

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.