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 H_2O_2 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