



Exploring Drought Tolerance in Wheat: Insights from Biochemical, Morphological, and Physiological Responses

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Authors' contributions

This work was carried out in collaboration among all authors. Author QAH designed the study, performed the statistical analysis, wrote the protocol and wrote the first draft of the manuscript. Whole studies about the Physiological responses are also carried by author QAH. Authors MA and EA managed the biochemical responses. Author MT carried out the morphological responses of the study. Author AR managed the literature searches. Authors MA wrote the summary of physiological and morphological markers. All authors read and approved the final manuscript.

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ABSTRACT

This review paper delves into the intricate biochemical foundations underlying drought tolerance mechanisms in wheat plants. This exploration encompasses multifaceted aspects, ranging from physiological adaptations to gene expression modulation. Plants like wheat employ repertoire of

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biochemical strategies to bolster their resilience against drought stress. It involves coordinating antioxidant enzymes, osmotic regulators, polyamines, and hormones to combat drought stress. The antioxidant system is crucial, countering reactive oxygen species produced during drought. Enzymes like SOD, CAT, and POD are activated to protect cells. Osmolytes like sugars and polyamines maintain cell integrity and water retention, while hormones like ABA control stomatal closure and water conservation. Gene expression highlights the plant's drought adaptability. AP2/ERF factors boost drought tolerance when overexpressed. Gene repression uses motifs like EAR to reduce expression for environmental adaptation. Gene expression shows the plant's drought adaptability. Overexpressed AP2/ERF factors enhance tolerance. Repression, like the EAR motif, aids variation. The morphological basis study examines how water scarcity affects different growth stages of wheat, such as germination, tillering, flowering, and grain filling. It identifies physio-morphological traits that could serve as the indicators of drought resilience, providing a new way to breed stress resistance. Furthermore, this article also explains plant characteristics important for adapting to drought, including photosynthesis, water relations, nutrient uptake, oxidative state, osmotic balance, and hormonal consequences. Each facet contributes to the intricate web of physiological adaptations that allow wheat plants to withstand and thrive under drought conditions. Comprehending these mechanisms aids breeding for drought-tolerant wheat, ensuring food security amid climate change.

Keywords: Biochemical; drought; morphological; physiological; traits; tolerances; wheat.

1. INTRODUCTION

Drought tolerance in plants refers to their remarkable ability to survive, grow, and reproduce even when water is scarce or irregularly available [1]. This natural talent is vital given the widespread challenge of drought, which significantly hampers plant development. It is a pressing concern for scientists and breeders, especially with the alarming prediction that by 2025, nearly 1.8 billion people might grapple with severe water shortages and 65% of the global population could find themselves in water-stressed environments. Understanding a plant's resilience to water stress is quite intricate, influenced by various plant traits [2]. It can be broadly separated into two strategies: tolerance for dehydration and avoidance of drought [3]. Drought avoidance involves clever root systems, efficient water utilization, and adapting behavior to maximize rainfall benefits. Dehydration tolerance, however, is about withstanding partial dehydration and rebounding when water becomes available again [4]. Adapting plants to thrive amidst drought stress is a critical pursuit, driving innovative methods to bolster stress-resistant plant varieties [5]. Many factors influence a plant's response to drought, like genetics, growth stage, stress severity and duration, physiological processes [6], gene activity patterns [7], respiration changes [8], photosynthesis activity [9], and environmental conditions [5]. Drought stress leaves a significant imprint on gene activity, emphasizing the need to

closely monitor genes during water scarcity episodes. As a result, scientists have identified a range of genes that respond to drought conditions [10].

Wheat (*Triticum aestivum* L.) holds the second position globally in cereal production but claims the top spot for cultivated land area [11,12]. In 2017 alone, a staggering 757 million metric tons of wheat were produced [11]. It's a vital source of nutrition, contributing to 41% of global cereal consumption: 74% in developed countries and 35% in developing countries. [13]. Interestingly, wheat is the second most consumed staple after rice. Of the wheat produced, 68% feeds people, 19% goes to livestock, and the rest serves various purposes, such as commercial biofuels [14].

Surprisingly, poorer nations are importing more wheat even in non-traditional regions like the tropics [14]. For instance, Sub-Saharan Africa has seen a yearly 2-3% increase in wheat demand [15]. This underscores the global significance of this adaptable cereal crop. Wheat plants navigate the perilous waters of water scarcity by orchestrating a multifaceted biochemical defense. Reactive oxygen species (ROS) generation, a hallmark of drought stress, can inflict oxidative damage on critical cellular components. However, wheat employs a sophisticated antioxidant system to combat the negative effects of ROS, which includes enzymes like superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD).

Additionally, the accumulation of stress-related compounds such as polyamines, glutathione MDHA, glybet, and soluble sugars provides further defense against drought-induced oxidative stress [16,17,18].

Wheat's ability to adapt to drought is intricately linked to the modulation of gene expression. Transcription factors like ERFs (ethylene response factors) play a pivotal role in orchestrating the plant's response to water deficit. For instance, TaERF3 overexpression enhances drought tolerance by promoting the accumulation of proline and chlorophyll, vital for stress adaptation [19]. Similarly, TaERF1 overexpression activates stress-related genes, bolstering wheat's resilience to drought, cold, and salinity [20]. These findings underscore the significance of manipulating gene expression to enhance drought tolerance in wheat. The inhibition of gene expression in response to drought stress has drawn more interest than gene activation, which has been the subject of extensive study. The identification of important regulatory motifs, such as the EAR motif, has made it easier to enlist co-repressors and chromatin modifiers to reduce gene expression. Across several plant species, the EAR motif emerges as a key participant in active transcriptional repression [21,22,23]. This article investigates the function of transcriptional repressors that contain the EAR motif and considers possible modes of action. Advances in molecular marker technology have revolutionized plant breeding, offering the promise of accelerated development of drought-tolerant wheat varieties. Marker-assisted breeding (MAB) leverages Key quantitative trait loci (QTLs) related to drought tolerance identified using DNA markers. These markers facilitate genome mapping and trait tagging, enabling the identification of promising candidates for breeding [24,25,26]. The integration of molecular markers, including AFLPs, SSRs, and SNPs, holds the potential for enhancing the efficiency of drought tolerance breeding programs.

The hunt for drought-tolerance genes in wheat has led researchers to investigate genetic markers associated with specific growth stages and traits. Despite the complexity of yield determination and the challenges of dissecting individual gene effects, studies have illuminated genetic markers tied to drought tolerance at different growth phases [27,28,29]. This review emphasizes the significance of concentrating on understudied regions, like reproductive organs

and root systems, to understand the genetic basis of wheat drought resistance.

Morphological adaptations are critical components of wheat's response to drought stress. Enhancing drought resistance through breeding requires an understanding of how drought affects leaf and root traits, growth phases, and overall plant shape. The links between leaf size, shape, aging, root weight, and length in response to drought stress have been clarified by recent studies [30,31,32]. These findings offer valuable insights into the morphological traits that underpin wheat's ability to withstand drought.

Wheat's physiological adaptations to drought stress encompass a range of intricate mechanisms that maintain water relations, nutrient uptake, and hormonal balance. The regulation of stomatal conductance, osmotic balance through solute accumulation, and the orchestration of Abscisic acid (ABA), a plant hormone, is essential for wheat's drought resistance [33,34,35].

Additionally, the antioxidant system's function in preventing oxidative stress, the effect of drought on nutrient availability, and nutrient transport all influence a plant's capacity to survive in a water-scarce environment.

2. FOCUSED STUDY SCHEDULE

This review study focuses on Pakistan's wheat shortage due to problems with water storage. We're going to look into current studies that try to solve this issue by figuring out how to use less water and lessen water scarcity. The main goal is to investigate many aspects of plant biology, including biochemical, morphological, and physiological properties. Understanding these characteristics will help us better understand how they affect plant growth and how they can reduce crop water needs while maintaining high yields.

In this study, are going to investigate the results of researchers that investigated new approaches for optimizing water use in wheat farming. We aim to provide useful insights into sustainable agricultural practices for wheat growing in water-scarce regions like Pakistan by identifying and understanding the individual plant characteristics that enable water-efficient growth. In the end, this study's goal is to help with continued efforts to deal with the critical issue of water scarcity along with how it affects wheat production. The goal of

these studies is to encourage agricultural practices that can efficiently reduce the need for water and increase crop output, hence promoting food security and stability in the area.

3. BIOCHEMICAL FOUNDATIONS OF DROUGHT TOLERANCE MECHANISMS IN WHEAT

Wheat and other plants improve their ability to withstand drought through a variety of biochemical processes. Reduced Rubisco efficiency, an increase in stress-related substances including glutathione MDHA, glybet, and polyamines, as well as the activation of antioxidant enzymes, are a few of these (SOD, POD, CAT, APX, GR, GST, GP, MDHAR). The antioxidant system of the plant responds positively, which is an essential component of drought tolerance. In times of drought, reactive oxygen species (ROS) like hydroxyls, superoxide, hydrogen peroxide, and singlet oxygen are produced, potentially causing harm to lipids, chlorophyll, proteins, and DNA. This insight is highlighted in the research of [16], emphasizing the significance of these biochemical processes in combating water stress effects [17]. Plants' ability to withstand drought stress is greatly aided by changes in enzyme activity. According to research, dryness causes oxidative damage because it increases the generation of reactive oxygen species (ROS) and weakens the plant's antioxidant defense mechanism. Osmotic regulators such as small molecules (Pro), ions (K+), and soluble sugars aid crops in absorbing water during drought conditions [36,37,38,39]. According to studies on wheat, genotypes with greater osmotic regulators and lower levels of malondialdehyde (MDA) are more drought-tolerant. These findings are supported by various citations [40,41,42,43,44]. During times of water stress, polyamines (PAs) are essential for preserving the integrity of cell membranes and nucleic acids [18]. Research conducted [45] indicates that increased

polyamine levels enhance crop growth when facing water stress, supported by earlier studies [46,47]. During drought, CAT, a rapidly reversible protein in leaf cells, experiences reduced activity, as observed in stress conditions.

In a study [48,49], Zincol-20's higher zinc content addresses zinc deficiency in drought-hit soils, enhancing its nutritional value and resilience. Akbar-19's strong yield potential ensures food production in drought, driven by its biochemical traits. Galaxy-2013's abundant chlorophyll sustains photosynthesis in dry conditions. Lasani-2008's proline buildup bolsters cell function during drought. Aas-2011's protein-rich biochemistry adds nutritional value during dry spells. NARC-2011's notable oil content, particularly oleic acid, elevates its economic worth for oil production amid drought. Table 1 underscores these biochemical distinctions in water scarcity combat.

3.1 Enhanced Gene Expression in Response to Drought Stress

Plant stress responses are well-known to be regulated by transcription factors of the AP2/ERF family [50]. They are divided into sub-families in wheat, including DREB, ERF, AP2, and RAV. [51]. ERFs are quickly activated during stress [52], and researchers have studied their overexpression to improve drought tolerance. Wheat with higher TaERF3 levels is more tolerant to salinity and drought [19]. Higher quantities of proline and chlorophyll, as well as the activation of downstream genes by binding to GCC-box cis-elements, are probably to blame for this [19]. Wheat TaERF1 overexpression increases resistance to salt, cold, and drought by activating stress-related genes [20]. AtERF019 supports drought resilience, delaying flowering and maturity [53]. Increasing its orthologs could boost wheat's drought tolerance without harming seed production.

Table 1. Physiological, morphological and biochemical properties of drought resistant varieties

Varieties	Physiological characters	Morphological characters	Biochemical characters
Zincol-20	Reduce transpiration and adjust its osmotic potential, which can help mitigate drought stress	Compact growth habit, reducing water loss through transpiration	Higher zinc content, which can help alleviate zinc deficiency in drought
Akbar-19	High photosynthetic trait and reduce oxidative damage, allowing it to	Shorter growth habit and extensive root system, reducing susceptibility to	High yield potential, which can help maintain productivity in drought

Varieties	Physiological characters	Morphological characters	Biochemical characters
	survive in dry conditions	drought-induced lodging	
Galaxy- 2013	Reduce stomatal conductance, making it suitable for cultivation in arid regions	Tall growth habit, providing shade to protect fruits from sunburn	High chlorophyll content, indicating good photosynthetic activity during drought.
Lasani-2008	High accumulation of proline, which induces drought resistance	Dense foliage, reducing water loss through transpiration	High vitamin C content and high leaf potassium, providing nutritional benefits to consumers during drought
Aas-2011	Tolerant to highly salt affected soil, which can help mitigate drought stress	Broad leaves, reducing water loss through transpiration	High protein content, which can help maintain nutritional value during drought
NARC-2011	Resistant to rust disease, which can help maintain plant health during drought	Large seed size and long spike length, providing high seed yield	High oil content with a high percentage of oleic acid, suitable for oil production during drought

3.2 Gene Repression in Drought Stress

While scientists have extensively explored how genes are turned on, our understanding of how genes are switched off in response to environmental changes has been limited. However, over the past decade, Significant progress has been made in understanding the characteristics and roles of the molecules involved in suppressing transcription [54]. It has been found that specific molecular patterns are involved in inhibiting gene transcription. The ethylene-responsive element binding factor is connected to the EAR motif [55] the TLLLFR motif [56], the R/KLFGV motif [57], and the LxLxPP motif [58]. Co-repressors and chromatin modifiers are drawn to these patterns, which helps to reduce gene expression [22]. The most common active transcriptional repression motif so far identified in plants is the EAR motif. Numerous investigations have shown that it is extremely constant over a wide spectrum of plant types [21,22,23,59,60,61,62]. In this discussion, we will center our attention on transcriptional repressors that incorporate the EAR motif and explore the potential ways they carry out their functions.

3.3 Molecular Marker-Assisted Breeding for Drought Tolerance in Winter Wheat

Today, researchers widely use molecular markers to locate drought-related genes. These markers aid genome mapping and trait tagging, crucial for stress-resistant wheat through Marker-

assisted breeding (MAB) [24]. This technique is vital for creating robust crops. Marker-assisted selection (MAS) involves choosing DNA markers linked to powerful QTLs, allowing the identification of drought tolerance QTLs [63]. By using molecular linkage maps, marker-assisted selection (MAS) is essential to increase plant drought resistance. To map QTLs for flag leaf senescence (FLS) in winter wheat under normal and water-stressed conditions, researchers used AFLP and SSR markers. This allowed them to pinpoint the relevant gene on chromosome 2D, which is linked to improved drought performance [25]. In the [26] study, wheat drought stress characteristics were identified using DNA markers from 2005 (RFLP, AFLP, SSR). By analyzing gene diversity, genotypes, and genetic mapping, molecular markers such as the SDS-protein, isozymes, and DNA sequences have also helped select drought tolerance features in wheat [64,65,66].

Certain markers in durum wheat are connected to grain yield and drought tolerance traits, with leaf water potential, canopy temperature, chlorophyll inhibition, and proline content showing strong links to molecular markers. Several DNA markers created, [67] including PCR indels, RAPDs, RFLPs, CAPS, AFLPs, microsatellites (SSRs), SNPs, and DNA sequences, to explore the inheritance of stress tolerance. In cereal research, DNA primers are frequently used for RAPDs among them [68]. To map the genomes of wheat and other crops, scientists used ISSRs. Wheat

has RAPD and ISSR markers connected to a gene associated with drought, according to [69]. For hexaploid wheat, RAPDs were useful [55,68]. Marker-assisted selection is advantageous when a molecular marker corresponds more closely with a trait than the trait's heritability. These markers have the potential to increase durum wheat's drought resistance. [70].

3.4 Deciphering Drought Tolerance QTLs in Wheat

Through research on wheat output and associated attributes under water-scarce conditions, scientists have discovered genetic markers connected to drought tolerance in wheat. [27,28,29,71,72]. Although yield is important, it's tricky to precisely measure in terms of water usage and locate specific gene regions. Although gene-based markers and genome sequencing are expected to make it easier to find specific genes [73], breeding methods cannot use the vast genomic regions connected to individual traits (QTL). Surprisingly, little genetic research has been done on reproductive tissues and roots, which are essential for drought resistance. The

impact of drought on cereal reproductive mechanisms has been thoroughly investigated [74]. Although [75] suggested that increasing floral fertility in water-stressed situations would be a worthwhile objective, no research has looked into the wheat genes that are in charge of this [76] recommended emphasizing improving root systems' capacity to absorb water. Molecular marker-assisted selection in breeding programs might benefit immensely from finding markers or genes associated with root growth and shape. Only a handful of research papers have looked into QTLs for wheat root characteristics. For instance, [77] discovered a QTL connected to the rate of root growth when exposed to aluminum. While employing relative root growth to map QTLs for tolerance to high soil boron levels, [78] discovered QTLs for a variety of root characteristics under different situations. However, the genetic factors influencing root architecture in dry conditions remain undiscovered for wheat. Despite numerous studies on genes linked to drought and stress resilience in challenging environments, the only successful markers applied in practical plant breeding deal with boron and aluminum tolerance [79].

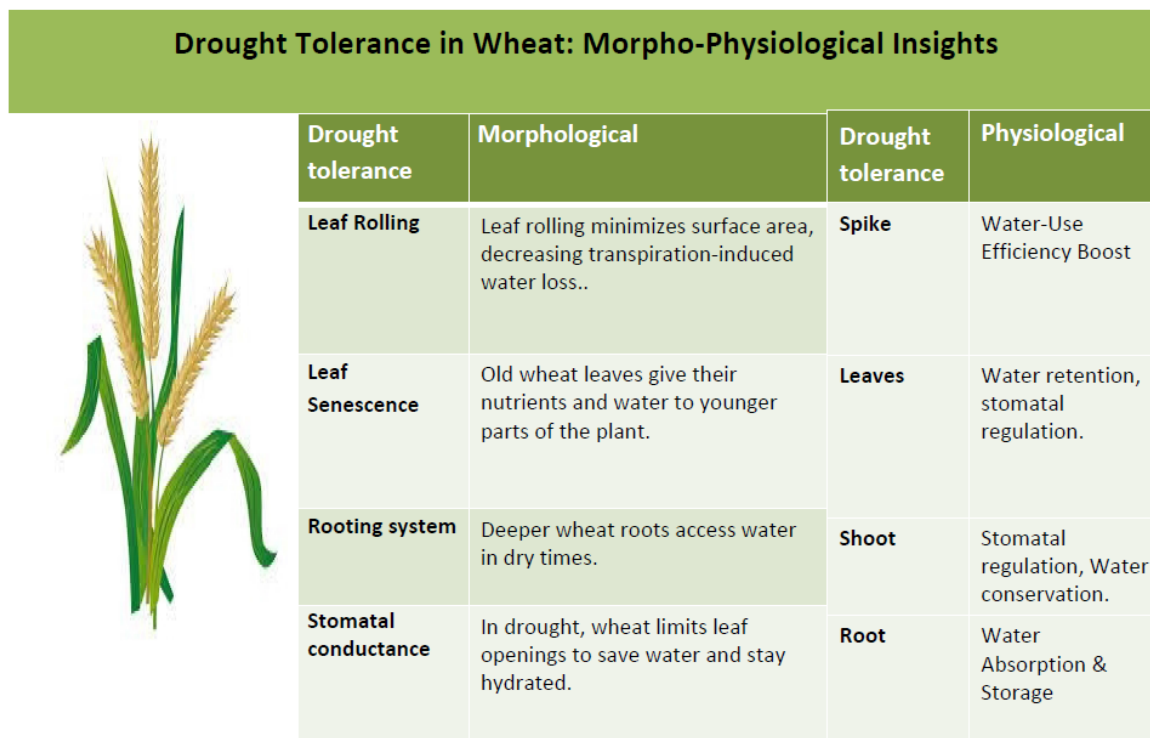


Fig. 1. Drought tolerance in wheat: morpho-physiological insights

4. EXPLORING THE MORPHOLOGICAL BASIS OF DROUGHT TOLERANCE IN WHEAT

The study [30] investigated the effects of drought on wheat's roots and leaves (size, shape, and age) (weight, length). In one more study [80] highlighted how dryness affects different stages of plant growth. Genetic improvements in breeding depend on this knowledge [30,80]. Early maturity, small plant size, and decreased leaf area are associated with drought tolerance, according to [32,81] discovered that wheat's main leaf length and area increase during drought, while width remains stable. This helps balance root water absorption with overall plant water status, as highlighted. The study [82] revealed that drought diminishes leaf area, leading to reduced photosynthesis. Water stress, as noted by [83], can shrink leaf count, size, and longevity. In wheat, [84] found leaf development particularly vulnerable to water stress. [85] emphasized the vital role of roots in seeking out water. When faced with drought stress, a plant's leaves are the first to be affected [86]. While roots keep growing in search of water, the growth of above-ground parts is limited. This divergent response aids the plant's survival in arid conditions. In drought, the ratio of the roots to the shoots rises, improving water absorption [87]. The ABA levels in the roots and shoots are related to this ratio change. Wheat roots grew more slowly when there was a moderate to severe drought. The reduction in root growth brought on by the drought in the case of wheat, however, was not very significant. In spring wheat, drought stress caused a drop in a crucial component called plant biomass [88]. Earlier investigations on wheat and other crops revealed similar results. According to research by, dryness for winter wheat resulted in a drop or change in yield while increasing water usage effectiveness [89,90].

In a study [48,49], Zincol-20's compact morphology curbs water loss, enhancing its drought resilience. Akbar-19's shorter stature and expansive roots bolster stability under drought by reducing lodging risk. Galaxy-2013's tall morphology provides fruit-saving shade, improving quality during drought. Lasani-2008's dense morphology minimizes water loss, elevating drought resistance. Aas-2011's broad morphology conserves water, aiding survival in drought. NARC-2011's large seeds and lengthy spikes ensure productivity even in drought [91]. Refer to Table 1.

4.1 Understanding Plant Traits: Physio-Morphological Insights

New ways of precisely understanding plant characteristics, combined with advanced genetic and molecular techniques in breeding, are set to enhance how breeding programs work. Instead of just aiming for higher yield, it's now seen as more effective to indirectly select according to earlier studies [92,93,94] for key physiological traits that affect yield. Indirect selection for higher yield is anticipated to perform better than direct selection [95,96]. This observation is made because traditional breeding masks the impact of the desired feature on grain output by focusing on the yield of thousands of plants after each cycle. Physio-morphological trait-based breeding, on the other hand, seeks out more straightforward features connected to yield [97]. By relying less on the final grain yield, evaluating yield-related physio-morphological variables separately increases selection efficiency. This method could enhance the chance of achieving successful crossbreeding outcomes by tapping into the potential of combined gene effects [96,98,99], as mentioned earlier. Moreover, it's beneficial if the heritability of the targeted physiological trait for selection in challenging conditions is higher than the yield itself. This provides a better opportunity for creating stress-resistant varieties.

4.2 Targeting Growth Stages

The breeder enhanced drought-resistant genes in wheat and produced different varieties. It is important to focus on specific growth stages. Understanding the impact of drought at different phases is very important. While the severity and frequency of drought matter, the duration of drought during growth also plays an important role. Critical stages include germination and tillering, stem elongation, and as well as heading, flowering, and grain filling [100,101,102,103].

4.3 Germination and Seedling Phases

For consistent seed germination when it comes to the effects of drought on wheat growth phases, having enough soil moisture and the proper temperature is crucial. This is especially important for drought-sensitive wheat cultivars. Under normal and water-limited conditions, many features of seed germination, such as how soon they sprout and the degree of cell damage, can

differ dramatically among various species of wheat. These variances have been emphasized in studies by [104,105,106,107].

4.4 Tillering and Stem Growth Phases

Spikelet initiation starts at the seedling stage and lasts until tillering after the plant has a double ridge, whereas floret initiation begins at tillering and continues as the stem lengthens. The spikelet and spike count at these stages directly affect grain yield. Wheat production and grains per spike are reduced by severe dryness during tillering and stem elongation [101,103]. For instance, [101] observed that water stress during the vegetative stage resulted in a 54 percent decrease in grain output (stem elongation to flowering).

4.5 Heading and Anthesis Stages

These are focused on decreasing grain yield due to decreased grain quantity and weight in research that shows that the blooming and anthesis stages of wheat are particularly vulnerable to drought [108]. Additionally, impacted, pollen viability results in spikelet sterility. The blooming and anthesis stages of wheat are particularly vulnerable to dryness, with a focus on decreasing grain production due to a reduction in grain number and weight, according to several studies [108]. Furthermore, impacted is pollen viability, which results in spikelet sterility [80,109]. Water stress during these stages has significant implications for wheat growth [104,110].

4.6 The Vital Grain Filling Phase

While one might expect drought during grain filling to be more damaging due to limited recovery opportunities, studies suggest this stage is not highly sensitive to drought. This implies potential ways to mitigate its impact. In fact, during grain filling, adequate water is crucial for nutrient movement, but reserves stored before flowering, like in the stem, can counter the negative effects of moisture stress on nutrient assimilation through photosynthesis [111].

5. NURTURING DROUGHT RESILIENCE IN WHEAT: INSIGHTS INTO PHYSIOLOGICAL ADAPTATIONS

When plants experience drought, they react by closing stomata, lowering photosynthesis activity,

and facing oxidative stress. This stress can harm cell walls, leading to the release of toxic compounds that eventually cause plant death [112]. Roots detect signals, turgor is lost, and osmosis adjusts. Leaves' water potential drops, internal CO₂ levels drop as stomatal conductance to CO₂ is reduced, and growth rates slow. Researchers have linked these responses to a plant's drought resistance. Factors like higher relative and potential water levels, along with membrane integrity, influence a plant's ability to withstand drought [113]. To gauge drought tolerance, scientists have examined how plant cell membranes hold up and function under water stress [114]. Early drought stress during grain filling can lower nutrient transport, reducing cell count and metabolic activity in the endosperm [115]. Cysteine proteinase's vital role in plant signaling, growth, development, and stress response was highlighted by [116]. They discovered increased cysteine expression in wheat leaves, leading to heightened proteolysis activity during drought [117].

The research [48,49] underscores distinctive physiological traits in drought-resistant varieties. Zincol-20 strategically reduces transpiration, adapting to aridity, while Akbar-19's adept photosynthesis and oxidative damage control support its dry condition survival. Galaxy-2013's reduced water loss suits arid regions, and Lasani-2008's proline accumulation bolsters cellular integrity during drought. AAS-2011's salt tolerance enhances resilience in dry environments, and NARC-2011's rust resistance ensures plant vitality amid drought (Table 1).

5.1 Plant Photosynthesis and Gaseous Exchange

Plant growth and crop yield are driven by photosynthesis. It is crucial to comprehend how plants react to drought. Variation in photosynthetic pigments indicates plant photosynthesis under water stress. Drought reduces photosynthesis in cereals [118]. Key limitations include CO₂ diffusion reduction due to early stomatal closure, enzyme activity decrease, biochemical changes, and photosystem II efficiency drop. Disruptions result from light capture/utilization imbalance, Rubisco activity decline, chloroplast damage [119], structure and machinery breakdown, chlorophyll oxidation, substrate depletion, biosynthesis hindrance, and increased chlorophylls activity [120]. Drought-induced photosynthesis limits are more complex

than stomatal ones due to pigment synthesis reduction [121].

5.2 Water Relations

Water content, water loss rate, and leaf water retention all play major roles in how plants and water interact. The relative water content (RWC), which measures a plant's level of hydration, is one important indicator. which drops during drought stress, impacting its well-being [33]. For instance, decreased leaf water potential during dry circumstances causes a drop in barley yield [122]. Understanding a plant's water relations can be gained by looking at how detached leaves lose water. This is particularly useful when contrasting leaves with adequate irrigation with those with inadequate irrigation. It indirectly indicates leaf protection and water loss. Less water loss from detached leaves suggests better drought tolerance and water conservation. During drought stress, detached leaves retain more water due to rolling or reduced surface area. This trait could aid in selecting drought-tolerant, high-yield crops. Research links water retention and leaf rolling to crop yield during drought [81,123,124].

5.3 Nutrient Relations

Drought reduces nutrient uptake in plants [34]. It limits water and nitrogen availability, affecting wheat yield and photosynthesis. Nutrient movement is restricted, especially phosphorus (P), due to decreased soil water [125,126]. Drought also impairs potassium (K⁺), calcium (Ca²⁺), and magnesium (Mg²⁺) uptake through roots [127]. Calcium (Ca²⁺) in plants drops during drought due to reduced transpiration [83,128]. Wheat experiences lower calcium, potassium, and phosphorus levels under water stress [34]. Micronutrients like manganese (Mn), iron (Fe), and molybdenum (Mo) may also decline during drought but become more available when watering resumes [129].

5.4 Oxidative Status

Plants suffer oxidative damage as a result of reactive oxygen species (ROS), which include singlet oxygen, superoxide radicals, hydrogen peroxide, and hydroxyl radicals. ROS upsets the balance of the cell by oxidizing essential substances like pigments, lipids, proteins, and DNA. This can lead to cell death, stunted growth, and reduced plant productivity [130]. The impact of drought stress on plants depends on its

duration, timing, and intensity [130]. ROS production increases with water stress severity, damaging membranes, organelles, enzymes, and nucleic acids [131]. Malonic dialdehyde (MDA) levels that are high signify lipid peroxidation brought on by ROS and represent membrane damage [132]. Wheat with low MDA levels is drought-tolerant [133]. Moreover, heightened lipoxygenase enzyme activity (LOX) accelerates lipid peroxidation by oxidizing fatty acids during stress [134]. LOX activities differ under drought stress compared to non-stressed plants [135].

5.5 Antioxidant System

When wheat and barley face water stress, they produce antioxidant enzymes like CAT, SOD, and POD to adapt. Barley's expression of APX, CAT, and SOD varies with growth stage and type under drought. Drought-tolerant wheat shows increased CAT, APX, and GPX gene expression, vital for drought management. Resilient wheat has higher SOD, POD, and CAT activities. Mild drought boosts wheat leaf APX, while prolonged shortage reduces it due to more MDA. Robust wheat types have high POD, phenolic content, and low damage, indicating better stomatal closure [70,136,137,138].

5.6 Osmotic Balance

The three types of plant adaptation to water scarcity are drought resistance, dehydration tolerance, and dehydration avoidance. One technique for managing cellular dehydration and the structural integrity of the membrane to provide tolerance to drought and cellular dehydration is osmolyte accumulation [138].

Plants subjected to drought may change their osmotic balance after storing low-molecular-weight organic solutes. The cytoplasm of the wheat plant builds up a variety of inorganic and organic solutes to reduce its osmotic potential and maintain cell turgor [138]. Plants create and store suitable solutes including sugars, polyols, and amino acids during drought stress to help maintain osmotic balance and promote water uptake and retention [139]. In addition to osmoprotection, osmotic adjustment, carbon storage, detoxification of reactive oxygen species, maintenance of membrane integrity, protection of macromolecules and DNA structures, and stabilization of enzymes and proteins, carbohydrates also serve several other important biological functions. Even more so than

proline, carbohydrates play a crucial role in replacing water in extremely dehydrated conditions by hydrating proteins around them. Wheat genotypes accumulate more soluble sugars during the grain-filling period than the pre-anthesis stage under drought stress [140]. On the other hand, the reduction of total soluble sugars could be ascribed to water-induced loss of solutes (mainly K⁺) from guard cells, which resulted in a selective reduction in guard cells' turgor leading to stomatal closure [141].

5.7 Hormonal Effect

Abscisic acid (ABA), a vital plant hormone, influences drought adaptation through water conservation and tolerance mechanisms. ABA helps plants endure harsh conditions like drought, salt, and extreme temperatures by signaling stress responses. It controls leaf growth, stomatal closure, and systemic reactions to stress before changes in water or nutrient levels are evident [34,142,143,144]. In wheat, ABA promotes root growth, vital for increased yield during drought. Osmotic stress triggers various growth regulators like auxins, cytokinins, and others, acting as signals in complex networks for physiological processes [145]. ABA fine-tunes root development, leaf growth, and water content through gene expression [146]. During drought, plants produce ABA in their xylem tissues, which then move to reproductive parts and affect grain filling by influencing certain genes related to carbohydrate breakdown and cell division. Leaves accumulate ABA, while cytokinin levels decrease. Mild drought with low ethylene and high ABA speeds up grain filling, but severe drought with excessive ethylene and ABA slows it down. Applying gibberellin A3 (GA3) to roots helps plants grow taller leaves in tough soil. Plants boost cytokinins and ABA to counter water stress effects [147,148,149,150].

6. CONCLUSION

In conclusion, the biochemical and physiological adaptations of wheat to drought stress are complex and multifaceted. Through various mechanisms, wheat plants enhance their tolerance to water scarcity, allowing them to survive and thrive under challenging conditions. The intricate interplay of biochemical processes, gene expression, morphological traits, and physiological responses contribute to the overall drought resilience of wheat. Plants use biochemical tricks, like building up stress-fighting substances and triggering antioxidant enzymes,

to fight off the damage caused by reactive oxygen molecules during droughts. Scientists have pinpointed important genes that help plants handle drought stress. By using special markers and advanced breeding methods, we're making progress in creating wheat plants that can better withstand drought conditions. The morphological basis when wheat plants face drought, they adapt to save water and survive. They adjust their water use, nutrient absorption, and internal balance. Hormones like Abscisic acid help them handle drought better. Think of it as the plant's survival plan, with hormones playing a crucial role. As we uncover the secrets of plants' adaptations to drought, we can develop drought-resistant wheat through targeted breeding and farming techniques. This benefits both crop yield and food security in dry regions. Ongoing research in this area offers potential for more resilient wheat crops.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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