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 CO_2 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