Mechanism of Wheat's Drought Tolerance: A Review

Khubaib Shakoor[1], Muhammad Irshad[2], Ghulam Hur[3], Saima Rasheed[4], Hafiza Mubeen Hayat[5], Zohaib Khan[6], Farhan Fareed Qureshi[7], Sajjad Hussain[8] and Sami Ullah[9]

https://doi.org/10.62345/jads.2023.12.2.6

Abstract

The majority of crops cultivated in tropical and subtropical regions across the world face significant risks due to climate change. Drought is one of the most critical environmental factors that might reduce agricultural productivity and yield. When crops are subjected to drought stress, they exhibit a variety of reactions on several levels, including the morphological, physiological, biochemical, and molecular levels. Polygenes regulate a sophisticated trait, drought tolerance, and a wide variety of environmental factors modulate the expression of these polygenes. In addition, drought stress affects plant protein changes, hormone composition, root depth and extension, osmotic adjustment, antioxidant generation, opening and closing of stomata, cuticle thickness, inhibition of photosynthesis, decreased transpiration, and growth may affect inhibition and chlorophyll content. In addition to various osmotic changes in their organs. Plants respond to drought by activating defense mechanisms, which cause a decrease in grain yield, changes in photosynthetic parameters, and an increase in specialized metabolic chemicals. This review article investigates water restriction and its effects on wheat's morphological, physiological, biochemical, and molecular responses concerning potential damage caused by drought stress.

Keywords: Drought Tolerance, Osmotic Adjustment, Wheat, Stomata Closure.

Introduction

Drought is one of the most prevalent environmental factors affecting plant development and growth. Drought continues to confront agricultural experts and plant breeders. By 2025, 1.8 billion people will face absolute water scarcity, and 65% of the world's population will live in water-stressed areas. Tolerance to water stress is a complex measure regulated by various factors (Seleiman et al., 2021). Tolerance includes drought avoidance and dehydration tolerance (Li et al., 2021). Root depth, water consumption, and lifestyle modifications help plants resist drought. Drought tolerance is a plant's capacity to dehydrate and grow again partly (Camaille et al., 2021). Adapting plants to drought stress is critical to developing stress-tolerant plants (Khan et al., 2021). Plant genotype, development stage, intensity and length of stress, physiological growth process

[1]*Department of Crop Genetics and Breeding, Huazhong Agricultural University Wuhan, China.*
[2]*Department of Plant Pathology, University of Agriculture, Faisalabad.*
[3]*College of Plant Science and Technology, Huazhong Agricultural University Wuhan. China.*
[4]*Department of Plant Breeding and Genetics, Pir Mehr Ali Shah, Arid Agriculture University Rawalpindi.*
[5]*Department of Horticulture, College of Agriculture, University of Sargodha.*
[6]*Department of Plant Breeding and Genetics, Pir Mehr Ali Shah, Arid Agriculture University Rawalpindi.*
[7]*Department of Plant Pathology, Pir Mehr Ali Shah, Arid Agriculture University Rawalpindi.*
[8]*Department of Plant Pathology, College of Agriculture, University of Sargodha.*
[9]*Department of Forestry, College of Agriculture, University of Sargodha. Email: samiullahzain168@gmail.com*

Compliance with ethical standards: There are no conflicts of interest (financial or non-financial). This study did not receive any funding.

(Ma et al., 2020), gene expression patterns (Laxa et al., 2019), respiration activity (Lal et al., 2021), photosynthetic machinery (Aliyeva et al., 2020) and environmental influences (Qaseem et al., 2019) might impact plants' responses to drought stress.

Drought tolerance is a plant's ability to grow and thrive despite the drought. Yield stability is linked to drought tolerance. Tolerance is complicated; plants have developed several physiological and biochemical adaptations to bestow it. Drought-tolerant accessions produce high yields even when conditions are dry. The seedling stage is the most critical time for survival (Wu et al., 2000). Later stages are less critical (Zhou et al., 2022). It is possible to increase wheat resilience to drought by addressing plant growth and development and its phenology, photosynthetic reserves, and grain filling (Bhardwaj et al., 2021). Osmoprotection in agricultural plants is achieved through osmotic adjustment and antioxidant scavenging. Other essential factors in plant drought tolerance include stress response proteins, water channel proteins, signaling pathways, transcription factors, and plant growth regulators.

In addition to various osmotic changes in their organs, drought stress may have an effect on plants in the areas of protein modifications, extension, opening and shutting of stomata, hormone composition, root depth, osmotic adjustment and antioxidant generation, suppression of plant development, reduction in transpiration, reduction in chlorophyll content, cuticle thickness, and restriction of photosynthesis (Sati et al., 2022).

Drought in Wheat

Drought is one of the essential abiotic stressors. It has a detrimental effect on at least 60 percent of wheat output in high-income nations and 32 percent of 99 million hectares in low-income in underdeveloped countries (Devaux et al., 2021). Depending on the severity of the water shortage, wheat grain production might drop by as much as 70% (Ahmad et al., 2022). Reduced output by 20.6% was recorded with a 40% water reduction (Hordofa et al., 2002). Because a lack of water during the double ridge to anthesis growth stage has a detrimental influence on the number of spikelets and, ultimately, kernels produced per spike, wheat production is particularly susceptible to the effects of a water shortage at this time. Grain production is reduced with little water since this slows the anthesis and grain filling process. Drought may reduce wheat's growth and output by decreasing turgor, stomatal conductance, photosynthesis, and leaf water potential (Herrera et al., 2022), reducing wheat's growth and yield. For this reason, the genetic development of wheat must examine wheat plant traits in response to drought stress to guarantee a fair yield under water-deficient scenarios.

The Food and Agriculture Organization of the United Nations (FAO) estimates that 480 million Africans will live in regions with acute water shortages by 2025. This region is categorized as highly water-limited (about 231661.295 square miles). Will be confronted with significant water shortages (Olivier, 2021). There are two main reasons why wheat is so essential for humanity: first, it is used as a staple food in most countries, and second, Wheat production is central to the farming practices and agricultural policies of many countries. Wheat contributes significantly to the global economy. As of 2009, the FAO estimated that 225 million hectares of agricultural land were used to grow wheat. This represents 15% of the world's arable land mass or 15 million hectares. Wheat production has to double by 2027. In 2013/14, Pakistan's wheat harvest contributed 4.44 percent to the country's gross domestic product (Saeed et al., 2022). *Triticum* wheat species are crucial to developing high-yielding cultivars and significantly contribute to human nourishment, even in water-limited settings (Tester & Langridge, 2010). Agricultural plants must strike a healthy balance between their production and the ever-increasing demand for human nourishment. As part of the "Green Revolution," high-yielding semidwarf mutants were produced to meet the ever-increasing need for human food (Buzdin et al., 2021). Research into the effects of drought aims, first and foremost, identifying genes and gene regions might facilitate the development of innovative cultivars for use in breeding programs and cultivation with a high output level in mind. Future strategies like the one proposed by Langridge and Reynolds (2021) provide a promising approach to engineering drought resistance. Some of these plants are the wild emmer wheat's forebears, which evolved without the ability to withstand drought yet nevertheless exist today.

Wheat's Physiological Basis of Drought Tolerance

The plant's physiology reacts by closing its stomata, slowing its rate of photosynthesis, experiencing oxidative stress, altering the integrity of its cell wall, and producing lethal and toxic metabolites (Bhattacharya et al., 2022) and recognizing a signal sent from the roots, losing turgor and making an osmotic adjustment, decreasing its leaf water potential, reducing its sensitivity to CO2, and slowing its rate of growth. Different physiological responses of plants, such as prospective water and high relative content and membrane integrity (Ahmad et al., 2022), have been shown to correlate with drought resistance functions in plants. Several researchers have examined membrane integrity and its role under water stress to learn about drought resistance (Ahmad et al., 2021). During early grain filling, drought stress may impair sink strength, affecting endosperm cell number and metabolic activity (Kishor et al., 2022). According to the research of Trono and Pecchioni (2022) cysteine proteinase is essential for proper plant development, growth, and adaptation to different types of stress. Wheat's leaf organs express cysteine, and their contribution to proteolysis rises under dry conditions (Shrawat et al., 2018). Cysteine's function was improved but adversely linked with the degree of drought tolerance among ten spring wheat lines (Zhang et al., 2021). Plants rely heavily on the efficiency of their transpiration (TE). Several researchers have speculated that cultivar and drought could have a role in TE (Mapuranga et al., 2022).

For this reason, choosing crops with a high TE value is the most essential step in developing drought-resistant plants. Reduced turgor pressure may affect growth, one of the physiological processes that is vulnerable to dryness. Water stress reduces turgor pressure, which stunts cell development and proliferation. Nevertheless, cell expansion may occur when turgor pressure exceeds the yield of the cell wall (Murali et al., 2021). The ability of plants to respond to water shortages via osmotic adaptation is remarkable (Ahmad et al., 2002).

Mechanisms of Tolerance Leaf Area Reduction

Plant cells shrink, and cell walls relax when water content lowers. This reduces cell volume, turgor pressure, and solute concentration. Because it covers less space, the plasma membrane thickens and compresses. Loss of this is the first biophysical response to water strand ess, and root and leaf elongation is very subtle to water deficit. Turgor-driven cell growth Because leaf growth relies on cell expansion, the two processes are comparable. Cell expansion inhibition slows leaf growth early in water deficiencies. Smaller leaf areas transpire less water, extending the soil's water supply. Reducing leaf area is a defense against drought (Ali et al., 2022).

Stomata Closure

Additional processes prevent plant desiccation when stress occurs too quickly or when the plant reaches the whole leaf area before stress. Under these conditions, leaf stomata are close to minimizing water loss through transpiration. The ability of stomata to open and close is controlled by the ability of guard cells to take in and release water. Evapotranspiration can cause guard cells in the leaf epidermis to lose turgor. Low turgor hydro causes passive stomatal closure. This closing mechanism kicks in when relative humidity levels drop below what is needed for guard cells to lose water at a rate that can be balanced by water flowing from neighboring epidermal cells.

Photosynthesis

When plants are under stress from drought, photosynthesis is one of the first and most important processes to suffer. Several factors are involved in a plant's photosynthetic response to dryness, including the location of the plant's leaves and the stage of the plant's development. A decrease in photosynthesis occurs due to drought stress affecting the proteins essential to the process, particularly ribulose-1,5-bisphosphate carboxylase/oxygenase (rubisco) (Demirevska et al., 2008). The photosynthetic reaction is based on the stress's pace, duration, and severity. For this reason, these elements determine whether or not acclimation-related mitigating activities will occur. Drought may affect photosynthesis either directly or indirectly. Suppose CO2 diffusion via stomata and mesophyll tissues is impeded, or there are other changes in the photosynthetic metabolism. In that case, the result will be an immediate reduction in CO2 availability and the associated effects. As an indirect result, oxidative stress, a primary component impacting the photosynthetic mechanism, would be negatively impacted. To preserve water status and encourage carbon absorption, a plant may lose leaves or slow its development as part of an acclimation response that indirectly affects photosynthesis (Mostofa et al., 2022).

Today, the heat-tolerant-associated physiological features seem to be an unparalleled accessibility instrument since they also display the necessary gene combination for drought tolerance. Photosynthesis is related to canopy design in the same way that drought is related to plant physiology. Since rising temperatures shorten the time that green areas remain green and decrease the leaf area index, research on quick ground cover and leaf senescence may assist in managing light intervention properties. Differences in primary and hereditary breeding objectives, such as specific leaf area, seed germination percentage, embryo size, and grain size, are observed in rapidly expanding plants. These goals include exact embryo size, leaf area, grain size, and seedling emergence rate. Wheat has diverse canopy structures; hence, enhancing light distribution mechanisms may boost light interception and radiation usage efficiency. The leaves' smaller size and more upright position in today's wheat cultivars are indicators of their greater effectiveness in absorbing radiation and using the light they receive. Enhanced wheat cultivars with enhanced light interception features would provide higher-yielding, higher-quality wheat (Wilkinson et al., 2019). Drought stress may be mitigated with additional progress made possible by optimizing light interception features. In such an approach, phenomena like dark respiration, photorespiration, and many other photosynthetic techniques may be investigated by manipulating radiation use efficiency.

Relationships with Water

The relative water content, often known as RWC, is an essential measure of water status in wheat under water deficit conditions (Pour et al., 2019). This indicator has been used in selecting drought-tolerant wheat cultivars (Paunescu et al., 2021). In wheat, the water relations, nutrient absorption, growth, and yield are negatively impacted more severely by drought-induced later in the plant's life cycle (after six weeks of emergence) than drought administered earlier (Jain et al., 2019). At the blooming stage, wheat cultivars that have been exposed to drought has significantly decreased levels of chlorophyll content, membrane integrity, and RWC (Ghasemi et al., 2022); bread wheat of four different genotypes saw a reduction in RWC of 45 percent, from 88 to 45 percent when subjected to drought stress (Sallam et al., 2019). A decreased RWC causes the stomata to shut down, slowing the photosynthesis rate. Osmotic regulation is hindered when there is a lack of water. Still, osmotic regulation may be created by alternating drying and watering, which improves a plant's ability to utilize water effectively even when there is a water shortage. High relative moisture content helps plants tolerate water deprivation by increasing osmotic control (Kartseva et al., 2021), showing a substantial association between photosynthetic rate and RWC in comparison to sensitive genotypes, drought-tolerant genotypes maintained high turgor potential and RWC, which indicated that restricting water did not have any effect on the protoplasmic structure of the plant. Contrary to sensitive genotypes, RWC and photosynthetic rate are negatively correlated (Mansour et al., 2020); under water stress, leaf turgor plays a significant function in stomatal regulation and photosynthetic activity (Habib et al., 2020).

Conversion of Signals

The process that results in the expression of genes that are responsive to drought stress agrees with the standard model of the cell. Drought-driven signal transduction mechanisms have begun to be dissected at the molecular level, primarily based on examinations of isolated drought-responsive genes, despite these studies being still in their early stages. This is mainly based on the fact that drought-responsive genes have been isolated. In numerous physiological investigations, a rise in endogenous abscisic acid levels was observed to occur due to water deficiency. Abscisic acid is believed to be implicated in signal transduction (Waseem et al., 2022). However, the fact that exogenous abscisic acid may induce drought-related genes does not certainly suggest that all of these genes are likewise controlled by abscisic acid in vivo. Many of the drought-related genes can be triggered by exogenous abscisic acid.

Natural master regulators of cellular activities and features that may be modified in response, transcription factors (TFs), can govern multistep complicated pathways by altering the fluxes of metabolites in a predictable form. This is how they can do this. The levels of transcription factors are responsible for regulating the stress-responsive pathways. Almost all research on the control of transcriptional factors has been done on the model plant Arabidopsis thaliana. Arabidopsis is known to have transcription factors (TFs) from more than 50 distinct families, each of which is transcribed by 1700 unique genes (Yang et al., 2010), abscisic acid-responsive element binding factors (AREB/ABF) are members of the basic leucine zipper (bZIP) TF family; they are involved in abscisic acid signaling under drought stress and seed maturation, AREB/ABF recognizes and binds abscisic acid-responsive two elements (ABRE) and conserves cis-element to regulate the expression of downstream genes (Soma et al., 2021), ABRE is a transcription factor that is activated in response to drought stress and confer (Wang et al., 2019), abscisic acid-independent dehydration responsive TF family is referred to as the DREB TF family (Hussain et al., 2021). These TFs serve as response regulators in conditions of drought stress and cold stress, and they are also necessary for the development of leaves, flowers, and seeds.

Signaling Pathway

Adaptive responses in plants may be roughly classified into three distinct categories: (a) osmotic homeostasis or osmotic adjustment; (b) detoxification, stress damage control, and repair; and (c) growth regulation (Punia et al., 2021), Following plant responses, drought stress signaling is again divided into three distinct functional groups: (a) detoxification stress to prevent and repair cell damage; (b) osmotic stress signaling to restore cellular homeostasis; and (c) signaling to maintain cell division and cell expansion to maintain growth. Both homeostasis and detoxification signals control physiological responses required for a plant to withstand drought and sustain growth. Protein phosphorylation is an integral part of the osmotic stress signaling process. The activation of protein kinases is seen as a reaction to osmotic stress. In response to osmotic stress, calcium signaling increases calcium-dependent protein kinases (CDPK), further controlling downstream reactions. Overexpression of CDPK protoplast constitutively controls the expression of specific genes sensitive to abscisic acid, cold, and osmotic stressors (Hussain et al., 2021). According to these results, calcium signaling is linked to gene expression induced in response to osmotic stress. Increases have been seen in the transcriptome for protein kinases such as MAPK, MAPKK, MAPKKK, and histidine kinase.

Osmotic Adjustment

In the context of osmotic adjustment, "generation of water gradient" refers to increasing water input to maintain turgor via a reduction in osmotic potential. The tissue water status may be maintained with the aid of osmotic adjustment. The buildup of solutes in cellular cytoplasm and vacuoles helps mitigate drought's negative consequences. Maintaining the physiological processes and the turgor potential with the support of osmotic adjustment provides protection (Paulino et al., 2020), enabling the organism to withstand the onslaught of the pathogen. The water status of a plant may be calculated using the plant's water potential, osmotic potential, turgor potential, and relative water content. The relative water content of a plant serves as an integrative metric for determining how well it can withstand drought. Stomata close, followed by a decrease in the buildup of carbon dioxide, which is the consequence of a decrease in the relative water content of the plant caused by drought stress. It enables plant growth and cell multiplication even in conditions of extreme water deficiency. It causes the stomata to remain partly open, allowing carbon dioxide (CO2) fixation to continue despite an inadequate water supply. Accumulating solutes or osmolytes that are compatible with the process makes it work. Osmolytes, also called osmoprotectants, are chemical compounds that are agnostic, non-toxic, and beneficial to plants. These osmolytes shield the proteins and membranes of the cells from the drying effects of the stress caused by drought. The plant can extract more of this water by adjusting its osmotic balance. Still, the overall amount of water accessible to the plant does not significantly increase. Comparing the water relations of acclimated and non-acclimated species reveals that the expense of osmotic adjustment in the leaf is counterbalanced by the fast-declining returns of the quantity of accessible water to the plant. This is because non-adjusting species cannot adjust their water relations. Research conducted by Kranzlein (2022) reveals this fact, which anybody may observe.

Role of Abscisic Acid

The manufacture of abscisic acid occurs in chloroplasts through the carotenoid route. Abscisic acid acts as a stress hormone and actively controls growth, development, and responses to stressors (Khan et al., 2020). When there is a lack of water, photosynthesis takes place in the leaf; there is a redistribution of carbon inside the mesophyll cell, an import of carbon from plant roots. There is recirculation of carbon from neighboring leaves. After the plant has been rewatered, the concentration of abscisic acid drops due to a reduction in the synthesis rate, as well as the breakdown and export of the compound from the leaf.

Antioxidant Enzymes

Crops are also subject to oxidative stress during drought, caused by generating reactive oxygen species (ROS) primarily in the plant's chloroplasts, peroxisomes, and mitochondria. This is because stomata are closing, which not only decreases the amount of net photosynthesis but also produces a restriction of CO2 levels. During periods of drought stress, several studies reported that there was a higher quantity of reactive oxygen species (ROS) as well as enhanced oxidative stress. In turn, they decrease CO2 fixation, resulting in decreased NADP+ regeneration, which increases ROS production. Because of this, the electron transport chain becomes too reduced, and the Mehler reaction allows electrons to escape into the oxygen. In wheat cultivars subjected to water stress, the Mehler reaction results in a rise of 50% in the amount of reactive oxygen species (ROS) compared to wheat cultivars that were not subjected to water stress. Because photorespiration is the dominant metabolic process when water availability is limited, it is also one of the most important contributors to the formation of ROS. During periods of drought, photorespiration results in a 70 percent increase in the formation of hydrogen peroxide (Morgun et al., 2019). ROS is responsible for inducing various signaling pathways, including defense or acclimatization mechanisms, both require hydrogen peroxides (as secondary messengers). Calcium ions and sugar inflow are engaged in the Abscisic acid-dependent signaling pathways further downstream and upstream, respectively. This pathway is also connected to the production of ROS in the body. An antioxidant enzyme system that fights off ROS under drought stress occurs to help organisms deal with the oxidative stress they experience.

On the other hand, if the drought stress is allowed to continue for an extended period, it may eventually overwhelm the system and cause cellular damage or death (Elakhdar et al., 2022). An experiment was conducted to investigate the possibility of antioxidant enzymes in determining the processes that confer drought tolerance in 10 genotypes of wheat cultivars. Five of these genotypes were resistant to drought, whereas the other five were vulnerable to the effects of dry conditions (Qayyum et al., 2021). They were all produced with regular watering as well as circumstances of water deficiency caused by a mannitol solution that was 6%. Compared to those grown in a controlled setting, the levels of catalase activity in drought-resistant genotypes were around fifty percent higher when grown in natural circumstances. Wheat seedlings with drought-tolerant genotypes showed enhanced glutathione reductase and peroxidase activity in their shoots and ascorbate peroxidase in their endosperms when subjected to water stress. It was shown that the activity of superoxide dismutase was not significantly altered. It was discovered that if three of these five enzymes were present in any genotype under water deprivation, it would likely be drought-tolerant (Casartelli et al., 2019). According to the research findings, the presence or absence of antioxidant enzymes is a beneficial factor in predicting whether a specific wheat genotype is drought-resistant or drought-susceptible. This is because the amount of superoxide dismutase was not increased in drought-tolerant plants. This might be explained by ascorbate oxidase directly reducing superoxide (Silva et al., 2019). The findings of this study suggest that genotypes with a high tolerance for drought also have a high capacity for oxidative stress tolerance.

Conclusion

Drought stress is one of the most significant constraints to agricultural production. The density of osmotic stress-related molecules and identifying their functions and positions within many biochemical, physiological, and gene regulatory networks are needed to develop improved crops with increased tolerance to drought stress. Drought affects agronomic traits differently in wheat and rice crops (Shamweira et al., 2022) because wheat responds to water deficit through better osmotic adjustment and stress recovery than rice (Du et al., 2022). Drought tolerance is a quantitative trait that is difficult to phenotyp (Saini et al., 2022). Tolerant wheat genotypes display particular physiological, morphological, biochemical, and molecular processes and traits (Pandy et al., 2022). A recent study indicates that it is challenging to cultivate drought-tolerant crops. In addition, dryness diminishes chlorophyll concentration (Mahpara et al., 2022). Wheat is a significant cereal crop that provides food for around one-fifth of the world's population. Wheat cultivar yield and quality losses may be averted by regulating and using drought-induced changes in wheat cultivars and their management strategies. In addition to discovering drought-tolerant genotypes, they are also necessary for developing screening procedures for drought-tolerant genotypes in breeding programs. Transgenic farming is a crucial alternative to the existing state of agriculture that has the potential to transform efforts to fulfill the rising food demands of the global population.

References

- Ahmad, A., Aslam, Z., Belliturk, K., Hussain, S., & Bibi, I. (2022). Soil Application of Cellulolytic Microbe–Enriched Vermicompost Modulated the Morpho-physiological and Biochemical Responses of Wheat Cultivars Under Different Moisture Regimes. *Journal of Soil Science and Plant Nutrition*, *22*(4), 4153-4167.
- Ahmad, A., Aslam, Z., Javed, T., Hussain, S., Raza, A., Shabbir, R., & Tauseef, M. (2022). Screening of wheat (*Triticum aestivum* L.) genotypes for drought tolerance through agronomic and physiological response. *Agronomy*, *12*(2), 287.
- Ahmad, A., Aslam, Z., Naz, M., Hussain, S., Javed, T., Aslam, S., & Jamal, M. A. (2021). Exogenous salicylic acid-induced drought stress tolerance in wheat (*Triticum aestivum* L.) grown under hydroponic culture. *PloS one*, *16*(12), e0260556.
- Ali, Z., Merrium, S., Habib-ur-Rahman, M., Hakeem, S., Saddique, M. A. B., & Sher, M. A. (2022). Wetting mechanism and morphological adaptation; leaf rolling enhancing atmospheric water acquisition in wheat crop—a review. *Environmental Science and Pollution Research*, 1-19.
- Aliyeva, D. R., Aydinli, L. M., Pashayeva, A. N., Zulfugarov, I. S., & Huseynova, I. M. (2020). Photosynthetic machinery and antioxidant status of wheat genotypes under drought stress followed by rewatering. *Photosynthetica*, *58*(5), 1217-1225.
- Bhardwaj, A., Devi, P., Chaudhary, S., Rani, A., Jha, U. C., Kumar, S., & Nayyar, H. (2021). 'Omics' approaches in developing combined drought and heat tolerance in food crops. *Plant Cell Reports*, 1-41.
- Bhattacharya, A. (2022). Effect of Low Temperature Stress on Photosynthesis and Allied Traits: A Review. *Physiological Processes in Plants Under Low Temperature Stress*, 199-297.
- Buzdin, A. V., Patrushev, M. V., & Sverdlov, E. D. (2021). Will Plant Genome Editing Play a Decisive Role in "Quantum-Leap" Improvements in Crop Yield to Feed an Increasing Global Human Population. *Plants*, *10*(8), 1667.
- Camaille, M., Fabre, N., Clément, C., & Ait Barka, E. (2021). Advances in wheat physiology in response to drought and the role of plant growth promoting rhizobacteria to trigger drought tolerance. *Microorganisms*, *9*(4), 687.
- Casartelli, A., Melino, V. J., Baumann, U., Riboni, M., Suchecki, R., Jayasinghe, N. S., & Heuer, S. (2019). Opposite fates of the purine metabolite allantoin under water and nitrogen limitations in bread wheat. *Plant Molecular Biology*, *99*(4), 477-497.
- Demirevska, K., Simova-Stoilova, L., Vassileva, V., & Feller, U. (2008). Rubisco and some

chaperone protein responses to water stress and rewatering at early seedling growth of drought sensitive and tolerant wheat varieties. *Plant Growth Regulation*, *56*(2), 97-106.

- Devaux, A., Goffart, J. P., Kromann, P., Andrade-Piedra, J., Polar, V., & Hareau, G. (2021). The potato of the future: opportunities and challenges in sustainable agri-food systems. *Potato Research*, *64*(4), 681-720.
- Du, L., Huang, X., Ding, L., Wang, Z., Tang, D., Chen, B., & Mao, H. (2022). TaERF87 and TaAKS1 synergistically regulate TaP5CS1/TaP5CR1-mediated proline biosynthesis to enhance drought tolerance in wheat. *New Phytologist*, *237*(1), 232-250.
- Elakhdar, A., Solanki, S., Kubo, T., Abed, A., Elakhdar, I., Khedr, R., & Qualset, C. O. (2022). Barley with improved drought tolerance: Challenges and perspectives. *Environmental and Experimental Botany*, 104965.
- Ghasemi, A., Farzaneh, S., Moharramnejad, S., Sharifi, R. S., Youesf, A. F., Telesinski, A., & Mojski, J. (2022). Impact of 24-epibrassinolide, spermine, and silicon on plant growth, antioxidant defense systems, and osmolyte accumulation of maize under water stress. *Scientific Reports*, *12*(1), 1-11.
- Habib, N., Ali, Q., Ali, S., Javed, M. T., Zulqurnain Haider, M., Perveen, R., & Bin-Jumah, M. (2020). Use of nitric oxide and hydrogen peroxide for better yield of wheat (*Triticum aestivum* L.) under water deficit conditions: growth, osmoregulation, and antioxidative defense mechanism. *Plants*, *9*(2), 285.
- Herrera, J. C., Calderan, A., Gambetta, G. A., Peterlunger, E., Forneck, A., Sivilotti, P., & Hochberg, U. (2022). Stomatal responses in grapevine become increasingly more tolerant to low water potentials throughout the growing season. *The Plant Journal*, *109*(4), 804- 815.
- Hordofa, A. T., Leta, O. T., Alamirew, T., & Chukalla, A. D. (2022). Response of Winter Wheat Production to Climate Change in Ziway Lake Basin. *Sustainability*, *14*(20), 13666.
- Hussain, Q., Asim, M., Zhang, R., Khan, R., Farooq, S., & Wu, J. (2021). Transcription factors interact with ABA through gene expression and signaling pathways to mitigate drought and salinity stress. *Biomolecules*, *11*(8), 1159.
- Jain, M., Kataria, S., Hirve, M., & Prajapati, R. (2019). Water deficit stress effects and responses in maize. In *Plant abiotic stress tolerance* (pp. 129-151). Springer, Cham.
- Kartseva, T., Dobrikova, A., Kocheva, K., Alexandrov, V., Georgiev, G., Brestič, M., & Misheva, S. (2021). Optimal nitrogen supply ameliorates the performance of wheat seedlings under osmotic stress in genotype-specific manner. *Plants*, *10*(3), 493.
- Khan, M. I. R., Palakolanu, S. R., Chopra, P., Rajurkar, A. B., Gupta, R., Iqbal, N., & Maheshwari, C. (2021). Improving drought tolerance in rice: ensuring food security through multi-dimensional approaches. *Physiologia Plantarum*, *172*(2), 645-668.
- Khan, N., Bano, A., Ali, S., & Babar, M. (2020). Crosstalk amongst phytohormones from planta and PGPR under biotic and abiotic stresses. *Plant Growth Regulation*, *90*(2), 189- 203.
- Kishor, P. B. K., Tiozon Jr, R. N., Fernie, A. R., & Sreenivasulu, N. (2022). Abscisic acid and its role in the modulation of plant growth, development, and yield stability. *Trends in Plant Science*.
- Kränzlein, M., Geilfus, C. M., Franzisky, B. L., Zhang, X., Wimmer, M. A., & Zörb, C. (2022). Physiological responses of contrasting maize (Zea mays L.) hybrids to repeated drought. *Journal of Plant Growth Regulation*, *41*(7), 2708-2718.
- Lal, M. K., Tiwari, R. K., Gahlaut, V., Mangal, V., Kumar, A., Singh, M. P., & Zinta, G. (2021). Physiological and molecular insights on wheat responses to heat stress. *Plant Cell Reports*, 1-18.

- Langridge, P., & Reynolds, M. (2021). Breeding for drought and heat tolerance in wheat. *Theoretical and Applied Genetics*, *134*(6), 1753-1769.
- Laxa, M., Liebthal, M., Telman, W., Chibani, K., & Dietz, K. J. (2019). The role of the plant antioxidant system in drought tolerance. *Antioxidants*, *8*(4), 94.
- Li, P., Ma, B., Palta, J. A., Ding, T., Cheng, Z., Lv, G., & Xiong, Y. (2021). Wheat breeding highlights drought tolerance while ignores the advantages of drought avoidance: A meta-analysis. *European Journal of Agronomy*, *122*, 126196.
- Ma, Y., Dias, M. C., & Freitas, H. (2020). Drought and salinity stress responses and microbe-induced tolerance in plants. *Frontiers in Plant Science*, *11*, 591911.
- Mahpara, S., Zainab, A., Ullah, R., Kausar, S., Bilal, M., Latif, M. I., & Zuan, A. T. K. (2022). The impact of PEG-induced drought stress on seed germination and seedling growth of different bread wheat (*Triticum aestivum* L.) genotypes. *Plos one*, *17*(2), e0262937.
- Mansour, E., Moustafa, E. S., Desoky, E. S. M., Ali, M. M., Yasin, M. A., Attia, A., & El-Hendawy, S. (2020). Multidimensional evaluation for detecting salt tolerance of bread wheat genotypes under actual saline field growing conditions. *Plants*, *9*(10), 1324.
- Mapuranga, J., Zhang, N., Zhang, L., Liu, W., Chang, J., &Yang, W. (2022). Harnessing genetic resistance to rusts in wheat and integrated rust management methods to develop more durable resistant cultivars. *Frontiers in Plant Science*, *13*.
- Morgun, V. V., Stasik, O. O., Kiriziy, D. A., Sokolovska-Sergiienko, O. G., & Makharynska, N. M. (2019). Effects of drought at different periods of wheat development on the leaf photosynthetic apparatus and productivity. *Regulatory Mechanisms in Biosystems*, *10*(4), 406-414.
- Mostofa, M. G., Rahman, M. M., Ghosh, T. K., Kabir, A. H., Abdelrahman, M., Khan, M. A. R., & Tran, L. S. P. (2022). Potassium in plant physiological adaptation to abiotic stresses. *Plant Physiology and Biochemistry*.
- Murali, M., Gowtham, H. G., Singh, S. B., Shilpa, N., Aiyaz, M., Niranjana, S. R., & Amruthesh, K. N. (2021). Bio-prospecting of ACC deaminase producing Rhizobacteria towards sustainable agriculture: A special emphasis on abiotic stress in plants. *Applied Soil Ecology*, *168*, 104142.
- Olivier, L. M. (2021). *Urban agroforestry: a regenerative approach for climate adaptation and resilience on schoolyards* (Doctoral dissertation, California State Polytechnic University, Pomona).
- Pandey, A., Khobra, R., Mamrutha, H. M., Wadhwa, Z., Krishnappa, G., Singh, G., & Singh, G. P. (2022). Elucidating the Drought Responsiveness in Wheat Genotypes. *Sustainability*, *14*(7), 3957.
- Paulino, M. K. S. S., de Souza, E. R., Lins, C. M. T., Dourado, P. R. M., de Carvalho Leal, L. Y., Monteiro, D. R., & de Carvalho Silva, C. U. (2020). Influence of vesicular trichomes of Atriplex nummularia on photosynthesis, osmotic adjustment, cell wall elasticity and enzymatic activity. *Plant Physiology and Biochemistry*, *155*, 177-186.
- Paunescu, R. A., Bonciu, E., Rosculete, E., Paunescu, G., Rosculete, C. A., & Babeanu, C. (2021). The Variability for the Biochemical Indicators at the Winter Wheat Assortment and Identifying the Sources with a High Antioxidant Activity. *Plants*, *10*(11), 2443.
- Pour-Aboughadareh, A., Omidi, M., Naghavi, M. R., Etminan, A., Mehrabi, A. A., Poczai, P., & Bayat, H. (2019). Effect of water deficit stress on seedling biomass and physio- chemical characteristics in different species of wheat possessing the D genome. *Agronomy*, *9*(9), 522.

- Punia, H., Tokas, J., Malik, A., Sangwan, S., Rani, A., Yashveer, S., & El-Sheikh, M. A. (2021). Genome-wide transcriptome profiling, characterization, and functional identification of NAC transcription factors in sorghum under salt stress. *Antioxidants*, *10*(10), 1605.
- Qaseem, M. F., Qureshi, R., & Shaheen, H. (2019). Effects of pre-anthesis drought, heat and their combination on the growth, yield and physiology of diverse wheat (*Triticum aestivum* L.) genotypes varying in sensitivity to heat and drought stress. *Scientific reports*, *9*(1), 1-12.
- Qayyum, A., Al Ayoubi, S., Sher, A., Bibi, Y., Ahmad, S., Shen, Z., & Jenks, M. A. (2021). Improvement in drought tolerance in bread wheat is related to an improvement in osmolyte production, antioxidant enzyme activities, and gaseous exchange. *Saudi Journal of Biological Sciences*, *28*(9), 5238-5249.
- Saeed, M., Ibrahim, M., Ahmad, W., Tayyab, M., Attacha, S., Khan, M. N., & Ma, C. (2022). Molecular Characterization of Diverse Wheat Genetic Resources for Resistance to Yellow Rust Pathogen (Puccinia striiformis). *Agronomy*, *12*(12), 2951.
- Saini, D. K., Chopra, Y., Singh, J., Sandhu, K. S., Kumar, A., Bazzer, S., & Srivastava, P. (2022). Comprehensive evaluation of mapping complex traits in wheat using genome- wide association studies. *Molecular Breeding*, *42*(1), 1-52.
- Sallam, A., Alqudah, A. M., Dawood, M. F., Baenziger, P. S., & Börner, A. (2019). Drought stress tolerance in wheat and barley: advances in physiology, breeding and genetics research. *International journal of molecular sciences*, *20*(13), 3137.
- Sati, D., Pande, V., Pandey, S. C., & Samant, M. (2022). Recent advances in PGPR and molecular mechanisms involved in drought stress resistance. *Journal of Soil Science and Plant Nutrition*, 1-19.
- Sciarresi, C., Patrignani, A., Soltani, A., Sinclair, T., & Lollato, R. P. (2019). Plant traits to increase winter wheat yield in semiarid and subhumid environments. *Agronomy Journal*, *111*(4), 1728-1740.
- Seleiman, M. F., Al-Suhaibani, N., Ali, N., Akmal, M., Alotaibi, M., Refay, Y., & Battaglia, M. L. (2021). Drought stress impacts on plants and different approaches to alleviate its adverse effects. *Plants*, *10*(2), 259.
- Shamuyarira, K. W., Shimelis, H., Mathew, I., Zengeni, R., & Chaplot, V. (2022). A meta-analysis of combining ability effects in wheat for agronomic traits and drought adaptation: Implications for optimizing biomass allocation. *Crop Science*, *62*(1), 139- 156.
- Shrawat, A. K., & Armstrong, C. L. (2018). Development and application of genetic engineering for wheat improvement. *Critical Reviews in Plant Sciences*, *37*(5), 335-421.
- Silva, S., de Oliveira, J. M. P. F., Dias, M. C., Silva, A. M., & Santos, C. (2019). Antioxidant mechanisms to counteract TiO2-nanoparticles toxicity in wheat leaves and roots are organ dependent. *Journal of hazardous materials*, *380*, 120889.
- Soma, F., Takahashi, F., Yamaguchi-Shinozaki, K., & Shinozaki, K. (2021). Cellular phosphorylation signaling and gene expression in drought stress responses: ABA- dependent and ABA-independent regulatory systems. *Plants*, *10*(4), 756.
- Trono, D., & Pecchioni, N. (2022). Candidate Genes Associated with Abiotic Stress Response in Plants as Tools to Engineer Tolerance to Drought, Salinity and Extreme Temperatures in Wheat: An Overview. *Plants*, *11*(23), 3358.
- Wang, W., Qiu, X., Yang, Y., Kim, H. S., Jia, X., Yu, H., & Kwak, S. S. (2019). SweetpotatobZIP transcription factor IbABF4 confers tolerance to multiple abiotic stresses. *Frontiers in Plant Science*, *10*, 630.

- Waseem, M., Ahmad, M., Saqib Naveed, M., Pasha, A., Hussain, M., Ali Zafar, S., & Rehman, R. S. (2022). Abscisic acid mediated abiotic stress tolerance in plants. *Asian Journal of Research in Crop Science*, 1-17.
- Wilkinson, A. (2019). *Improving the agronomic management and utilisation of organic bread making wheat* (Doctoral dissertation, Newcastle University).
- Wu, B. M., Subbarao, K. V., & Van Bruggen, A. H. C. (2000). Factors affecting the survival of Bremia lactucae sporangia deposited on lettuce leaves. *Phytopathology*, *90*(8), 827-833.
- Zhang, Y., Zhou, J., Wei, F., Song, T., Yu, Y., Yu, M., & Zhang, X. (2021). Nucleoredoxin gene TaNRX1 positively regulates drought tolerance in transgenic wheat (*Triticum aestivum* L.). *Frontiers in Plant Science*, *12*.
- Zhou, J., Li, P., & Wang, J. (2022). Effects of Light Intensity and Temperature on the Photosynthesis Characteristics and Yield of Lettuce. *Horticulturae*, *8*(2), 178.