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REVIEW

Drought Stress in Pulse Crops: Consequences and Mitigation Options

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Pulses are essential for global food security and nutrition, serving as crucial sources of protein, vitamins, and essential micronutrients for humans. They are well-known for their high protein levels, their ability to enhance soil fertility through nitrogen fixation, and their role in sustainable farming practices. Nonetheless, climate change has exacerbated the frequency and intensity of droughts around the globe, posing significant problems for pulse cultivation. The extent of yield loss in pulse crops can differ between species and even among varieties within a species, depending on the intensity of drought stress and factors such as growth stages, soil types, and agro-climatic conditions. Understanding how drought stress impacts pulses and investigating effective mitigation strategies to ensure food security amid changing climate conditions is vital. This review article compiles reliable information from first-hand sources to highlight the detrimental effects of drought stress on the growth, yield, and physiological activities of pulses. It also recommends mitigation strategies, including agronomic practices, the use of phytohormones, and plant breeding techniques, to reduce yield losses caused by drought. Additionally, it is advised to enhance farmers' awareness of drought stress management and for the government to provide support to growers to help them effectively tackle this challenging issue.

Key words: drought stress, pulse, phytohormones, breeding, yield loss

It is projected that by 2050, the global population will exceed 9.7 billion, with over 65% of people relying on agriculture for their livelihoods. In developing countries, this figure could rise to 90% (Castañeda *et al.*, 2016). Consequently, agriculture will play a significant role not only in national economies but also in food supply. However, agricultural practices face numerous challenges, including limited access to adequate irrigation systems, small and fragmented landholdings, lack of high-quality seeds, insufficient machinery, and excessive use of chemical fertilizers and pesticides. These issues can lead to poor soil health, erosion, and increased vulnerability to natural disasters (Dev, 2012).

Water scarcity is a critical challenge to global food security, with drought being the most significant threat. Historically, droughts have triggered major famines. As the global demand for food increases due to population growth, limited water resources are expected to worsen the impact of drought (Somerville and Briscoe, 2001). The unpredictability of drought severity relies on factors such as rainfall distribution, evaporation rates, and soil moisture capacity (Wery *et al.*, 1994).

Legumes are an essential, low-cost source of protein and play a crucial role in agriculture due to their ability to fix atmospheric nitrogen. However, these crops are highly susceptible to various abiotic stresses, especially drought, which is a primary factor limiting yields. Legumes are typically cultivated in rainfed areas, and models predict an increase in the frequency and intensity of drought conditions, highlighting the risk of water shortages. Water scarcity during any growth stage can hinder plant development, notably affecting grain filling and reproductive phases. Drought impacts grain yield, plant biomass, and other aspects of legume production, with the extent of yield reduction depending on drought intensity, duration, crop developmental stage, and genetic factors (Nadeem *et al.*, 2019).

To survive drought, plants implement various coping strategies, such as producing reactive oxygen species, stress hormones like ethylene and abscisic acid, and adapting their root and shoot structures. These responses can be short-term or long-term. Short-term adaptations happen during short stress periods and include reduced carbon assimilation, stomatal closure, and growth inhibition. If normal conditions return quickly, these responses usually don't cause significant damage. However, prolonged stress can lead to more severe, lasting injury, such as stunted growth, metabolic changes, reduced transpiration area, yield loss, and plant aging (Ahluwali *et al.*, 2021).

Implementing strategies like developing drought-tolerant traits, innovative breeding techniques, and efficient water usage methods such as drip irrigation and mulching may help alleviate the severe impacts of drought. While previous reviews have addressed drought effects on various crops, there is a lack of updated, comprehensive studies on the impact of drought stress on pulses. Thus, advancing new methods to enhance drought tolerance in pulses is vital for reducing yield losses in drought conditions. Our research on drought stress effects on pulses and potential mitigation strategies aims to manage the adverse impacts of drought stress to decrease production losses in these crops.

Physiological Effects of Drought Stress

Drought stress is the results of decreased water availability, leading to various physiological changes in plants. In pulses, this condition triggers stomatal closure to reduce water loss, which subsequently limits photosynthesis and causes stunted growth and reduced biomass. A lack of sufficient transpiration can disrupt nutrient uptake, further impeding plant growth.

Photosynthesis

Under moisture stress, the rate of photosynthesis declines due to reductions in leaf area and the leaf area index, which are caused by inhibited cell division and elongation. Ethylene production during stress conditions also contributes to decreased leaf area by promoting leaf abscission. Stomatal closure, driven by abscisic acid (ABA) signaling and reduced stomatal conductance, limits carbon dioxide diffusion into mesophyll chloroplasts. This reduction results in the production of reactive oxygen species that can damage thylakoid membranes and inhibit photosynthetic activity and productivity. Moreover, drought stress downregulates noncyclic photophosphorylation, obstructing ATP synthesis necessary for photosynthesis. Low tissue water potential can lead to the formation of inhibitors that occupy the carboxylation site of RUBISCO, impairing its activity (Subbramamma *et al.*, 2017).

Drought affects the photosynthetic machinery by influencing its key components, including the regulation of stomatal CO_2 supply, electron transport, and the carbon reduction cycle. During drought conditions, partial stomatal closure or turgor loss in mesophyll cells can lead to variations in leaf photosynthesis. Consequently, carboxylation processes and ribulose-1,6-bisphosphate (RuBP) regeneration are suppressed, resulting in increased photorespiration. Inhibitors of Rubisco binding become more active when tissue water content declines. Additionally, non-cyclic electron transport is inhibited to align with lower NADPH production, which results in decreased ATP synthesis. While increased watering can enhance photosynthesis in common beans, it may inhibit photosynthesis in lablab and cowpea (Khatun *et al.*, 2021).

Assimilate Flux into Developing Pods

Drought stress often leads to increased allocation of dry matter to the roots, which can strengthen the root system and enhance water uptake prior to flowering and pod formation in grain legumes. However, drought can lower current photosynthetic rates and disrupt carbohydrate metabolism, leading to reduced sucrose levels in leaves and decreased export rates. This phenomenon is likely linked to increased activity of acid invertase triggered by drought stress (Kim *et al.*, 2000). Limited photosynthesis and sucrose accumulation can impair the rate at which sucrose is transported to sink organs, ultimately affecting reproductive development. The resultant carbohydrate shortage due to drought, along with elevated internal abscisic acid concentrations, can hinder the utilization of incoming sucrose by reproductive sinks, which may contribute to flower and seed abortion in pulses. Reduced acid invertase activity might stall the development of reproductive tissues due to insufficient phloem unloading and a low supply of hexose sugars to developing ovules, inhibiting cell division in embryo and endosperm tissues. This diminished sink activity can ultimately result in pod abortion (Subbramamma *et al.*, 2017).

Plant–Water Relations

Various factors influence plant water relations, such as relative water content, stomatal resistance, leaf water potential, transpiration rate, leaf temperature, and canopy temperature. Lower water availability significantly affects plant water relations, particularly the opening and closing of stomata. Additionally, the management of leaf water status during drought may be affected by changes in leaf temperature (Farooq *et al.*, 2009). Water stress tends to be higher in cells with elevated water potential. Interestingly, the common bean exhibited the most stress under partial water availability, while the water potential in cowpea and lablab remained stable (Sohrawardy and Hossain, 2014).

Transpiration and Stomatal Conductance

Reduced leaf area leads to diminished water uptake from the soil and lower transpiration rates. In common beans, transpiration increased with rising water content, except in dry conditions. Under partially dry and moderately hydrated scenarios, lablab experienced slight increases in evaporation with increasing water content, while transpiration increased in both partially and fully hydrated conditions (Sohrawardy and Hossain, 2014). As an initial response to drought, plants often close their stomata, restricting gas exchange and resulting in reduced transpiration and stomatal conductance in different chickpea varieties subjected to drought stress (Mafakheri *et al.*, 2010).

Respiration

Drought typically leads to a decline in respiration rates across various plant parts, including leaves, shoots, roots, and flower apices, as well as in the overall plant. While some studies have reported unaffected or even increased respiration rates under limited water availability, all forms of respiration were halted at low water potentials (–35 bars) (Hussain *et al.*, 2019).

Production of Reactive Oxygen Species

Under water stress conditions, the production of reactive oxygen species (ROS) such as superoxide anion radicals (O_2^{-}), hydroxyl radicals (OH^-), hydrogen peroxide (H_2O_2), alkoxy radicals (RO), and singlet oxygen (O_2^{-1}) is increased (Blokhina *et al.*, 2003). These

ROS interact with lipids, proteins, enzymes, and DNA, leading to lipid peroxidation, degradation of vital structural and functional proteins, inactivation of enzymes, and damage to nucleic acids. Consequently, this results in membrane injury and disruption of normal cell functions (Sairam *et al.*, 2005).

Drought stress disrupts the equilibrium between ROS production and the antioxidant defense mechanisms, leading to an accumulation of ROS and oxidative stress. Carotenes, which are isoprenoid compounds, play a crucial role in plant defense, yet they are susceptible to oxidative damage. Increased dryness contributes to osmotic stress and ion toxicity, causing the concentration of salts and ions to rise in the soil layers surrounding the roots. The reduction of CO_2 in leaves decreases the carboxylation process and shifts more electrons towards ROS production. Water stress degrades beta-carotene, a component of the PSI and PSII core complexes, through ROS formation in the thylakoids, resulting in significantly elevated levels of ROS (such as O_2^{-}, H_2O_2, and OH^{-} radicals) that cause oxidative damage to proteins, lipids, and genetic material. One of the most damaging physiological responses to water stress is lipid peroxidation in cell membranes, which increases the production of the highly reactive molecule malondialdehyde (MDA), associated with oxidative damage. In pea plants, drought stress quadruples protein and lipid peroxidation compared to normal conditions (Khatun *et al.*, 2021).

Plant Nutrient Relations

Drought typically leads to a decrease in the overall uptake of nutrients and their concentrations within plant tissues due to reduced water availability. The most significant impact of reduced water supply is on the ability of roots to absorb nutrients and transfer them to the shoots. Essential elements such as nitrogen (N), silicon (Si), magnesium (Mg), and calcium (Ca) which are usually absorbed with water are hindered in their transport during dry conditions, inhibiting plant growth (Barber, 1995). Disruption in nutrient uptake, unloading mechanisms, and diminished transpirational flow can also lead to decreased absorption of inorganic nutrients. Generally, moisture stress results in increased nitrogen levels but a marked reduction in phosphorus (P), with little impact on potassium (K) (Garg, 2003). Drought may negatively affect nutrient assimilation due to insufficient energy for the uptake of nitrate (NO_3^{-}) and ammonium (NH_4^{+}), phosphate (PO_4^{-}), and sulfate (SO_4^{-}), as these ions must undergo energy-consuming transformations before being utilized by the plant (Grossman and Takahashi, 2001). Overall, drought stress hampers nutrient availability, absorption, translocation, and metabolism. For instance, it can diminish biological nitrogen fixation in legumes due to reduced availability of assimilates and oxygen flow into root nodules. Drought also limits (i) leaf nitrate reductase activity and root nitrate levels, leading to decreased nitrogen availability, and (ii) the supply of carbohydrates to nodules and the functionality of the sucrose synthase enzyme, which hydrolyzes sucrose in nodules, resulting in diminished nitrogenase activity. Furthermore, drought stress reduces the nutrient-use efficiency in grain legumes by adversely affecting nitrate reductase and sucrose synthase activity and disrupting the legume–rhizobium symbiotic relationship (Ullah and Farooq, 2021).

Effect of Drought Stress on Yield

Drought has a direct effect on the yield of pulse crops. During critical growth phases—such as flowering and pod formation—water stress can lead to flower drop and pod abortion, resulting in significant yield losses. Studies reveal that yield reductions due to drought can range from 20% to 60%, influenced by the severity and timing of the stress. Water stress impacts various physiological processes that determine yield. It tends to lower crop yields by affecting photosynthetically active radiation, radiation efficiency, and harvest index. Plants that experience stress during the vegetative stage but not later on tend to yield significantly more than those that encounter stress during flowering or throughout both stages. For example, moisture stress before anthesis can shorten the time to anthesis, while stress after anthesis decreases the grain-filling period. Water stress during the post-anthesis period is particularly detrimental to grain yield, regardless of drought intensity. Different stages of crop growth are affected by drought stress, leading to yield reductions in grain legumes (Khatun *et al.*, 2021). Annually, drought causes

40% of global yield losses in chickpeas (Jukanti *et al.*, 2015). Drought also diminishes soybean yields, impacting both total and branch seed production. The effects of drought stress on grain legume yields vary across phenological stages, soil types, and agro-climatic regions, differing by species. For instance, groundnut demonstrates greater drought resistance compared to common beans or black gram, even in severe water shortage scenarios (Daryanto *et al.*, 2015).

Table 1: Yield losses (%) in important pulses under drought stress conditions (Nadeem *et al.*, 2019)

Pulse crops	Growth stage	Yield loss (%)
Soybean	Reproductive phase	46-71
	Pod set	45-50
	Grain filling stage	42
Chickpea	Reproductive phase	45-69
	anthesis	27-40
	Ripening	50
Cowpea	Reproductive phase	60
	Pod filling stage	29
Common bean	Reproductive phase	58-87
	Pod filling stage	40
	Flowering stage	49
Pigeon pea	Reproductive phase	40-55
Mung bean	Reproductive phase	26
	Flowering stage	31-57
Faba bean	Grain filling stage	68
Lentil	Reproductive phase	24
	Pod development	70

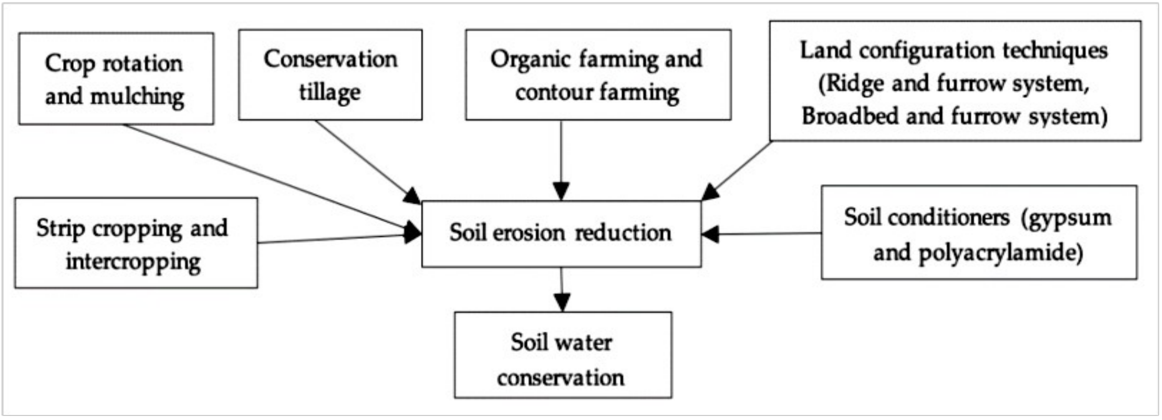

Figure 1. Agronomic options for soil and water conservation to mitigate drought stress (Kumawat *et al.*, 2020).

Mitigation of Drought Stress

Agronomic Options

Addressing the impacts of drought stress on pulse production necessitates a comprehensive approach that combines agronomic practices, breeding initiatives, and technological innovations. Seed priming has been demonstrated to enhance germination metabolism and facilitate early crop establishment under both normal and stressful conditions. Adjusting sowing times, plant density, and overall farm management can also help adapt to drought conditions. The application of potassium fertilization during periods of drought has been shown to enhance drought resistance by promoting cell membrane stability. Additionally, hardening seedlings can improve drought resilience by reducing stomatal regulation and osmotic potential while enhancing new root growth and cell membrane stability. Soil erosion poses a significant threat to the degradation of soil and water resources. To safeguard these resources, it is crucial to utilize natural resources wisely and implement effective management strategies. Various practices aimed at minimizing soil erosion can also alleviate water stress by conserving soil moisture and decreasing water loss (Khatun *et al.*, 2021).

Nutrient Utilization

Potassium is crucial for the survival of crop plants facing water stress. The application of potassium can help mitigate the negative impacts of water scarcity on plant growth. Enhancing potassium levels can counteract the yield-reducing effects of water deficits. Under stressful conditions, potassium application reduces the formation of reactive oxygen species (ROS) and the consequent oxidative damage to cells. Additionally, potassium influences the plant's water management and growth by affecting water uptake, root development, turgor maintenance, transpiration, and stomatal regulation. It aids plants in adapting to lower water potentials during drought stress. The application of silicon externally has been shown to reduce the shoot-to-root ratio, promoting root growth while maintaining higher photosynthetic rates and stomatal conductance compared to plants without silicon under drought conditions (Subbaramamma *et al.*, 2017). Moreover, Safar-Noori *et al.* (2018) found that combining potassium with salicylic acid enhances drought tolerance under water-deficient conditions.

Sowing Time and Plant Density

The timing of planting is a critical factor for drought evasion in subtropical, tropical, and rainfed conditions. Early planting in dry conditions can enhance water use efficiency (WUE) and help ensure that plants do not experience drought stress during key growth phases. A cropping system that balances adequate water availability and nutrient supply can improve canopy development and yield through increased biomass production. A larger canopy leads to higher evapotranspiration rates. Consequently, optimizing biomass production relative to transpiration through adjusted planting dates can serve as an effective strategy for enhancing drought tolerance or fostering drought escape (Hussain *et al.*, 2019). Adjusting planting times can significantly influence vital developmental stages, such as flowering and grain filling, thereby mitigating the detrimental effects of drought during these periods. Early planting with higher plant density can effectively utilize rainfall and improve yield. By aligning critical growth stages with periods of water availability, legume crops can thrive in arid regions and minimize yield losses. Maintaining optimal plant density is essential for maximizing the use of natural resources such as water, light, space, and nutrients. In rainfed regions, excessively high planting density can lead to soil moisture depletion before maturity and increased water losses through transpiration, whereas low planting density may leave soil moisture unutilized (Nadeem *et al.*, 2019).

Utilizing Plant Growth Regulators and Osmoprotectants

The application of exogenous plant growth regulators (PGRs) has been shown to enhance chlorophyll content and increase cellular water potential. PGRs, which include auxins, gibberellins, ethylene, cytokinins, and abscisic acid (ABA), can significantly improve legume growth. Numerous compounds exhibiting clear growth-promoting effects have been identified, some of which have potential applications in bolstering crop growth, yield, and quality. In kidney beans (*Phaseolus vulgaris* L.), a reduction in stomatal conductance was associated with increased ABA levels induced by re-watering. ABA enhances root hydraulic conductivity, thereby improving a plant's water absorption and transport efficiency. It also increases the production of $O2^-$ and H_2O_2 radicals, leading to enhanced activity of antioxidant enzymes such as glutathione reductase (GR). Therefore, overexpressing ABA synthesis genes may be an effective strategy for combating drought. Plants can counter ROS's harmful effects by maintaining higher levels of antioxidants. Osmoprotectants play a protective role for cell membranes against damage from inorganic ions and oxidative stress, suggesting that developing osmoprotectant production pathways could contribute to creating stress-resistant crops. For instance, applying glycine betaine can improve crop performance under drought by enhancing stomatal conductance, proline accumulation, and photosynthetic rates (Khatun *et al.*, 2021). Elevated levels of abscisic acid and decreased cytokinins promote stomatal closure, thereby reducing water loss through transpiration during water stress. Ethylene is also thought to regulate leaf performance and influence both natural senescence and drought-induced senescence. Additionally, polyamines can interact with negatively charged membrane components, protecting lipid bilayers from stress-related degradation (Subbramamma *et al.*, 2017).

Furthermore, endogenous plant growth regulators or phytohormones play a vital role in managing the effects of abiotic stress by adjusting the plant's growth and development. They aid in adaptation to diverse environments through regulating growth, development, nutrient distribution, and transitions between sources and sinks (Fahad *et al.*, 2015). PGRs significantly influence physiological processes related to drought tolerance. While auxin production usually declines under drought stress, the synthesis of abscisic acid and ethylene often increases. Auxins can enhance drought tolerance by breaking root apical dominance and promoting new root development (Abobatta, 2019).

Breeding for Drought Resistance

Traditional breeding approaches have primarily relied on empirical selection of crops based on their yield. However, a deeper understanding of the physiological and molecular basis of yield can help identify key traits that limit productivity. Although screening germplasm lines for drought tolerance in natural environments can be challenging, it is more feasible in controlled stress settings. Significant efforts have been dedicated to the genetic analysis of secondary traits, such as root system architecture, leaf water potential, osmotic adjustment, and relative water content (Jongdee *et al.*, 2002). An ideal secondary trait should: (1) correlate genetically with grain yield under drought; (2) be highly heritable; (3) be stable and easy to measure; and (4) not compromise yield under optimal growing conditions (Edmeades *et al.*, 2001). Drought-tolerant species manage water loss by either reducing leaf area or restricting stomatal opening, often resulting in less impact on biomass production (Subbramamma *et al.*, 2017). Plants adopt various physiological and morphological strategies, such as osmotic adjustment, production of phytohormones, and reduction of transpiration rates, to cope with drought stress (Sahoo *et al.*, 2013). Extensive gene discovery and manipulation efforts have led to the identification and mapping of numerous quantitative trait loci (QTLs). This progress allows for the modification of proteins and transcription factors involved in signaling and regulatory pathways, enhancing drought tolerance attributes. By altering these proteins, drought tolerance could be significantly improved through the increased production of phytohormones and osmotic adjustments (Hu and Xiong, 2014).

CONCLUSION

Pulses serve as a primary source of protein and are a vital complement to cereal-based diets. Drought stress adversely affects plant growth and development, resulting in smaller plant organs, reduced flower production, and impaired grain filling. During drought conditions, stomata gradually close, leading to a decrease in net photosynthesis and water-use efficiency, which ultimately hinders crop growth and lowers grain yields. As drought events become more frequent and severe, it is crucial to comprehend their negative effects on pulse crops and to adopt effective mitigation strategies. Implementing targeted breeding practices, optimizing agronomic techniques, and providing education can significantly improve the resilience of pulses to drought stress. By focusing on sustainable practices, we can ensure the future of pulse production, thereby contributing to food security and nutritional balance for growing populations in a rapidly changing climate. Additionally, it is essential to educate farmers on drought management strategies through training and extension services. Workshops and field demonstrations can assist smallholder farmers in adopting innovative practices that bolster their resilience to drought conditions. Furthermore, government and agricultural organizations can play a vital role by offering support mechanisms such as drought insurance, subsidies for drought-resistant seeds, and funding for research into sustainable farming practices.

Author’s contributions

All authors have equally contributed to this article.

CONFLICTS OF INTEREST

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

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