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Review Article

Abiotic stress tolerance in wheat with emphasis on drought

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Abstract

Environmental change presents a significant hazard to most tropical and subtropical crops across the world. Drought stress is among the negative repercussions of environmental modification that affects agricultural development and output. It has a significant influence on the vegetative and propagative phases of plants. Considering the current and prospective nutrition demands of a growing populace, it is critical to target crop production in drought-prone rainfed areas. Crops respond to drought stress in various manners, including structural, physio-chemical, and molecular responses. Drought tolerance encompasses processes that operate at several geographical and temporal dimensions, ranging from immediate stomatal closure to crop production management. There are multiple genes in wheat that are responsible for drought resistance and generate various enzymes and proteins under drought conditions. This review focusses the current advances in wheat physio-chemical, and molecular adaptation to drought tolerance. The experimental data revealed that drought stress negatively impacts multiple physiological processes that occur in wheat plants during their various growth phases, including germination, vegetative growth, reproductive development, and maturity. Therefore, studying the drought-induced damage in wheat plants, as well as strategies for boosting drought tolerance, is critical for increasing wheat output. Furthermore, molecular genetics and breeding strategies for developing drought tolerance in wheat to boost yield and quality are discussed.

Keywords: Drought stress, Drought adaptations, Wheat, Breeding, Food security.

1. Introduction

Drought is becoming a foremost threat to plant production being a yield-limiting factor. The growth, physiology, and reproduction of plants are negatively impacted during extreme drought conditions, causing substantial failure in crop yields. Water being an ultimate element of plant life, constitutes almost 90% of the plant's weight. It is becoming a continuous challenge to agronomists and plant breeders. By 2025, around 1.8 billion population will suffer water scarcity and 65% will confront low water availability. Resilience to water pressure is a perplexing threshold wherein harvests can be influenced by numerous quality factors (Nezhadahmadi *et al.,* 2013). Plants have diverse systems for overcoming drought stress that can be categorized into four portions including drought avoidance, drought tolerance, drought escape, and drought recovery. The two principle means for plant drought resistance are drought avoidance and drought tolerance, which are among the four constituents of dehydration resistance

(Fang and Xiong 2015). Root density, sustainable use of freshwater resources by flora, and modifications in plant lifestyle to harness rainfall are all factors in drought avoidance. Drought resilience refers to a plant's propensity to partially dry and rehydrate while the rain continues to fall (Nezhadahmadi *et al.,* 2013). Drought escape relates to the process of reconfiguring the life cycle, to avoid an correspondence between the developing period and local periodic drought (Shanmugavadivel *et al.,* 2019). Plant ends its life cycle by the advent of drought stress and forms viable drought-resistant seeds. The seeds later germinate when they encounter enough amount of water in the environment (Fang and Xiong 2015). Farmers prefer genotypes with brief life cycles that end their growing period before the commencement of seasonal drought stress or generally require minimal moisture (Kumar *et al.,* 2019). Drought recovery refers to a plant's ability to restore vigor and productivity after being subjected to extreme water shortage, which causes significant decrease in turgor pressure and leaf dehydration (Shanmugavadivel *et al.,* 2019).

Drought can have an impact on gene expression and detecting genes under this condition is critical for studying their responses (Nezhadahmadi *et al.,* 2013). Several drought-induced genes have already been recognized (Ingram and Bartels 1996). The contribution of genes can be differentiated by their expression to increased resistance rates between cultivars (Nezhadahmadi *et al.,* 2013). Dehydration being multidisciplinary stress can also trigger pollen incompatibility, grain mortality, abscisic acid (ABA) deposition in spikes of drought-prone wheat cultivars, and ABA biosynthesis genes in the anthers (Ji *et al.,* 2010). Plants have established such processes to withstand stress conditions. They can be influenced by drought stress in terms of antioxidant production, protein modifications, osmoregulation, hormonal composition, root outgrowth, stomatal movement, cuticle thickness, photosynthesis, and photosynthetic pigments, reduced transpiration, and growth arrest, in addition to some osmotic adjustments in their organ systems. (Lawlor and Cornic 2002, Nezhadahmadi *et al.,* 2013, Szegletes *et al.,* 2000, Yordanov *et al.,* 2000, Zhu 2002).

Water deficit flora can be broadly categorized into three types including hydrophytes (suitable to high moisture content), mesophytes (semi-arid and sub-humid geographical zone), and xerophytes (arid zones). Mesophytes are an important model for researching drought. Plants exhibit several intricate pathways for drought tolerance at various developmental phases, and at each developmental phase, a sequence of events such as photosynthesis, production of various macromolecules, stomatal movement, and cell osmotic control occur. Furthermore, natural drought stress is dynamically erratic. As a result, assessing drought resistance is challenging (Fang and Xiong 2015). Plants growing under extreme habitats (Xerophytes) exhibits particular adaptations to deal with long periods of dry weather conditions. The perennials avoid drought conditions either by having a long root system that digs deep into the soil to acquire low water table (e.g., Prosovis sp.) or having considerable water storage capacity that they gather during the brief rainy season (e.g., Sciguaro) Simultaneously, they reduce transpirational loss by shutting their stomata during the day time and lowering surface area by replacing leaves with spines (Srivastava 2002).

Wheat is the earliest cultivated staple cereal crop fulfilling most of the carbohydrates, proteins, and energy demands of mankind. It is utilized by 1/3rd of the human population to meet their nutritional needs. With a yearly output of 735 million tonnes, it is the most significant cereal after rice and ahead of maize (Ihsan *et al.,* 2016). Fluctuating climate is expected to affect various biotic as well as abiotic stresses on wheat (Prasad *et al.,* 2021). The constantly rising temperature of the planet has resulting in water depletion thus limiting the agricultural yield of the crops (Khare *et al.,* 2022). Drought has a very negligible influence on the incidence of kernel filling in wheat, but it does reduce the period between fermentation and maturity, resulting in lowering the dry weight at maturity (Wardlaw and Willenbrink 2000). Wheat has a higher water-use efficiency under drought circumstances than properly irrigated plants. This is due to stomatal closure, which lowers the transpiration rate (Monclus *et al.,* 2006). The cell membrane of wheat cells becomes more stable when they are subjected to water stress. This is because it is a strategy for increasing drought resilience (Blum and Ebercon 1981). Hardening, or physiological adaptation to dryness, is a key consequence of drought that has recently gained greater attention. The importance of osmotic adjustment in such adaptations cannot be overstated (Begg and Turner 1976). In this study, we have focused on morpho-

physiological features related to the processes enabling drought resistance in crop plants, and then we concisely highlight the achievements in the characterization of the genes for drought response in plants. Furthermore, we also discussed the effect of drought on photosynthesis, leaf senescence, respiration, antioxidant defense system, as well as cell membrane stability.

2. Risks associated with drought

Plants face various environmental stresses which cause yield reduction resulting in an increased threat to food security. Adverse environmental conditions resulting from abiotic stresses can result in the lowering of yield from 50% to even 70% (Francini and Sebastiani 2019). The average global temperature will rise 1.4 to 5.8 by the turn of 19th century. One of the major factors affected by the increase in temperature is water deficiency resulting in serious water crises like drought (Assad *et al.,* 2004). Under heat and water shortage conditions, the plant's nutrients absorption capacity and photosynthetic efficiency are reduced. These risk factors not only shorten the growth time but also diminish the size of the leaf, tiller, and spikes at different phases of tillering, booting, anthesis, heading, and grain filling (Ihsan *et al.,* 2016). Plant genetic constitution, morpho-physiological system of growth, expression patterns, activity of photosynthetic machinery, and environmental exposures are all factors that can influence plant responses to drought stress (Mohammadi 2018, Nezhadahmadi *et al.,* 2013). Droughts happen due to a variety of factors, most of which impair the environment's hydrologic cycle. One of these factors is a substantial reduction in rainfall, which may contribute to a reduced water content in the ground, and lakes. When the water demand is inadequate to meet domestic requirements, a water stress period is unavoidable (Lockwood 1986). Summing up the entire list of problems may be beyond the scope of this review; hence, the attention has been focused on a few prominent dangers; nevertheless, the list is not exhaustive:

1. Plants become dehydrated when droughts persist for an extended period. Symptoms include halted development, sudden leaf, and fruit loss, and eventually wilting. Drought conditions harm pastures and harvest yields (Fig 1).
2. Food shortages may develop in addition to water shortages. In the worst-case situation, hunger may result after a lengthy period of drought.
3. Not only does wind cause soil erosion, but also can flood under dry conditions.
4. Another severe effect of protracted droughts may be sinking, which is extremely perilous for the entire area.
5. If a certain location is repeatedly subjected to drought circumstances, it may cause irreversible harm to the ground, from which it will be unable to recuperate.
6. Desertification is based on drought circumstances.
7. Drought causes environmental modifications such as a lack of biodiversity, modifications in migration patterns, rise in soil erosion, and poor air quality (Cook *et al.,* 2007, Namias 1983, Schubert *et al.,* 2004, Trenberth and Branstator 1992).

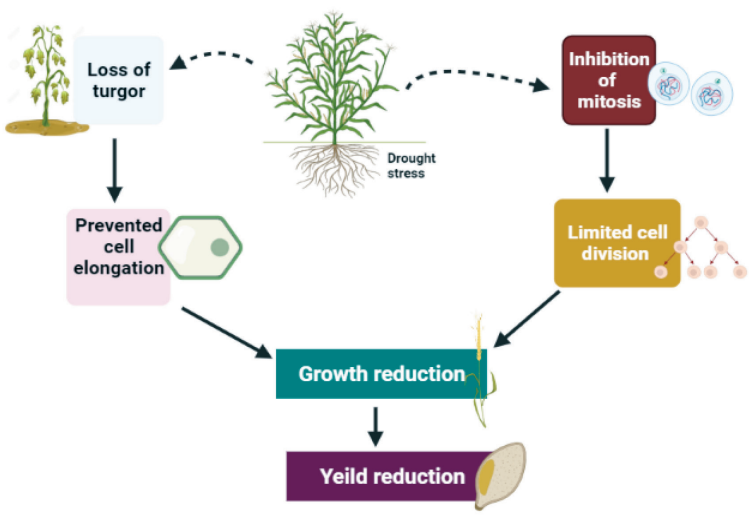

Figure 1: Mechanism of growth reduction under drought conditions.

3. Morphological, and physio-chemical deviation of wheat under drought conditions

Drought tolerance has two basic effects on the plants: physiological impacts which have impacts that are later visible to the naked eye and molecular impacts including changes in biochemical responses and enzymatic activity. Physiological stresses have an adverse impact on photosynthesis, transpiration, stomatal functioning, plant enzymes, and many more pathways which get disturbed. The biochemical stresses impact osmotic adjustment, osmolyte biosynthesis, plant homeostasis, ion transport, and many more balances are disturbed (Hasegawa *et al.,* 2000). Upon the arrival of favorable conditions after the desiccation period, plants show two types of responses including rapid recovery response in which the plant quickly recovers its normal physiological and biochemical responses. The other response is the slow recovery in which the plant may take hours to come back to normal physiological and biochemical activity or it may have some permanent damage and not be able to develop normally even after the onset of favorable moisture conditions. (Kollist *et al.,* 2019). Fig 2 illustrates the diverse structural and biochemical responses of a plant during water shortage.

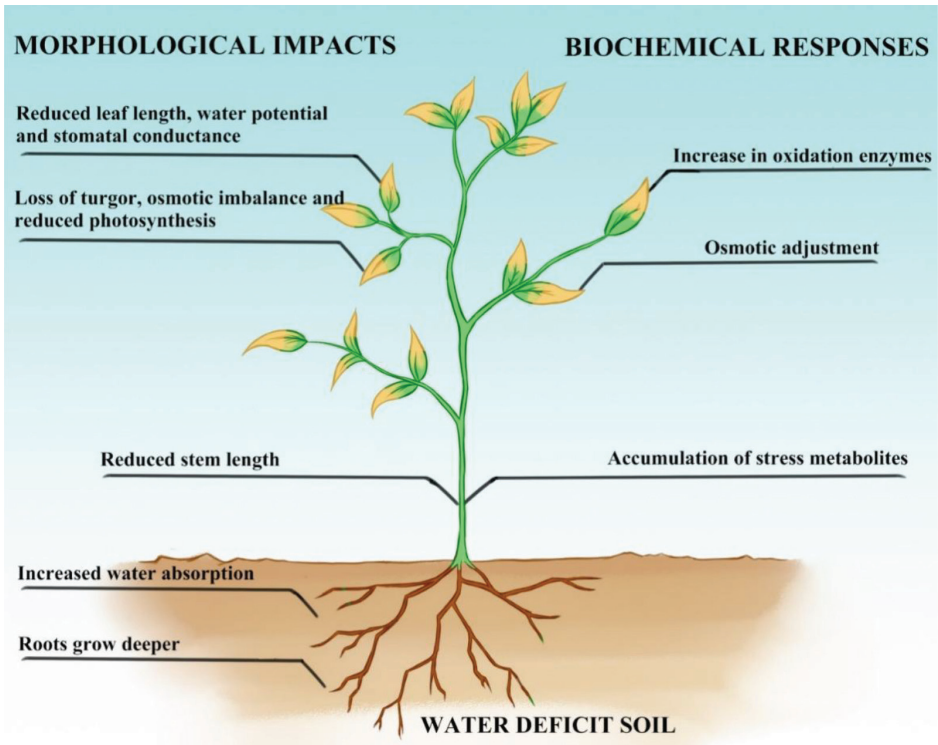

Figure 2: Structural and biological responses of plants due to water deficit.

3.1 Water deficit and leaf senescence

Drought increases foliar senescence and reduces the plant canopy size as well (Aliche *et al.,* 2018). Leaf senescence is one of the constraints which are used to judge the level of drought stress a wheat plant is facing (Miloud and Ali 2020). The first phase of drought impacts the leaf's color and shape. The leaves start to wilt and then dry along with the degradation of chlorophyll resulting in loss of the original plant color usually leading to a darker brown shade. As the cellular mechanisms are water-dependent, loss of water results in slowing down and ultimate halt in the biochemical processes. Chlorophyll molecules degrade and the leaves lose their green color which was provided by chlorophyll which depleted because of drought stress (Fig 2). The loss or degradation of chlorophyll molecules inside a plant is known as chlorosis which is a big indicator of drought stress. As days go by, the heat of the sun dries out the soil and the plants ultimately die out due to prolonged drought stress. The loss of leaves has a deleterious impact on the plant's overall functions and in the case of wheat, the flag leaves are very important as they provide for 30 to 40% of the energy assimilates (sugar) during the developmental stage of the

wheat grains. (Farooq *et al.,* 2014) The loss of flag leaves is one of the main indicators for drought stresses faced by wheat plants which not only leads to lower yields but can also cause ultimate death of the entire wheat plant due to prolonged absence of water (Yang *et al.,* 2006).

3.2 Water deficit and yield loss

During drought stress, plants usually halt their productive growth and focus only on the vegetative parts which are essential for the survival of the plant. This results in floral senescence and the flowers meaning no fruits and loss in yield. If a drought hits at the fruiting stage, then fruit senescence occurs resulting in premature fruit dropping, fruit spoilage, and shrinking in fruit size (da Silva *et al.,* 2013)</style> 2013. The wheat plant confronts the most detrimental impacts of drought stress during its flowering and grain-filling stages like any other plant. Loss of flowers and shrivelled grains result in significant yield loss (Shamsi K *et al.,* 2010). Wheat has shown extreme sensitivity towards drought pressure during the post-anthesis period as well. Wheat plants facing mild drought at the post-anthesis stage reduce the yield between 1 to 30% depending upon the tolerance of the wheat cultivar against drought stress. However, a protracted moderate drought during the blooming and grain filling periods reduces the yield from 58 to 92%. This shows that the complete absence of water may cause the death of the entire plant, but mild droughts can significantly reduce the yields. Mild droughts are also economically devastating because the realization hits at the end when yield is obtained that all the effort to grow wheat was wasted because of a prolonged mild drought (Zhang *et al.,* 2018). Fig 3 illustrates how different parts of a wheat plant are affected by drought stress.

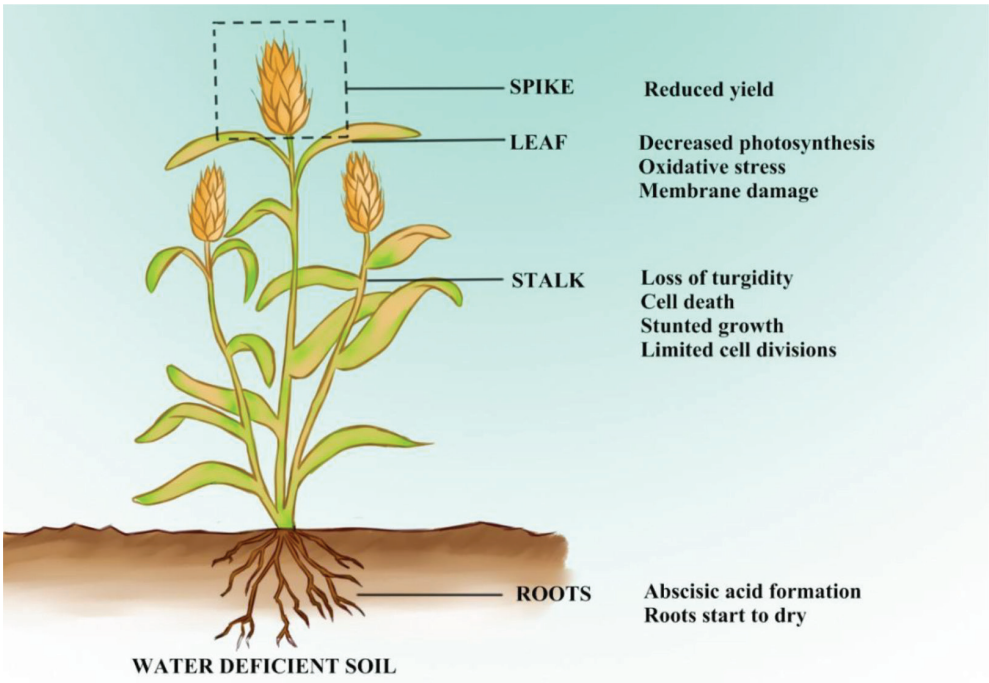

Figure 3: Impact of water deficiency on different parts of a wheat plant.

3.3 Water deficit and photosynthetic response

Photosynthesis is the driving force of plants which forms sugars that are utilized by plants as food sources and storage purposes. Photosynthesis occurs normally in plants having all the vitals including CO_2, water, and sunlight. However, taking out water disturbs the entire photosynthetic pathway, and an extremely complex response is received from plants undergoing water stress. The response is also related to the type of plant, the intensity of drought, and time period. Normally plants recover their normal physiological and biochemical activities upon the availability of water after drought, but some plants do not recover when the stress exceeds their capacity to tolerate the stress (Siddique *et al.,* 1999). The most important enzyme in photosynthesis is RuBisCO (ribulose-1,5-bisphosphate carboxylase/oxygenase) which gets affected and as a result photosynthetic activity declines (Perdomo *et al.,* 2017). Drought has many negative

impacts on the photosynthetic pathway but some of them are common for all plants including stomatal leaf-gas exchange, photosynthetic enzymes, and readily available forms of energy production. The main points are discussed as follows:

3.3.1 Influence on stomatal oscillations

The first response against drought stress is stomatal closure to prevent further loss of water. However, this response is only feasible until the plant can actively maintain turgor pressure which is lost in the case of a prolonged water deficit environment. Moreover, the closure of stomata also stops the gaseous exchange which is extremely important for obtaining CO_2 and releasing O_2 into the environment for the process of photosynthesis (Brodribb and Holbrook 2003). In case of stomatal closure, there are more electrons available for the generation of ROS (Reactive Oxygen Species) which help in maintaining the normal growth of plants and helping them get by the drought period (Huang *et al.,* 2019). The water volume of soil also helps in regulating the stomatal movement because when the water content in the soil surrounding the roots depletes, roots start to dry out and it results in the production of abscisic acid. The stomata respond to abscisic acid signals even when the leaf water content is sufficient. This aids the plant in maintaining turgor pressure despite the soil has dried out of water content (Brodribb and Holbrook 2003). When water depletes from soil and roots start to dry out, the pH of the soil decreases, and it results in the deposition of abscisic acid and a diminution in the stomatal activity. On the other hand upsurge in the production of cytokinin in the xylem stimulates stomatal opening along with affecting the stomatal sensitivity towards abscisic acid. (Wilkinson and Davies 2002) When gaseous exchange stops, CO_2 is unable to be carried out by the plant culminating in carbon dioxide deprivation effects including severe inhibition of photosynthesis, respiration, chlorophyll production, and starch buildup (Banerjee *et al.,* 2019). The stomatal functioning is regulated by several internal and external factors, but it is evident that drought stress alters the normal functionality of the stomata.

3.3.2 Influence on photosynthetic enzymes

One of the most deleterious effects of drought is the slow down and ultimate inactivation of the enzyme RuBisCO. Rubisco enzyme plays a key role in photosynthesis by fixing CO_2 which is the first step of the photosynthesis process. Since carbon dioxide fixation is the first major step, the entire photosynthesis process halts due to the unavailability of CO_2 (Perdomo *et al.,* 2017) Moreover, the reduction in water content also creates a viscous environment that increases the protein-protein interactions resulting in collisions of toxic substances with the Rubisco enzyme and its ultimate degradation. The degradation can be due to enzymes that digest Rubisco or part of it rendering it useless or toxic substances that alter the normal functioning of the enzyme (Parry *et al.,* 2002) Plants undergoing stress also show that Rubisco acts more as an oxygenase than a reductase during water deficit conditions. Drought stress also limits the regeneration ability of Rubisco resulting in further decline of the photosynthesis process (Demirevska *et al.,* 2009).

3.3.3 Influence on ATP synthesis

PMF (Proton Motive Force) is responsible for CO_2 fixation by harnessing the energy from light and have significant function in the feedback mechanism regulation of PSII (Photosystem II) antenna. Prolonged droughts harm the balance between these two roles played by the PMF. A study on balance between carbon fixation and feedback mechanism regulation roles showed that a nearly 34% increase in electron influx was observed in the PSI (Photosystem I) cyclic electron flow. However, a 5-fold reduction in the conductivity of protons was also noted across the thylakoid membrane showing that drought stress had an undesirable impact on PMF in plants. (Kohzuma *et al.,* 2009) The reduced conductivity of the protons also impacts the ATP synthase which functions by transfer of proton through the ATP synthase and converting ADP to ATP with the addition of Pi. When this process halts, ATP synthesis is also reduced and the plant starts to lose readily available ATPs for cellular activities (Golding and Johnson 2003).

3.4 Water deficit and oxidative damage

Oxidative damage occurs due to ROS including singlet oxygen, hydroxyl and superoxide anion radicals. ROS interact with nucleic acids, proteins, lipids, and membranes causing oxidative harm to their structures. ROS are formed by enzymatic and non-enzymatic pathways; though, the two pathways are regulated by the flow of oxygen under water deficit conditions. ROS formed by the enzymatic process is generate from the mitochondrial ETC (Electron Transport Chain) and the ROS formed by

the non-enzymatic process result from electron reduction by oxygen when there is a high level of oxygen available. (Alvarez *et al.,* 1998) ROS species damage the plant DNA, enzymes, phospholipid bilayer, and several important plant structures. ROS are formed in plants naturally as well and are indicative of plant aging, however, the rapid increase in ROS levels results in wilting, growth stunting, leaf senescence, halt of photosynthesis, and premature death of the plant.

3.5 Water deficit and antioxidant defense system

Antioxidants are the components that help prevent oxidative damage to the plant organelles and important structures for plant sustainability. The defense against oxidation is called an antioxidant defense strategy which involves both enzymatic and non-enzymatic components. Enzymes include catalases, peroxidases, superoxide dismutases, glutathione reductases, and ascorbic peroxidases. On the other hand, the non-enzymatic antioxidant defense scheme includes cysteine, ascorbic acid (Vitamin C), and reduced glutathiones for defense. Several components including antioxidant enzymes, water or lipid-soluble scavenging molecules help the oxidative damage creating components. Apart from ROS, lipid peroxyl radicals also increase oxidative damage to plants. Antioxidants help scavenge the ROS directly or with the help of other antioxidant components. Antioxidants are also sensors playing a key role in sensing the cellular oxidation-reduction (redox) status of the plant. They help keep a balanced plant redox status which also keeps the pH of the plant in check. (Hernández *et al.,* 2012) Several plant pigments are excellent antioxidants keeping the redox status of the plant in check. A study done on plant pigments with antioxidant abilities showed 13 different pigments harnessing the ability to scavenge oxidative damage creating components. (Boo *et al.,* 2011).

3.6 Water deficit and cell membrane stability (CMS)

Cell membrane stability (CMS) is a measure of drought conditions faced by a plant. The drought tolerance of wheat starts to decrease as the plant ages and the leaves are no longer able to bear the stress (Blum and Ebercon 1981). PEG (Poly Ethylene Glycol) has been used to measure the stability of plant cell membrane which is indicative of the stability of the structure and impacts due to drought stress. (Premachandra and Shimada 1988, Premachandra and Shimada 1987) Some markers including wmc9, wmc596, wmc603, and barc108 have been identified in a study related to wheat drought tolerance and consequent cell membrane stability. They are weak yet significantly associated with the cell membrane stability of the wheat plant. (Ciuc and Petcu 2009) A investigation on 50 diverse genotypes of wheat revealed that CMS was also dependent upon the type of wheat cultivar and those promising wheat cultivars should be used for future breeding. CMS has been found to be greatly influenced by drought and heat stress especially at the young seedling stage and anthesis stage which are both the most vulnerable states for wheat during drought stress. Therefore, germplasm isolation of resistant varieties can be promising for future drought-resistant cultivars of wheat. (Rehman *et al.,* 2016).

3.7 Compatible solutes and osmotic modification

Osmotic adjustment is a drought tolerance mechanism that allows the accumulation of solute under drought stress resulting in osmotic potential lowering. (Nio *et al.,* 2018) When water is deficient, it is important to provide water to the most important parts of the plant either through changes in the cell wall elasticity or osmotic adjustments. The adjustment of available water is important to drive physiological functions in the plant without which it cannot survive. (Hsiao *et al.,* 1976) Osmotic adjustment helps in conferring drought tolerance by accumulating abscisic acid resulting from a signal from roots that start to dry out resulting in the ultimate induction of dehydrins that prevent drought stress-related physiological damage. (Boyer *et al.,* 2008) One of the most notable functions of osmotic adjustment involves maintenance of the turgor pressure in the stomata to help them remain closed preventing water loss. (Zivcak *et al.,* 2016) However, this is only helpful in cases where drought stress is not for a long time, or the plant has an internal reserve of water that can be utilized for a long duration. (Chen and Jiang 2010) In wheat, the process of osmotic adjustment helps the translocation of pre-anthesis partitioning of carbohydrates in the grain filling stage. The turgor pressure maintained by osmotic adjustment helps the plant to sustain a greater rate of photosynthesis and ultimately a higher growth rate from the higher rate of photosynthesis. (Serraj *et al.,* 2002) There are certain organic compounds, like proline, which help the plant have a more stable and protected cell membrane. The proline content can be measured using spectrophotometry and research-based analysis

of the proline contents of different wheat genotypes revealed that a substantial contrast exists between different genotypes in terms of osmotic adjustments. Genotypes either showed high or low osmotic adjustments which showed a correlation with stomatal closure. The genotypes which show more osmotic adjustments were also showing delayed stomatal closure resulting in the continuation of the process of photosynthesis. The process of photosynthesis continues which is beneficial for wheat as the plant continued to grow and showed greater yield in terms of grain filling and overall quality. (Živčák *et al.,* 2009).

4. Selection of traits for drought tolerance in wheat

4.1 Physiological trait selection for drought tolerance in wheat

Increased availability to moisture with a proactive root system and water conservation to guarantee that it will not drain out when the crop longevity is finished seem to be the two main strategies for boosting production in water shortages areas (El Sabagh *et al.,* 2019). The second method, unlike the first, is crucial in situations where deep water is unavailable or when the subsoil is poisonous to the root system owing to toxic metals, salts, or other factors. Although transpiration efficiency (TE) is likely desired among both circumstances, it is more so in the latter. Despite the difficulty of measuring TE precisely on the ground, carbon isotope discrimination (CID) can be employed as a substitute. CID is holistic and genotypic; however, it is costly to quantify because it necessitates mass spectrometry (Juliana *et al.,* 2019). Interestingly, roots' exposure to subsurface water may be monitored in the field at maximum throughput by estimating canopy temperature (CT). Research findings on mapping populations revealed genetic factors basis, and recent work not just validated the representation of profound roots in rows with "cool canopy" quantitative trait loci (QTL), but even demonstrated that the same lines represented cooler canopies under hot, irrigated conditions and had been aligned with a greater root mass throughout all depth profiles in the field (Chapman *et al.,* 2018). Although differences in height and phenology can skew CT measurements, these parameters are well controlled in such experiments, and the root data corroborated the CT measurement while also indicating a greater root: shoot ratio, least during drought (Langridge and Reynolds 2021).

4.2 Drought tolerance in wheat through genomic selection (GS)

GS is a method of evaluating the influence of loci throughout the complete genomic sequence to compute a genomic estimated breeding value (GEBV) which may be utilized to forecast the phenotype of lines predicated on their genetic makeup (Juliana *et al.,* 2019). The quantity and variety of the population utilized to train the model to calculate breeding standards, as well as intensity of the molecular markers utilized in genotyping lines, affect the predictability of the results. Genomic selection in wheat breeding is a relatively new concept, with early ideas reaching back just around ten years. Moreover, currently, it has been frequently exploited in wheat breeding projects (Juliana *et al.,* 2018). Although, GS is essentially a breeding approach, and few papers are documenting its use. An overview of how it may be used to boost yield. The use of GS to improve wheat's temperature and drought tolerance, that has yielded promising outcomes, especially when coupled with latest high-throughput phenotyping approaches (Juliana *et al.,* 2019). There have been reports of yield estimating precision of 0.56 and 0.62 in drought and extreme temperature respectively. These findings imply that integrating GS with better phenotyping in order to increase wheat endurance might yield considerable benefits (Langridge and Reynolds 2021).

5. Plants adaptations to drought

Drought stress harms the plant water relations resulting in significant damage from delayed physiological functions. The plant develops a variety of structural, biological, and physiological responses to coping with stress (Beck *et al.,* 2007, Chaves and Oliveira 2004). The following are some of the plant's defense mechanisms in the event of a water shortage:

5.1 Drought escape

Drought escape is a phenomenon that occurs when the life cycle (vegetative and reproductive phases) of a plant is shortened. The plant reproduces using this strategy before the water supply in the environment becomes inadequate (Araus *et al.,* 2002). Varieties have an efficient approach for minimizing yield loss during drought by maturing

early, therefore, developing short life cycles (Kumar and Abbo 2001).

5.2 Drought avoidance

Drought avoidance entails controlling transpiration through stomata and maintaining water absorption through massive radicle growth. Root characteristics like biomass and depth are key drought avoidance features that contribute to ultimate productivity during water scarcity (Turner *et al.,* 2001). The use of a deep root system makes it easier to extract water from great depths (Kavar *et al.,* 2008).

5.3 Phenotypic flexibility

Phenotypic flexibility refers to the limitation of area and number of leaves to reduce water use efficiency. A shortage of water significantly impedes plant growth. Plant drought tolerance is highly reliant on roots and shoots (Schuppler *et al.,* 1998). Leaf pubescence (hairs) is a feature that protects the leaf from extreme temperatures by reducing transpiration (Sandquist and Ehleringer 2003). Drought stress stimulates trichomes to develop on both upper and lower sides of wheat leaves, but they have minimal effect on boundary layer resistance (Nerd and Neumann 2004).

5.4 Osmotic adjustment

Osmotic adjustment is the process by which the osmotic potential of a plant cell is dropped due to accumulation of solutes (Kramer and Boyer 1995). During dehydration, osmotic adjustment, in conjunction with cell wall elasticity, modulates turgor (Blum 2017). In the earlier reports, osmotic potential of plants was decreased to higher degree along with the decreased water potential of leaves and growing media but its reason is unknown as if it was caused by high concentration of organic solutes or due to the change in adaptation of cellular environment according to the development of plant (Turner 2018).

6. Molecular approaches of drought tolerance in wheat

When drought conditions prevail, several physiological and metabolic systems are triggered in plants in order to persist, grow, and produce. Inheritance's pattern of drought tolerance is intricate, and the accompanying characteristics are multifaceted and controlled by various genes, enabling the development of drought resilient varieties more challenging. Plants being motile have multiple mechanisms to recognize and adapt to different environmental situations. The interpreted signal is transduced, resulting in the activation of underlying genes that code for proteins conferring resistance under drought (Gupta *et al.,* 2017) (Fig 4). Researchers have recently been able to uncover certain genes associated with drought resistant wheat because of advance laboratory methods and computational biology tools (Budak *et al.,* 2013).

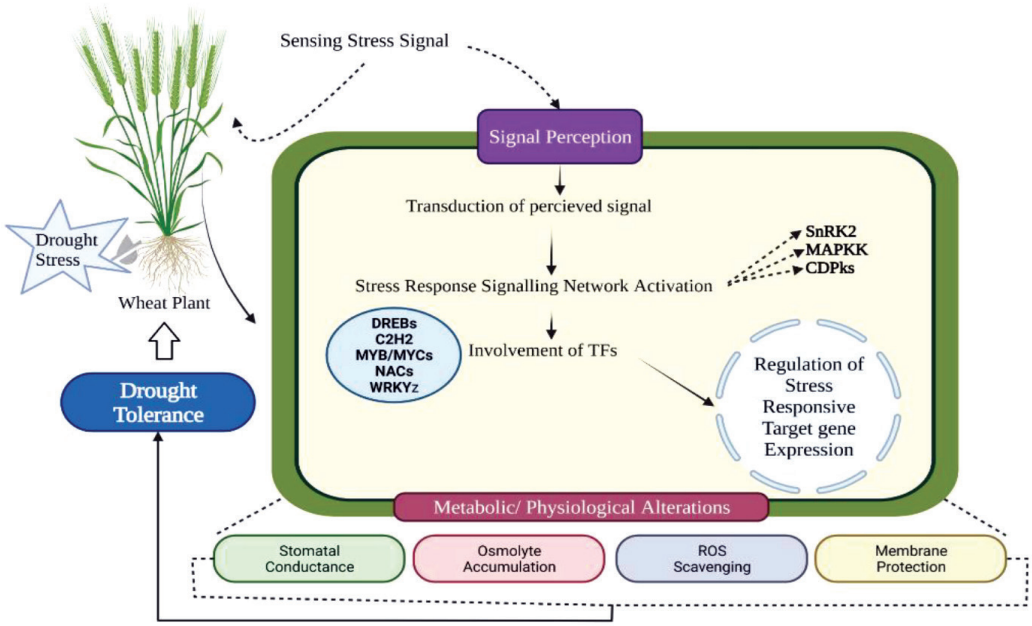

Figure 4: Series of steps involved in drought tolerance.

6.1 Molecular marker-assisted practices

Abiotic stresses are the potential source of food insecurity in ecosphere, owing to the high populace and poverty in developing nations. Innovative methods such as screening of existing germplasm, breeding new crop cultivars, exogenous practices of osmoprotactants, and the establishment of genetically modified organisms must be developed to resolve the needs. Various molecular methods are being explored to improve plant resistance to abiotic stresses. Water stress tolerance is a quantitative polygenic characteristic. QTLs are made up of the genes that function to determine the phenotype (physical properties) of quantitatively acquired characteristics. Crop changes can be identified via QTL mapping (Nezhadahmadi *et al.,* 2013).

6.1.1. Development of transgenic cultivars

Drought resistance genes may be found in a variety of plants. Drought resistance genes may be found in a variety of plants. These genes may be inserted into wheat using rDNA technology to induce drought resistance. To confer drought tolerance, the HAV1 gene is inserted into wheat from barley. DREB is another transcription factors (TF) family determined to have function in the regulation of numerous genes that participate in developing drought tolerance (Nezhadahmadi *et al.,* 2013). Moreover, NAC TFs are intriguing candidates for drought-tolerant breeding. When *TaSNAC8-6A* was significantly expressed in *Arabidopsis* and *Triticum*, drought endurance of transgenic varieties improved substantially (Mao *et al.,* 2020).

6.1.2. Molecular breeding (MB)

Exploiting molecular techniques in plant breeding is known as molecular breeding. Single genes influence several traits such as blooming time of flower, osmotic stability, and plant height, implying that these genes may have critical function in drought adaptation. In wheat genome, there is just one *OR* gene on the short arm of the 7A chromosome (Morgan and Tan 1996). Thus, breeding of *OR* gene can enhance plant production under water stress circumstances (Morgan 2000). Exploring collections in drought-tolerant locations may result in the identification of novel drought-tolerant genotypes (Morsy *et al.,* 2021).

6.1.3. Molecular assisted selection (MAS)

In MAS, a marker is being utilized for the indirect selection of candidate genes for the trait of interest. Marker-assisted selection has been considered because it facilitates the selection and breeding of drought-tolerant cultivars by enabling the identification of quantitative gene markers. If the markers are near a gene's stress-related region, the producer will be more efficient (Haque *et al.,* 2021).

6.1.4. Molecular assisted backcrossing

The most basic type of MAS is molecular mediated backcrossing, which attempts to introduce a significant gene from a less desirable source into a breeding line. Because of the complex stress-associated dehydration gene, comprehensive evaluation of drought-linked QTLs or genes is indispensable. To discover drought-related genes, molecular markers are used for gene mapping. Plants can adapt to water deficit conditions by modulating the gene encoding particular protein expression. Among the highly expressed proteins during dehydration are vacuolar acid invertase (VIN), glutathione S-transferase (GSTs), late embryogenesis abundant proteins, and dehydrin (Anderson and Davis 2004, Close 1996, Pnueli *et al.,* 2002, Trouverie *et al.,* 2003). Techniques such as omics investigations and QTL mapping are being used to uncover stress-sensitive molecular markers. These molecular markers are exploited to screen wheat genetic constitution for water stress (Budak *et al.,* 2013).

6.1.4.1. Marker-Assisted Breeding

Drought-induced genes are currently being identified using genetic markers. This technique is based on the employment of DNA markers to identify quantitative trait loci that are responsible for drought-tolerant (Ashraf 2010). The integration of Amplified Fragment Length Polymorphism (AFLPs) and microsatellites have contributed to the mapping of flag leaf senescence in both regular and water deficit situations. On the wheat chromosome, QTL concomitant with enhanced performance under water stress situations has been identified. To label the QTLs for water stress in wheat DNA markers such as ALFP, SSR, and RFLPs are used (Verma *et al.,* 2004).

6.1.4.2. Omics Investigation

The study of metabolome, genome, proteome of an organism is known as omics. In the instance of drought,

the omics method assists in the detection of drought-linked genes. The evaluation of drought response mediated by differential deposition of drought-related ingredients prompted the use of genetic sequence datasets. Drought-induced transcripts and proteins have also been reported in hexaploid (bread) and tetraploid (durum) wheat with variable drought sensitivity in these omics studies (Kumar and Abbo 2001). Proteomic reports of tetraploid wheat embryos have been developed as a result of the embryos' ability to germinate under severe desiccation conditions (Irar *et al.,* 2010). The metabolomics reports indicated that the genotype resistant to water scarcity had a greater accumulation of tricarboxylic acid (TCA) cycle products and drought-related metabolites such as glycine, glucose, aspartate, proline, and trehalose. The combination of metabolomic and transcriptome data revealed that drought adaptation comprises optimal modulation and signal transduction pathways that influence the effectiveness of cell homeostasis, carbon metabolism, and bio-energetic activities.

6.1.4.3. QTL Mapping

QTLs are the sites where certain genes affect the phenotype of quantitatively inherited traits. Polygenes can be used to investigate a crop's genetic variability (Ashraf *et al.,* 2008). QTLs are the sites where certain genes affect the phenotype of quantitatively inherited traits. Polygenes can be used to explore genetic diversity in crops (Ashraf et al., 2008). Water deficit is a polyploidy characteristic with challenging quantitative properties. Productivity QTLs in tetraploid wheat have been detected using linkage mapping. Drought tolerant QTLs in wheat were identified utilizing production parameters in a desiccated condition (Maccaferri *et al.,* 2008). Drought and crop productivity are two complicated traits comprising genotype, and phenotype and environment (Bennett *et al.,* 2012). Furthermore, various yield-related QTLs have been identified using RAC875/Kukri doubled haploid lines of *T. aestivum* that have been proven to mature across a wide range of environmental circumstances. A multi-environmental study provides a foundation for precise mapping along with cloning of the genes associated with a yield-associated QTL (Bonneau *et al.,* 2013). Recent research, as well as advancements in DNA sequencing technology and established techniques for associating linkage studies with omics investigations have suggested that the information collected from these types of experiments will eventually come for actual drought-resistant wheat breeding projects (Fleury *et al.,* 2010, Habash *et al.,* 2009)

6.2. Transcription factors regulated under drought in wheat

6.2.1. C_2H_2 zinc finger proteins (ZFPs)

ZFP is grouped into subclasses depending on the arrangement of Cysteine (Cys) and Histidine (His) such as C2H2-type, C2HC, C3H, C4, C3HC4, C6, and C8. Amongst them, C_2H_2 ZFPs genes make ~0.7 percent of the *Arabidopsis thaliana* genome, 0.8 percent of the yeast genome, and 3 percent of the mammalian and dipteran genome. The first C2H2 type ZFP gene, EPF1 was discovered from petunia. It encodes a protein with 2 C_2H_2 ZF motifs (Han *et al.,* 2020). Many C2H2 type ZFP genes have been investigated and cloned in *A. thaliana*, *Glycine max, Oryza sativa,* and *Triticum aestivum* (Gao *et al.,* 2011, Hong *et al.,* 2016, Sun *et al.,* 2012, Zhang *et al.,* 2014). In C2H2-type ZFPs, Zn^{+2} forms an independent protein region by binding to the conserved amino acid residues. C2H2 ZFP contain 25-30 conserved protein sequence: C-X2~4-C-X3-P-X5-L-X2-H-X3-H. Two sets of His at the C-terminal of alpha-helix and two Cys at the beta-strand link with Zn^{+2} to appear like a tetrahedral structure. Zn^{+2} at the center ensures the stability and maintenance of the helical structure. In plants, mostly C2H2 ZF proteins contain a highly conserved zinc finger domain (QALGGH) and such proteins are regarded as Q-type ZF proteins. C2H2-type proteins lacking QALGGH conserved motif are regarded as C-type ZF proteins. Evidence has revealed that ZF proteins have a crucial role in development, growth, and abiotic conditions (Han *et al.,* 2020). Under drought and water scarcity, plants activate the upregulation of dry mass by sending signals from roots to aerial parts (Tardieu 1996).

6.3. Role of TaZFP under drought

TaZFP15: This gene has a significant function under drought. It sends the signals from the root to the aerial plant part and triggers the accumulation of starch in the foliage (JasonKam et.al 2008).

TaZFP22, TaZFP34, and TaZFP46: These genes show high expression pattern in roots and drought stimulated C_2H_2 ZF transcriptional repressors (Chang *et al.,* 2016).

TaZFP24: *TaZFP24* is responsible for growth and development and is repressed under drought. Thus, plants need favorable conditions to store food and energy to survive in stressed environments (Ali *et al.,* 2020).

TaZFP33: This gene is upregulated under water scarcity in the embryo and aleurone layer of the endosperm tissue within the duration of grain ripening to guard the cells from the DHN (dehydrin) gene (Ali *et al.,* 2020).

TaZFP34: This gene is upregulated under dehydration, heat, salt, and chilling stresses. In wheat, increased expression of this gene maintains the radicle to shoot ratio by improving the root growth while reducing the shoot growth (Chang *et al.,* 2016).

TaZFP42: Investigations revealed that *TaZFP42* take part in fabrication of biological reserves in the kernel and accretion of polysaccharides (starch) (Ali *et al.,* 2020).

6.3.1. bZIP

The basic leucine zipper is responsible for governing numerous growth-related and physiological functions along with synchronizing stress responses. So far, 13 bZIP homologs groups have been discovered in angiosperms (Ying *et al.,* 2012). These TFs contain 40 to 80 amino acids rich bZIP domain (Wang *et al.,* 2021). This domain is composed of a leucine zipper motif that is important in TF dimerization and a 16 amino acid long basic region that regulates the transcription factor's pecularity to its target DNA. The basic region of bZIP is about 18 amino acids long followed by the N-x7-R/K-x9 motif (Gai *et al.,* 2020). It is rich in basic amino acids (arginine, lysine) (Nieva *et al.,* 2000). The leucine zipper region of bZIP consists of α-helices having amphipathic nature. This region is stabilized through heptad repeats of hydrophobic amino acids (Nieva *et al.,* 2000). The hinge is the protein sequence that links the basic region to the leucine zipper. bZIP TFs often attach to genome sequences with an ACTG core. Plant bZIP encoding proteins are said to bind to A, C, and G-box sequences, although interactions with non-palindromic sequences have also been studied (Na *et al.,* 2021, Rahaie *et al.,* 2013)</style> 2021, Rahaie<style face="italic"> et al.,</style> 2013. bZIP TF modulates the expression of drought triggered genes and their cumulative impact causes changes such as root growth maintenance, leaf development inhibition, higher concentration of chaperones, and stomatal closure (Hamanishi and Campbell 2011).

ABF4 is mostly manifested in vegetative tissues and is stimulated under drought as well as abscisic acid (ABA) levels. It regulates the expression of *, CHS, ICK1, ABI1, RAB18, SKOR, ADH1*, *KAT2,* and *RD29B* genes. When there is a lack of water, *ABF4* and *ABF3* enhance the plant survival rate and stomatal closure. In the vegetative tissues, *ABF2* is reported to regulate ABA and drought-inducible genes. This TF also regulates *LEA* genes, which are responsible for alleviating desiccation mostly through chaperone activities (Wang *et al.,* 2003). Moreover, the *Wlip19* gene has enhanced the expression under low water and high ABA levels.

Gene expression studies in wheat indicated that *TabZIP* expression changed under high temperature, salt, and water shortage, indicating that bZIP might have a prominent role in stress alleviation processes. Arabidopsis plant expressing *TabZIP* disclosed high tolerance to salt, drought, ROS, and heat stress (Agarwal *et al.,* 2019). Furthermore, overexpression of *TabZIP60* in *A. thaliana* boosted tolerance to dehydration, salt, and cold stressors, as well as improved plant response to ABA in seedling development. In addition, *TabZIP60* was noticed to be capable of binding ABA-responsive cis-elements found in the promoters of numerous known ABA-responsive genes. Further investigations discovered that overexpression of *TabZIP60* activate several stress-responsive genes as well as alterations in various physiological parameters (Zhang *et al.,* 2015). Similarly, *TabZIP8-7A* was discovered to interact with *TaFDL2-1A* in the nuclear region, and elevated expression of *TabZIP8-7A* in *Arabidopsis* executed higher drought tolerance and ABA sensitivity (Wang *et al.,* 2021).

6.3.2. WRKY

WRKY TFs have a diversified function in plant defense and developmental processes. These TFs are distinguished by their DNA binding domain, that comprises of an distinct WRKY sequence at their N-terminus. They also have a zinc finger as a characteristic at their C-terminus. WRKY TF have a fundamental role in drought signaling by interacting with MAPK cascade, Histone de-acetylases, Calmodulin, 14-3-3 proteins, and resistance proteins to up or down-regulate certain genes. WRKY TFs can be antagonistic to Salicylic acid (SA), Jasmonic acid (JA), Ethylene, as well as control through indole-3-acetic acid and cytokinin (Agarwal *et al.,* 2011, Antoni *et al.,* 2011, Eulgem *et al.,* 2000). Under drought, many WRKY TFs,

including *WRKY1, WRKY72, WRKY77, WRKY11*, and *WRKY45*, appear to have been activated by the Abscisic acid pathway, resulting in the synthesis of Galactinol through the stimulation of the *Gols1* gene (Qiu and Yu 2009, Rushton *et al.,* 2012). *TaWRKY2* has previously been demonstrated to have an important function in drought stress resistance. Notably, the current study showed that *TaWRKY2* overexpression boosted biomass under drought stress. Transgenic wheat had longer panicles and high number of grains/spike under drought stress than wild-type, showing that these agricultural traits resulted in higher yield. Similarly, *TaWRKY2* and *TaWRKY19* have recently reported to provide drought resistance in recombinant plants (Gao *et al.,* 2018). 48 drought-sensitive WRKY genes were identified in wheat. *TaWRKY46* overexpression in wheat increased drought stress tolerance. Furthermore, *TaWRKY46* overexpressing plants had higher survival rates, levels of soluble sugar, proline, and superoxide dismutase (SOD), as well as enhanced catalase (CAT) and peroxidase (POD) activity, but lower levels of MDA and H_2O_2. These findings showed that *TaWRKY46* regulates osmotic balance and ROS scavenging serving as a positive factor during drought stress (Yang *et al.,* 2021).

6.3.3. NAC

NAC TFs are members of most diverse transcription factor identified specifically in plants. The NAC is made up of **N**AM, **A**TAF, and **C**UC genes: The **N**AM stands for no apical meristem, **A**TAF stands for Arabidopsis transcription activation factor, and **C**UC stands for cup-shaped cotyledon. The NAC protein has an N and C-terminal. The C-terminus possessing protein binding activities work as a transcriptional activator or repressor (Hu *et al.,* 2006). The N-terminus, on the other hand, is a conserved region that comprises the DNA-binding domains, which have around ~150-160 amino acids and are further catagorized into 5 sub-domains (Ooka *et al.,* 2003). The NAC domain is responsible for DNA binding, and dimer formation with other NAC proteins (Ali *et al.,* 2020).. *TaNAC4* and *TaNAC8* were discovered to be wheat TFs that act as transcription activators and are implicated in biotic as well as abiotic stress factors (Bian *et al.,* 2021, Wang *et al.,* 2021). TaNAC2 overexpression enhanced tolerance to dehydration, salinity, and low temperature (Wang *et al.,* 2021). *TaNAC69* is shown to be up regulated by drought and is involved in root cellular activities. Overexpression of this transcription factor gene family showed improved drought resistance and water consumption efficiency (Mathew *et al.,* 2020).

6.3.4. ERF

Ethylene Responsive Factors (ERF) family TF act as key regulators of the ethylene-dependent genes concerned with stress tolerance. They play a role in biotic stress and guide particular plant responses to ethylene signals (Zhang *et al.,* 2021). The ERF domain, which comprises of 40-70 highly conserved amino acid sequences, provides ERF with an affinity for the GCC box located within the promoter region of ethylene-sensitive genes (Xie *et al.,* 2019, Yamaguchi-Shinozaki and Shinozaki 2005). In addition to the GCC box, the ERF proteins interact with the DRE/CRT motif which is known as the cis-acting element in response to water deficit and cold stress (Yamaguchi-Shinozaki and Shinozaki 2005). The C-terminal putative phosphorylation site (TPDITIS) was shown to be a phosphorylation substrate for TaMAPK1 protein kinase in protein interaction studies. The MAPK cascade participates in both environmental and non-environmental stress (Frismantiene *et al.,* 2018, Muñoz 2018). The drought-induced cDNA library approach was utilized to isolate the ERF gene in *T. aestivum* in prior work. *TaERF1* found on the 7A chromosome of *the TaERF* gene is thought to code for a 355-amino-acid protein. Another TF gene, *TaERF3* is an intriguing engineering target in targeted attempts to promote abiotic stress tolerance in wheat and other crops because it positively affects wheat adaptation responses to salt and drought conditions via stress-related gene activation (Ali *et al.,* 2020).

6.3.5. DREB

Dehydration-responsive element-binding factors (DREB) is a large class of transcription factor encoding proteins that bind to dehydration responsive element (DRE) present in the promoter sequence of abiotic stress-responsive genes with two subclasses i.e., DREB2 leads to desiccation induced drought and DREB1/CBF resulting in cold-induced drought (Khan 2011, Sakuma *et al.,* 2002, Sazegari and Niazi 2012). DREB binding to a particular region of the target gene, known as the CRT/DRE sequence, is quite specific which is composed of the C-repeat sequence, with 5 base pair conserved sequence (Hu *et al.,* 2020). Abscisic acid (ABA) is synthesized under dehydration and enhance the promoter activity of wheat DREB genes *viz*., *TaDREB2*

thus exogenous ABA is responsible for generating critical signaling routes for water deficit tolerance via DREB proteins, such as suppressing seed germination, inhibiting stomatal opening for limited transpiration, and enhancing senescence (Kobayashi *et al.,* 2008). So far, DREB genes have been divided into 6 subfamilies with 210 *T. aestivum* DREB protein-encoding genes whereas elevated expression of the *TaDREB3-AI* gene improved drought tolerance (Niu *et al.,* 2020).

6.3.6. MYB

MYB superfamily was initially found in avian myeloblastosis virus whereas *ZmMYBC1* gene was the first plant-specific MYB identified and isolated in *Zea mays* having a regulating role in anthocyanin biosynthesis (Paz-Ares *et al.,* 1987, Salih *et al.,* 2016). MYB domain is made up of three imperfect repeats of fifty-two amino acids residue in each domain which makes a helix-turn-helix-conformation that twists itself in the major groove of the DNA to be targeted (Jin and Martin 1999). *TaMYB31* gene encoding TF participates in conferring enhanced drought tolerance in *A. thaliana* when ectopically expressed as a transgene (Zhao *et al.,* 2018). Differentially expressed genes (DEGs) of wheat were identified with RNA-seq technology and R2R3-MYB TFs were classified in 15 subclasses containing 411 genes, among them 28 TFs were suppressed under the effect of silicon treatment (Hao *et al.,* 2021).

6.4 Priming induced tolerance in wheat

Wheat is an extensively cultivated crop in the entire world and is essential for human nutrition. However, it is cultivated in hot, dry climates, resulting in poorer yields in certain seasons (Langridge and Reynolds 2021). Plants are disposed to a numerous abiotic stresses, thus is imperative to scrutinize plant response, when subjected to drought and other stresses, either simultaneously or sequentially (Han *et al.,* 2019). Various investigations have shown that when drought and heat are coupled, the impact is more acute rather than solely drought stress application (Hussain *et al.,* 2019). Plants are pre-disposed to slight levels of drought stress at their juvenile stage and the stages of primary growth to enhance tolerance levels at later developmental or growth stages with drastic stress events (Avramova 2019).

6.4.1. SO_2 induced drought priming in wheat

Another prevalent cause restricting plant growth and production is drought stress. Sulphur dioxide (SO_2) has been shown to boost plants by protecting them from stressful conditions (Corpas and Palma 2020). The impact of SO_2 on the molecular mechanisms and physiological functions of wheat plants at early developmental and growth phases to drought stress was investigated (Li *et al.,* 2021). Under abiotic stresses e.g., drought, pre-treatment of wheat seedlings with 10 mg/m3 SO_2 improved the chances of survival and relative water content (RWC), showing that pre-disposition to an adequate dose of SO_2 might improve plant tolerance towards drought. A recent study found that pre-treatment of foxtail millet seedlings with SO_2 protected these plants against drought stress damage (Han *et al.,* 2019).

For a long time, SO_2 was considered to be a prevalent air contaminant with deleterious impacts on the crop (Liu *et al.,* 2017). SO_2 toxicity is primarily caused by oxidative stress, which is regulated by an increase in ROS production, comparable to drought stress. Low concentrations of SO_2 were shown to stimulate transcriptome reprogramming in grape berries, which is linked to oxidative signaling, indicating that SO_2 indeed has a physiologically metabolic role under defensive processes(Xue and Yi 2018). These reactions were linked to the increased proline build-up produced by SO_2 pre-treatment in drought-stricken wheat seedlings. Whilst, in drought-treated wheat seedlings, SO_2 pre-treatment elevated the functions of superoxide dismutase (SOD) and peroxidase (POD) (Corpas and Palma 2020). However, these treatments had significantly lowered the concentration of hydrogen peroxide (H_2O_2) and malondialdehyde (MDA), implying that mitigate drought-induced oxidative injury can be mitigated through SO_2 by bolstering antioxidant processes and pathways in wheat plants (Li *et al.,* 2021). Gene expression analyses of transcription factor NAC, MYB, and ERF in wheat after SO_2 pre-treatment lowered the expression of TaNAC69. Whereas the expression of TaERF1 and TaMYB30 altered a little and remained at elevated amounts in wheat seedlings in drought stress tolerance (Baillo *et al.,* 2019) (Table 1). Interestingly, SO_2 pre-treatment caused a crucial enhancement in hydrogen sulfide (H_2S) build-up upon exposing juvenile wheat plants to desiccation (Ausma and De Kok 2019). The activities of antioxidant enzymes

and TF genes expression were reduced when H2S was scrounged by spraying Hypotaurine (HT), whereas the concentration of H_2O_2 and MDA enhanced to the level of drought treatment solely, implying a central role in the regulation of SO2-induced H_2S in plant tolerance to drought stress (Corpas and Palma 2020). Overall, this research found that SO_2 increased drought endurance in wheat seedlings via H_2S signaling, indicating a novel method for culminating drought tolerance in wheat crops (Li *et al.,* 2021).

Table 1. Physiological Alterations upon pretreatment of wheat plants with chemicals to develop drought tolerance

Abiotic Stress	Pretreatment of wheat seedlings	Metabolic Alterations	Stress Response Genes		Physiological Alterations	References
			Up-Regulation	Down-Regulation		
Drought Stress	SO_2	*Increased:* SOD, POD, Proline *Decreased:* H_2O_2, MDA, soluble sugar	TaERF1, TaMYB30,	TaNAC69	Increased survival rate Relative Water Content	(Li *et al.,* 2021)
	PEG	ABA Biosynthesis NO biosynthesis H2O2 biosynthesis	P5CS BADH	PDH	Osmolyte accumulation (Proline, glycine betaine)	(Wang *et al.,* 2021)
	Jasmonic Acid and	*increased:* anti-oxidant enzyme activity	APX, CAT, POD, SOD	LOX	Osmo-protectant accumulation, Total water content	(Wang *et al.,* 2021)
	Kinetin	*Decreased:* anti-oxidant enzyme activity		LOX	Chlorophyll content stability	(Wang *et al.,* 2021)

Δ1-pyrroline-5-carboxylate synthetase (P5CS)
Betaine Aldehyde Dehydrogenase (BADH)
Proline Dehydrogenase (PDH)
Lipoxygenase (LOX)
Super oxide Dismutase (SOD)
Catalase (CAT)

6.4.2. NO-induced drought priming in wheat

Utilizing different concentration of polyethylene glycol (Nitrogen Reductase) enable the plant for NR-dependent NO generation, which is linked to drought stress endurance in wheat. NO2 is reduced to NO via the reduction of nitrate (NO_3) to NO_2 by NR and (Nitrogen Oxide Synthase) NOS that facilitates drought priming as well (Tejada-Jimenez *et al.,* 2019). The nitric oxide (NO) scavenger boosted activity of nitric oxide synthase, and the fact that the NOS inhibitor reduced NO synthesis in maize seedlings under drought-stress suggests that NOS is responsible for most of NO generation under water shortages. Drought priming increased NO content in an experiment, while scavengers and NO inhibitors application inhibited the rise in NO caused by drought priming (Wang *et al.,* 2021). During priming events, the concentrations of NO, in forager or inhibitors for treatments with NO were greater than those with similar treatments in non-primed crop plants under dehydration conditions. Grain filling stage, however implies that scouring of NO might restrict NO generation in primed wheat plants (Wang *et al.,* 2019). Plants' swift production and accumulation of osmolytes seem thought to be an adaptation strategy to cope with dehydration conditions. Drought augmented the levels of endogenous NO and proline in leaves of *Oryza sativa*, according to research. Exogenously administered NO reduced osmotic stress in wheat and rice under drought stress, by increasing osmolyte accumulation and reducing oxidative damage (Farooq *et al.,* 2017). During this grain filling stage, higher sucrose content was reported in plants primed under dehydration conditions in comparison with non-primed plants. Osmolyte accumulation in higher contents is validated by drought priming application on wheat plants when NO biosynthesis was induced under ABA-dependent pathways causing drought tolerance in plants (Avramova 2019). Primed plants with inhibited NO activity depicted low sugar contents than their

corresponding non-primed plants. This links the crucial role of NO in osmolyte accumulation for inducing drought tolerance and their involvement in drought priming (Wang *et al.,* 2021).

6.4.3. H_2O_2 induced drought priming in wheat

Second messengers such as NO and hydrogen peroxide (H_2O_2) are actively engaged in phytohormone signalling along a wide spectrum of biological reactions to abiotic factors (Tejada-Jimenez *et al.,* 2019). Decreased stomatal conductance in maize was induced by a substantial rise in O_2 and H_2O_2 contents, along with abscisic acid (ABA) levels in leaves under dehydration conditions. H_2O_2 is being demonstrated to increase wheat drought tolerance by acting as a secondary messenger for the JA-induced antioxidant defense (Wang *et al.,* 2021). Drought priming at an initial stage of development caused stress tolerance against drought in future growth stages, while H_2O_2 mediates the abscisic acid (ABA) involvement in drought priming, therefore boosting wheats' drought endurance capacity. NO generation is triggered by H_2O_2, according to several streams of research (Wang *et al.,* 2019). The elimination of NO did not influence H_2O_2 production, however, the elimination of H_2O_2 caused suppression in NO concentration. These studies reveal that H_2O_2 was involved in NO generation during drought priming. Primed plants might considerably reduce the level of H_2O_2 amid dehydration conditions during grain filling to minimize injuries to cellular compartmentation induced by excessive H_2O_2 accumulation (Table 3.2.) (Wang *et al.,* 2021).

6.4.4. Jasmonic acid and kinetin

Foliar application of jasmonic acid (JA) or kinetin (K) effectively imparted drought tolerance to susceptible cultivars, enabling them to endure brutal environments before their development and function similarly to tolerant cultivars. Application of phytohormones caused an unambiguous switch from downregulation to overexpression. This affected all drought resistance characteristics via a reconfiguration of photo-assimilates to vegetative parts, boosting development, improving the aggregation of certain osmoregulatory chemicals, strengthening tissue vigor, and regulating antioxidant enzymatic activity. It also included structural modification achieved by restoring the shoot/root ratio (Abeed *et al.,* 2021).

Conclusion

This paper focuses evidence-based knowledge on the deleterious impacts of water inadequacy on wheat productivity during the last few decades. Drought directly affects the physiology of wheat, resulting in lower grain output. This research also emphasizes the significance of the selection environment in the development of productive, resilient wheat varieties for drought-prone areas. Besides this, the indirect choice of physiological features contributing to harvest index has enormous potential for optimizing the efficacy for optimizing the efficacy of drought resilience breeding is also discussed. Moreover, a multidisciplinary physio-morphological approach, as indicated in this study, is a highly promising way ahead for enabling the breeding of wheat for drought conditions. To attain this aim, a concerted effort is required to develop optimize platforms for phenotypic selection, as outlined in the preceding sections, in conjunction with biological, marker-assisted, and genomic selection.

Compliance with ethical standards

NA

Conflict of interest

Authors declares there is no conflict of interest

Author contributions

AA: Conceptualization, Data curation, Writing & updating the manuscript for publication, MA and NA: Writing, MI: Conceptualization, Writing, TSB: Conceptualization, Writing, ME: Conceptualization, AG: Conceptualization, Supervision, and Validation. All the listed authors read and approved the manuscript.

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