

Drought Mediated Morphological and Physiological Alterations in legumes

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Abstract:

Drought stress significantly impedes plant growth and agricultural productivity, especially with the increasing global population and climate change. Legumes, which account for a significant portion of global agricultural output and protein supply, are particularly vulnerable to drought, affecting their growth, development and yield. Despite the well-documented adverse effects of drought on various crops, there is a lack of comprehensive research on the responses and adaptive mechanisms of legume crops to drought stress. This review explores the multifaceted impacts of drought stress on legumes, from seed germination, morphology, physiological processes to yield outcomes and also the adaptive mechanisms that enable them to tolerate such stress. Understanding these mechanisms is vital for developing strategies to enhance legume productivity under drought conditions.

Keywords: drought stress, drought tolerance, legumes, tolerance mechanism.

1. Introduction:

The rapid growth of the world population has aggravated the challenge of food production in the twenty-first century (Priyanka et al., 2019). Chemical fertilizers are widely employed to increase crop yields, but they pose major environmental and health risks, climate change further exacerbates the situation by introducing environmental pressures such as drought and salinity, which impede plant development and reduce agricultural productivity (Kaushal and Wani, 2016). Climate change has resulted in more frequent

extreme weather events, such as inconsistent precipitation, which add to drought stress and reduce crop yields (Ye et al., 2018). Drought stress is projected to impact about one-third of soils, posing challenges for maintaining typical plant growth (Asma et al., 2021). Drought is a prolonged period of low rainfall, which is a major issue for plant development and agricultural output in many areas (Priyanka et al., 2019). It is viewed as a severe and unpredictable jeopardy to world crop output, with serious consequences (Anjum, 2017; Hussain et al., 2018). Drought impairs several plant activities, including leaf gas exchange, carbon absorption, oxidative damage and turgor maintenance, contributing to less production (Chowdhury et al., 2016). Plant vulnerability to drought is complex and impacted by factors such as genetic potential, growth stage and the duration and severity of the stress (Zhu, 2002).

Legumes are the second most important food crop after cereals, accounting for 27% of worldwide agricultural output and 33% of protein requirements. They may be grown in a variety of climates and soil types, accounting for more than 35% of global vegetable oil production, mostly from groundnuts and soybeans (Pradhan et al. 2019). Legumes are an inexpensive and healthy protein source that play an important role in agriculture because of their knack to fix atmospheric nitrogen (Rubiales&Mikic, 2015). Legumes lower the demand of synthetic fertilizers and increases crop output (Khatun et al., 2021). Legumes are commonly employed in crop rotation systems to reduce weed populations and insect pests, hence improving farm production and income for smallholder farmers. Cultivating legumes in rotation with grains helps to avoid soil erosion, improve nutrient profiles and reduce soil pollution (Daryanto et al., 2015). Given these advantages, legumes are viewed as a prospective cornerstone of the climate smart agriculture concept (Araujo et al., 2015). However, legume crops are subject to a variety of abiotic challenges, with drought being the most significant constraint on crop productivity (Farooq et al., 2016). Insufficient water supply at any growth stage can lower crop yield, especially during filling of grains and reproductive stages (Pushpavalli et al., 2015). Dry spell frequency and intensity reduce grain output and plant biomass, (Baroowa&Gogoi, 2013; Ghassemi-golezani et al., 2013).

Although the adverse consequences of dry spell on other crops have been widely documented, but there is a paucity of current, systematic research on drought stress responses and adaptive mechanisms in legume crops. Plants have evolved complex morphological, biochemical and physiological systems to deal with drought stress (Baroowa&Gogoi, 2013). Plant tolerance to drought varies significantly based on the duration and severity of the stress, as well as the species and developmental stage of the plant (Ghassemi-golezani et al., 2013). This review focuses on the detrimental effects of drought on legume crops and adaptive mechanisms of drought tolerance, which may provide improved strategies for managing drought stress.

2. Drought Stress and Legumes:

Drought stress interferes with all stages of legume plant development, from germination to yield, as outlined below.

2.1. Efficacy of Dry Spell on Germination: The establishment of a plant relies heavily on the crucial stages of seed germination and early seedling development. Seed shape and physiology have a substantial impact on germination, as do environmental conditions like as soil moisture (Gao et al., 2023). Alfalfa, an important legume crop is extremely vulnerable to dry spell ((Atumo et al., 2021; Diatta et al., 2021), particularly during germination and early seedling phases (Li et al., 2013). Slight drought stress can improve alfalfa seed sprouting, but intermediate to severe drought stress greatly reduces it (Gao et al., 2023). Drought during germination can have a significant influence on the quality of emergent plants, as well as the expected output (Muscolo et al., 2014). Increased drought severity caused by increased PEG concentrations significantly reduced the germination percentage in clover plants (Kintl et al., 2021).

2.2 Effect of Drought on Morphology:

Water scarcity has an impact on growth processes such cell division, differentiation and expansion (Khatun et al., 2021). Cell growth is one among the most drought-sensitive biological processes because it lowers the turgor pressure (Taiz&Zeiger, 2006). Acute water scarcity disrupts water passage from the xylem to the neighboring expanding cells, thereby halting plant cell elongation (Farooq et al., 2008). Drought inhibits mitosis and cell expansion resulting in decreased plant height, leaf area and crop development (Khatun et al., 2021). Soil moisture deficiency can also limit root development and nutrient absorption (Garg, 2003). Dryness inhibits the growth of roots and shoots, which slows the growth and development of plants (Fathi&Tari, 2016). It dehydrates mesophyll cells in plants, limiting cell proliferation and leaf growth when water deprivation occurs (Fathi&Tari, 2016). Plants may lose leaves in response to increased production and response to stress hormones under water stress (Kabiri et al., 2012). Drought induces structural changes in *Rhizobia*, lowering the infection and nodulation in legumes (Busse and Bottomley, 1989). Reduced soil moisture decreases the number of infection threads in faba beans as well as the size of nodules in soyabeans (Lu et al., 2021).

2.3. Effect of Drought Stress on Physiology:

Chlorophyll content drops under drought stress but the extent and duration of the reduction depend on the conditions (Fathi&Tari, 2016). A prolonged drought lowers overall amount of chlorophyll in both the vegetative and blooming stages. However, certain

cultivars of *Vignamungo* showed an increase in chlorophyll content under moisture stress, while others showed negative trends (Ashraf & Karim, 1991). Significant reductions in chlorophyll a and b content in both the vegetative and blooming stages occur when drought stress strikes during the vegetative stage.

Furthermore, dry spell during the flowering stage affects these chlorophyll levels negatively (Mafakheri et al., 2010). Drought impairs the key components of the photosynthetic system, including carbon reduction cycle, stomatal CO₂ control and electron transport (Awasthi et al., 2014). The decrease in total chlorophyll quantity during drought indicates a reduced potential for light gathering, hence lowering photosynthesis (Fathi & Tari, 2016). Reductions in turgor under drought lead to fractional stomatal closure, which alters leaf photosynthesis (Farooq et al., 2009). This condition increases photorespiration and suppresses carboxylation and ribulose-1,6-bisphosphate reformation (Lu et al., 2021). Reduced water content activates RUBISCO binding inhibitors and non-cyclic electron transport is blocked resulting in decreased ATP synthesis (Farooq et al., 2009). Some studies proposed that low ATP levels are the fundamental reason of impaired photosynthesis during drought conditions (Tang et al., 2002).

Reduced leaf area decreases the soil water uptake and transpiration rates (Fathi and Tari, 2016). The closure of stomatal is an early plant response to water deficiency. When exposed to drought stress, chickpea showed lower transpiration and stomatal conductance (Mafakheri et al., 2010). Plant-water relations are regulated by parameters such as stomatal resistance, relative water content, leaf temperature, leaf water potential, transpiration rate and canopy temperature (Khatun et al., 2021). Plant-water relations are altered by water scarcity in many ways, but stomatal opening and closure are most impacted. Variations in leaf temperature under drought stress may also influence leaf water status adjustment (Farooq et al., 2009). It is believed that cells with more water potentials tend to be stressed under dry spell. Under partial drought, the common bean seemed most stressed due to its greater water potential, whereas cowpea and lablab's cell water potential remained consistent (Sohrawardy & Hossain, 2014). Water stress reduces leaf water potential in soybean at different phases of pod formation (Makbul et al., 2011). As per Omae et al. (2007), water stress caused a decrease in the relative water content (RWC) of common beans.

A primary effect of water shortage is decreased nutrient uptake by roots and their subsequent transfer to shoots (Farooq et al., 2009). Along with water, roots take up necessary elements including Mg, N, Ca and Si however, dry conditions prevent these elements from being transported by mass flow and diffusion, which slows down plant growth (Barber, 1995). According to Garg (2003), drought generally results in a spike in nitrogen uptake and a substantial drop in phosphorus uptake. Furthermore, drought stress reduces sucrose synthase, nitrate reductase and the symbiotic relationship between

legumes and *Rhizobium*, resulting in decreased the nutrient-use efficiency of legumes (Ullah&Farooq, 2021).

2.4. Impact of Drought Stress on Crop Yield:

Numerous physiological systems that control plant productivity are impacted by drought (Farooq et al., 2009). According to Fathi and Tari (2016), a prolonged dry spell lowers harvest index and photosynthetic active radiation, which in turn lowers agricultural output. According to Mafakheri et al. (2010), plants that experienced stress during growth but not afterwards produced significantly more than those that did so at anthesis. Post-anthesis drought stress decreased legume yields regardless of the severity of the drought (Samarah, 2005). Legume yields were reduced during several phenological stages of crop growth by drought stress. Drought stress accounts for 40% of annual yield losses in chickpeas worldwide (Jukanti et al., 2015). The drought affected both total and branch seed production of soybeans (Frederick et al., 2001). Legumes with relatively significant N₂ fixation, such as cowpea, green gram, and black gram, yield more during droughts as compared to those with limited fixation, such as groundnut and faba bean (Daryanto et al., 2015).

3. Mechanisms of drought resistance in legumes:

Understanding tolerance mechanisms is critical for increasing legume output under dry spell (Nadeem et al., 2019). Plants have evolved many adaptations to resist drought stress, as discussed below:

3.1. Drought Avoidance:

A fundamental adaptation approach is rapid plant growth and development in order to complete the life cycle before drought strikes (Nadeem et al., 2019). Legume crops can endure drought by decreasing their life cycle while maintaining higher tissue water potential through increased water intake and decreased water loss (Siddique et al., 1993). This occurs when the period of phenological growth coincides with soil moisture (Farooq et al., 2014). Flowering period coincides with the end of the rainy period, demonstrating an adaptive approach. Early blooming and seed development prior to an impending drought is a significant characteristic of legumes (Shavrukov et al., 2017).

3.2. Phenotypic Plasticity:

Plants reduce the quantity and size of their leaves as a morphological adaptation to drought in order to conserve water and avoid yield loss (Varshney et al., 2018). *Phaseolus vulgaris* responds to drought stress by increasing root density and growth rate as the root system is the sole way for plants to take water from the soil (Kavar et al., 2008). The number

of metaxylems in soybeans has been associated with drought resilience, and a higher metaxylem count facilitates water flow in the roots (Prince et al., 2017). By changing the number of fibrous roots, lateral root diameter and root biomass, drought stress modifies the adaptability of the root system (Salazar et al., 2015).

3.3. Compatible Solute Accumulation:

Accumulating solutes is an important approach for osmoprotection and osmotic adjustment during dry spell. These solutes aid in the maintenance of leaf turgidity in cells during dry conditions (Tomer and Singh 2020). They accumulate in drought-stressed cells without interacting with macromolecules such as proline, amino acids and polyamines (Majumdar et al., 2016). The Osmo-protection strategy is based on the connection of non-toxic substances with cell components, whereas osmotic regulation promotes turgor by retaining cell water content (Slama et al., 2016). Compatible solutes, such as polysaccharides and amino acids, are essential for osmoregulation and may help protect enzymes and membrane structures while also eliminating active oxygen free radicals (Fathi&Tari, 2016). Proline, in particular, functions as a signaling molecule, activating genes required for stress recovery to regulate mitochondrial activity and cell proliferation (Solanki&Sarangi, 2015). Proline buildup sustains cellular redox potential, reduces lipid oxidation and eliminates free radicals to support membrane integrity (Shinde et al., 2016). Non-reducing sugars, such as di and polysaccharides, keep the membrane intact (Ramanjulu& Bartels, 2002). Mannitol stabilizes macromolecule structures such as ferredoxin, glutathione and phosphoribulo-kinase and hunts hydroxyl radicals (Bhauso et al., 2014). Similarly, trehalose stabilizes membrane lipids, proteins and biological structures which enhances photosynthetic performance during droughts (Khater et al., 2018).

3.4. ABA Coordinated Stomatal Closure:

Stress signal that triggers stomatal closure is abscisic acid (ABA) (Schachtman and Goodger, 2008). The roots produce ABA as a result of transmitting a signal cascade to the shoots through the xylem when soil dries. After that, ABA is transferred to the shoot through the xylem streams. There, it inhibits stomatal opening and leaf growth, hence affecting the nutritional status and water content of the leaf (Tomer& Singh, 2020).

3.5. Antioxidant Defense:

Antioxidant defense systems enable plants to reduce oxygen damage and sustain healthy functioning of cells. When plants are stressed by drought, they produce reactive oxygen species, which acts as a signal to activate defense mechanisms (Choudhury et al., 2017). Reactive oxygen species, which harm macromolecules and cell structure are produced

under low water stress. These species include hydroxyl radicals, hydrogen peroxide, singlet oxygen and superoxide radicals (Farneset al., 2016). While reactive oxygen species act as signaling chemicals at low concentrations, but excessive buildup overtakes the plant's defensive capability, resulting in oxidative stress that damages proteins, lipids and nucleic acids, eventually leading to cell death (Kurutas, 2016). Plants fight oxidative stress via antioxidant defenses, the most substantial of which are enzymatic (Farooq et al., 2008). Enzymatic antioxidants include superoxide dismutase, catalase, glutathione peroxidase, ascorbate peroxidase, dehydroascorbate reductase, glutathione reductase, and monodehydroascorbate reductase, while non-enzymatic antioxidants include ascorbate, glutathione, carotenoids, tocopherols, ascorbic acid, and phenolics (Chakrabarty et al., 2016). Enzymes like superoxide dismutase, catalase, and peroxidase scavenges reactive oxygen species by regulating non-enzymatic defense mechanisms (Desoky et al., 2011). Drought stress significantly enhances the non-enzymatic and enzymatic antioxidant activity in *Vicia faba* compared to normal conditions (Desoky et al., 2021). During oxidative stress, antioxidant often increase more during the restoration phase than during the stress phase, as observed in soybeans (Guler & Pehlivan, 2016), chickpeas (Patel et al., 2011) and green beans (Yasar et al., 2013). Drought induced, increased activities of ascorbate peroxidase, superoxide dismutase, glutathione reductase and peroxidase have been recorded in resistant cultivars of *Macrotyloma uniflorum* (Bhardwaj & Yadav, 2012). In a nutshell enhanced antioxidant activities in legumes improves the drought tolerance by protecting against oxidative stress.

3.6. Molecular Mechanisms:

Drought stress can lead to changes in plant gene expression. Several genes are activated at the transcriptional level, and their products are essential for drought resistance (Kavar et al., 2008). Stress or injury can directly activate gene expression (Abobatta, 2019). Plants make specialized proteins in order to endure stressful environments, such as drought. The majority of shock-related proteins are water-soluble, and keep cellular structures hydrated which is critical for stress tolerance (Wahid et al., 2007). Transcriptome analysis has found several drought-induced genes, which are separated into two groups: operational and regulatory genes (Chinnusamy et al., 2004). The first set of genes encodes antifreeze proteins, LEA proteins, chaperones, detoxifying enzymes, osmoprotectants, enzymes for osmolyte production, free radical scavengers and water-channel proteins. These compounds directly protect cells against stress (Bray, 2002). The second set of genes controls the expression of other genes in response to dry spell which includes protein phosphatases, transcription factors, and kinases (Xiong, 2002). Moreover, such genes produce signaling molecules such calmodulin-binding protein and enzymes that regulate phospholipid metabolism (Ali et al., 2017). Several stress-inducible transcription factor

genes have been found, and they control networks of stress-responsive genes (Abe et al., 2003). Stress-inducible genes that encode enzymes for the biosynthesis of compatible solutes have been shown to improve abiotic stress tolerance in transgenic plants (Bartels, 2005).

4. Conclusion and future perspective

Today's world is facing more and more serious issues due to population expansion, water scarcity, food shortages and climate change. Drought stress is one of these problems that needs to be addressed immediately since it poses a serious risk to agricultural crops and worldwide agricultural productivity. Dry spells are likely to become more frequent and intense in the near future, making these problems worse. Legumes, which are critical for food security and sustainable agriculture, are highly susceptible to drought, particularly during the vegetative and reproductive stages. Reduced germination, stunted development, disrupted photosynthetic machinery, decreased net photosynthesis and decreased nutrient intake are all consequences of drought stress in legumes. Understanding the physiological, agronomic, and genetic components that contribute to drought tolerance is crucial to reducing the negative impacts of drought on legumes. This review focuses on how drought affects the physiological characteristics of legumes, such as production and growth metrics, as well as germination, photosynthesis and nutrient and water intake. Additionally, it delves into the vital adaptive strategies legumes use to deal with drought stress, including phenotypic plasticity, ABA-regulated stomatal closure, osmoprotection and antioxidant defense. These mechanisms show legume's resilience and complexity in responding to adverse environmental conditions. Comprehending these adaptation strategies is essential for formulating sustainable management approaches to augment legume yield under drought circumstances.

Future research should concentrate on identifying and using genetic markers linked with drought resistance in legumes. Advanced breeding techniques, like as marker-assisted selection and genome editing, can be used to create drought-tolerant legume types. Furthermore, investigating the possibility of transgenic techniques to introduce stress-responsive genes from other species could improve bean drought resistance.

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