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Physiological Responses of Photosynthetic Characteristics and Antioxidant Systems in Wheat Leaves under Drought Stress

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Received: 29 Jul., 2026

Accepted: 31 Aug., 2026

Published: 15 Sep., 2026

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Preferred citation for this article:

Jin L., 2026, Physiological responses of photosynthetic characteristics and antioxidant systems in wheat leaves under drought stress, Genomics and Applied Biology, 17(5): 284-298 (doi: [10.5376/gab.2026.17.0022](https://doi.org/10.5376/gab.2026.17.0022))

Abstract Drought stress is one of the major environmental constraints limiting wheat growth, productivity, and yield stability, particularly under increasing climate variability. This review summarizes the physiological responses of wheat leaves to drought stress, with emphasis on photosynthetic characteristics and antioxidant defense mechanisms. Drought-induced reductions in leaf water status and stomatal conductance restrict CO₂ diffusion and progressively impair photosynthetic carbon assimilation. Meanwhile, disturbances in photosynthetic electron transport enhance the production and accumulation of reactive oxygen species (ROS), resulting in oxidative damage to cellular membranes and photosynthetic structures. Wheat responds to oxidative stress by activating enzymatic antioxidant defenses, including superoxide dismutase, catalase, peroxidase, ascorbate peroxidase, and glutathione reductase, together with non-enzymatic antioxidants involved in the ascorbate-glutathione cycle. The coordinated regulation of stomatal behavior, chlorophyll fluorescence, photoprotection, ROS scavenging, hormonal signaling, and redox homeostasis contributes to drought adaptation. Case studies further demonstrate differences among drought intensity, duration, and rewatering conditions in determining photosynthetic recovery and antioxidant capacity. Finally, strategies involving irrigation management, nutritional regulation, exogenous substances, drought-tolerant cultivar selection, and precision agriculture are discussed. Integrating physiological, biochemical, and molecular approaches will improve the understanding and practical management of wheat drought tolerance.

Keywords Wheat; Drought stress; Photosynthesis; Antioxidant system; Reactive oxygen species

1 Introduction

Wheat is one of the world's most important staple crops and provides a substantial share of human calories and protein, so its stability under water-limited environments is tightly linked to global food security. Yet drought has become one of the most serious abiotic constraints on wheat production worldwide, and climate change is increasing both the frequency and severity of water scarcity across major wheat-growing regions (Franco-Navarro et al., 2025). Projections suggest that the area exposed to drought in wheat-producing regions could expand markedly during this century, with simultaneous severe water scarcity affecting far more wheat land than at present even under mitigation scenarios. This threat is especially serious because much of global wheat production already occurs in water-stressed breadbaskets; one analysis estimated that 65% of wheat produced across major global breadbaskets faces high water scarcity. At regional scales, winter wheat frequently experiences serious crop water deficit in major production zones such as the North China Plain and northwestern China, especially from greening to jointing and from jointing to anthesis, and these deficits can reduce yield by 60% and 55%, respectively, when water supply is insufficient. Future modeling further indicates that concurrent meteorological and agricultural drought can widen wheat yield gaps more than single-type drought, with projected impacts on wheat often stronger than on maize and strongly shaped by soil moisture constraints. Although global mean production losses may appear moderate in some projections, the burden is highly uneven, with many countries expected to face large drought-related crop losses, reinforcing the need for drought adaptation in wheat systems (Kraklow et al., 2025). Because reproductive and grain-filling stages are particularly sensitive to water deficit, drought not only depresses biomass accumulation and grain formation but also threatens the reliability of wheat production under increasingly unstable climates (Bohra et al., 2024).

The harmful effect of drought on wheat productivity is mediated through a cascade of physiological disturbances, among which impairment of photosynthesis is one of the earliest and most consequential responses (Nyaupane et al., 2024). Under water deficit, wheat leaves rapidly close stomata to limit transpirational water loss, but this protective response also restricts CO₂ diffusion and reduces carbon assimilation, leading to declines in net photosynthetic rate and stomatal conductance. Experimental studies across wheat genotypes consistently show that drought reduces net photosynthesis, stomatal conductance, relative water content, chlorophyll content, and grain yield, although the magnitude of decline differs among cultivars according to drought tolerance capacity. In the early phase of drought, photosynthetic inhibition is often dominated by stomatal limitation, whereas under prolonged or severe stress non-stomatal limitations become increasingly important, including chlorophyll loss, reduced Rubisco-related activity, inhibition of PSII electron transport, and damage to the oxygen-evolving complex and light-harvesting system (Todorova et al., 2022). Chlorophyll fluorescence measurements confirm that drought decreases Fv/Fm, ΦPSII, qP, and electron transport rate, while often increasing energy dissipation pathways, indicating progressive photochemical impairment and photoinhibition risk. This physiological progression is further intensified when drought co-occurs with heat, because high temperature amplifies declines in PSII efficiency, carbon uptake, and water use efficiency, particularly above critical thermal thresholds and in sensitive genotypes. At the same time, drought disturbs photosynthetic electron flow and enhances the incomplete reduction of oxygen, promoting the formation of reactive oxygen species such as superoxide and hydrogen peroxide that damage lipids, proteins, membranes, and the photosynthetic apparatus if not effectively detoxified. Accordingly, antioxidant defense is a central component of drought tolerance in wheat. Water deficit commonly elevates the activities of superoxide dismutase, catalase, peroxidase, and ascorbate peroxidase, together with osmotic regulators such as proline, soluble sugars, and related metabolites that help preserve membrane integrity and cellular hydration. Tolerant genotypes generally sustain lower hydrogen peroxide and lipid peroxidation, stronger or longer-lasting antioxidant activity, and better recovery after rewatering, indicating that resistance depends not only on limiting water loss but also on maintaining redox homeostasis and protecting photosynthetic tissues.

Against this background, understanding the coordinated responses of photosynthetic characteristics and antioxidant systems in wheat leaves is essential for clarifying how drought injury develops and how tolerance is expressed at the physiological level. Existing research has established that drought affects gas exchange, chlorophyll fluorescence, pigment stability, osmotic adjustment, and antioxidant metabolism, but several important questions remain open, particularly regarding the temporal coupling between photosynthetic decline and oxidative defense, the extent to which stomatal versus non-stomatal limitation predominates under different stress intensities, and which leaf traits best distinguish tolerant from susceptible wheat genotypes. There is also strong practical value in identifying physiological indicators that respond sensitively to drought and recovery, because such traits can support cultivar screening, mechanistic phenotyping, and management strategies aimed at improving water productivity and resilience. Therefore, this study is framed to examine how drought stress alters leaf photosynthetic performance and antioxidant defense in wheat, with emphasis on changes in gas exchange, chlorophyll-related traits, reactive oxygen metabolism, and protective enzyme activities. The central scientific questions are whether drought-induced reductions in photosynthetic capacity are accompanied by coordinated activation of antioxidant enzymes, whether these responses are sufficient to limit oxidative injury in leaves, and which physiological indices can most effectively explain variation in drought tolerance). By integrating these dimensions, the study can help bridge the gap between whole-plant drought outcomes and leaf-level mechanisms, and provide a physiological basis for breeding and management strategies that enhance wheat adaptation to increasingly water-limited environments.

2 Effects of Drought Stress on Leaf Water Status and Physiological Processes in Wheat

2.1 Changes in leaf water status and water relations

Drought stress first disrupts leaf water balance in wheat by lowering leaf water potential and relative water content, thereby weakening turgor maintenance and impairing normal physiological activity. This decline in water status is consistently accompanied by higher leaf or canopy temperature, indicating reduced evaporative cooling and

tighter hydraulic constraints on leaf function. Across genotypes, the magnitude of these changes depends on their capacity to preserve hydration through osmotic regulation, elastic adjustment, and sustained water transport, rather than through simple dehydration avoidance alone. In drought-tolerant wheat, maintenance of higher relative water content and leaf water potential is often associated with better xylem exudation, stronger membrane stability, and improved chlorophyll retention under stress (Akter et al., 2023).

The physiological basis of these water-relation differences lies in the coordination between osmotic adjustment and hydraulic behavior. Resistant wheat genotypes commonly accumulate soluble sugars and other osmolytes that lower osmotic potential, improve soil water uptake, and help preserve cell function under declining soil moisture. By contrast, increasing water deficit causes sharper declines in relative water content, water potential, and membrane stability in susceptible materials, showing that inadequate adjustment accelerates dehydration injury. Leaf structural and anatomical integrity also matters, because maintaining functional leaf hydraulic properties and internal diffusion pathways helps sustain photosynthetic capacity as drought progresses (Yang et al., 2026). For this reason, traits such as relative water content, excised leaf water retention, relative water loss, leaf rolling, and waxiness are widely treated as practical indicators of drought tolerance in wheat.

2.2 Stomatal regulation and transpiration responses

Stomatal regulation is one of the earliest and most decisive responses of wheat leaves to drought stress because it directly controls both carbon dioxide influx and transpirational water loss. As soil dries, stomatal conductance usually declines before many other gas-exchange traits, and this reduction lowers transpiration and leaf cooling while progressively constraining photosynthesis (Pflüger et al., 2024). Experimental evidence further shows that stomatal conductance in wheat is positively linked with leaf water potential and hydraulic conductance, but negatively associated with abscisic acid accumulation and, under severe stress, with altered stomatal traits such as density and pore area. Thus, stomatal behavior reflects not only passive water loss control but also active integration of hydraulic and hormonal signals across stress intensities.

Wheat does not rely on a single stomatal strategy under drought. Under mild stress or early drying, some genotypes maintain relatively high conductance and behave more anisohydrically, allowing continued carbon assimilation despite falling hydraulic conductance. With increasing drought severity, however, stomata shift toward a more conservative, isohydric pattern, reducing transpiration to protect leaf water status and hydraulic safety. Genotypic differences are important in this transition: drought-tolerant lines can delay full stomatal closure during reproductive stress, whereas sensitive lines often close stomata earlier and enter a passive survival mode sooner (Onyemaobi et al., 2021). In parallel, structural stomatal traits contribute to performance, since smaller or more numerous stomata, depending on genetic background, can support faster regulation and improved transpiration efficiency under drought.

2.3 Water use efficiency and drought adaptation

Water use efficiency in wheat under drought is shaped by the balance between conserving water and sustaining assimilation. Moderate restriction of stomatal opening often increases instantaneous or integral water use efficiency because transpiration declines faster than photosynthesis, even though absolute carbon gain may still be reduced. Drought-resistant cultivars tend to achieve this balance more effectively, showing lower lifetime water consumption or transpiration together with better maintenance of productive photosynthesis under stress. This trade-off is central to wheat adaptation, since excessive water saving can protect tissues but penalize biomass accumulation, whereas insufficient control accelerates dehydration and oxidative damage. As a result, drought adaptation depends on optimizing, rather than maximizing, stomatal restriction and tissue hydration (Franco-Navarro et al., 2025).

At the whole-plant level, improved water use efficiency emerges from the integration of stomatal behavior, root water acquisition, osmotic adjustment, and management context. Deficit irrigation imposed at suitable growth stages can raise wheat water use efficiency, especially when stress is moderated and rewatering occurs after sensitive periods such as heading. Management interventions can also enhance efficiency: combining deficit irrigation with soil amendments improved water use efficiency in pot experiments, indicating that agronomic

measures can complement intrinsic physiological tolerance (Irkiso et al., 2025). At the genetic level, wheat lines with tighter stomatal control, improved root development, and lower relative water loss show higher instantaneous water use efficiency and less physiological damage under water limitation. Together, these findings show that drought adaptation in wheat is best understood as coordinated regulation of water loss, water capture, and photosynthetic protection rather than as a single-trait response (Figure 1).

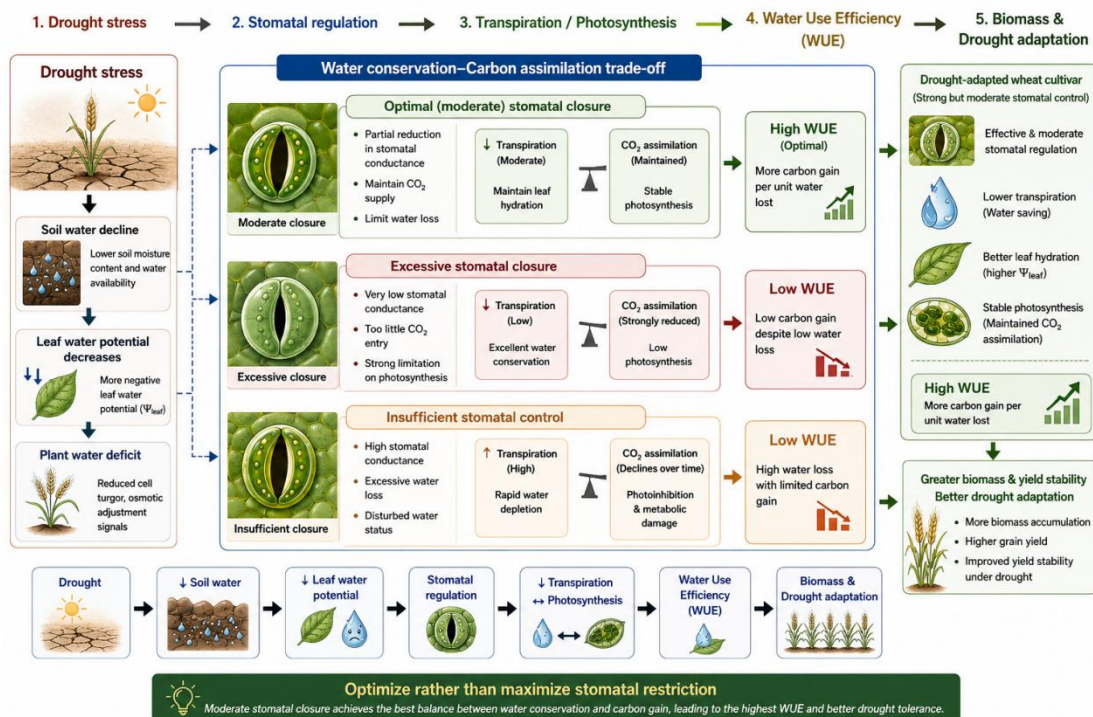


Figure 1 Trade-off between water conservation and carbon assimilation in wheat under drought stress. Moderate stomatal restriction can improve water use efficiency by reducing transpiration while maintaining relatively stable photosynthetic carbon assimilation, whereas excessive stomatal closure can restrict carbon gain and biomass accumulation. Drought-adapted wheat cultivars optimize stomatal regulation and tissue hydration to balance water conservation with productive photosynthesis

3 Changes in Leaf Photosynthetic Characteristics of Wheat under Drought Stress

3.1 Dynamic responses of gas exchange parameters

Drought stress suppresses leaf gas exchange in wheat primarily through progressive declines in net photosynthetic rate, stomatal conductance, and transpiration, and these changes often appear early during soil drying. Across experiments, stomatal conductance is typically the most sensitive gas-exchange trait, and once it falls sufficiently, limitations on CO_2 supply begin to constrain photosynthetic carbon gain more strongly (Pflüger et al., 2024). This early phase is therefore dominated by stomatal limitation rather than irreversible biochemical damage, especially under mild to moderate stress. As drought intensifies, reduced stomatal opening also weakens evaporative cooling and accelerates feedback effects on leaf metabolism, which further depresses assimilation.

With longer or more severe drought, gas-exchange inhibition becomes increasingly shaped by non-stomatal factors, including reductions in carboxylation capacity and electron transport. In wheat, this transition is often reflected by lower chlorophyll content, smaller assimilating leaf area, and rising intercellular constraints that indicate impairment beyond stomatal closure alone (Guizani et al., 2023). Genotypic differences are substantial: tolerant cultivars generally maintain higher photosynthesis and conductance under stress, whereas sensitive genotypes adopt stronger water-conserving closure at the cost of carbon uptake. After rewatering, gas exchange can recover markedly, but recovery depends on how far drought has progressed before relief.

3.2 Chlorophyll fluorescence and photosystem function

Chlorophyll fluorescence shows that drought alters the photochemical functioning of wheat leaves even when visible injury is limited. Sensitive fluorescence traits usually include declines in Φ_{PSII} , qP , and ETR, together

with stronger non-photochemical energy dissipation as the use of absorbed light for photochemistry becomes restricted (Abdullaev et al., 2024). Consistent with this, droughted wheat often exhibits lower Fv/Fm and Fv/F0, linking reduced gas exchange with reduced photochemical efficiency of PSII. These responses indicate that the photosynthetic apparatus is not only receiving less CO₂ because of stomatal closure, but is also redistributing excitation energy toward protective heat dissipation.

However, PSII damage is usually limited during mild drought and becomes pronounced mainly under severe dehydration, when protective mechanisms are no longer sufficient (Sommer et al., 2023). Under stronger stress, wheat shows increases in F0 and decreases in Fm, Fv/Fm, qP, and ETR, while OJIP-based indices such as RC/ABS, PIabs, and PI_{tot} also decline, revealing fewer active reaction centers and lower overall PSII performance. Mechanistically, drought reduces PSII electron transport and leaves a larger fraction of absorbed energy to be handled by alternative electron sinks and cyclic electron flow, which appear to contribute to photoprotection. Fluorescence traits therefore capture both injury and acclimation, making them useful indicators for distinguishing tolerant and sensitive wheat genotypes.

3.3 Photosynthetic pigments, carbon assimilation, and photosynthetic product accumulation

Drought commonly reduces photosynthetic pigment content in wheat leaves, including chlorophyll and carotenoids, and this loss contributes directly to lower light capture and weaker carbon assimilation. Reviews and experiments converge on the point that drought-induced chlorophyll decline is associated with chloroplast damage, thylakoid disruption, and reduced activity of Calvin-cycle components such as Rubisco, which together depress atmospheric carbon fixation. At the molecular level, drought also down-regulates many wheat genes linked to PSI, PSII, light-harvesting complexes, cytochrome b6f, and ATP synthase, providing a transcriptional basis for declining pigment function and photochemical capacity (Karami et al., 2025). Because tolerant cultivars usually retain chlorophyll more effectively, pigment stability is often treated as a practical marker of drought resilience.

The reduction in leaf carbon assimilation under drought also changes downstream carbohydrate metabolism and assimilate accumulation. As photosynthesis falls, starch accumulation is often reduced, while soluble sugars and sucrose-related metabolism become more dynamic and can increase as part of osmotic adjustment or stress reallocation (Nyaupane et al., 2024). In developing wheat grains, drought during early grain filling significantly increases soluble sugars and sucrose synthase activity, while sucrose and total starch can first decline and then rebound, indicating a temporal restructuring of carbon partitioning rather than a uniform shutdown. Experimental manipulation also shows that improving stress protection can preserve chlorophyll and moderate drought-induced shifts in sucrose and starch pools, reinforcing the close coupling between leaf photosynthetic performance and whole-plant carbon economy.

4 Drought-Induced Oxidative Stress and Reactive Oxygen Species Metabolism

4.1 Production and accumulation of reactive oxygen species

Drought stress triggers a rapid increase in reactive oxygen species (ROS) production in wheat leaves because stomatal closure restricts CO₂ fixation, causing absorbed light energy and reducing power to exceed the utilization capacity of the Calvin cycle. This excess excitation energy drives electron leakage to molecular oxygen, primarily generating superoxide (O₂^{•-}) and hydrogen peroxide (H₂O₂) in chloroplasts, peroxisomes, and mitochondria. Under normal conditions, only a small fraction of electrons passing through the electron transport chain incompletely reduce oxygen, but drought shifts this balance toward uncontrolled ROS generation. The resulting overaccumulation of ROS disrupts cellular redox homeostasis and initiates oxidative cascades that damage biomolecules (Panda et al., 2024).

ROS accumulation in wheat is highly dependent on drought severity and duration. Under progressive drought, ROS levels remain stable during early stress phases but increase significantly once drought exceeds a critical threshold, indicating that the ROS generation rate eventually overwhelms the plant's scavenging capacity. Drought-sensitive wheat cultivars accumulate higher ROS levels than tolerant ones, reflecting greater photosynthetic inhibition and a higher potential for oxidative damage. Tolerant cultivars mitigate ROS accumulation through enhanced non-photochemical quenching and sustained antioxidant enzyme activity, which

together prevent the oxidative burst (Moloi et al., 2024). Severe drought further accelerates ROS production by impairing PSII electron transport, leaving a larger fraction of absorbed energy to be processed by alternative electron sinks.

4.2 Membrane lipid peroxidation and cellular oxidative damage

Excessive ROS production during drought causes direct oxidative damage to cellular structures, with membrane lipid peroxidation being one of the most damaging consequences. Malondialdehyde (MDA) content is widely used as a biochemical marker for lipid peroxidation, and drought-stressed wheat consistently shows elevated MDA levels alongside increased hydrogen peroxide and superoxide generation. Drought-sensitive wheat varieties exhibit substantially greater MDA accumulation in both leaves and roots compared to tolerant varieties, indicating more severe membrane damage from uncontrolled ROS spread (Moloi et al., 2024). Tolerant varieties, by contrast, limit MDA increases through stronger enzymatic antioxidant capacity and lower tissue ROS content.

Beyond lipid peroxidation, ROS attack proteins, nucleic acids, and other macromolecules, causing base substitutions, structural protein alterations, and eventual cell death. Electrolyte leakage serves as a direct physiological indicator of this membrane disruption, and drought-stressed wheat shows elevated electrolyte leakage proportional to the severity of oxidative injury (Muslemyar & Kaya, 2025). Drought acclimation can moderate this damage; wheat seedlings exposed to initial mild stress exhibit better membrane stability and lower electrolyte leakage during subsequent severe stress compared to non-acclimated plants. Exogenous applications of antioxidants such as thiourea, selenium, and melatonin further reduce MDA and electrolyte leakage by enhancing ROS-scavenging enzyme activities.

4.3 ROS signaling and drought stress adaptation

At low concentrations, ROS function as signaling molecules that activate acclimatory and defense responses rather than causing damage. Hydrogen peroxide acts as a secondary messenger in signal transduction pathways, triggering stress-defense gene expression and coordinating adaptive responses to water deficit. ROS signaling is tightly linked to abscisic acid (ABA) pathways, calcium fluxes, and sugar sensing, positioning ROS both upstream and downstream of ABA-dependent drought signaling cascades. Maintaining ROS homeostasis is therefore essential for drought tolerance, as balanced ROS levels enable protective signaling without triggering destructive oxidative cascades (Yang et al., 2026).

Wheat exploits this signaling role through transcriptional and enzymatic networks that regulate ROS levels. Mitogen-activated protein kinase cascades, including the TaMYB2-TaMAP3K17 module, enhance drought tolerance by promoting ROS scavenging and reducing malondialdehyde accumulation under water deficit. SnRK2 protein kinases interact with catalase to modulate ROS detoxification, while MAPK6 and antioxidant gene expression respond rapidly to short-term osmotic stress (Bhanbhro et al., 2025). Drought acclimation further refines this signaling: transcription factors such as TaWRKY2 and TaNAC1 are upregulated during severe stress, priming antioxidant defenses for subsequent drought events. Together, these signaling networks allow wheat to integrate ROS signals into coordinated physiological and molecular adaptations that improve survival under recurring drought.

5 Responses of the Wheat Leaf Antioxidant System to Drought Stress

5.1 Enzymatic antioxidant defense system

Drought activates the wheat leaf enzymatic antioxidant system because excess reactive oxygen species must be detoxified before they disrupt membranes, proteins, and the photosynthetic apparatus (Nyaupane et al., 2024). The first defensive step is usually the conversion of superoxide to hydrogen peroxide by SOD, followed by H₂O₂ removal through CAT, POD, and especially APX working in coordinated sequence. This response is not random but reflects a functionally integrated network in which enzymatic antioxidants act as the main biochemical barrier against oxidative injury. In wheat under drought, activities of SOD, CAT, APX, and related enzymes therefore commonly increase as stress intensity rises.

The magnitude and stability of this induction differ strongly among genotypes and stress histories. Drought-tolerant wheat generally shows stronger increases in CAT, POD, APX, and SOD, together with lower

H₂O₂ and lipid peroxidation, whereas susceptible genotypes show weaker antioxidant activation and greater oxidative damage. Some field studies indicate that CAT can decline under severe or late-stage stress even when APX and guaiacol peroxidase remain highly responsive, suggesting that H₂O₂ detoxification shifts toward enzymes with higher substrate affinity in stressed leaves (Dvojković et al., 2023). Short-term osmotic stress also alters the expression of CAT, APX, and related antioxidant genes, showing that drought regulation occurs at both biochemical and transcriptional levels. Repeated drought exposure can further strengthen this system, since acclimated wheat seedlings maintain more coordinated antioxidant induction than non-acclimated plants under later severe stress.

5.2 AsA-gsh cycle and non-enzymatic antioxidants

The AsA-GSH cycle is a central pathway for H₂O₂ scavenging in wheat leaves under drought because it links APX-dependent peroxide removal with continuous regeneration of reduced ascorbate and glutathione pools. In this cycle, APX uses AsA to reduce H₂O₂, while MDHAR, DHAR, and GR restore the reduced state of AsA and GSH and thereby preserve antioxidant capacity across cellular compartments (Laus et al., 2021). Drought commonly stimulates this pathway, and wheat tissues often show increased APX, GR, DHAR, and MDHAR activities as oxidative pressure intensifies. This pattern supports the view that AsA-dependent detoxification is one of the most consistent biochemical features associated with drought defense.

Non-enzymatic antioxidants complement the AsA-GSH cycle by directly quenching radicals and buffering the intracellular redox environment. AsA and GSH are the core soluble antioxidants in this system, but phenolic compounds, carotenoids, tocopherols, proline, and related metabolites also contribute to ROS neutralization and membrane protection (Dvojković et al., 2023). Under drought, wheat often shows depletion of reduced AsA with parallel increases in APX activity, while glutathione turnover and GR activity rise to sustain redox cycling. Genotypic differences are again important: tolerant materials can maintain higher GSH-related buffering capacity or faster AsA recovery, whereas sensitive lines often show sharper depletion of antioxidant pools and greater oxidative injury. In some traditional cultivars, enhanced phenolic accumulation appears to add a further protective layer by limiting lipid peroxidation during early drought response.

5.3 Antioxidant systems and maintenance of redox homeostasis

Drought tolerance in wheat depends less on the absolute abundance of a single antioxidant than on the coordinated maintenance of redox homeostasis across leaf compartments. Enzymatic and non-enzymatic antioxidants work jointly to minimize, buffer, and scavenge excess ROS, thereby preventing a shift from signaling-level oxidation to destructive oxidative stress. This coordination is especially important because ROS have dual roles: at controlled levels they participate in stress signaling, but at high levels they trigger lipid peroxidation, metabolic disruption, and cell death. Accordingly, wheat drought adaptation requires both efficient ROS removal and preservation of the reduced AsA/GSH redox state that stabilizes cellular metabolism. When this balance fails, oxidative damage accumulates rapidly and leaf function declines (Duvnjak et al., 2024).

Evidence from acclimation and signaling studies shows that redox homeostasis is actively regulated rather than passively maintained. Drought-acclimated wheat preserves the ascorbate-glutathione redox pool, restricts H₂O₂ accumulation, and limits membrane damage through coordinated induction of APX and related detoxifying enzymes. ABA and H₂O₂ also interact with the AsA-GSH cycle, and inhibition studies indicate that they regulate different components of this pathway during drought stress. At the signaling level, drought-induced modules such as TaMYB2-TaMAP3K17 enhance tolerance by promoting ROS scavenging and stabilizing ROS homeostasis under water deficit (Yang et al., 2026). Together, these findings indicate that the wheat leaf antioxidant system functions as an integrated redox regulatory network, and its effectiveness is a major determinant of drought tolerance and post-stress recovery.

6 Coordinated Regulation of Photosynthetic and Antioxidant Systems

6.1 Coupling between photosynthetic electron transport and ROS production

Under drought stress, the coordination between photosynthetic and antioxidant systems begins with the tight coupling between restricted carbon assimilation and over-reduction of the photosynthetic electron transport chain.

Stomatal closure lowers CO₂ availability, decreases Calvin-cycle consumption of NADPH, and leaves more electrons without productive sinks, which promotes ROS generation through pathways such as the Mehler reaction (Vijayaraghavareddy et al., 2022). In wheat leaves, this imbalance appears as a mismatch between electron excitation and electron use, so drought-induced declines in assimilation directly increase the formation of superoxide and hydrogen peroxide in chloroplasts. The result is not simply a passive side effect of dehydration, but a mechanistic link between impaired photosynthesis and oxidative stress that intensifies as water deficit progresses.

This coupling also explains why photochemical injury deepens when excess electrons are not safely redistributed. Drought gradually decreases PSII electron transport in wheat, yet a substantial fraction of electron flow is diverted away from carbon assimilation and photorespiration, indicating activation of alternative electron sinks. At the same time, enhanced PSI cyclic electron flow helps prevent over-reduction of the PSI acceptor side and lowers the risk of oxidative stress in chloroplasts. When stress becomes severe, however, ROS accumulation can suppress PSII repair and damage core proteins such as D1, shifting the system from regulated photoprotection toward photoinhibition and structural injury. This is why the balance between electron dissipation, PSI protection, and antioxidant capacity is central to drought tolerance in wheat (Figure 2).

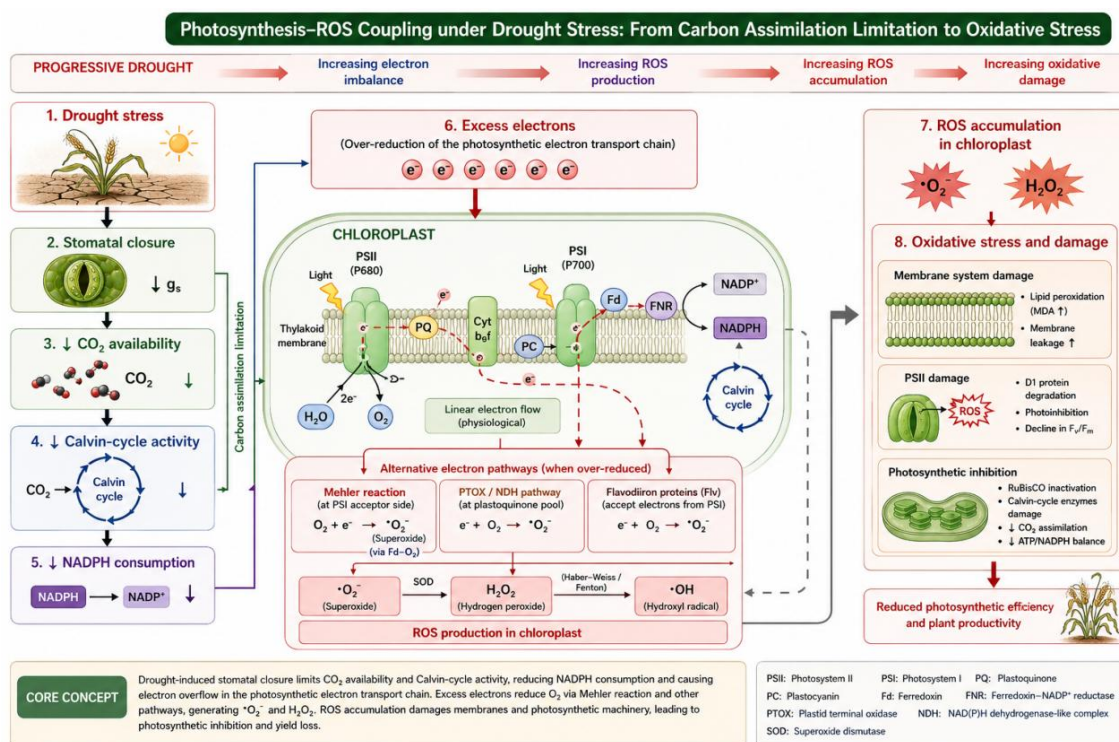


Figure 2 Coupling between drought-induced photosynthetic limitation, electron over-reduction, and reactive oxygen species generation in wheat leaves. Stomatal closure restricts CO₂ availability and decreases Calvin-cycle consumption of NADPH, thereby increasing the probability of electron over-reduction and ROS formation in chloroplasts. Progressive drought stress can consequently establish a mechanistic connection between impaired carbon assimilation and oxidative stress

6.2 Coordination between photosynthetic protection and antioxidant defense

Wheat limits oxidative damage under drought by coordinating photoprotective energy dissipation with biochemical ROS scavenging. Non-photochemical quenching rises under drought as a rapid feedback mechanism that dissipates excess excitation energy as heat and thereby restrains ROS overaccumulation before antioxidants become overwhelmed. In parallel, carotenoids contribute both to excess-energy dissipation and to direct protection of the photosynthetic apparatus, linking pigment-based photoprotection with antioxidant defense at the chloroplast level (Qiao et al., 2024). This coordination is especially important because PSII is highly vulnerable to oxidative damage, and preservation of its function depends on keeping excitation pressure and ROS production below damaging thresholds.

The evidence indicates that tolerant wheat genotypes do not rely on scavenging alone, but combine lower ROS production with stronger detoxification capacity. Higher carotenoid levels in tolerant leaves help dissipate excess excitation energy and likely restrain ROS formation at its source, while soluble sugars appear to support antioxidant capacity and redox buffering during drought. Consistent with this, droughted wheat can maintain lower ROS accumulation when NPQ increases effectively, even without disproportionately larger transcript increases of scavenging enzymes, showing that preventing ROS formation is as important as removing it. Earlier cultivar comparisons also showed that the more sensitive wheat cultivar displayed stronger xanthophyll de-epoxidation and non-radiative dissipation only after larger declines in PSII efficiency, suggesting that photoprotection can be protective yet still insufficient once stress injury has advanced. Together, these responses show that drought tolerance depends on synchronizing light-energy management with antioxidant metabolism rather than maximizing either system in isolation.

6.3 Molecular regulation, hormones, and signaling networks

At the molecular level, this coordination is governed by signaling networks that connect chloroplast redox status with hormone-mediated stress responses. Chloroplast-derived ROS act not only as toxic by-products but also as retrograde signals that alter nuclear transcription and induce antioxidant and stress-response genes. ABA is a major integrating signal in this network, because drought-responsive regulators can simultaneously enhance ABA biosynthesis or sensitivity and increase ROS-scavenging capacity, as shown by TaFDL2-1A overexpression, which increased endogenous ABA content, stomatal hypersensitivity, and SOD and GPX activities under drought. This coupling allows wheat to coordinate water-saving stomatal responses with protection of chloroplast metabolism.

Downstream of ABA perception, wheat uses interconnected signaling modules to regulate osmotic adjustment, stomatal movement, and ROS detoxification in a coordinated way. The TaPYL9/TaPP2C6/TaSnRK2.8/TabZIP1 pathway links ABA signaling to activation of TaP5CS2, TaSLAC1-1, and TaCAT2, thereby integrating proline biosynthesis, stomatal control, and ROS scavenging. Transcriptomic evidence also shows coordinated up-regulation of PP2C, SnRK2, and MAPKKK genes under drought, together with repression of LHCB1-related light-harvesting genes, which likely reduces excess light capture while strengthening antioxidant defense and stomatal regulation (Wu et al., 2026). Other regulators, including TaPPR13, further connect chloroplastic ROS homeostasis, chloroplast structural integrity, ABA signaling, and photosynthetic efficiency under water deficit. Overall, the molecular network that coordinates photosynthetic protection and antioxidant defense in wheat under drought is a redox-sensitive, hormone-linked system that optimizes survival, recovery, and productivity under limited water supply.

7 Case Studies: Photosynthetic and Antioxidant Responses of Wheat Leaves under Different Drought Conditions

7.1 Case study 1: photosynthetic responses to progressive drought stress

Progressive drought stress in wheat leaves is characterized by an early decline in stomatal conductance, followed by reductions in transpiration and net photosynthetic rate as soil water becomes increasingly limiting (Pflüger et al., 2024). In controlled progressive-drying experiments, stomatal closure responded faster than the decline in photosynthesis, indicating that the first limitation is usually diffusive rather than fully biochemical. As drought deepens, chlorophyll content and photochemical efficiency also decrease, and these changes become more evident when water deficit is prolonged or combined with additional atmospheric demand. Genotypic variation is substantial, but across cultivars the overall pattern remains consistent: declining water availability progressively constrains CO₂ uptake, leaf cooling, and carbon assimilation.

The later phase of progressive drought involves stronger impairment of the photosynthetic apparatus itself. A month-long progressive drought reduced the quantum yield of PSII photochemistry while increasing the fraction of absorbed energy released as fluorescence, showing a shift away from productive electron use as stress intensified (Jia et al., 2023). Field-capacity gradients from mild to severe drought similarly reduced net photosynthesis, stomatal conductance, relative water content, and chlorophyll retention across diverse wheat

genotypes, although tolerant materials maintained higher function under severe stress. These case studies indicate that progressive drought in wheat begins with stomatal restriction but eventually extends to pigment loss, altered PSII energy partitioning, and broader metabolic inhibition. They also show that evaluating drought response against available soil water, rather than stress duration alone, gives a clearer view of physiological thresholds.

7.2 Case study 2: antioxidant system responses to drought stress

A second case-study pattern is the strong activation of the wheat leaf antioxidant system under drought-induced oxidative stress. Water deficit increases hydrogen peroxide, malondialdehyde, and proline while stimulating the main enzymatic defenses, including SOD, CAT, and APX, and these responses become stronger as stress severity increases (Nasirzadeh et al., 2020). In a separate greenhouse study across growth stages, drought likewise increased SOD, CAT, POD, and APX activities in leaves, supporting the view that enzymatic detoxification is a core component of wheat drought defense. This antioxidant activation reflects the need to detoxify ROS generated when drought restricts carbon assimilation and disturbs cellular redox balance. At the same time, the response is not uniform across all genotypes or all enzymes, which makes antioxidant profiling useful for distinguishing different drought-response strategies.

Case comparisons further show that drought tolerance depends on the coordination, rather than the mere presence, of antioxidant defenses. Drought-resistant varieties often rely more heavily on enhanced ROS-detoxifying enzyme activity, whereas drought-sensitive genotypes can depend more on non-enzymatic antioxidant components that become particularly important during recovery. Repeated stress exposure can also prime the antioxidant machinery: in acclimated wheat seedlings, severe subsequent drought caused less H₂O₂ accumulation and membrane damage because APX activity and the ascorbate-glutathione redox pool were maintained more effectively. These findings suggest that the most informative antioxidant case studies are those that integrate ROS levels, membrane injury, osmolyte accumulation, and enzyme coordination across contrasting genotypes or stress histories. They also underline that antioxidant capacity contributes directly to preserving leaf function under drought, not merely to damage repair after stress has already occurred.

7.3 Case study 3: photosynthetic recovery and antioxidant regulation during drought-rewatering cycles

Drought-rewatering case studies show that many wheat leaf responses are reversible, but recovery depends strongly on prior stress severity and genotype. After rewatering, photosynthetic traits such as net assimilation, stomatal conductance, transpiration, and water use efficiency can show full or even over-compensatory recovery following drought, indicating substantial physiological resilience when stress has not exceeded critical thresholds (Todorova et al., 2022). This reversibility is not unlimited, however, because moderate stress tends to permit near-complete restoration of photosynthetic processes, whereas severe drought often leaves persistent impairment in membranes, ROS balance, and final productivity. Recovery therefore reflects both the extent of prior injury and the plant's ability to reactivate gas exchange, re-establish water relations, and restore redox control. In this context, fast recovery of photosynthesis is a meaningful indicator of drought tolerance rather than a simple return to pre-stress values.

Antioxidant regulation during rewatering is equally dynamic and can persist even after visible stress relief. In winter wheat, most pigment, photosynthetic, and antioxidant traits recovered effectively after stress relief within a certain range, but after longer combined stress, antioxidant activities remained elevated while oxidative damage was still not fully mitigated. Repeated drought-rewatering cycles can even enhance post-stress performance: intermittent drought increased the maximum photosynthetic rate after rewatering and strengthened stress-response indicators relative to non-primed plants, with ABA responding particularly rapidly. Lower-ranked but important recovery studies extend this picture by showing that after atmospheric-soil drought, stomatal conductance and photosynthetic rate recovered relatively quickly, whereas leaf hydraulic conductance recovered more slowly, suggesting different repair kinetics within the same leaf system (Wang et al., 2025). Taken together, these case studies show that rewatering success in wheat depends on coordinated restoration of photosynthesis, antioxidant defenses, and hydraulic function, with moderate prior stress often producing the strongest recovery capacity.

8 Agricultural Applications and Comprehensive Evaluation of Drought-Resistance Regulation in Wheat

8.1 Water management and irrigation regulation

Water management in drought-prone wheat production aims to avoid severe inhibition of photosynthesis while improving water-use efficiency through controlled deficit rather than continuous full irrigation. Across irrigation-gradient studies, mild water stress generally maintained a relatively high photosynthetic rate and sometimes even improved biomass accumulation and 1 000-grain weight compared with fully irrigated controls, indicating that moderate restriction can enhance water productivity without a major physiological penalty (Zhao et al., 2020). A similar conclusion emerged from stage-based field-capacity experiments, in which mild stress around 65%-70% field capacity improved canopy photosynthesis, assimilate allocation to grain, yield, and water-use efficiency, whereas moderate and severe stress increasingly constrained these responses. These results suggest that irrigation scheduling should target the threshold at which stomatal regulation conserves water but does not yet trigger major non-stomatal damage to the photosynthetic system.

The timing and delivery mode of irrigation are as important as total water supply. Growth-stage-based deficit irrigation sustained a high photosynthetic rate when soil relative water content was maintained at 60%-75%, and the treatment irrigated from jointing to filling achieved the best balance between water saving and acceptable yield loss in Northwest China. Under drip irrigation, mild deficit imposed at tillering or jointing increased antioxidant enzyme activity, reduced ROS and lipid peroxidation, delayed flag-leaf senescence, and improved yield relative to stronger deficit treatments, with the tillering-stage mild deficit giving the clearest agronomic advantage (Che et al., 2025). Complementary field management can strengthen this effect: ridge-furrow mulching with moderate deficit irrigation improved soil water status, raised flag-leaf photosynthesis, enhanced SOD, POD, CAT, and APX activities, and reduced oxidative damage, making it a practical water-saving strategy in semi-arid systems.

8.2 Nutritional regulation and application of exogenous substances

Adequate mineral nutrition can buffer the drought-induced decline in photosynthetic and antioxidant function in wheat leaves. Nitrogen supply is especially important because drought-stressed plants receiving moderate or high N maintain higher photosynthesis and N-metabolism activity than low-N plants, while also showing stronger SOD, POD, CAT, GR, and APX responses and better osmotic adjustment (Ru et al., 2022). At vegetative stages, higher N also helped wheat sustain leaf water potential, chlorophyll and Rubisco content, and lower lipid peroxidation under drought, indicating that nutritional regulation supports both carbon assimilation and ROS detoxification. Thus, fertilizer management should be viewed as part of drought regulation rather than a separate yield-input issue.

Exogenous substances provide an additional tool for protecting wheat leaves when drought cannot be avoided. Root-applied strigolactones enhanced the expression of antioxidant-defense, chlorophyll-biogenesis, and light-harvesting genes, and this was accompanied by higher SOD, POD, and CAT activities, increased chlorophyll, and a higher photosynthetic rate under drought (Song et al., 2023). Foliar salicylic acid, zinc, and glycine betaine reduced H_2O_2 , $\text{O}_2^{\bullet-}$, MDA, and lipid oxidation while promoting antioxidant enzymes, osmolyte accumulation, and grain yield under reproductive-stage drought, with glycine betaine showing the strongest overall effect in that study. Other regulators act through related mechanisms: Zn increased SPAD, Fv/Fm, ascorbate, glutathione, phenolics, and flavonoids while reducing H_2O_2 and lipid peroxidation, and GABA increased phenolic acids and antioxidant enzyme activity, further supporting the use of exogenous compounds to reinforce redox protection under water deficit.

8.3 Drought-tolerant cultivar screening and precision agriculture applications

Drought-tolerant cultivar screening is most effective when it integrates photosynthetic, antioxidant, water-status, and yield-related traits rather than relying on any single indicator. Field evaluation in the North China Plain reduced 24 conventional traits to a smaller set of practical drought indicators, identifying canopy temperature, leaf water content, photosynthetic rate, intercellular CO_2 concentration, POD, MDA, and ABA among the most

informative variables for cultivar discrimination. Controlled screening studies similarly showed that tolerant genotypes maintain higher chlorophyll content, relative water content, membrane stability, gas exchange, and antioxidant activity than sensitive lines, confirming that drought tolerance in wheat is a composite physiological syndrome rather than a single trait (Ahmad et al., 2022). This supports selection frameworks that combine carbon-assimilation traits with oxidative-stress markers.

Precision agriculture tools now make this integrated screening scalable at breeding and field levels. Canopy temperature is already a low-cost, large-scale indicator with a negative linear relationship to grain yield during grain filling under drought. Spectral approaches further improve throughput: NDWI and the red-edge chlorophyll index closely tracked drought-tolerance indices in field trials and can serve as inexpensive alternatives for identifying tolerant genotypes, while multi-environment phenotyping showed that NDVI and MTSI are effective tools for identifying stable drought-tolerant germplasm across locations. UAV-based crop-health indices also correlated with yield in sodic rain-fed environments and successfully separated tolerant from sensitive genotypes, and sensor-based irrigation-gradient platforms validated NDVI, PRI, and fluorescence-related indices as non-destructive selection tools for breeding programs (Soares et al., 2025). Overall, agricultural regulation of wheat drought resistance is most effective when mild, stage-specific water deficit, targeted nutritional or exogenous support, and integrated phenotyping-based cultivar selection are used together. In the context of wheat leaves, these approaches converge on the same physiological objective: preserving photosynthetic capacity while strengthening antioxidant protection under limited water supply.

9 Conclusions and Future Perspectives

Drought stress imposes a coordinated physiological challenge on wheat leaves, simultaneously disrupting carbon assimilation and accelerating reactive oxygen species (ROS) accumulation. The initial response is predominantly stomatal: as leaf water potential declines, stomata close to conserve water, which restricts CO₂ influx and immediately reduces net photosynthetic rate. This stomatal limitation is the earliest diffusive barrier to photosynthesis, but it rapidly triggers downstream metabolic constraints. With restricted CO₂ fixation, the Calvin cycle slows, NADP⁺ regeneration fails to keep pace, and the photosynthetic electron transport chain becomes over-reduced. This excess excitation energy drives electron leakage to molecular oxygen, generating superoxide and hydrogen peroxide primarily in the chloroplasts, peroxisomes, and mitochondria. The resulting oxidative stress damages membranes through lipid peroxidation, impairs PSII repair cycles, and degrades photosynthetic pigments, creating a destructive feedback loop where impaired photosynthesis generates more ROS, and ROS further inhibit photosynthesis. Tolerant wheat genotypes break this cycle through the coordinated activation of photoprotective and antioxidant mechanisms. Non-photochemical quenching dissipates excess light energy as heat, while enzymatic antioxidants-superoxide dismutase, catalase, ascorbate peroxidase, and glutathione reductase-detoxify ROS in a compartment-specific manner. The ascorbate-glutathione cycle plays a central role in maintaining redox homeostasis by continuously regenerating reduced antioxidant pools. Non-enzymatic antioxidants, including ascorbate, glutathione, carotenoids, and proline, provide additional buffering capacity. Crucially, ROS at controlled concentrations also function as signaling molecules, activating ABA-dependent and ABA-independent pathways that upregulate stress-responsive genes. This dual role of ROS-as toxic byproducts and essential signals-means that drought tolerance is not achieved by maximizing ROS elimination but by maintaining redox balance within a signaling-compatible range. The integration of photosynthetic protection, antioxidant defense, and hormone-mediated signaling networks ultimately determines whether a wheat leaf survives, acclimates, or suffers irreversible damage under drought.

Despite extensive documentation of drought-induced physiological changes in wheat, several critical gaps remain in understanding the temporal and spatial coordination of photosynthetic and antioxidant responses. Most studies measure antioxidant enzyme activities and photosynthetic parameters at discrete time points, providing only a snapshot of dynamic processes that unfold over hours to weeks. The real-time kinetics of ROS generation, antioxidant activation, and photosynthetic decline within specific subcellular compartments remain poorly resolved. Furthermore, the threshold at which ROS shift from signaling molecules to destructive agents is not clearly defined for wheat leaves under field-relevant drought conditions. This knowledge gap limits the ability to

identify precise intervention points for enhancing drought tolerance through targeted genetic or chemical strategies. A second major gap concerns the translation of controlled-environment findings to field conditions where drought interacts with heat, high vapor pressure deficit, and variable soil nutrient availability. Most mechanistic studies are conducted in growth chambers or greenhouses with uniform stress application, yet field drought is inherently heterogeneous in timing, severity, and duration. The interactive effects of drought with other abiotic stresses on photosynthetic electron transport and antioxidant redox signaling are insufficiently characterized in wheat. Additionally, the genetic architecture underlying the coordination of photosynthetic efficiency and antioxidant capacity is not fully resolved. While individual transcription factors and signaling modules have been identified, the regulatory networks that integrate chloroplast-to-nucleus retrograde signaling, ABA pathways, and antioxidant gene expression under recurrent drought cycles remain largely uncharacterized. These gaps raise key questions about how priming and acclimation memory are molecularly encoded and whether they can be reliably induced in diverse wheat genetic backgrounds.

Future research should prioritize dynamic, non-destructive monitoring of photosynthetic and antioxidant responses in wheat leaves under realistic field drought scenarios. Advances in chlorophyll fluorescence imaging, thermography, and hyperspectral reflectance offer the potential to track spatial and temporal heterogeneity in photosynthetic performance and canopy temperature at high resolution. Coupling these phenotyping tools with real-time ROS detection probes and redox-sensitive reporters would enable researchers to map the kinetics of oxidative stress and antioxidant activation at the tissue and subcellular levels. Such approaches could reveal the critical thresholds at which protective mechanisms fail and identify the earliest markers of irreversible photosynthetic damage. Integrating these physiological measurements with unmanned aerial vehicle-based multispectral imaging would further bridge the gap between leaf-level mechanisms and canopy-level drought responses in breeding nurseries and production fields. A second priority is the dissection of regulatory networks that coordinate photosynthetic protection with antioxidant defense through multi-omics integration. Combining transcriptomics, proteomics, metabolomics, and redox proteomics across time-series drought and rewatering cycles could identify the key nodes where ABA, ROS, and retrograde signaling converge to regulate both systems. Genome-wide association studies and CRISPR-based functional validation should target genes controlling the balance between ROS signaling and oxidative damage, particularly those governing the AsA-GSH cycle and PSII repair. Finally, research should explore how exogenous substances-such as strigolactones, melatonin, and glycine betaine-can be deployed under field conditions to prime antioxidant capacity and sustain photosynthesis during critical reproductive stages. Translating these findings into precision agriculture frameworks, where irrigation timing, nutrient management, and cultivar selection are optimized together, will be essential for maintaining wheat productivity under increasingly unpredictable drought regimes.

Acknowledgments

The author expresses deep gratitude to Professor R. Cai from the Zhejiang Agronomist College for his thorough review of the manuscript and constructive suggestions. The author also extends thanks to the two anonymous peer reviewers for their valuable revision recommendations.

Conflict of Interest Disclosure

The author affirms that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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