

Review Article

Drought stress and its tolerance mechanism in wheat

Abstract

Plants encounter diverse forms of stress in response to fluctuations in their surrounding environment. Drought is a very detrimental environmental stressor that negatively impacts crop *Plants*. The phenomenon of drought stress in *Plants* is characterized by its intricate nature, arising from many environmental factors, including limited soil water availability, elevated soil salinity levels, and increased ambient temperature. The latter is referred to as physiological drought. The wheat plant exhibits high sensitivity to dry conditions, particularly during the flowering and grain-filling stages. The phenomenon led to a significant decline in the growth and production of wheat crops. Water stress during crucial growth stages, including tillering, grain filling, and flowering, has been identified as a significant factor leading to substantial reductions in crop output. Drought stress in wheat induces morphological, physiological, biochemical, and molecular alterations. *Plants* employ three fundamental survival strategies, stress avoidance, escape, and tolerance, in response to drought-induced stress. The cultivation of drought-tolerant cultivars and the implementation of agronomic practices play a crucial role in the development of novel water-use strategies for effective drought management. Drought tolerance is a multifaceted characteristic governed by multiple genes, with their expressions modulated by diverse environmental factors. Therefore, the challenge of breeding for this particular trait is considerable, necessitating the utilization of novel molecular techniques such as molecular markers, quantitative trait loci (QTL) mapping procedures, and gene expression patterns to generate genotypes that exhibit tolerance to drought conditions. Wheat possesses multiple genes that contribute to drought stress tolerance by encoding various enzymes and proteins, such as late embryogenesis abundant (LEA), abscisic acid-responsive (RAB), rubisco, helicase, proline, glutathione-S-transferase (GST), and carbohydrates, which are involved in mitigating the effects of drought stress. This review paper has focused on examining the impact of water limitation on several aspects of wheat, including its morphology, physiology, biochemistry, and molecular

responses. Additionally, it explores the potential losses incurred by wheat due to drought-induced stress.

Keywords: Crop growth, Drought stress, Quantitative trait loci (QTLs), Reactive oxygen species.

INTRODUCTION

Wheat, scientifically known as *Triticum aestivum* L., is a prominent cereal crop crucial in sustenance for approximately one-fifth of the global population (FAO, 2011). According to Foresight (2011), there is a pressing need to double wheat output by the year 2050 to meet the growing demands of a rapidly increasing global population. Common wheat serves as the primary crop in a total of forty-three nations. The escalating impacts of climate change have led to a rise in severe natural occurrences, hence exacerbating environmental strain. This strain has emerged as a prominent factor contributing to global crop depletion, with significant annual reductions in yield exceeding 50% for essential agricultural commodities (Chaves and Oliveira, 2004). The irregularity of the monsoon has been observed to impact the exacerbation of drought conditions significantly. According to Singh and Bhalla (1994), following illnesses, drought stress is the second most significant limitation to crop productivity. According to a global-scale study conducted by Cumani and Rojas (2016), the regions prone to agricultural drought include eastern and southern Africa, the Mediterranean region, the western United States, South American countries, India, China, and Sri Lanka. The frequency of drought occurrences in South and Southeast Asia is increasing. According to Miyan (2015), several countries, including Bangladesh, Nepal, Bhutan, Cambodia, and the Philippines, are in the monsoon climate zone. The adverse impact of drought is more severe on the agriculture sector and the overall livelihood of developing nations (Cumani and Rojas, 2016). Drought stress can be characterized as a deficiency of water leading to significant alterations in morphology, biochemistry, physiology, and molecular processes (Sallam *et al.*, 2019). Drought stress in *Plants* is characterized by many symptoms, including reduced leaf water potential and turgor pressure, stomatal closure, and decreased cell development and enlargement (Farooq *et al.*, 2009). The crop's performance is influenced by the presence of water during many crucial stages (Jamal *et al.*, 1996). The occurrence of moisture stress has been observed to have a detrimental impact on various plant characteristics, including biomass production, tillering capacity, grains per spike, and grain size. The impact of moisture stress is influenced by the extent and duration of the stress (Bukhat,

2005). The occurrence of water stress during later stages of growth can lead to a reduction in both the quantity and weight of kernels per ear (Gupta *et al.*, 2001). Drought stress can result in crop losses at any point throughout the growing season (Blum, 2005). However, its most significant impact on reducing crop output occurs during the anthesis stage. The occurrence of water stress during the anthesis stage of plant growth has been found to have a detrimental effect on the pollination process, reducing the number of grains produced per spike and subsequently decreasing overall grain production. Providing sufficient water either during or after the process of anthesis enables the plant to augment its photosynthetic rate and extend the duration of glucose translocation to the grains (Zhang and Oweis, 1998).

Consequently, this leads to more prominent grains and an increase in overall grain yield. Drought conditions occurring throughout crucial growth stages, including tillering, booting, earing, anthesis, and grain formation, reduces radiation utilization efficiency, ultimately leading to a decline in growth rate. The crop's performance is contingent upon the presence of water during these crucial periods (Jamal *et al.*, 1996). The response of *Plants* to drought is determined by multiple criteria, such as growth rate, severity of the drought, genotype of the plant, duration of the stress period, activity of the photosynthetic machinery, respiration, transpiration, and prevailing environmental circumstances. Nezhadahmadi *et al.* (2013) have identified multiple genes in wheat that enhance tolerance to drought stress. These genes are responsible for the production of various enzymes and proteins, including late embryogenesis abundant (LEA), responsive to abscisic acid (Rab), rubisco, helicase, proline, glutathione-S-transferase (GST), and carbs. Three recognized mechanisms exist for mitigating drought stress's effects: tolerance, escape, and avoidance. Implementing avoidance or tolerance mechanisms can mitigate the adverse impacts of drought on plant species. The capacity of *Plants* to maintain a high water potential in conditions of limited water supply in the soil, hence preventing dehydration, is referred to as drought avoidance. The concept of tolerance to dehydration in *Plants* refers to their capacity to endure minor water damage and internal water deficiencies. An alternative approach to addressing the issue of drought is the concept of seeking refuge or relocating. This is the location where the plant concludes its life cycle well in advance of the initiation of a drought event. In order to address the issue of drought, it is imperative to use an interdisciplinary strategy encompassing several fields, such as *Agronomy*, plant breeding, plant physiology, plant biotechnology, water engineering, and related disciplines. This comprehensive approach is

essential for developing creative strategies and techniques to optimize water usage. Agronomic approaches such as mulching, conservation tillage, intercropping, early sowing, crop selection and variety selection, and micro-irrigation have been identified as effective strategies for enhancing crop resilience in drought conditions. Researchers are currently working on developing drought-tolerant wheat cultivars through contemporary methodologies, including physiological trait-based breeding, molecular breeding, marker-assisted backcrossing, aerial phenotyping, water budgeting, and resource allocation (Ahmad *et al.*, 2018). This review aims to compile relevant information about the impact of drought stress on the growth and production of wheat.

1. Responses of Wheat Plants to Drought Stress

Determining the impact of drought on wheat output, in conjunction with several co-varying elements such as phenological phases, agroclimatic areas, and soil texture, is a challenging task, unlike other crops. This complexity arises due to the intricate structure of the relationship, as highlighted by Hasanuzzaman *et al.* (2014) and Daryanto *et al.* (2016). Drought stress frequently intersects with other stressors, such as elevated temperatures, exacerbating the overall impact. According to a recent study conducted by Daryanto *et al.* (2016), it was found that a mere 40% loss in soil moisture might lead to a significant decrease of approximately 21% in wheat yield. The decline in wheat production caused by drought can be attributed to various factors, including diminished cell division and growth, decreased photosynthetic activity, membrane deterioration, impaired water and nutrient absorption and distribution, aberrant reproductive growth, and oxidative stress (Hasanuzzaman *et al.*, 2014).

1.1. Effect of drought on Seed Germination

The seed germination process is the initial and pivotal phase in the life cycle of a plant. The determination of eventual growth aspects of a seed is crucial for its survival as a healthy seedling. If this critical phase is disrupted, it may lead to significant harm to the plant's growth, development, and productivity. Several factors can impact the process of seed germination. Like other cereal crops, wheat seed germination is contingent upon essential factors such as moisture, air, light, temperature, and various other variables. In conditions characterized by a scarcity of water, seeds encounter a lack of moisture that impedes the process of seed imbibition, which is a

crucial requirement for the proper initiation of germination. Several studies have elucidated the adverse effects of drought stress on the germination of wheat seeds. Several critical parameters that indicate germination characteristics have been extensively investigated by researchers (Timmus *et al.*, 2014). These parameters include mean germination time (MGT), time to 50% emergence (E50), coefficient of uniformity of emergence (CUE), mean daily germination (MDG), germination index (GI), coefficient velocity germination (CVG), and final germination percentage (FGP). Farooq *et al.* (2013) observed a delay in the mean emergence time (MET) and E50 of two wheat types when grown under conditions where the soil's water retention capacity was maintained at 35%. According to Timmus *et al.* (2014), the germination rate of the Stava cultivar was 50% under drought conditions, while in the control group of *Plants* that were irrigated, the germination rate was 72%. The research mentioned above demonstrates that drought stress greatly disrupts the process of wheat seed germination.

1.2. Effect of drought on Plant Growth

The detrimental impact of drought stress on plant growth has long been recognized, except for xerophytes. Wheat, a crop that exhibits sensitivity to water supply, undergoes significant alterations in its growth patterns when subjected to drought conditions. Furthermore, the potential alterations are also influenced by factors such as the length, category, and intensity of drought, as well as the developmental stage of the *Plants*. The growth of *Plants* is influenced by both the duration and type of drought. In their study, Shamsi and Kobraee (2011) implemented a two-factor experimental design to examine the effects of three distinct wheat cultivars and three varying stages of wheat growth. Drought stress was applied during stem elongation, booting, and grain-filling stages and persisted until harvest. The study's findings indicate that *Plants* experiencing water stress during stem elongation had more significant negative impacts than the two other growth stages. The height of *Plants* experiencing drought decreased by 35% and 23% during the stem elongation and booting stages, respectively. However, *Plants* subjected to dehydration during the grain-filling stage exhibited a comparatively minor reduction in height, with just a 7% decrease. In a study conducted by Shahbaz *et al.* (2011), it was shown that the growth of wheat types was significantly hindered under drought conditions for seven weeks. This hindrance was evident in various aspects, including a notable decrease in shoot length, shoot fresh weight (FW), shoot dry weight (DW), root fresh weight (FW), and root dry weight (DW).

Previous studies have documented decreased root and shoot growth in various wheat cultivars when subjected to prolonged drought conditions (Abdel-Motagally and El-Zohri, 2016). In the study conducted by Kang *et al.* (2012), it was observed that the fresh weight (FW) and dry weight (DW) of seedlings exhibited a decrease after a three-day exposure of wheat seedlings to a 15% polyethylene glycol (PEG) solution. Alavi *et al.* (2014) observed comparable decreases in plant height, fresh weight (FW), dry weight (DW), relative dry weight increase rate (RDIR), and root length in wheat *Plants* subjected to PEG treatment for a duration of 2 to 8 days.

1.3. Effect of drought on Plant Water Relations

Water is an essential constituent necessary for the sustenance of all organisms, encompassing both flora and fauna. Based on the *Food and Agriculture Organization* (FAO, 2015) findings, the wheat plant requires a range of 450-650 mm of water to optimize its growth and output. The specific water requirements are contingent upon the prevailing climate conditions and the plant's growth cycle duration. During drought, *Plants* face challenges in meeting their substantial water requirements. Consequently, cellular-level damage ensues in *Plants*, resulting in diminished crop productivity or possibly plant mortality. In a study conducted by Akram (2011), various parameters, including relative water contents (RWC), water potential (Ψ_w), osmotic potential (Ψ_s), and turgor potential (Ψ_p), were examined in two different wheat cultivars. The study observed that *Plants* experiencing drought stress exhibited a decrease in relative water content (RWC) and other related indicators. However, Inqlab-91, in contrast, demonstrated higher RWC and Ψ_w levels, indicating a greater tolerance to drought conditions. In a study conducted by Wang *et al.* (2010), it was shown that the leaf relative water content (RWC), water potential (Ψ_w), and osmotic potential (Ψ_s) of wheat seedlings decreased during a brief period of drought exposure lasting approximately 6-7 days.

Furthermore, the researchers conducted measurements of osmotic adjustment (OA), which refers to the disparity in water potential at full turgor between seedlings subjected to stress and those not. In a recent Bukhari *et al.* (2015) study, the researchers examined various parameters in two distinct wheat cultivars. Their findings revealed that the tolerant cultivar, Chakwal-50, had significantly higher values for relative water content (RWC), water potential (Ψ_w), osmotic potential (Ψ_s), and turgor potential (Ψ_p) in comparison to the sensitive cultivar Sehar-06. Similar findings were documented in other trials involving different wheat cultivars and varying

durations of drought (Yavas and Unay, 2016). Nevertheless, when considering water use efficiency (WUE), it has been seen that a brief duration of drought exposure (specifically, ten days) led to a decrease in WUE, according to Timmus *et al.* (2014). In contrast, a longer duration (49 days) increased WUE, as reported by Shahbaz *et al.* (2011). This is because water usage efficiency (WUE) is defined as the disparity between the overall dry mass of a plant and the total amount of water utilized.

1.4. Effect of drought on Nutrient Uptake by the plant

Plants want adequate water within their rhizosphere to facilitate the absorption of vital nutrient ions from the soil. Consequently, water scarcity significantly impacts nutrient absorption by plant roots (Nawaz *et al.*, 2015). In a study conducted by Shahbaz *et al.* (2011), the concentrations of crucial fundamental elements (nitrogen, phosphorus, and potassium) were assessed in wheat seedlings' shoots and roots following a drought stress lasting seven weeks. The findings of their study demonstrated a considerable reduction in both phosphorus (P) and potassium (K) levels in both the shoot and root tissues under water deficit conditions. Additionally, it was observed that the nitrogen (N) content declined significantly only in the root tissue. However, Hafez and Gharib (2016) found in their latest study that the nitrogen content exhibited a drop in both the grain and straw due to the imposition of drought stress. Bukhari *et al.* (2015) also documented decreased phosphorus and potassium intake in response to drought stress. In their study, El Tayeb and Ahmed (2010) examined the secondary essential elements, namely Ca^{2+} , Mg^{2+} , and K^+ . They observed a decrease in the levels of these elements in both the shoot and root after 14 days under a 30% field capacity (FC) condition. The study conducted by Bukhari *et al.* (2015) yielded comparable findings for Mn^+ , Zn^{2+} , and Si. Additionally, similar results were seen in the research conducted by Nawaz *et al.* (2015) for Na^+ and Ca^{2+} . A study conducted by Nawaz *et al.* (2015) showed that the absorption of $\text{Fe}^{2+}/\text{Fe}^{3+}$ was decreased in the presence of drought conditions.

1.5. Effect of drought on Photosynthesis

Photosynthesis is an exceptional mechanism of light absorption in *Plants*, intricately associated with the development and viability of plant organisms. The primary requirement for photosynthesis is the presence of water and carbon dioxide. Drought stress induces a deficiency

in water availability to *Plants*, impeding the generation of carbohydrates through photosynthesis. Drought stress has a significant impact on various parameters that drive photosynthesis. In their study, Wang *et al.* (2010) documented a decrease in various photosynthetic gas exchange parameters, such as net photosynthesis rate (Pn), transpiration rate (Tr), stomatal conductance (gs), and intercellular CO₂ concentration (Ci), in the flag leaves of wheat seedlings that were exposed to drought stress for 6-7 days. Other researchers have also shown similar reductions in the case of Pn (Prasad *et al.*, 2011), gs (Timmus *et al.*, 2014), or both Pn and gs (Wei *et al.*, 2013). In a recent study conducted by Nawaz *et al.* (2015), it was shown that wheat seedlings cultivated under 60% field capacity (FC) for the entire duration of the growth period saw a reduction of 43% in photosynthetic rate (Pn), 30% in transpiration rate (Tr), and 27% in stomatal conductance (gs). According to Timmus *et al.* (2014), the net assimilation rate (NAR) exhibited a notable decrease in both sensitive and tolerant cultivars when subjected to a period of water scarcity lasting for ten days, namely from 10 days after sowing (DAS) to 20 DAS. Photosynthetic pigments, including chlorophyll (chl) a chlorophyll (chl) b, and carotenoids, play a crucial role in facilitating photosynthesis. Any decrease in the levels of chlorophyll content can disrupt the photosynthetic process. Abdel-Motagally and El-Zohri (2016) observed a decrease of 26% in chlorophyll a and 18% in chlorophyll b levels in wheat *Plants* subjected to drought stress over the entire growth period. In contrast, Alavi *et al.* (2014) observed a 25% decrease in chlorophyll content in wheat seedlings after a period of 3-day exposure to artificial drought induced by polyethylene glycol (PEG).

1.6. Effect of drought on Reproductive Growth

Drought stress in wheat has been found to harm the life cycle and duration of grain filling. According to previous studies conducted by Madani *et al.* (2010) and Wei *et al.* (2010), the grain filling time of wheat is shortened under situations of limited water availability due to a combination of factors, including reduced photosynthesis, accelerated leaf senescence, and decreased sink activity. Consequently, this reduction in the grain filling period ultimately leads to a drop in grain size. The early microspore phase of pollen development is a critical step frequently impacted by drought stress, resulting in pollen sterility and a subsequent decrease in grain production (Ji *et al.*, 2010). Meiosis and anthesis failure due to drought conditions have been found to harm grain number. It ultimately leads to reduced grain production, as observed by

Cattivelliet al. (2008). According to Manjarrez-Sandoval et al. (1989), the occurrence of drought stress during the meiosis phase of pollen mother cells disrupts the process of microsporogenesis, leading to the sterility of pollen and a significant decrease of 40-50% in grain set. During the transition from the initial phases of growth to maturity, drought significantly reduced wheat yield, ranging from 27% to 37% (Shamsi and Kobraee, 2011). During the heading stage, the impact of drought stress on wheat resulted in a significant drop of 57% in yield, as Balla et al. (2011) reported. According to the findings of Raza et al. (2012), the application of drought stress throughout the tillering, flower initiation, and milking stages has resulted in a decrease in the uptake of nitrogen (N), potassium (K), and sodium (Na), as well as a reduction in photosynthesis, therefore impeding the production of grain. According to Dhanda and Sethi (2002), prolonged mild stress resulted in a significant reduction in yield, ranging from 58% to 92%, namely during the heading and grain filling period. According to Majid et al. (2007), drought stress prior to anthesis reduced yield from 18% to 53%. During the period of anthesis, Akram (2011) documented a decrease of 8% in grain yield, Sangtarash (2010) saw a fall of 19%, in grain output. According to Gúoeth et al. (2009), the crop yield can be reduced by 9-78% due to a drought spell during the grain-filling stage, depending on the intensity and duration of the stress.

1.7. Effect of drought on Yield

Scarcity of water or drought stress is one of the vital environmental constraints affecting crop yield worldwide. Water scarcity during wheat *Plants'* vegetative and reproductive stages caused a severe reduction in grain yield (Maqbool et al., 2015). Decreasing photosynthesis rate, as well as lower growth of *Plants* induced by drought stress, is one of the significant reasons for yield loss of *Plants* (Yordanov et al. 2000). Water insufficiency at the vegetative phase is very dangerous because assimilates of the vegetative portion of *Plants* contribute in yield. On the other hand, drought stress at the reproductive phase directly hampers the yield of the plant by hindering the tiller survival rate, number of spikes, length of spike, number of fertile spikelets, grain ear-1, grain size, and weight (Hasanuzzaman et al. 2013). Prasad et al. (2011) withdrew water for 22 days from wheat *Plants* and found that the spikelet fertility rate decreased by 22% and grain number decreased by 38%. The creation of drought onset of the stem elongation stage reduced grain and biological yield by 47% and 23%, respectively (Shamsi and Kobraee 2011). Irrigation skipped at tillering, heading, or anthesis stage considerably decreased grain yield in

different wheat cultivars by hampering the yield contributing factors (Naveed *et al.* 2014). Nawaz *et al.* (2015) observed that grain weight, yield, and biological yield decreased by 39%, 40%, and 38% due to water scarcity (60% FC) in *T. aestivum* cv Pasban-90. Daryanto *et al.* (2016) recently conducted two experiments under different water deficit conditions and recorded yield reduction. Daryanto *et al.* (2016) observed that grain yield reduced by about 21% due to 40% water reduction. So, it can be concluded that wheat yield reduction depends on genotype, stress intensity, stress duration, and age of *Plants*.

2. Drought-Induced Oxidative Stress in Wheat

Drought is a significant manifestation of environmental stress that hinders various aspects of *Plants'* biochemistry and physiology. The plant's root system is the primary organ that experiences the initial impact of water scarcity during drought-induced stress. In addition to facilitating the transport of water and mineral nutrients to the leaves via the xylem sap, plant roots also transmit several stress signals (Cruz de Carvalho, 2008). In drought stress, *Plants* must employ mechanisms to mitigate excessive water loss. Under such circumstances, the hormone abscisic acid (ABA) transmits a stress signal from the plant's root to its leaves. Upon the arrival of the drought stress signal, the closing of the stomata is activated (Cruz de Carvalho, 2008).

Consequently, *Plants* adopt a water-saving strategy by controlling the aperture of their stomata, decreasing the transpiration rate and limiting the influx of carbon dioxide. Hence, the internal concentration of CO₂ experienced a decline, leading to a significant decrease in the rate at which CO₂ is reduced by the Calvin cycle. Consequently, the regeneration of NADP⁺ is hindered, resulting in an excessive reduction of the photosynthetic electron transport chain (Hasanuzzaman *et al.*, 2013). Drought stress leads to a decrease in the availability of carbon dioxide (CO₂) and hinders the process of carbon fixation. Consequently, the chloroplasts within leaf cells are subjected to an excessive amount of excited energy originating from photosystem I (PSI), leading to an augmentation in the generation of several hazardous reactive oxygen species (ROS) (Hasanuzzaman *et al.*, 2013). The excessive production of reactive oxygen species (ROS) during drought stress can be attributed to the compromised electron transport mechanisms inside the chloroplasts and mitochondria of plant cells. However, when the activity in Photosystem II (PSII) is disrupted, there is an imbalance between the production and utilization of electrons, leading to a change in the quantum yield. These alterations in chloroplast photochemistry in the

leaves of *Plants* experiencing drought stress lead to the accumulation of excessive light energy in PSII.

Consequently, this excess energy generates various free radicals or reactive oxygen species (ROS), which have the potential to cause harm and induce oxidative stress in *Plants* (Hasanuzzaman *et al.*, 2013). Reactive oxygen species (ROS) exhibit high reactivity and disrupt the normal metabolic processes of *Plants* through the peroxidation of lipids, oxidation of proteins, and damage to nucleic acids and DNA. The plant's antioxidant system is activated when the cellular redox potential is little affected by the presence of reactive oxygen species (ROS). It protects against the damage inflicted by ROS. *Plants* possess a robust array of nonenzymatic antioxidants that safeguard against oxidative stress, as indicated by Hasanuzzaman *et al.* (2012).

The occurrence of drought stress leads to a significant increase in oxidative damage. It induces changes in the antioxidant defence system, which depends on the drought's intensity and the plant's specific growth phases. Under mild stress conditions, oxidative stress markers such as MDA and H₂O₂ increased, concomitant with the plant's overexpression of some antioxidant components. However, a significant decrease in water availability has been observed to impact antioxidant activity negatively. A temporary water scarcity within a controlled setting has been observed to induce rapid changes in the physiological processes of *Plants* (Khan *et al.*, 2012). The application of 15-20% polyethylene glycol (PEG) on wheat genotypes for 24 hours resulted in a significant elevation of oxidative stress. This was shown through an increase in the membrane stability index, content of malondialdehyde (MDA), and formation of superoxide radicals (O₂⁻) (Khan *et al.*, 2012). The study conducted by Alexieva *et al.* (2001) observed that exposure to 10% polyethylene glycol (PEG) generated stress in *Triticum aestivum* (cv. Centauro) *Plants*. This stress condition was associated with elevated levels of hydrogen peroxide (H₂O₂) and reduced activities of superoxide dismutase (SOD), catalase (CAT), and peroxidase (POX). In addition to short-term severe drought stress, *Plants* exhibit comparable oxidative damage under long-term low-level water scarcity conditions. In the study conducted by Ibrahim (2014), irrigation was intentionally delayed throughout the late tillering to early flowering stage of *Triticum aestivum* (cv. Giza 168). The researcher noted significant MDA, H₂O₂, and proline (Pro) levels, increase by 194%, 93%, and 193%, respectively.

Conversely, the membrane stability index and root viability decreased by 40% and 58%, respectively. The activities of CAT and SOD also decreased by 46% and 42% respectively. However, the activity of POD (guaiacol peroxidase) exhibited a notable increase of 178%. Additionally, the ascorbate (AsA) content decreased, while the glutathione (GSH) and α -tocopherol contents increased. Similarly, Naveed *et al.* (2014) observed a significant rise in lipid peroxidation and proline content by 216% and 22%, respectively, in response to water scarcity stress, namely the omission of irrigation during the flowering stage. The authors also reported that the levels of catalase (CAT), glutathione reductase (GR), and ascorbate peroxidase (APX) activities exhibited a significant rise of 75%, 145%, and 235%, respectively. Nawaz *et al.* (2016) have identified alterations in Pro, phenol, protein, free amino acid, and soluble sugar concentrations as additional indicators of drought stress in wheat *Plants*.

Furthermore, the soluble protein content of the root and shoot exhibited a significant rise of 97% and 29%, respectively, in response to drought stress. Similarly, the root and shoot soluble sugar content experienced a notable increase of 269% and 51%, respectively, under the influence of drought stress. However, a study by Karmollachaab and Gharineh (2015) demonstrated that prolonged exposure to drought stress, specifically using PEG at a concentration of 20% for 42 days, significantly reduced leaf-soluble sugar levels. Consequently, there was a substantial rise in electrolyte leakage by 291% and proline content by 262%. In a study conducted in 2013, Farooq *et al.* observed that the retention of 35% water holding capacity in soil resulted in a 23% reduction in membrane stability index and a 37% increase in MDA content compared to the control plant. An increase of 30% in soluble phenolics and 57% in leaf-free Pro content was also detected. The extent of oxidative damage in wheat *Plants* resulting from drought stress is primarily contingent upon the severity of water shortage, the developmental stage of the plant, and the duration of the stress period.

3. Management of drought stress

3.1. Agronomic management of drought stress

Drought management strategies safeguard water resources, including precipitation, irrigation water, and snow. Drought stress mitigation in wheat can be achieved by utilizing drought-tolerant wheat genotypes and implementing appropriate agronomic practices, such as modifying

plant density, sowing time, and soil management techniques. These strategies must be designed to guarantee the alignment of the crop-sensitive stages of wheat development with a period of minimal drought risk. According to Hussain *et al.* (2019), implementing agronomic techniques such as optimizing irrigation water usage, adjusting sowing times, and employing seed priming can effectively alleviate the adverse impacts of drought. Seed priming is a technique that enhances the vigour, germination, and emergence of seedlings. According to Rakshit *et al.* (2020), using mulches restricts the growth of weeds by reducing the amount of light that reaches the soil.

Consequently, this practice enhances the availability of water to crop *Plants*, particularly in drought situations. Surface residue plays a crucial role in mitigating evaporation throughout the growing season. Drought management approaches primarily focus on optimizing soil moisture extraction, promoting effective crop establishment, enhancing biomass production, facilitating growth, and maximizing grain yield. During periods of water scarcity, it is imperative to prioritize the preservation of yield stability. The implementation of crop rotation and diversification practices has been found to contribute to the conservation of water resources. Crop rotation is believed to contribute to the improvement of water retention in soils, as well as the increase in crop production and biomass (Pierce and Rice, 1988).

Similarly, applying macro and micronutrients externally to wheat has been found to enhance its capacity to withstand drought conditions. The utilization of exogenous silicon (Si) has been employed to mitigate the impacts of drought on wheat, as demonstrated by Gautam *et al.* (2016). According to Ma *et al.* (2016), the application of silicon (Si) on *Plants* resulted in increased antioxidant activity, elevated levels of photosynthetic pigments, and alterations in the expression of genes associated with the ascorbate-reduced glutathione cycle, flavonoid biosynthesis, and antioxidant response. In drought-induced stress, applying an appropriate quantity of nitrogen fertilizer has been observed to facilitate the augmentation of re-mobilization and grain-filling processes. This, in turn, mitigates the negative impact of diminished photosynthesis and reduced grain filling (Yang and Zhang, 2006). Applying organic manure has positively impacted the soil's ability to retain water. Consequently, applying organic manure to the wheat field enhances the susceptibility of crops to drought, thus affecting their output.

3.2.Drought tolerance in wheat

In an ecosystem characterized by limited water availability, escaping drought is a crucial adaptation for ensuring survival. The phenomenon of a plant's capacity to survive in an arid climate is commonly known as drought tolerance. Drought tolerance is a multifaceted polygenic trait wherein multiple factors contribute to a plant's capacity to endure drought. The phenomenon of drought significantly influences various levels of plant biology, including cellular, tissue, and organ levels (Beck *et al.*, 2007). Drought-tolerant *Plants* respond to drought conditions by engaging many defence mechanisms, the comprehensive understanding of which is crucial for developing drought-tolerant cultivars (Chaves and Oliveira, 2004). Farooq *et al.* (2009) stated that drought resistance can be attributed to various morphological, physiological, and molecular adaptations. Drought escape is a morphological process characterized by the capacity of *Plants* to successfully undergo their life cycle prior to the commencement of the drought period (Mitra, 2001). Drought avoidance pertains to the capacity of a plant to enhance water retention by augmenting water absorption and reducing water loss through decreased transpiration. This is facilitated by the plant's extensive and compact root system and specific leaf and stomatal characteristics. Osmotic adjustment (OA) is a vital mechanism that enables the reduction of a cell's osmotic potential while preserving turgor, hence facilitating the survival of *Plants* in water-limited environments (Farooq *et al.*, 2009). The presence of a waxy coating, known as glaucousness, on the cuticle of wheat *Plants* has been recognized as a viable means of enhancing water usage efficiency and providing mechanisms for drought tolerance. Drought tolerance indicators offer an enhanced opportunity for selecting genotypes that exhibit favourable performance under optimal and stress-induced circumstances. Scientists have devised multiple methodologies for assessing drought tolerance as a selection factor.

3.2.1. Various approaches to induce drought tolerance in wheat

3.2.1.a. Molecular breeding for drought tolerance in wheat

Drought tolerance is a well-reported quantitative trait in several plant species. Drought tolerance can be understood conceptually as a crucial adaptation that facilitated the shift of *Plants* from aquatic to terrestrial environments. The primary function of drought tolerance was to enable this change (Bowles *et al.* 2021). Several quantitative trait loci (QTLs) are linked with several aspects related to drought tolerance. These include root architecture, plant biomass, water-soluble carbohydrates, membrane stability index, and grain production. Specific Quantitative Trait Loci

(QTLs) have been found to exhibit associations with agronomic or physiological characteristics related to drought-induced stress. These QTLs have the potential to account for a substantial proportion, up to 20%, of the observed phenotypic variation for each particular trait being studied (Bennani, 2022). Luo *et al.* (2021) conducted an analysis employing QTL mapping to examine the presence of genes associated with drought resistance in wheat. Identifying quantitative trait loci (QTLs) linked to drought resistance holds significant significance in crop breeding, as it offers essential focal points for genetic enhancement tactics. The investigation and analysis of quantitative trait loci (QTL) have demonstrated their efficacy in examining and dissecting QTL. Many studies have extensively utilized crop gene exploration (Liu *et al.*, 2019). Significant efforts have been made in wheat research to uncover quantitative trait loci (QTLs) correlated with drought resistance. The researchers have specifically directed their attention towards physiological characteristics, such as net photosynthesis, relative water content, and cell membrane stability (Gupta *et al.*, 2017). A wide array of drought tolerance characteristics are linked to many quantitative trait loci (QTLs). Luo *et al.* (2021) have found many quantitative trait loci (QTLs) that may account for up to 20% of the observed phenotypic variance. The utilization of genome-wide association study (GWAS) in the investigation of wheat has facilitated the identification and mapping of quantitative trait loci (QTLs) that are linked to the trait of seedling drought tolerance (Maulana *et al.*, 2020). Several significant quantitative trait loci (QTLs) linked to seedling drought tolerance were detected on chromosomes 1B, 2A, 2B, 2D, 3A, 3B, 3D, 4B, 5A, 5B, 6B, and 7B. Twelve stable quantitative trait loci (QTLs) exhibited responsiveness to drought stress across many characteristics. Notably, two of these QTLs were associated with branch length and leaf chlorophyll fluorescence, both identified as reliable indicators of drought stress tolerance. Maulana *et al.* (2020) identified some quantitative trait loci (QTLs) in wheat that exhibited co-localization with previously documented QTLs. These QTLs were associated with (i) root and shoot attributes during the seedling stage and (ii) canopy temperature during the grain-filling stage. El Gataa *et al.* (2022) revealed noteworthy single-nucleotide polymorphisms (SNPs) among candidate genes associated with plant abiotic stress responses. These findings have the potential to facilitate marker-assisted selective breeding aimed at enhancing drought resistance at the seedling stage. The study conducted by Sallam *et al.* (2022) employed a combination of Genome-Wide Association Studies (GWAS) and Quantitative Trait Locus (QTL) mapping techniques to investigate the genetic factors underlying

the characteristics of recovery and tolerance to drought in seedlings of winter wheat. The researchers identified candidate genes and SNP networks crucial in regulating these traits through this approach.

3.2.1.b.Epigenetic Modifications for drought tolerance in wheat

Epigenetics is the study of heritable phenotypic changes that do not entail altering the genetic code itself. The field of epigenetics encompasses various molecular mechanisms that contribute to the regulation of gene expression. These mechanisms include DNA methylation (Deng *et al.*, 2018), changes in histones, the presence of histone variants, and modifications of non-coding RNA molecules. These processes collectively impact the structure and accessibility of chromatin, hence influencing the interaction between transcription apparatus and genes, ultimately leading to alterations in gene expression (Kim *et al.*, 2015; Duan *et al.*, 2018). A growing body of research indicates the involvement of epigenetic mechanisms in the plant's response to abiotic stressors, as demonstrated by numerous investigations (Singroha and Sharma, 2019). Hence, investigating and interpreting the epigenetic mechanisms underlying plant stress response have considerable importance in developing drought-resistant crops (Chang *et al.*, 2020). *Plants* exhibit diverse short-term and long-term responses, which are contingent upon the nature of the stressor, whether it is of a permanent or temporary nature. Short-term tactics encompass modifications in plant homeostasis, whereas long-term strategies involve trans-generational alterations that entail the formation of heritable changes in gene expression. The strategy mentioned above involves the generation of novel epigenetic modifications while concurrently removing existing ones, including the upregulation of specific genes and the downregulation of others (Zhang *et al.*, 2021). Epigenetic reprogramming, which occurs in response to various environmental stimuli, significantly shapes phenotypic variety and enhances tolerance to these challenges. According to the study conducted by Priyanka et al. (2021), the epigenetic process can be delineated into three distinct stages. (i) An epigenator refers to a stimulus, such as dietary factors, environmental pollutants, radiation exposure, or hormonal influences that modifies the cellular microenvironment, leading to an epigenetic phenotype. The stimuli mentioned above that elicit a strong emotional response are temporary but persist sufficiently to begin the epigenetic mechanism. (ii) The epigenetic initiator is responsible for

converting the epigenator signal into an alteration of chromatin that is epigenetic. The process of epigenetic initiation involves the priming of an epigenator, which then designates the specific chromosomal site to be marked. (iii) The epigenetic maintainer is responsible for preserving the chromatin environment across present and future generations. The maintenance of the chromatin configuration may necessitate collaborative efforts between the initiator and maintainer.

3.2.1.c. Histone Modifications for drought tolerance in wheat

According to Bandurska (2022), *Plants* can retain information on abiotic stress at initial exposure, enhancing their tolerance towards such stress when reencountered. The process of memorization facilitated by modifications to DNA and histones involves several mechanisms:

1. The enhancement of small RNAs, such as micro-RNAs (miRNAs) and short-interfering RNAs (siRNAs)
2. The suppression of repressor proteins that impede transcription
3. The suppression of specific siRNAs, which in turn promotes the activation of factors necessary for the regulation of plant hormones and transcription

In the model plant *Arabidopsis*, it has been demonstrated that long non-coding RNAs (lncRNAs) have a role in modulating the expression of stress-responsive genes by facilitating DNA de novo cytosine methylation. This process occurs through the RNA-directed DNA methylation (RdDM) pathway and the involvement of small interfering RNAs (siRNAs). Small interfering RNAs (siRNAs) produced by RNA polymerase IV (RNAPIV) can associate with Argonaute 4 (AGO4) and form a complex with long non-coding RNAs (lncRNAs) formed by RNA polymerase II (RNAPII). This complex, known as the siRNA-AGO4-lncRNA silencing complex, then attracts the DMT domains rearranged methyltransferase 2 (DRM2) to facilitate the process of de novo cytosine methylation on DNA. According to Kong *et al.* (2020), it was shown that mutants lacking NRPD2, a crucial subunit of RNAPIV, exhibited heightened sensitivity to heat stress. This finding implies that the RdDM pathway plays a vital role in governing the plant's response to stress. The intricate interaction between histone changes and DNA methylation affords *Plants* a diverse and resilient regulatory network for transcriptional reprogramming in reaction to stress. The HDA9-PWR-ABI4 complex is pivotal in regulating the molecular response to drought stress by impeding the breakdown of ABA, leading to increased levels of active ABA. Consequently, this mechanism safeguards *Plants* from dehydration. Abscisic acid (ABA) plays a

crucial role in regulating various physiological processes, such as plant growth and development, flowering time, and determining leaf size and morphology. Additional research is necessary to have a comprehensive understanding of the mechanisms by which this intricate entity controls the genes that ABI4 activates at the chromatin level (Ali and Yun, 2020).

3.2.1.d. Chromatin Structure modification for drought tolerance in wheat

The chromatin immunoprecipitation (ChIP) technique is employed to examine the dynamic interactions between specific proteins and DNA locations. Interactions between molecules have a crucial role in many biological processes, including but not limited to replication, transcription, DNA damage repair, genome stability, and gene control (Nikitakiet *al.*, 2018). This methodology enables the investigation of several biological systems within cells based on protein-DNA interactions. The utilization of CHIP-seq technology in the analysis of chromatin in seedlings of allohexaploid wheat facilitated the identification of discrete chromatin architectural characteristics in the vicinity of different functional components, such as genes, promoters, enhancer-like elements, and transposons (Li *et al.*, 2019). A multitude of novel gene regions, as well as trans- and cis-regulatory elements, were discovered through the analysis of chromatin characteristics and their combinatorial patterns. Consistent with expectations, the subset of regulatory elements within the genome, specifically promoters and enhancer-like elements, comprising approximately 1.5% of the total genome, exhibit notable characteristics such as a pronounced level of chromatin accessibility, histone acetylation, a substantial presence of CpG islands, and relatively low levels of DNA methylation. These attributes are attributed to their association with genes predominantly residing within the A compartment (Talbert and Henikoff, 2021). An analysis of sub-genomes demonstrated a discernible focus of negative selection on sequence and chromatin characteristics that play a role in gene regulation. The differential concentration of cis-regulatory elements between enhancer-like sequences and promoters suggests that these functional components are subject to distinct transcription factors (Li *et al.*, 2019).

3.2.1.e. Use of Transcription Factors (TFs) for drought tolerance in wheat

Transcription factors (TFs) facilitate *Plants'* response to abiotic stress by initiating priming stimuli and promoting the accumulation of transcription factors and signalling chemicals in an

inactive state. According to Wiszniewska (2021), a primed state is a state of preparedness in *Plants* for subsequent stress events, enabling them to activate stress-protective mechanisms more rapidly and efficiently. Transcription factors (TFs) are pivotal components within signal transduction networks, concurrently exerting control over many pathways. This characteristic has spurred the development of pragmatic approaches to enhance plant stress tolerance by genetic engineering (Ahmed *et al.*, 2020; Manna *et al.*, 2021). Wang *et al.* (2021) discovered several crucial genes and transcription regulators that significantly govern morpho-physiological traits related to root architecture and stomatal development. These traits are essential for extracting and retaining soil moisture, making them suitable targets for molecular breeding strategies aimed at selectively breeding for drought tolerance. An instance of this is DUO-B1, a gene that encodes an APETALA2/ethylene response factor (AP2/ERF) protein, belonging to one of the most extensive families of transcription factors associated with several biological processes. AP2/ERFs were categorized into several groups based on their DNA binding domain (DBD). These groups include AP2, RAV (which is connected to Abscisic acid insensitive3/Viviparous1), DREB (specifically subgroup A1–A6), ERF (specifically subgroup B1–B6), and other groups, as described by Martignago *et al.* (2020). The RAV transcription factor family, which is highly prevalent in *Plants*, and the ethylene response (ERF) subfamily are commonly involved in phytohormone signalling, disease resistance, and response to abiotic stress. The utilization of CRISPR-Cas9 genome editing has provided evidence that the wild gene plays a significant role in regulating meristem activity and branching in orthologues derived from *Brachypodium distachyon* (L.) P. Beauv., bread wheat, and Arabidopsis. The introduction of CRISPR-induced mutations in DUO-B1 resulted in the development of minor supernumerary spikelets, an increase in the number of grains per spike, and a subsequent increase in overall yield when evaluated in field circumstances. Notably, these mutations had no discernible impact on other significant agronomic characteristics. Exploiting DUO-B1 alleles to enhance yield potential can be expanded by incorporating loci associated with enhanced photosynthesis and nitrogen use efficiency (Wang *et al.*, 2022).

CONCLUSION

Drought stress leads to a significant decline in both the growth and productivity of wheat crops. Drought stress induces a range of morphological, physiological, and biochemical alterations in

wheat. Understanding these alterations in wheat will enable researchers to discern the mechanisms underlying drought tolerance and facilitate the development of wheat cultivars with enhanced resilience to drought conditions. Wheat is susceptible to drought-induced stress, particularly during the critical flowering and grain-filling periods. Drought conditions lead to significant reductions in wheat yield, primarily due to the disruption of the equilibrium in reactive oxygen species (ROS) production inside plant cells. This disruption subsequently triggers an excessive generation of ROS, leading to the onset of oxidative stress. The detrimental effects of drought-induced reactive oxygen species (ROS) extend to several macromolecules, such as proteins and nucleic acids, leading to the eventual demise of plant cells. The potential strategy for increasing wheat's tolerance to drought is improving its antioxidative defence mechanism. The utilization of markers linked to quantitative trait loci (QTLs) presents a valuable approach for implementing marker-assisted selection (MAS) strategies to develop drought-tolerant wheat cultivars. Enhancing the accessibility of moisture to crops via diverse agronomic techniques, crop diversification, varietal improvement, water conservation and harvesting, and watershed development constitutes a crucial element in managing drought conditions. To effectively address the challenges of drought stress, it is imperative to adopt a multidisciplinary strategy encompassing all relevant components. This approach should aim to develop novel water-use strategies and promote climate-resilient agriculture. By integrating many disciplines and considering the interplay between different factors, we may effectively alleviate the adverse effects of drought stress. Drought forecasting and the early delivery of pertinent advice to farmers are crucial strategies for mitigating drought and minimizing possible economic losses.

Reference

- Abdel-Motagally FMF, El-Zohri M (2016). Improvement of wheat yield grown under drought stress by boron foliar application at different growth stages. *J Saudi Soc Agric Sci*.
- Ahmad Z, Waraich EA, Akhtar S, Anjum S, Ahmad T, Mahboob W, Hafeez OB, Tapera T, Labuschagne M and Rizwan M, (2018). Physiological responses of wheat to drought stress and its mitigation approaches. *Acta Physiologiae Plantarum*, 40, 4.

- Ahmed, R.F.; Irfan, M.; Shakir, H.A.; Khan, M.; Chen, L. 2020. Engineering drought tolerance in *Plants* by modification of transcription and signalling factors. *Biotechnol. Biotechnol. Equip.*, 34, 781–789.
- Akram M (2011). Growth and yield components of wheat under water stress of different growth stages. *Bangladesh J Agril Res* 36:455–468
- Alavi SMN, Arvin MJ, Kalantari KM (2014). Salicylic acid and nitric oxide alleviate osmotic stress in wheat (*Triticum aestivum* L.) seedlings. *J Plant Interact* 9:683–688
- Alexieva V, Sergiev I, Mapelli S, Karanov E (2001). The effect of drought and ultraviolet radiation on growth and stress markers in pea and wheat. *Plant Cell Environ* 24:1337–1344
- Ali, A.; Yun, D.J. (2020). Chromatin remodeling complex HDA9-PWR-ABI4 epigenetically regulates drought stress response in *Plants*. *Plant Signal. Behav.*, 15, 1803568.
- Balla K, Rakszegi M, Li Z, Békés F, Bencze S, Veisz O (2011). Quality of winter wheat in relation to heat and drought shock after anthesis. *Czech J Food Sci* 29:117–128
- Bandurska, H. (2022). Drought stress responses: Coping strategy and resistance. *Plants*, 11, 922.
- Beck EH, Fettig S, Knake C, Hartig K and Bhattarai T. (2007). Specific and unspecific responses of *Plants* to cold and drought stress. *Journal of biosciences*, 32, 501-510.
- Bennani, S.; Birouk, A.; Jlibene, M.; Sanchez-Garcia, M.; Nsarellah, N.; Gaboun, F.; Tadesse, W. Drought-tolerance QTLs associated with grain yield and related traits in spring bread wheat. *Plants* 2022, 11, 986.
- Blum A, 2005. Drought: Drought stress and its impact. <https://Plantstress.com/drought/>
- Bowles, A.M.C.; Paps, J.; Bechtold, U.2021. Evolutionary origins of drought tolerance in spermatophytes. *Front. Plant Sci.*, 12, 655924.
- Bukhari MA, Ashraf MY, Ahmad R, Waraich EA, Hameed M (2015) Improving drought tolerance potential in wheat (*Triticum aestivum* L.) through exogenous silicon supply. *Pak J Bot* 47:1641–1648

- Bukhat NM, 2005. Studies in yield and yield associated traits of wheat (*Triticum aestivum* L.) genotypes under stress conditions. Thesis for M.Sc., Department of Agronomy, Sindh Agriculture University Tandojam and Pakistan.
- Chang, Y.N.; Zhu, C.; Jiang, J.; Zhang, H.; Zhu, J.K.; Duan, C.G. Epigenetic regulation in plant abiotic stress responses. *J. Integr. Plant Biol.* 2020, 62, 563–580.
- Chaves MM and Oliveira MM, 2004. Mechanisms underlying plant resilience to water deficits, prospects for water-saving agriculture. *Journal of Experimental Botany*, 55, 2365-2384.
- Cruz de Carvalho MH (2008) Drought stress and reactive oxygen species: production, scavenging and signaling. *Plant Signal Behav* 3:156–165
- Cumani M and Rojas O, 2016. Characterization of the agricultural drought prone areas on a global scale. *Food and Agriculture Organization for the United States*, Rome, 30p. ISBN 978-92-5-109286-6
- Daryanto S, Wang L, Jacinthe P (2016) Global synthesis of drought effects on maize and wheat production. *PLoS One* 11:e0156362.
- Deng, J.; Kou, S.; Zhang, C.; Zou, Q.; Li, P.; Zhang, C.; Yuan, P. 2018. DNA methylation and plant stress responses. *J. Plant Physiol. Pathol.*, 6, 4
- Dhanda SS, Sethi GS (2002) Tolerance to drought stress among selected Indian wheat cultivars. *J Agric Sci* 139:319–326
- Duan, C.G.; Zhu, J.K.; Cao, X. 2018. Retrospective and perspective of plant epigenetics in China. *J. Genet. Genom.*, 45, 621–638.
- El Gataa, Z.; Samir, K.; Tadesse, W. 2022. Genetic dissection of drought tolerance of elite bread wheat (*Triticum aestivum* L.) genotypes using genome wide association study in Morocco. *Plants*, 11, 2705.
- El Tayeb MA, Ahmed NA (2010) Response of wheat cultivars to drought and salicylic acid. *Am-Euras J Agron* 3:1–7

- Eskandari H, Kazemi K (2010) Response of different bread wheat (*Triticum aestivum* L.) genotypes to post-anthesis water deficit. *Not Sci Biol* 2:49
- FAO (2011) Crop prospects and food situation. *Food and Agriculture Organization*, Rome
- FAO (2015) http://www.fao.org/nr/water/cropinfo_wheat. Accessed 15 Dec 2016
- Farooq M, Irfan M, Aziz T, Ahmad I, Cheema SA (2013) Seed priming with ascorbic acid improves drought resistance of wheat. *J Agron Crop Sci* 199:12–22
- Farooq M, Wahid A, Kobayashi N, Fujita D and Basra SMA, 2009. Plant drought stress: Effects, mechanisms and management. *Agronomy for sustainable development*, 29, 185-212.
- Foresight (2011) The future of food and farming: challenges and choices for global sustainability. Final project report. The Government Office for Science, London
- Gautam P, Lal B, Tripathi R, Shahid M, Baig MJ, Raja R, Maharana S and Nayak AK, 2016. Role of silica and nitrogen interaction in submergence tolerance of rice. *Environmental and Experimental Botany*, 125, 98-109.
- Gúoth A, Tari I, Gallé A, Csiszár J, Pécsvaradi A, Cseuz L, Erdei L (2009) Comparison of the drought stress responses of tolerant and sensitive wheat cultivars during grain filling: changes in flag leaf photosynthetic activity, ABA levels, and grain yield. *J Plant Growth Regul* 28:167–176
- Gupta NK, Gupta S and Kumar A, 2001. Effect of water stress on physiological attributes and their relationship with growth and yield of wheat cultivars at different stages. *Journal of Agronomy and Crop Science*, 186, 55-62.
- Gupta PK, Balyan HS and Gahlaut V, 2017. QTL analysis for drought tolerance in wheat, present status and future possibilities. *Agronomy*, 1, 5.
- Hafez EM, Gharib HS (2016) Effect of exogenous application of ascorbic acid on physiological and biochemical characteristics of wheat under water stress. *Int J Plant Prod* 10:579–596
- Hasanuzzaman M, Hossain MA, Teixeira da Silva JA, Fujita M (2012) Plant responses and tolerance to abiotic oxidative stress: antioxidant defense is a key factor. In: Bandi V,

- Shanker AK, Shanker C, Mandapaka M (eds) Crop stress and its management: perspectives and strategies. *Springer*, Berlin, pp 261–316
- Hasanuzzaman M, Nahar K, Gill SS, Fujita M (2014) Drought stress responses in *Plants*, oxidative stress and antioxidant defense. In: Tuteja N, Gill SS (eds) Climate change and plant abiotic stress tolerance. *Wiley, Weinheim*, pp 209–250
- Hussain S, Hussain S, Qadir T, Khaliq A, Ashraf U, Parveen A, Saqib M and Rafiq M, 2019. Drought stress in *Plants*. An overview on implications, tolerance mechanisms and agronomic mitigation strategies. *Plant Science Today*, 6, 389-402.
- Ibrahim HM (2014) Selenium pretreatment regulates the antioxidant defense system and reduces oxidative stress on drought-stresses wheat (*Triticum aestivum* L.) *Plants. Asian J Plant Sci* 13:120–128
- Jamal M, Nazir MS, Shah SH and Ahmed N, 1996. Varietal's response of wheat to water stress at different growth stages III. Effect on grain yield, straw yield, harvest index and protein content in grains. *Rachis*, 2, 38-45.
- Ji X, Shiran B, Wan J, Lewis DC, Jenkins CLD, Condon AG, Richards RA, Dolferus R (2010) Importance of pre-anthesis anther sink strength for maintenance of grain number during reproductive stage water stress in wheat. *Plant Cell Environ* 33:926–942
- Kang G, Li G, Xu W, Peng X, Han Q, Zhu Y, Guo T (2012) Proteomics reveals the effects of salicylic acid on growth and tolerance to subsequent drought stress in wheat. *J Proteome Res* 11:6066–6079
- Karmollachaab A, Gharineh MH (2015) Effect of silicon application on wheat seedlings growth under water-deficit stress induced by polyethylene glycol. *Iran Agric Res* 34:31–38
- Khan SU, Bano A, Jalal-ud-din GA (2012) Abscisic acid and salicylic acid seed treatment as potent inducer of drought tolerance in wheat (*Triticum aestivum* L.) *Pak J Bot* 44:43–49
- Kim, J.-M.; Sasaki, T.; Ueda, M.; Sako, K.; Seki, M. 2015. Chromatin changes in response to drought, salinity, heat, and cold stresses in *Plants. Front. Plant Sci.*, 6, 114.

- Kong, L.; Liu, Y.; Wang, X.; Chang, C. 2020. Insight into the role of epigenetic processes in abiotic and biotic stress response in wheat and barley. *Int. J. Mol. Sci.*, 21, 1480
- Li, Z.; Wang, M.; Lin, K.; Xie, Y.; Guo, J.; Ye, L.; Zhuang, Y.; Teng, W.; Ran, X.; Tong, Y.; et al. The bread wheat epigenomic map reveals distinct chromatin architectural and evolutionary features of functional genetic elements. *Genome Biol.* 2019, 20, 139
- Liu C, Sukumaran S, Claverie E, Sansaloni C, Dreisigacker S and Reynolds M, 2019. Genetic dissection of heat and drought stress QTLs in phenologycontrolled synthetic-derived recombinant inbred lines in spring wheat. *Molecular Breeding*, 39,1-8.
- Luo L, Xia H and Lu BR, 2021. Crop breeding for drought resistance. *Frontiers in Plant Science*, 10, 314.
- Ma D, Sun D, Wang C, Qin H, Ding H, Li Y and Guo T, 2016. Silicon application alleviates drought stress in wheat through transcriptional regulation of multiple antioxidant defense pathways. *Journal of Plant Growth Regulation*, 35, 1-0.
- Madani A, Rad AS, Pazoki A, Nourmohammadi G, Zarghami R (2010) Wheat (*Triticum aestivum* L.) grain filling and dry matter partitioning responses to source: sink modifications under postanthesis water and nitrogen deficiency. *Acta Sci Agron* 32:145–151
- Manjarrez-Sandoval P, Gonzales-Hernandez VA, Mendoza-Onofre LE, Engleman EM (1989) Drought stress effects on the grain yield and panicle development of sorghum. *Can J Plant Sci* 69:631–641
- Manna, M.; Thakur, T.; Chirom, O.; Mandlik, R.; Deshmukh, R.; Salvi, P. 2021. Transcription factors as key molecular target to strengthen the drought stress tolerance in *Plants*. *Physiol. Plant.*, 172, 847–868
- Maqbool MM, Ali A, Haq T, Majeed MN, Lee DJ (2015) Response of spring wheat (*Triticum aestivum* L.) to induced water stress at critical growth stages. *Sarhad J Agric* 31:53–58

- Martignago, D.; Rico-Medina, A.; Blasco-Escámez, D.; Fontanet-Manzaneque, J.B.; Caño-Delgado, A.I. Drought resistance by engineering plant tissue-specific responses. *Front. Plant Sci.* 2020, 10, 1676.
- Maulana, F.; Huang, W.; Anderson, J.D.; Ma, X.F. 2020. Genome-wide association mapping of seedling drought tolerance in winter wheat. *Front. Plant Sci.* 11, 573786.
- Mitra J, 2001. Genetics and genetic improvement of drought tolerance in crop *Plants*. *Current Science*, 80, 758-763.
- Miyan MA, 2015. Droughts in Asian Least Developed Countries: Vulnerability and sustainability. *Weather and Climate Extremes*, 7, 8-23.
- Naveed M, Hussain MB, Zahir ZA, Mitter B, Sessitsch A (2014) Drought stress amelioration in wheat through inoculation with *Burkholderia phytofirmans* strain PsJN. *Plant Growth Regul* 73:121–131
- Nawaz F, Ahmad R, Ashraf MY, Waraich EA, Khan SZ (2015) Effect of selenium foliar spray on physiological and biochemical processes and chemical constituents of wheat under drought stress. *Ecotoxicol Environ Saf* 113:191–200
- Nezhadahmadi A, Proadhan ZH and Faruq G, 2013. Drought tolerance in wheat. *The Scientific World Journal*.
- Nikitaki, Z.; Holá, M.; Donà, M.; Pavlopoulou, A.; Michalopoulos, I.; Angelis, K.J.; Georgakilas, A.G.; Macovei, A.; Balestrazzi, A. Integrating plant and animal biology for the search of novel DNA damage biomarkers. *Mutat. Res. Rev. Mutat. Res.* 2018, 775, 21–38.
- Pierce FJ and Rice CW, 1988. Crop rotation and its impact on efficiency of water and nitrogen use. *Cropping strategies for efficient use of water and nitrogen*, 51, 21- 42.
- Prasad PVV, Pisipati SR, 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

- Priyanka, V.; Goel, N.; Dhaliwal, I.; Sharma, M.; Kumar, R.; Kaushik, P. Epigenetics: A key to comprehending biotic and abiotic stress tolerance in family Poaceae. Preprints 2021, 2021070135.
- Rakshit A, Singh HB, Singh AK, Singh US and Fraceto L, 2020. New frontiers in stress management for durable agriculture. *Springer Nature*.
- Raza MAS, Saleem MF, Ashraf MY, Ali A, Asghar HN (2012) Glycine betaine applied under drought improved the physiological efficiency of wheat (*Triticum aestivum* L.).
- Sallam A, Alqudah AM, Dawood MFA, Baenziger PS and Börner A, 2019. Drought Stress Tolerance in Wheat and Barley: Advances in Physiology, Breeding and Genetics Research. *International Journal of Molecular Sciences*, 20, 3137.
- Sallam, A.; Eltaher, S.; Alqudah, A.M.; Belamkar, V.; Baenziger, P.S. 2022. Combined GWAS and QTL mapping revealed candidate genes and SNP network controlling recovery and tolerance traits associated with drought tolerance in seedling winter wheat. *Genomics*, 114, 110358.
- Sangtarash MH (2010) Responses of different wheat genotypes to drought stress applied at different growth stages. *Pak J Biol Sci* 13:114–119
- Shahbaz M, Masood Y, Perveen S, Ashraf M (2011) Is foliar-applied glycine betaine effective in mitigating the adverse effects of drought stress on wheat (*Triticum aestivum* L.)? *J Appl Bot Food Qual* 84:192–199
- Shamsi K, Kobraee S (2011) Bread wheat production under drought stress conditions. *Ann Biol Res* 2:352–358
- Singh G and Bhalla V, 1994. Differential response of wheat genotypes to moisture stress for seed germination and early seedling growth. *Indian Journal of Agricultural Research*, 28, 99-104.
- Singroha, S.; Sharma, P. 2019. Epigenetic modifications in *Plants* under abiotic stress. In *Epigenetics*; Meccariello, R., Ed.; IntechOpen: London, UK,.

- Talbert, P.B.; Henikoff, S. 2021. The Yin and Yang of Histone marks in transcription. *Annu. Rev. Genom. Hum. Genet.*, 22, 147–170.
- Timmusk S, Abd El-Daim IA, Copolovici L, Tanilas T, Kaännaste A, Behers L, Nevo E, Seisenbaeva G, Stenstroöm G, Niinemets U (2014) Drought-tolerance of wheat improved by rhizosphere bacteria from harsh environments: enhanced biomass production and reduced emissions of stress volatiles. *PLoS One*9:e96086.
- Wang GP, Hui Z, Li F, Zhao MR, Zhang J, Wang W (2010b) Improvement of heat and drought photosynthetic tolerance in wheat by overaccumulation of glycine betaine. *Plant Biotechnol Rep* 4:213–222
- Wang, J.; Li, C.; Li, L.; Reynolds, M.; Mao, X.; Jing, R. Exploitation of drought tolerance-related genes for crop improvement. *Int. J. Mol. Sci.* 2021, 22, 10265.
- Wang, Y.; Du, F.; Wang, J.; Wang, K.; Tian, C.; Qi, X.; Lu, F.; Liu, X.; Ye, X.; Jiao, Y. Improving bread wheat yield through modulating an unselected AP2/ERF gene. *Nat. Plants* 2022, 8, 930–939.
- Wei J, Li C, Li Y, Jiang G, Cheng G (2013) Effects of external potassium (K) supply on drought tolerances of two contrasting winter wheat cultivars. *PLoS One*8:e6973
- Wiszniewska, A. 2021. Priming strategies for benefiting plant performance under toxic trace metal exposure. *Plants*, 10, 623.
- Yang J and Zhang J, 2006. Grain filling of cereals under soil drying. *New phytologist*, 169, 223-236
- Yavas I, Unay A (2016) Effects of zinc and salicylic acid on wheat under drought stress. *J Anim Plant Sci* 26:1012–1018
- Yordanov I, Velikova V, Tsonev T (2000) Plant responses to drought, acclimation, and stress tolerance. *Photosynthetica* 38:171–186
- Zhang HP and Oweis T, 1998. Water yield relation and optimal irrigation scheduling of wheat in Mediterranean regions. *Agriculture Water Management*, 38, 195-211.

Zhang, X.; Li, C.; Tie, D.; Quan, J.; Yue, M.; Liu, X. 2021. Epigenetic memory and growth responses of the clonal plant *Glechoma longituba* to parental recurrent UV-B stress. *Funct. Plant Biol.*, 48, 827–838.

UNDER PEER REVIEW