

REVIEW



Wheat Production under Drought Stress Conditions: Physiological and Biochemical Responses and Mitigation Options

Mohammad Safar Noori

¹ Associate professor of Agronomy department, Faculty of Agriculture, Takhar University, Afghanistan

ORCID: <https://orcid.org/0000-0003-2545-6760>

Scopus Author ID: 57203974245

*E-Mail: safar_noori@yahoo.com

Received December 12, 2022

Drought is a global problem, limiting crop production and quality, and it is more detrimental under climate change conditions. It decreases crop yield by affecting the key plant metabolic pathways. Drought triggers a wide variety of plant responses, ranging from cellular metabolism to changes in growth rates and crop yields. Wheat is one of the most important cereal crops and extensively cultivated in wide ranges of altitudes in Afghanistan. With an alarming population growth in the era of climatic change, there is a need for further crop improvement for sustainable production. Understanding the physiological and biochemical responses wheat to drought is essential for a holistic perception of resistance mechanisms to drought conditions. This review article has been divided into two parts, i.e., Physiological and biochemical responses of wheat to drought stress, and drought stress mitigation approaches. In the first part, physiological and biochemical responses of wheat to stress were discussed. Drought stress reduces relative water content of leaves, chlorophyll content, and membrane stability. It adversely affects photosynthesis by changing the inner structure of chloroplasts, mitochondria, and chlorophyll content and minerals. Drought stress induces generation of active oxygen species, and the production of antioxidant enzymes in response to water stress as an adaptive mechanism against oxidative damage. This review article elucidates the physiological and biochemical responses of wheat to drought stress conditions and provides drought mitigation options that could contribute in food security under changing climate.

Key words: *wheat, drought stress, antioxidant enzymes, photosynthesis, osmolytes*

Drought stress is considered the most detrimental factor for crop growth and productivity and a serious threat to sustainable crop production in the face of climate change. Drought triggers a variety of plant responses, ranging from changes in cellular metabolism to changes in growth rates and yields. Drought stress gradually reduces CO₂ assimilation rates due to reduced stomatal conductivity. It reduces leaf size, stem elongation, and root proliferation, disturbs plant water quality, and reduces water utilization efficiency. Drought interferes with photosynthetic pigments and reduces gas exchange, resulting in reduced plant growth and productivity (Anjum *et al.*, 2011a). Drought stress occurs when water supply to the roots is restricted or transpiration rates are too high. Low water availability impairs photosynthetic activity and causes oxidative stress due to the imbalance between light uptake and utilization (Celik and Cimen, 2012). Global food security is plagued by rapid population growth and dramatic climate change (Lesk *et al.*, 2016). With climate change, drought and heat stress are major limiting factors for crop yields and, ultimately, food security. Droughts are becoming more frequent around the world due to decreased precipitation and changes in precipitation patterns (Lobell *et al.*, 2011). Water shortages caused by irregular and inadequate rainfall are causing enormous losses to agriculture around the world. In Russia, drought and other natural disasters are estimated to have cost over 800 million US\$ in 2000 alone. Drought affects all stages of plant development, from germination to vegetative and reproductive growth, grain filling and crop maturity (Hossain *et al.*, 2012).

Among plants, wheat (*Triticum aestivum* L.) is an excellent health food and an excellent source of minerals, fiber, protein and B vitamins. Wheat is cultivated for its starch and protein. It is the world's most important cereal crop and, along with rice and corn, is an integral part of the diet of over 4.5 billion people. Wheat's success in temperate regions of the world offers distinct advantages over other temperate crops due to its adaptability and high yields, as well as its unique flour properties (Shewry 2007). Demand for wheat is estimated to increase by 60% by 2050, but

environmental pressures from climate change could reduce production by 29% (Manickavelu *et al.*, 2012). Understanding physiological and biochemical responses of wheat crop to drought stress is essential for a holistic understanding of plant tolerance mechanisms to water-limited conditions. It provides a framework for work on the development of wheat plants with increased drought stress. This article, aims to provide an overview of the physiological and biochemical responses of plants, especially wheat, to drought stress, and to provide management options to minimize the detrimental effects of drought stress on wheat productivity.

Drought stress

Drought is a polygenic stress that reduces crop productivity (Kilic and Tacettin, 2010) and quality (Waraich *et al.*, 2010, 2011) and limits effective use of land potential worldwide (Liu *et al.*, 2016). Drought reduces the uptake and utilization of nitrogen (N) by plants. Decreased nutrient uptake is due to impaired membrane permeability and active transport, and reduced transpiration rates, resulting in reduced root absorptive capacity. In semi-arid and arid regions of the world, drought is one of the main causes of limiting agricultural production. Many plant growth parameters and functions are affected by drought stress (Nezhadahmadi *et al.*, 2013). Drought is one of the major abiotic pressures, affecting at least 60% of wheat production in high-income countries and around 32% of 99 million hectares in low-income least developed countries (Chen *et al.*, 2012). Water scarcity can reduce wheat yields from 17% to 70% (Nouri-Ganbalani *et al.*, 2009).

Drought severely limits the production and quality of the crops, and recent global climate change has exacerbated this situation. Drought stress affects plant growth, dry matter and yield. The timing, duration, severity, and rate of development undoubtedly play an important role in determining how plants respond to drought. After drought, stomata gradually close, resulting in a simultaneous decrease in net photosynthesis and water use efficiency (Anjum *et al.*, 2011a). Cell proliferation is considered one of the most drought-sensitive physiological processes due to reduced turgor pressure. Growth is the result of mitotic

cell division and subsequent massive expansion of young cells to produce daughter cells. Grain yield is the result of the expression and association of multiple plant growth components. Water deficit leads to severe deterioration of crop yield-related traits, possibly by perturbing leaf gas exchange properties. This not only limits the size of source and sink tissues, but also affects phloem loading, anabolic translocation, and dry matter partitioning (Farooq *et al.*, 2009a). Drought stress suppresses dry matter production, primarily through an inhibitory effect on leaf elongation and leaf development, resulting in reduced shading (Nam *et al.*, 1998). Drought during flowering often leads to infertility. The main, if not the only, cause was that assimilate flux to the developing ear fell below the threshold required to maintain optimal grain growth (Yadav *et al.*, 2004). Decreases in grain yield and could be attributed to stomatal closure and reduced CO₂ uptake in response to lower soil water content, resulting in reduced photosynthesis (Flexas *et al.*, 2004). Drought reduces plant growth and development, resulting in impaired flower production and grain filling, resulting in smaller and less grains. It occurs due to decreased partitioning and activity of sucrose and starch synthases (Anjum *et al.*, 2011a).

RESPONSES OF WHEAT TO DROUGHT STRESS

Water relation

Relative water content (RWC) is considered a measure of the water status of plants, reflecting tissue metabolic activity and used as the most important indicator of dehydration tolerance. Leaf RWC is high during the early stages of leaf development and decreases as dry matter accumulates and leaves mature. RWC is associated with water uptake by roots and water loss through transpiration (Anjum *et al.*, 2011a). When plants are exposed to drought stress, leaf water potential, relative water content, and transpiration rate decrease significantly, while leaf temperature increases (Siddique *et al.*, 2001). Although the water-related component of plants is affected by the reduction in available water, in fact stomatal opening and closing is more affected. In addition, changes in leaf

temperature could be a key factor in controlling leaf water status under drought stress. Drought-tolerant species maintain water-use efficiency by reducing water loss. However, water use efficiency was also significantly reduced when plant growth was more constrained (Anjum *et al.*, 2011a).

Drought at a later stage of plant growth (6 weeks after germination) had a greater effect on water status, nutrient uptake, growth and yield than drought imposed at earlier stage (3 weeks after seedling germination) in wheat (Nawaz *et al.*, 2014). Drought significantly reduces chlorophyll content, membrane stability and RWC of wheat cultivars at flowering stage (Moayedi *et al.*, 2010). As the RWC decreases, the stomata close and the photosynthetic rate slows down. Although water deficit hampered osmotic regulation, alternating drying and rewatering induced osmotic regulation and improved plant water use efficiency under drought conditions due to the large regulation of osmotic pressure (Keyvan, 2010). Drought-tolerant genotypes retained high turgor potential and relative water content, suggesting that limited water had little effect on plasma structure compared to sensitive genotypes, indicating a highly positive correlation between RWC and photosynthetic rate (Moayedi *et al.*, 2010). Maintaining leaf turgor is an important adaptive mechanism that plays a key role in regulating stomatal and photosynthetic activity under drought conditions (Lipiec *et al.*, 2013).

Antioxidant enzyme

The production of antioxidant enzymes such as catalase (CAT), superoxide dismutase (SOD), peroxidase (POD), ascorbate peroxidase (APX), and glutathione peroxidase (GPx) in response to water stress is a well-known adaptive mechanism in plants. Plants increase peroxidase and glutathione activity against oxidative damage caused by water stress. APX is a major antioxidant enzyme that scavenges chloroplast superoxide radicals and H₂O₂ under conditions of drought (Gill and Tuteja, 2010). Similarly, in wheat cultivars, APX activity varied by leaf development stage and drought duration. Wheat exposed to mild drought increases APX activity in leaves, whereas prolonged water deficit reduced that

activity due to increased malondialdehyde (MDA) production (Nikolaeva *et al.*, 2010). Peroxidase plays an important role in removing H_2O_2 produced by SOD-catalyzed disproportionation of O_2^- . CAT is a key enzyme for H_2O_2 removal in mitochondria and microbodies (Shigeoka *et al.*, 2002) and helps mitigate the detrimental effects of oxidative stress. Although it occurs in peroxisomes, it is thought to be essential for the breakdown of H_2O_2 during stress. Maintaining higher levels of antioxidant enzyme activity may help in reducing oxidative damage (Sharma and Dubey, 2005). The ability of antioxidant enzymes to mitigate the effects of drought may be correlated with plant drought tolerance. SOD, glutathione reductase, and APX contribute significantly to the reduction of reactive oxygen species (ROS) generated by drought stress (Hernández *et al.* 2012). As hydrogen peroxide scavengers, CAT and POD convert toxic levels of endogenous H_2O_2 to water and oxygen. Similarly, CAT activity in wheat leaves exposed to severe drought was examined and an increase in the CAT activity of wheat plants was found in particularly susceptible cultivars (Simova-Stoilova *et al.*, 2010). Ascorbic acid applied to leaves mitigates drought by affecting stomatal closure, nutrient uptake, total chlorophyll content, protein synthesis, transpiration, flowering and photosynthesis (Xu *et al.*, 2015). Leaf-applied ascorbic acid increased wheat yield and chlorophyll content in combination with leaf water potential regulation by transporting minerals from leaves to flowers and enhancing CAT and APX activity (Hafez and Gharib, 2016).

Chlorophyll content and photosynthesis

Chlorophyll is one of the most important chloroplast components for photosynthesis, and relative chlorophyll content is positively correlated with photosynthetic rate. Decrease in chlorophyll content under drought stress is considered a typical symptom of oxidative stress and may be the result of pigment photo-oxidation and chlorophyll degradation. Photosynthetic pigments are important to plants primarily for capturing light and photosynthesis. Both chlorophyll a and b are susceptible to soil water-deficit conditions (Farooq *et al.*, 2009b). Depending on cultivar, plant growth, and various

environmental factors, the ratio of chlorophyll a to b is 3:1. However, the highest chlorophyll content is found in early flowering plants (Simova-Stoilova *et al.*, 2009). Severe drought stress in wheat is associated with changes in leaf chlorophyll content (Fotovat *et al.*, 2007) and leaf photosynthesis (Prasad *et al.*, 2011). A decrease in wheat chlorophyll content is associated with leaf age. Chlorophyll content increased in young leaves due to activation of enzymes in the photoreaction of chlorophyll synthesis, but decreased by 13-15% in older leaves due to activation of chlorophyllase and deactivation of enzymes under drought (Nikolaeva *et al.*, 2010). Differences in chlorophyll content were not only caused by drought stress, but also existed between genotypes. Higher chlorophyll content resulted in better seed yields under water stress conditions (Alaei 2011). Kilic and Tacettin (2010) evaluated the yield and physiological characteristics of 14 durum wheat cultivars under drought stress and found differences between grain yield and chlorophyll content, grain filling time, and number of grains per ear (Mir *et al.*, 2012). Dehydration adversely affects photosynthesis by altering the internal structure of chloroplasts, mitochondria, chlorophyll content, and minerals (Huseynova *et al.*, 2016). However, stomatal responses under drought conditions vary greatly among plant species (Lawlor and Cornic, 2002). Photosynthesis is limited by reduced stomatal conductivity during mild droughts, but dysfunction of Rubisco becomes a major factor affecting photosynthesis (Bota *et al.*, 2004). Low concentrations of photosynthetic pigments may directly limit photosynthetic potential and thus primary production. From a physiological point of view, leaf chlorophyll content is an independent parameter of considerable interest. Most studies of plant chlorophyll loss in response to drought stress occur in mesophyll cells, with lesser loss from bundle sheath cells (Anjum *et al.*, 2011a). Drought-stressed plants have been reported to have higher concentrations of chlorophyll a compared to chlorophyll b (Jain *et al.*, 2010)

Accumulation of osmolytes

Osmotic adaptation as a plant defense mechanism improves plant drought tolerance and allows cell growth and plant growth in severe water deficits (Shao *et al.*,

2005). Plants accumulate a wide variety of organic and inorganic solutes in the cytosol to reduce osmotic pressure and thereby maintain cellular turgor (Rhodes and Samaras, 1994). The stomata remain partially open to continue CO₂ fixation during periods of water deficit. Accumulation of osmolytes allows cells to cope with desiccation and membrane structural integrity and achieve resistance to desiccation and cellular desiccation (Loutfy *et al.*, 2012). Osmotic adaptation of drought-exposed plants may follow storage of low-molecular-weight organic solutes. Wheat plants accumulate several inorganic and organic solutes in their cytosol to reduce osmotic pressure to maintain cellular turgor (Zahoor *et al.*, 2018).

Leaf turgor can also be maintained during drought by osmotic adjustment in response to accumulation of proline, sucrose, soluble carbohydrates, glycine betaine, and other solutes in the cytoplasm. The process of such solute accumulation under drought stress is known as osmotic adaptation, which is highly dependent on the rate of plant water stress. Wheat is characterized by low levels of these compatible solutes, and proline accumulation and mobilization have been observed to increase resistance to water stress (Nayyar and Walia, 2003). Compatible osmolytes present in higher plants are glycine betaine, proline, and soluble carbohydrates and proteins. Glycine betaine protects cells from dehydration by maintaining an osmotic balance between the extracellular and intracellular environment and protein quaternary structure. It also regulates intracellular osmotic pressure, regulates cytosolic pH, and stabilizes cell membrane structure in wheat under drought stress (Huseynova *et al.*, 2016). Among these solutes, proline has been the most extensively studied as it is of great importance in stress tolerance. Accumulation of proline is the first response by water-stressed plants to reduce cellular damage. Progressive drought stress led to significant accumulation of proline in water-stressed maize plants. Proline levels increased as drought stress progressed, peaked as recorded after 10 days of stress, and decreased under severe water stress, as observed after 15 days of stress (Anjum *et al.*, 2011b). Accumulation of proline under stress in many plant species is correlated with stress tolerance,

and its concentrations have been shown to be generally higher in stress-tolerant than stress-sensitive plants. It affects protein solvation, maintains complex protein quaternary structure, maintains membrane integrity under drought stress, and reduces oxidation or photo-inhibition of lipid membranes (Demiral and Turkan, 2004).

Wheat plants accumulate more proline than other osmolytes, especially in leaves (Farshadfar *et al.*, 2008). This is due to increased protein degradation and an immediate decrease in its synthesis during the grain filling stage under water deficit (Nazarli and Faraji, 2011). Wheat genotypes accumulate more soluble sugars during the grain-filling stage than during the anthesis stage under drought stress. The optimal stages for screening drought-tolerant cultivars are the ripening and post-flowering stages (Farshadfar *et al.*, 2008). Qayyum *et al.* (2011) reported that hyperosmotic stress increased the endogenous content of soluble sugars in wheat from 1.49 mg in controls to 2.65 mg per gram leaf under -8 bar osmotic stress. Proline levels increased under imposed stress, with the greatest increase (69.8%) occurring under combined (drought and heat) stress compared to controls. Individual drought and heat stress increased proline levels by 53% and 58.9%, respectively, compared to controls. Soluble protein was also affected by the imposed stress, with minimal values observed in control treatments. Increases in soluble protein of 3.6 mg g⁻¹, 4.3 mg g⁻¹ and 4.5 mg g⁻¹ were recorded under drought, heat and combined stress, respectively, compared to control treatments. A minimal level of soluble sugars (1.46 mg g⁻¹) was observed in the control treatment. Drought stress increased soluble protein by 61% compared to controls (Abdul-Sattar *et al.*, 2020). Evaluation of wheat genotypes under drought stress showed that drought-tolerant genotypes accumulated higher concentrations of physiological indices such as free proline, glycine betaine, total sugars and potassium content. These organic and inorganic substances help maintaining osmoregulation under water stress. In addition, high concentrations of these solutes provide wheat with the advantage of withstanding drought stress (Muhammad *et al.*, 2016).

Reactive oxygen species

Generation of reactive oxygen species (ROS) is one of the earliest biochemical responses of eukaryotic cells to biotic and abiotic stress. Generation of ROS in plants, known as oxidative burst, is an early event in plant defense responses to water stress and acts as a secondary messenger that triggers subsequent defense responses in plants. ROS, including oxygen ions, free radicals, and peroxides, are natural byproducts of normal oxygen metabolism and play important roles in cell signaling. However, environmental stresses such as drought dramatically increase ROS levels, causing oxidative damage to proteins, DNA, and lipids (Apel and Hirt, 2004). Drought stress increases production of ROS. However, the main source of ROS generation is the electron transport chain that occurs in the chloroplast. Disruption of the photosystem II (PSII) oxygen-releasing complex and reaction center impedes electron production and utilization, generating ROS that expose cell membranes to lipid peroxidation (Wang *et al.*, 2014). High concentrations of singlet oxygen (1O_2), superoxide radicals (O_2^-), hydrogen peroxide (H_2O_2), and hydroxyl radicals (OH) caused oxidative damage in plants, depending on endogenous levels. ROS are deoxyribonucleic acids, lipids, and proteins cause photosynthetic-related oxidative damage, enzyme inactivation, and disruption of cellular structure by affecting normal functioning of cells (Huseynova *et al.*, 2016). ROS production is linear with the severity of water stress that induces membrane lipid peroxidation and nucleic acid degradation. Organelles such as Chloroplasts, mitochondria and peroxisomes are cytological sites and primary targets for reactive oxygen species. An alternative nitric oxide-mediated pathway enhances photosynthesis under water deficit by avoiding severe reduction of the photosynthetic electron transport chain and ultimately inhibiting the ROS production and oxidative damage in wheat leaves (Wang *et al.*, 2016). ROS are highly reactive and can seriously damage plants by increasing lipid peroxidation, protein degradation, DNA fragmentation, and ultimately cell death. Drought induces oxidative stress in plants through the formation of ROS (Farooq *et al.*, 2009a). Drought reduces wheat leaf water potential due to solute

accumulation, but genotypic variation may exist depending on water potential under well-watered and drought conditions (Nawaz *et al.*, 2014). The amount of soluble sugars, the concentration of proline, and the activity of radical scavenging enzymes were significantly increased under stress conditions to combat the accumulation of reactive oxygen species (Manuchehri and Salehi, 2014)

Assimilate Partitioning

Drought upsets the balance of assimilates and most of them migrate to the roots to improve water uptake. The export of assimilates from source to sink generally depends on the rate of photosynthesis and the concentration of sucrose in leaves. Drought impairs the photosynthetic process, lowering sucrose levels and ultimately reducing the rate of export from source to sink. Drought also limits the ability of sinks to efficiently utilize incoming assimilates. In addition, invertase activity is adversely affected and phloem charging and discharging is disrupted. Thus, dry matter distribution is severely affected under water stress (Fahad *et al.*, 2017).

Drought stress and nutrients

Many essential nutrients such as nitrogen, silicon, magnesium and calcium are taken up by the roots along with the water. Drought conditions limit the diffusion and mass transfer of these nutrients, retarding plant growth (Barber, 1995). A lack of soil moisture temporarily reduces root growth and reduces the uptake of less mobile nutrients such as phosphorus (Garg, 2003). Soil microbial colony composition and activity are adversely affected by soil moisture deficit, ultimately disrupting plant nutrient balance (Schimel *et al.*, 2007). Responses to mineral uptake under water stress vary among plant species. In general, under drought conditions, N uptake increases, P uptake decreases, and potassium remains unaffected. However, nutrient relationships are more complex as different nutrients interact with each other, complicating overall plant physiology. This aspect requires detailed studies at a sophisticated molecular level (Fahad *et al.*, 2017).

Drought can lead to nutrient deficiencies in the agricultural sector, as individual nutrient intakes depend on soil physicochemical properties (Nawaz *et al.*, 2020).

Water deficit conditions have a significant impact on nutrient uptake by roots and transport to shoots. It has been found that drought stress causes an increase in plant N content, a decrease in P content, and generally does not affect K content (Farooq *et al.*, 2009b). Under drought stress conditions, roots are ineffective at uptake of nutrients from the soil due to poor root function and slow water diffusion rates (Dubey and Pessarakli, 2001). Water deficit conditions also lead to stomatal closure, reduced transpiration, and restricted movement of nutrients from the roots to the upper part of the plant. Thus, drought conditions reduce soil nutrient availability and reduce the consistency of plant nutrient migration (Bashir *et al.*, 2022).

DROUGHT STRESS MITIGATION

Plant natural defense

Some plants have different morphological, physiological and biochemical adaptation strategies that enable them to cope with water stress conditions. Plant responses to water stress are influenced by several factors, including developmental stage, stress intensity and duration, and cultivar genetics (Tefera *et al.*, 2021). To cope with oxidative stress, plants usually rely on enzymatic or non-enzymatic antioxidant defenses. Enzymatic defenses are generally considered to be the most effective (Farooq *et al.*, 2008). The main enzymes involved in this system are SOD, GR, POD and CAT (Farooq *et al.*, 2009b). In addition to these enzymes, certain carotenoids and glutathione may also be involved as non-enzymatic components of the antioxidant system which indirectly protects plants (Anjum *et al.*, 2011c). Therefore, maintaining higher levels of antioxidants may be a good strategy for plants to counteract the negative effects of ROS (Sharma and Dubey, 2005). Phytohormones are also natural defense molecules in plants that maintain high levels of antioxidants even under stress. They help plants adapt to different environments by mediating growth, development, source/sink transitions, and nutrient allocation (Fahad *et al.*, 2015).

Application of growth regulators

Exogenous application of growth regulators and osmoprotectants at different growth stages may play an

important role in inducing drought tolerance. Hydration of seeds before sowing initiated germination metabolism but prevented the emergence of radicles (Farooq *et al.*, 2006). It has been reported that several wheat cultivars performed better under drought conditions after priming with potassium chloride (Eivazi, 2012). Priming wheat seeds with ascorbic acid improved proline accumulation, increased drought tolerance, and maintained tissue water content and membrane stability (Farooq *et al.*, 2013). External application of Salicylic acid (SA) also improves drought tolerance (Azooz and Youssef, 2010). Studies conducted primarily at the physiological level, suggest that drought tolerance by SA is associated with enhanced antioxidant defense mechanisms (Horváth *et al.* 2007). It has been reported that applying SA at the seedling stage to mitigate drought may result in real economic yields from wheat genotypes grown under water stress. Safar-Noori *et al.* (2018) reported that combined application of SA and appropriate levels of potassium (K) fertilizer can ameliorate the adverse effects of post-anthesis drought stress, improves wheat productivity, and partially enhances grain minerals content, and nutritional quality of wheat. Anjum *et al.* (2011c) reported that exogenous application of brassinolide improved maize performance under drought conditions by improving water balance and antioxidant defenses. Application of glycine betaine helps improve plant performance under drought conditions (Hussain *et al.*, 2008). It improves stomatal conductivity, photosynthetic rate and proline accumulation in plants (Ma *et al.*, 2007). Other studies also highlighted the potential application of silicon to improve drought tolerance of wheat mainly through root growth, stomatal conductance, photosynthetic rate, and antioxidant defense (Gong *et al.*, 2005).

Selection and genetic improvement

Screening and selection of drought tolerant genotypes of wheat can be considered as a good approach to minimize the deleterious effect of drought stress. In drought conditions, cell membrane stability (CMS) is another important selection criterion for drought-tolerant genotypes. Genotypes with values below 50% and with 71–80% are considered sensitive or tolerant to drought, respectively (Bilal *et al.*, 2015). In

drought-tolerant wheat, higher CMS protects the plant from ROS, which cause decreased membrane stability through the generation of lipid peroxidation. Physiological responses such as chlorophyll levels, stomatal closure and decreased photosynthetic activity, generation of oxidative stress, changes in cell wall integrity, and metabolite production play important roles in water-limited wheat. Therefore, these physiological traits can be considered as potential indicators for indirect selection of resistant wheat genotypes under drought conditions (Negisho Daksa, 2018). Transgenic wheat plants rapidly close stomata under drought stress conditions, reducing transpiration and water loss, thereby improving drought tolerance of wheat (Yu *et al.*, 2017). Some studies have shown that photosynthesis under drought stress is directly related to wheat grain production due to reduced stomatal openings, resulting in reduced CO₂ fixation levels and reduced photosynthesis (Mafakheri *et al.*, 2010). Genetic modification of root shoot structure can improve water and mineral uptake in water-stressed wheat. The wheat tiller inhibitor gene (Zinn) strongly affects root shoot structure. This gene improves root-to-shoot ratio and root biomass during early stem elongation and also increases root depth at maturity in a wheat near-isogenic line (NIL). It also slows soil moisture utilization by lowering canopy temperature, increasing stomatal conductivity, and keeping the grain green during filling of these NILs. These changes can increase harvest index and ultimately yield (Hendriks *et al.*, 2016).

Opportunities in Drought Tolerance Development

The following factors are known to pose challenges in developing drought-tolerant wheat cultivars. These include timing (growth stage), genetic diversity, drought intensity, complex and large genome, low heritability and quantitative/polygenicity of drought responsive traits, epistatic qualitative trait loci (QTL) interactions, interaction between genotype and environment, and co-occurrence of abiotic and biotic factors. The genetics of drought tolerance/susceptibility are complex, and the traits involved are complex and polygenic, complicating the task of developing drought-tolerant cultivars. However, current high-throughput techniques

(transcriptomics, proteomics, metabolomics, genotyping, SNP chip assays) for accurate phenotyping and analysis of the wheat genome and the bioinformatics software employed to identify drought-tolerant wheat. Therefore, recent technologies such as high-throughput phenotyping, next-generation sequencing (NGS), and genetic engineering can be utilized for drought tolerance improvement in wheat (Mwadingeni *et al.*, 2015). Climate change conditions that make plants more susceptible to abiotic stresses, emphasis should also be placed on breeding for stress tolerance. Recently, studies have been initiated to improve plant stress tolerance using conventional and molecular breeding approaches (Farooq *et al.*, 2009b). Higher plants have evolved distinct but interrelated strategies to survive and overcome stress. On the contrary, these strategies are not equally present in most crops. In addition, for crops, traditional breeding programs involving the transfer of desirable genetic traits from wild relatives are often used to manipulate resistance traits. However, it is not effective because breeding is objectively difficult. Especially in cereals, most traits of abiotic stress tolerance are localized in landraces and related wild species, whereas most of these traits are yet to be identified in grasses. Wheat, rye, and barley have good levels of abiotic stress tolerance compared to maize and rice, but information on the genes and mechanisms involved is very sparse or sometimes absent, so it is difficult or impossible to improve commercial varieties for stress-tolerant traits. A future challenge for abiotic stress research is therefore needed to bridge the gap between knowledge and translation of relevant traits into promising materials (Lichtfouse and Goyal, 2015).

CONCLUSION

Drought stress is a key constraint that limits wheat growth and productivity. Wheat exhibits a wide range of responses to drought stress, which are mainly expressed by various changes in plant growth, morphology and physiology. The effects of drought stresses including damaged photosynthetic machinery, oxidative damage, and membrane instability. As a natural defense mechanism, wheat plants produces many organic and inorganic solutes to reduce osmotic pressure and maintain cellular turgor under drought

stress conditions. Scavenging of reactive oxygen species by enzymatic and non-enzymatic systems, cell membrane stability, and expression of stress proteins are vital mechanisms of drought tolerance. Application of some phytohormones and osmoprotectants can play an important role in mitigation of drought stress. The ability of plants to withstand damaging effects of drought stress varies greatly between wheat genotypes. Genotypes with higher yields under drought stress can be considered as tolerant one. Therefore, screening of wheat varieties for their yield under drought stress condition and identification drought tolerant genotypes is a powerful tool to minimize the loss of yield due to drought stress. Employing genetic approaches and plant breeding techniques my help in avoiding the yield loses by inducing stress tolerance. Cultivation of transgenic wheat varieties which close their stomata under drought stress conditions, and therefore improves drought tolerance through reducing transpiration and water loss could be another approach to successful wheat production under drought stress condition. However, there is great advances in genetic approaches such as conventional breeding and transgenic approaches, there is still much opportunities for improvement of drought tolerant wheat varieties.

CONFLICTS OF INTEREST

The author declare that has no potential conflicts of interest.

REFERENCES

- Abdul-Sattar, Sher A., Ijaz M., Sami Ul-Allah, M., Mubshar Hussain S. R., Jabran K., Mumtaz Cheema A. (2020). Terminal drought and heat stress alter physiological and biochemical attributes in flag leaf of bread wheat. *PLOS ONE*. <https://doi.org/10.1371/journal.pone.0232974>.
- Alaei, Y. (2011). The effect of amino acids on leaf chlorophyll content in bread wheat genotypes under drought stress conditions. *Middle-East J Sci Res.*, 10:99–101.
- Anjum, S.A, Xiao-yu Xie, Long-chang W., Farrukh Saleem M., Chen M. and Wang L. (2011a). Morphological, physiological and biochemical responses of plants to drought stress. *Afr. J.Agril. Res.*, Vol. 6(9): 2026-2032.
- Anjum, S.A., Wang L.C., Farooq M., Khan I., Xue L.L. (2011b). Methyl jasmonate-induced alteration in lipid peroxidation, antioxidative defense system and yield in soybean under drought. *J. Agron. Crop Sci.*, doi:10.1111/j.1439-037X.2010.00468.x.
- Anjum, S.A., Wang, L.C., Farooq, M., Hussain, M., Xue, L.L., and Zou, C.M. (2011c). Brassinolide application improves the drought tolerance in maize through modulation of enzymatic antioxidants and leaf gas exchange. *J. Agron. Crop Sci.* 197, 177–185. doi: 10.1111/j.1439-037X.2010.00459.x
- Apel, K., Hirt H. (2004). Reactive oxygen species: metabolism, oxidative stress, and signal transduction. *Annu. Rev. Plant Biol.*, 55: 373-399.
- Azooz, M.M., and Youssef M.M. (2010) Evaluation of heat shock and salicylic acid treatments as inducers of drought stress tolerance in Hassawi wheat. *Am J Plant Physiol* 5:56–70
- Barber, S. A. (1995). *Soil Nutrient Bioavailability: A Mechanistic Approach*, 2nd Edn. New York, NY: Wiley.
- Bilal, M., Iqbal, I., Rana, R.M., Shoaib, U.R., Rehman, Haidery, Q.A., Ahmad, F., Ijaz, A. & Umar, H.M.I. (2015), "A comprehensive review of effects of water stress and tolerance in wheat (*Triticum aestivum* L.)", *Tropil Plant Res.* 2(3): 271–275.
- Bota, J., Flexas, J., and Medrano, H. (2004). Is photosynthesis limited by decreased Rubisco activity and RuBP content under progressive water stress? *New Phytol.* 162, 671–681. doi: 10.1093/aob/mcn244.
- Celik, O., Cimen A. (2012). The effect of salt stress on antioxidative enzymes and proline content of two Turkish tobacco varieties. *Turk. J. Biol.*, 36:339 – 356.
- Chen, X., Min D., Yasir T.A., Hu Y.G. (2012). Field crops research evaluation of 14 morphological, yield-related and physiological traits as indicators of drought tolerance in Chinese winter bread wheat revealed by analysis of the membership function value of drought tolerance (MFVD). *F. Crop. Res.*, 137:195–201. DOI: 10.5897/AJAR10.027

- Demiral, T., and Turkan I. (2004). Does exogenous glycinebetaine affect antioxidative system of rice seedlings under NaCl treatment? *J. Plant Physiol.*, 161: 1089-1110.
- Dubey, R.S., Pessaraki M. (2001). Physiological mechanisms of nitrogen absorption and assimilation in plants under stressful conditions. In: Pessaraki M, editor. Handbook of plant and crop physiology. Boca Raton (FL): CRC Press; p. 659–678
- Eivazi, A. (2012). Induction of drought tolerance with seed priming in wheat cultivars (*Triticum aestivum* L.). *Acta Agric. Slov.* 99, 21–29. doi: 10.2478/v10014-012-0003-6
- Fahad, S., Bajwa A.A., Nazir U., Anjum S.A., Farooq A., Zohaib A., Sadia S., Nasim W., Adkins S., Saud S., Ihsan M.Z., Alharby H., Wu C., Wang D. and Huang J. (2017). Crop Production under Drought and Heat Stress: Plant Responses and Management Options. *Front. Plant Sci.*, 8:1147. doi: 10.3389/fpls.2017.01147.
- Fahad, S., Hussain, S., Matloob, A., Khan, F. A., Khaliq, A., Saud, S. (2015). Phytohormones and plant responses to salinity stress: a review. *Plant Growth Regul.*, 75, 391–404. doi: 10.1007/s10725-014-0013-y
- Farooq. M., Basra S, Wahid A. (2009a). Improving the drought tolerance in rice (*Oryza sativa* L.) by exogenous application of salicylic acid. *J Agron Crop Sci.*, 2009; 195 (4):237–246.
- Farooq, M., Aziz, T., Basra, S. M. A., Cheema, M. A., and Rehman, H. (2008). Chilling tolerance in hybrid maize induced by seed priming with salicylic acid. *J. Agron. Crop Sci.*, 194, 161–168. doi: 10.1111/j.1439-037X.2008.00300.x
- Farooq, M., Basra, S.M.A., and Wahid, A. (2006). Priming of fieldsown rice seed enhances germination, seedling establishment, allometry and yield. *Plant Growth Regul.*, 49, 285–294. doi: 10.1007/s10725-006-9138-y
- Farooq, M., Irfan, M., Aziz, T., Ahmad, I., and Cheema, S. A. (2013). Seed priming with ascorbic acid improves drought resistance of wheat. *J. Agron. Crop Sci.*, 199, 12–22. doi: 10.1111/j.1439-037X.2012.00521.x
- Farooq, M., Wahid, A., Kobayashi, N., Fujita, D., and Basra, S. M. A. (2009a). Plant drought stress: effects, mechanisms and management. *Agron. Sustain. Dev.* 29, 185–212. doi: 10.1051/agro:2008021
- Farshadfar, E., Ghasempour H., Vaezi H. (2008) Molecular aspects of drought tolerance in bread wheat (*T. aestivum*). *Pak. J. Biol. Sci.*, 11:118–122.
- Flexas, J., Bota J., Loreto F., Cornic G., Sharkey T.D. (2004). Diffusive and metabolic limitations to photosynthesis under drought and salinity in C3 plants. *Plant Biol.*, 6: 1-11.
- Fotovat, R., Valizadeh M., Toorchi M. (2007). Association between wateruse efficiency components and total chlorophyll content (SPAD) in wheat (*Triticum aestivum* L.) under well-watered and drought stress conditions. *J. Food Agric. Environ.*, 5:225–227
- Garg, B. K. (2003). Nutrient uptake and management under drought: nutrient-moisture interaction. *Curr. Agric.*, 27, 1–8.
- Gill, S., Tuteja N. (2010). Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. *Plant Physiol Biochem.*, 48:909–930.
- Gong, H., Zhu, X., Chen, K., Wang, S., and Zhang, C. (2005). Silicon alleviates oxidative damage of wheat plants in pots under drought. *Plant Sci.*, 169, 313–321. doi: 10.1016/j.plantsci.2005.02.023
- Hafez, E.M., Gharib H.S. (2016) Effect of exogenous application of ascorbic acid on physiological and biochemical characteristics of wheat under water stress. *GUASNR Int J Plant Prod* 10:579–596.
- Hendriks, P.W., Kirkegaard J.A., Lilley J.M., Gregory P.J., Rebetzke G.J. (2016) A tillering inhibition gene influences root-shoot carbon partitioning and pattern of water use to improve wheat productivity in rainfed environments. *J. Exp. Bot.*, 67:327–340.
- Hernández, I., Cela J, Alegre L, Munné-Bosch S. (2012). Antioxidant defenses against drought stress. In: Plant responses to drought stress. *Springer, Berlin*, pp 231–258

- Horváth, E., Pál M., Szalai G., Páldi E., Janda T. (2007). Exogenous 4-hydroxybenzoic acid and salicylic acid modulate the effect of short-term drought and freezing stress on wheat plants. *Biol Plant.*, 51:480–487.
- Hossain, A., Teixeira da Silva J.A., Lozovskaya M.V., Zvolinsky V.P. (2012). High temperature combined with drought affect rainfed spring wheat and barley in South-Eastern Russia: I. Phenology and growth. *Saudi J. Biol. Sci.*, 19:473–487.
- Huseynova, I.M., Rustamova S.M., Suleymanov S.Y., Aliyeva D.R., Mammadov A.C., Aliyev J.A. (2016). Drought-induced changes in photosynthetic apparatus and antioxidant components of wheat (*Triticum durum* Desf.) varieties. *Photosynth Res.*, 130:215–223
- Hussain, M., Malik, M. A., Farooq, M., Ashraf, M. Y., and Cheema, M. A. (2008). Improving Drought tolerance by exogenous application of glycinebetaine and salicylic acid in sunflower. *J. Agron. Crop Sci.*, 194, 193–199. doi: 10.1111/j.1439-037X.2008.00305.x.
- Jain, M., Tiwary, S., and Gadre, R. (2010). Sorbitol-induced changes in various growth and biochemical parameters in maize. *Plant Soil Environ.*, 56, 263–267.
- Keyvan, S. (2010). The effects of drought stress on yield, relative water content, proline, soluble carbohydrates and chlorophyll of bread wheat cultivars. *J. Anim. Plant Sci.*, 8:1051–1060.
- Kilic, H., Tacettin Y. (2010) The effect of drought stress on grain yield, yield components and some quality traits of durum wheat (*Triticum turgidum* ssp. durum). *Not Bot Horti Agrobot Cluj-Napoca* 38:164–170.
- Lawlor, D. W., and Cornic, G. (2002). Photosynthetic carbon assimilation and associated metabolism in relation to water deficits in higher plants. *Plant Cell Environ.*, 25, 275–294. doi: 10.1046/j.0016-8025.2001.00814.x.
- Lesk, C., Rowhani, P., and Ramankutty, N. (2016). Influence of extreme weather disasters on global crop production. *Nature*, 529, 84–87. doi: 10.1038/nature16467.
- Lichtfouse, A E. Goyal (eds.), Sustainable Agriculture Reviews, *Sust. Agri. Rev.*, 16, DOI: 10.1007/978-3-319-16988-0_3
- Lipiec, J., Doussan C., Nosalewicz A., Kondracka K. (2013). Effect of drought and heat stresses on plant growth and yield: a review. *Int. Agrophys.*, 27:463–477.
- Liu, Y., Liang H., Lv X., Liu D., Wen X., Liao Y. (2016). Effect of polyamines on the grain filling of wheat under drought stress. *Plant Physiol Biochem.*, 100:113–129
- Lobell, D. B., Schlenker, W., and Costa-Roberts, J. (2011). Climate trends and global crop production since 1980. *Science*, 333, 616–620. doi: 10.1126/science.1204531
- Loutfy, N., El-Tayeb M.A., Hassanen A.M., Moustafa M.F.M., Sakuma Y., Inouhe M. (2012). Changes in the water status and osmotic solute contents in response to drought and salicylic acid treatments in four different cultivars of wheat (*Triticum aestivum*). *J. Plant Res.*, 125:173–184
- Ma, X. L., Wang, Y. J., Xie, S. L., Wang, C., and Wang, W. (2007). Glycinebetaine application ameliorates negative effects of drought stress in tobacco. *Russ. J. Plant Physiol.* 54, 472–479. doi:10.1134/S1021443707040061
- Mafakheri, A., Siosemardeh, A., Bahramnejad, B., Struik, P. & Sohrabi, E. (2010). Effect of drought stress on yield, proline and chlorophyll contents in three chickpea cultivars. *Aust. J. Crop Sci.*, 4: 580–585.
- Manickavelu, A., Kawaura, K., Oishi, K., Shin-I., T., Kohara, Y., Yahiaoui, N. (2012). Comprehensive functional analyses of expressed sequence tags in common wheat (*Triticum aestivum*). *DNA Res.* 19, 165–177. doi: 10.1093/dnares/dss001
- Manuchehri, R., and Salehi H. (2014). Physiological and biochemical changes of common bermudagrass (*Cynodon dactylon* [L.] Pers.) under combined salinity and deficit irrigation stresses. *South Afr. J. Bot.*, (9) 2: 83–88, 2014.
- Mir, R. R., Zaman-Allah M., Sreenivasulu N., Trethowan

- R., Varshney R.K. (2012). Integrated genomics, physiology and breeding approaches for improving drought tolerance in crops. *Theor Appl Genet.*, 125: 625–645.
- Moayedi, A.A., Nasrulhaq Boyce A., Shahar Barakbah S., Author C., Akbar Moayedi A., Nasrulhaq Boyce A., Shahar Barakbah S. (2010). The performance of durum and bread wheat genotypes associated with yield and yield component under different water deficit conditions. *Aust. J. Basic. Appl. Sci.*, 4:106–113
- Muhammad, H.C., Nazir, A.C., Qamaruddin, C., Sheikh, M.M., Sadaruddin, C. & Zaid, C. (2016). "Physiological characterization of six wheat genotypes for drought tolerance", *Intl. J. Res. Granthaalayah*, (4) 2:184-196
- Mwadingeni, L., Shimelis, H., Dube, E., Laing, M.D. & Tsilo, T.J. (2015). Breeding wheat for drought tolerance: Progress and technologies. *J. Integ. Agri.*
- Nam, N.H., Subbaroa G.V., Chauhan Y.S., Johansen C. (1998). Importance of canopy attributes in determining dry matter accumulation of pigeon pea under contrasting moisture regimes. *Crop Sci.*, 38: 955-961.
- Nawaz, F., Ashraf M.Y., Ahmad R., Waraich E.A., Shabbir R.N. (2014). Selenium (Se) regulates seedling growth in wheat under drought stress. *Adv Chem.*, 2014:1–7
- Nawaz, F., Shehzad MA, Majeed S. (2020). Role of mineral nutrition in improving drought and salinity tolerance in field crops. Singapore: *Springer*; 129–147.
- Nayyar, H., Walia D.P. (2003). Water stress induced proline accumulation in contrasting wheat genotypes as affected by calcium and abscisic acid. *Biol. Plant.*, 46: 275-279.
- Nazarli, H., Faraji F. (2011). Response of proline, soluble sugars and antioxidant enzymes in wheat (*Triticum aestivum* L.) to different irrigation regimes in greenhouse condition. *Cercet Agron în Mold* 44:27–33.
- Negisho, K. and Daksa J. (2018). Morphological, Physiological, Biochemical and Molecular Responses of Wheat vs Drought Stresses: A Review. *J. of Natural Sci. Res.* (8) 9.
- Nezhadahmadi, A., Prodhon Z.H., Faruq G. (2013). Drought tolerance in wheat. *Sci. World J.*, 610721
- Nikolaeva, M.K., Maevskaya S.N., Shugaev A.G., Bukhov N.G. (2010). Effect of drought on chlorophyll content and antioxidant enzyme activities in leaves of three wheat cultivars varying in productivity. *Russ. J. Plant Physiol.*, 57:87–95
- Nouri-Ganbalani, A., Nouri-Ganbalani G., Hassanpanah D. (2009). Effects of drought stress condition on the yield and yield components of advanced wheat genotypes in Ardabil, Iran *J. Food Agric. Environ.*, 77:228–234.
- Prasad, P.V.V., Pisipati S.R., Momčilović I., Ristic Z. (2011). Independent and combined effects of high temperature and drought stress during grain filling on plant yield and chloroplast EF-Tu expression in spring wheat. *J. Agron. Crop Sci.*, 197:430–441
- Qayyum, A., Razaq A., Ahmad M., Jenks M.A. (2011). Water stress causes differential effects on germination indices, total soluble sugar and proline content in wheat (*Triticum aestivum* L.) genotypes. *Afr. J. Biotechnol.*, 10:14038–14045.
- Rhodes, D. Samaras Y. (1994). Genetic control of osmoregulation in plants. In cellular and molecular physiology of cell volume regulation. Strange, K. Boca Raton: *CRC Press*, pp. 347-361.
- Safar-Noori, M., Assaha D.V.M. and Saneoka H. (2018). Effect of Salicylic Acid and Potassium Application on Yield and Grain Nutritional Quality of Wheat under Drought Stress Condition. *C.R.C.*, 46(3), pp. 558–568 (2018).
- Schimel, J., Balsler, T.C., and Wallenstein, M. (2007). Microbial stress response physiology and its implications for ecosystem function. *Ecology*, 88, 1386–1394. doi: 10.1890/06-0219
- Shao, H.B., Liang Z.S., Shao M.A., Sun Q. (2005). Dynamic changes of antioxidative enzymes of 10 wheat genotypes at soil water deficits. *Colloids Surf. Biointerfaces*, 42:187–195.
- Sharma, P., Dubey R.S. (2005). Drought induces

- oxidative stress and enhances the activities of antioxidant enzyme in growing rice seedling. *Plant Growth Regul.*, 46: 209-221
- Sheikh, S. B., Hussain A., Hussain S. J., Wani O. A., Nabi S. Z, Niyaz A.D., Baloch F.S. and Sheikh M. (2022). Plant drought stress tolerance: understanding its physiological, biochemical and molecular mechanisms. *Biotec. Biotechnol. Equipment*, (35)1. <https://doi.org/10.1080/13102818.2021.2020161> .
- Shewry, P.R. (2007) Improving the protein content and composition of cereal grain. *J. Cereal Sci.*, 46:239–250
- Shigeoka, S., Ishikawa T., Tamoi M., Miyagawa Y., Takeda T., Yabuta Y., Yoshimura K. (2002). Regulation and function of ascorbate peroxidase isoenzymes. *J. Exp. Bot.*, 53: 1305-1319.
- Siddique, M.R.B., Hamid A., Islam M.S. (2001). Drought stress effects on water relations of wheat. *Bot. Bull. Acad. Sin.*, 41: 35-39.
- Simova-Stoilova, L., Vaseva I., Grigorova B., Demirevska K., Feller U. (2010). Proteolytic activity and cysteine protease expression in wheat leaves under severe soil drought and recovery. *Plant Physiol Biochem.*, 48:200–206
- Tefera, A., Mulugeta K., Tadesse K., and Getahun T. (2021). Morphological, Physiological, and Biochemical Characterization of Drought-Tolerant Wheat (*Triticum* spp.) Varieties. *Int. J. Agron.*, Article ID 8811749. <https://doi.org/10.1155/2021/8811749>
- Wang, H., Huang J., Li Y., Li C., Hou J., Liang W. (2016). Involvement of nitric oxide-mediated alternative pathway in tolerance of wheat to drought stress by optimizing photosynthesis. *Plant Cell Rep.*, 35:2033–2044.
- Wang, X., Vignjevic M., Jiang D., Jacobsen S., Wollenweber B. (2014) Improved tolerance to drought stress after anthesis due to priming before anthesis in wheat (*Triticum aestivum* L.) var, Vinjett. *J. Exp. Bot.*, 65:6441–6456
- Waraich, E.A., Ahmad R., Ashraf M.Y. (2011). Role of mineral nutrition in alleviation of drought stress in plants. *Aust J Crop Sci.*, 5:764–777
- Waraich, E.A., Ahmad R., Saifullah Ahmad S., Ahmad A. (2010). Impact of water and nutrient management on the nutritional quality of wheat. *J. Plant Nutr.*, 33:640–653
- Xu, Y, Xu Q., Huang B. (2015). Ascorbic acid mitigation of water stress inhibition of root growth in association with oxidative defense in tall fescue (*Festuca arundinacea* Schreb.). *Front. Plant Sci.*, 6:807
- Yadav, R.S., Hash C.T., Bidinger F.R., Devos K.M., Howarth C.J. (2004). Genomic regions associated with grain yield and aspects of post flowering drought tolerance in pearl millet across environments and tester background. *Euphytica*, 136: 265-277.
- Yu, T.F., Xu, Z.S., Guo, J.K., Wang, Y.X., Abernathy, B., Fu, J.D., Chen, X., Zhou, Y.B., Chen, M., Ye, X.G. & Ma, Y.Z. (2017). Improved drought tolerance in wheat plants over expressing a synthetic bacterial cold shock protein gene SeCspA. *Scientific Rep.*
- Zahoor, A., Waraich E.A., Akhtar S, Anjum S., Tanveer A., Mahboob W., Bin Abdul Hafeez O., Terence T., Labuschagne M., Rizwan M., (2018). Physiological responses of wheat to drought stress and its mitigation approaches. *Acta Physiologiae Plantarum*, 40:80. <https://doi.org/10.1007/s11738-018-2651-6>.