plant development (Nasir, et al., 2022). Plant growth and development is affected by different abiotic and biotic stresses (Nazar, et al., 2015).

A persistent deficit in precipitation (meteorological drought) along with increased evapotranspiration demand leads to drought stress (Farooq, et al., 2012). Effects of drought are quite vivid, impacting morphology, plant growth, yield, membrane integrity, pigment content, osmotic adjustment water relations, and photosynthetic activity. Drought stress is shaped by a combination of climatic, soil-related, and agricultural factors, alongside the severity of the stress, accompanying stressors, plant species, and their growth stages. Plants undergo acclimatization to cope with water deficits, undergoing adaptive changes in growth and physiological processes. These adaptations include changes in plant structure, growth rate, tissue osmotic potential, and the augmentation of antioxidant defence (Anjum, et al., 2011). Certainly, studying plants resilience to drought stress remains significant for ensuring stable grain quality and yield, particularly in arid and semi-arid regions. Research in this area necessitate ongoing attention to develop drought-tolerant crops and sustainable agricultural practices to address the challenges posed by water scarcity (Seleiman, et al., 2021). To improve yield and crop production best solution is to produce water deficit stress tolerant crop varieties (Siddique, et al., 2000).

Growth and yield of plants

In order to meet the demands of a growing population, it's imperative to have a thorough grasp of crop growth and development processes to guide agronomic practices effectively. Maximizing plant performance and ensuring crop sustainability under varying environmental stresses hinges upon our ability to regulate vegetative and reproductive growth patterns. The intricate balance between root and shoot systems, managing sources and sink limitations, determines plant growth. Among environmental factors, water deficit, whether temporary or permanent, poses the most significant hindrance to plant growth and development (Anjum, et al., 2011). Water paucity stress which can takes place at any stage of plant growth and development can have effects like changes in crop structure, function and biochemical processes (Sewore, et al., 2023). Drought stress leads to reduction of growth, low Specific Leaf Area, decreased photosynthesis, closure of stomata, decline in respiration, protein degradation and reduction in biomass production (Akhtar, I., & Nazir, N. 2013).

Various morphological changes can be seen in different plants. During drought stress, soybean roots adapt by growing deeper into moist soil layers while reducing growth in dry surface layers. Leaf area diminishes due to decreased cell division and enlargement. Photosynthesis rates decline as stomatal closure and leaf senescence occur under stress. Shoot characteristics during flowering, like main stem height and leaf area, play a crucial role in soybean yield, with drought stress influencing node number and pods per node (Tarumingkeng, et al., 2003). Water deficit stress significantly altered wheat plant morphology, reducing root length, plant height, and dry weights of both roots and aboveground parts while increasing the root-shoot ratio. Moreover, it impacted wheat caryopses by decreasing starch accumulation but increasing protein accumulation, indicating a shift in endosperm enrichment under stress conditions (Chen, et al., 2021). In soybean drought stress leads to decline in total seed yield and the branch seed production (Frederick et al., 2001). Drought pressure significantly alters wheat growth, particularly in its initial phases. It impedes seed germination by thwarting water absorption, resulting in inadequate plant establishment. Throughout the plant's lifecycle, drought suppresses cell expansion and growth, impacting root development and leaf senescence. This leads to a shortened grain filling period and reduced size, ultimately diminishing the yield of wheat plants (Dhakal, A. 2021). Reduction in water supply during flowering and fruit development stages to pepper leads to decline in final fruit production (Okunlola, et al., 2017).

Maize crop grain yield reduces due to water scarcity if the drought place takes place during important growth stages (Aslam, et al., 2012). In Maize Water paucity stress leads to decline in grain and biomass yield (Traore, et al., 2000). In species of plant like *Populus*. Drought stress mostly reduced growth of leaf and also leaf area (Jaleel, et al., 2009).

During the grain-filling phase water deficit stress didn't decrease the moisture content of grain however reduced the grain-filling phase and abbreviated yield (Samarah, N. H. 2005). Stress due to scarcity of water decreases the biomass production (Kamara, et al., 2003)

Water scarcity stress is the perilous abiotic stress that cause enormous losses around the globe to crop production. (Ahmad, et al., 2022). Barrenness occurs due to drought at flowering it occurs as a result of assimilate flux reduction which is necessary for optimal growth of the grain (Farooq, et al., 2009). Due to suppression of lateral root meristem activation growth of lateral roots is reduced under water deficit stress (Basu, et al., 2016). With increasing drought stress plant biomass and height decreases (Ahanger, et al., 2016). Water stress leads to reduction of leaf area also supress leaf expansion. (Kaur, G., & Asthir, B. 2017). The Root growth is relatively less afflicted than growth of the shoot (Franco, J. A. 2011). The Soybean is most vulnerable to drought during pod filling which leads to loss of yield. This occurs because more flowers and pods are shed during this stage (Tarumingkeng, et al., 2003). Rice yield changes with drought depending on growth stage, with flowering stage being more vulnerable, followed by booting and grain filling. Water scarcity cause more yield loss during flowering, mainly due to less fertile panicles and reduced percentage of filled grain (Moonmoon, et al., 2017).In Lemongrass reduction in leaf area under water stress a higher density of the oil glands that leads to in accumulation higher amount of oil(Singh, et al., 1994).

Photosynthesis

Drought is a major abiotic stress that effects the biological processes which takes place inside an organism. Ascribed to the decline in turgor pressure, closure of stomata, limitation of gas exchange, reduction in CO_2 assimilation, PSI & PSII is, hampered and elevated metabolite fluxes, there is reduction in photosynthesis (Zargar, et al., 2017). Studies in recent times renews the interest whether metabolic or stomatal limitations does affect photosynthesis under low water deficit stress. Decline in ATP synthesis and RuBP regeneration hamper photosynthesis, closure of stomata is seen as major cause of reduction of CO_2 uptake. It is seen stomatal conductance reduces before photosynthesis under drought and stomatal limitations obstruct CO_2 diffusion (Chaves, et al., 2003). Water scarcity also affects the photosystem II efficiency, as Fv/Fm ratio decreases, which is a marker for photoinhibition. (Rahbarian, et al., 2011). In Phaseolus vulgaris under drought there is major reduction in rates of photosynthesis which is due to stomatal and non-stomatal limitations. Stomatal closure reduces CO_2 intake, but even under CO_2 saturating conditions, the photosynthetic apparatus is damaged. Reduction in electron transport and increased heat dissipation indicate a reduced capacity for photosynthetic reactions Ru5PK a Calvin cycle enzyme, critical for RuBP regeneration, is identified as the significant limiting factor for photosynthesis under water scarcity stress (Dias, et al., 2010). In soybean leaves photosynthesis was limited due to stomatal regulation which deduced efficiency to protect the photosynthetic systems from damage caused by light energy (Wang, et al., 2018). In wheat Water deficit adversely effects chloroplast membrane integrity and photosynthesis, resulting in minimized thylakoid stability and chlorophyll degradation. Water scarcity contributes to chlorophyll content reduction, majorly affecting chlorophyll a than chlorophyll b. Decreased photosynthetic efficiency leads to reduction in chlorophyll producing lower crop yields due to impairment in leaf expansion and reduction in Calvin cycle enzyme activity. There is minimization of stomatal conductance under water scarcity stress, leading to reduction in carbon assimilation. there is increase abscisic acid (ABA) levels under drought tolerance (Sharifi, et al., 2016). In higher plants foliar photosynthetic rate reduces with lower relative water content (RWC) and leaf water potential. Water deficit stress mainly affects photosynthesis due to stomatal closure, which decreases CO_2 concentration internally. Alteration in rubisco activity and ribulose-1,5-bisphosphate (RuBP) regeneration, also leads to this decline. Water paucity affects rubisco activity and its production (Reddy, et al., 2004). In high water deficit stress, the impairment of photosystem II and antioxidant enzyme system is a limitation factor for the decline of the photosynthesis rate (Jianhui Li, et al., 2004). In tomato increase in water deficit severity decreases maximum quantum yield of PSII and effective quantum yield. In the beginning, non-photochemical quenching (NPQ) aids in dissipation of excess energy, but this capability also reduces under severe water scarcity, resulting in PSII damage. SOD, POD, CAT antioxidant enzyme activities escalate with low drought stress and reduces with high water scarcity stress, resulting in increased malondialdehyde (MDA) levels. Eventually, photosynthetic rates decrease as there is severe water scarcity (Liang, et al., 2020). The dehydration of plant tissue under drought causes elevated oxidative stress which eventually impairs structure of chloroplast, ascribing to loss in chlorophyll (Mohammadkhani, et al., 2007).

Oxidative damage

Incomplete reduction of atmospheric oxygens forms Reactive oxygen species (ROS), ROS is alternatively called active oxygen species (AOS) or as reactive oxygen intermediate (ROI) (Ilyas et al., 2021). Under water scarcity stress production of reactive oxygen species (ROS) inexorable, the ROS are deleterious which leads to damage to cell and cell death (Verma et al., 2019). To perform cellular functions, such as signaling and defense responses at basal levels ROS are necessary for plants (Schneider et al., 2019). At normal conditions when there is no water stress ROS is produced in minute quantities. ROS acts as an alarm signal that triggers defence response and help the plant adjust to water deficit (Nadarajah 2020). Although, under stress ROS levels are escalated (Kaur, G., & Asthir, B.2017). An imbalance between generation and removal of ROS cause oxidative damage under abiotic stress situations affecting normal cellular functions (Hasanuzzaman et al., 2020). During stress conditions like drought Reactive oxygen species (ROS) are produced primarily in chloroplasts, peroxisomes, mitochondria and ROS, includes superoxide radicals and hydrogen peroxide, which can cause damage to proteins, lipids, and DNA, leading to oxidative stress. Plants manages ROS through antioxidant enzymes like superoxide dismutase and catalase. Elevated ROS production during stress increases lipid peroxidation and cellular damage (Farooq et al., 2009). These processes may give rise to reactive molecules such

as ketones, aldehydes, and hydroxyl acids, while others can lead to changes in proteins by amino acid residues oxidation. Glutathionylation, carbonylation, nitrosylation, and disulfide bond formation are the protein changes that may cause protein function (Bijalwan, et al., 2022). Water deficit is a major abiotic stress which leads to the formation of various reactive oxygen species (ROS), including free radicals like superoxide, hydroxyl radicals, hydrogen peroxide, and alkoxy radicals, as well as non-radical forms such as singlet oxygen and. Hydroxyl radicals are the most reactive among these (Impa et al., 2012).

The Protein content declines in plant varieties probably because of increase in reactive oxygen species (ROS), due to which protein synthesis can be inhibited (Fazeli et al., 2007). Reactive oxygen species (ROS) in living systems can arise from both non-enzymatic and enzymatic reactions. The balance between these pathways, especially during oxygen stress, can be influenced by the available oxygen concentration. In Electron transport chains of chloroplasts reactive oxygen species are formed as by-products (Apel and Hirt, 2004). Drought stress leads to decrease in chlorophyll amount which gives rise to production of reactive oxygen species (ROS) like O_2^- and H_2O_2 that brings about lipid peroxidation chlorophyll degradation occurs in plants eventually (Nxele et al., 2017). Oxidative damage to the biomolecules such as carbohydrates, proteins, lipids and nucleic acids that results in reduction of the photosynthesis, respiration and growth of plants is caused by ROS which is produced under water scarcity stress (Seleiman et al., 2021). The Plants are affected by water deficit stress that leads to damage to plasma membrane majorly by ROS excess production. physiological markers like proline, CAT, POD, ABA, SOD etc. are released to cope with cellular ROS (Sun, Yuan, et al., 2021). As a response to drought stress stomata closes to reduce water loss because of transpiration.There is decrease in carbon dioxide (CO2) concentration which leads to stimulation of ribulose–1,5–bisphosphate oxygenation and therefore in peroxisomes photorespiratory hydrogen peroxide (H2O2) are formed(Laxa, et al., 2019).

Proline accumulation

When plants are susceptible hyperosmotic stresses, predominantly drought and soil salinity, proline plays a primary role as an osmoregulatory solute. Proline (Pro) is generated from either glutamate (Glu) or ornithine (Orn) (Delauney, et al., 1993). Proline functions as an Osmo protectant exposed to water deficit conditions (Yamada, et al., 2005). In Maize variety proline accumulation was seen in both warm, humid environment and a semi-desert under drought. Proline buildup might be a symptom of water deficit. Furthermore, chloroplasts are essential role for proline biosynthesis, a systemic water sensor provoke proline production under water scarcity (Ibarra-caballero, et al., 1988). The levels of Pro elevated particularly in leaves and roots pertaining to intensity of water scarcity (Sofo, et al., 2004). Drought-tolerant crop peanut withstand water stress attributing to its ability to maintain relative water content (RWC). Water deficit tolerant varieties exhibit higher RWC, protein content, and proline accumulation than susceptible ones, helping them in osmotic regulation and drought resilience. In stabilizing cellular structures under stress proline plays a key role, and its more accumulation in tolerant varieties is associated to improved drought adaptation. Proline accumulation can be an indicator of drought tolerance in peanut varieties (Solanki, et al., 2014). In water stressed Sorghum Accumulation of free proline in the leaves is associated to recovery resistance because Pro facilitate recovery by equipping respiratory energy (Blum & Ebercon 1976). During initial drought phase and pre-anthesis in wheat Pro assimilation acts as indicator (van Heerden, et al., 1996). In the Sorghum, accumulation in drought-stressed plants, but its adaptive significance is yet to be studied, but play a role in plant adjustment to drought. Proline accumulation most of it took place in the green parts of leaves, and levels returned to normal after normal condition (Sivaramakrishnan, et al., 1988). Water stress can be overcome by accumulation of proline through osmoregulation (Al-Khayri, et al., 2004). With decrease in water content there is elevated amount of free proline in cotton cultivars (De Ronde, et al., 2000). Under water deficit conditions genotypic variation occurs in free proline accumulation between tolerant and sensitive soybean genotypes (Mwenye, et al., 2016). Proline acts as osmoprotectant stabilizing cellular structures and helping in tolerance of the water scarcity (Mohammadkhani & Heidari 2008). Proline plays a role as an osmolyte also has complex role in drought tolerance by stabilizing proteins, scavenging free radicals, and aiding protection against photoinhibition (Gomes, et al., 2010). Proline aids dehydrated plant cells to tolerate dehydration by preserving turgor,buffering opposed to ROS and redox homeostasis maintenance (Zegaoui, et al., 2017). In Wheat Proline has pivotal role in RWC maintenance (Maghsoudi, et al., 2018). Proline accumulation has been proposed as a selection parameter for tolerance of stress (Saha, et al., 2019). Higher amount of proline accumulated indicates the plant to be more resilient to stress (Giancarla, et al., 2011). In all varieties of Sunflower under drought proline content increased in root in all phases and Pro accumulation supplies energy for growth under stress (Manivannan, et al., 2007). In many plants accumulation proline is widespread physiological response in response to water scarcity (Mafakheri, et al., 2010).

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