Stomatal closure lowers CO_2 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).

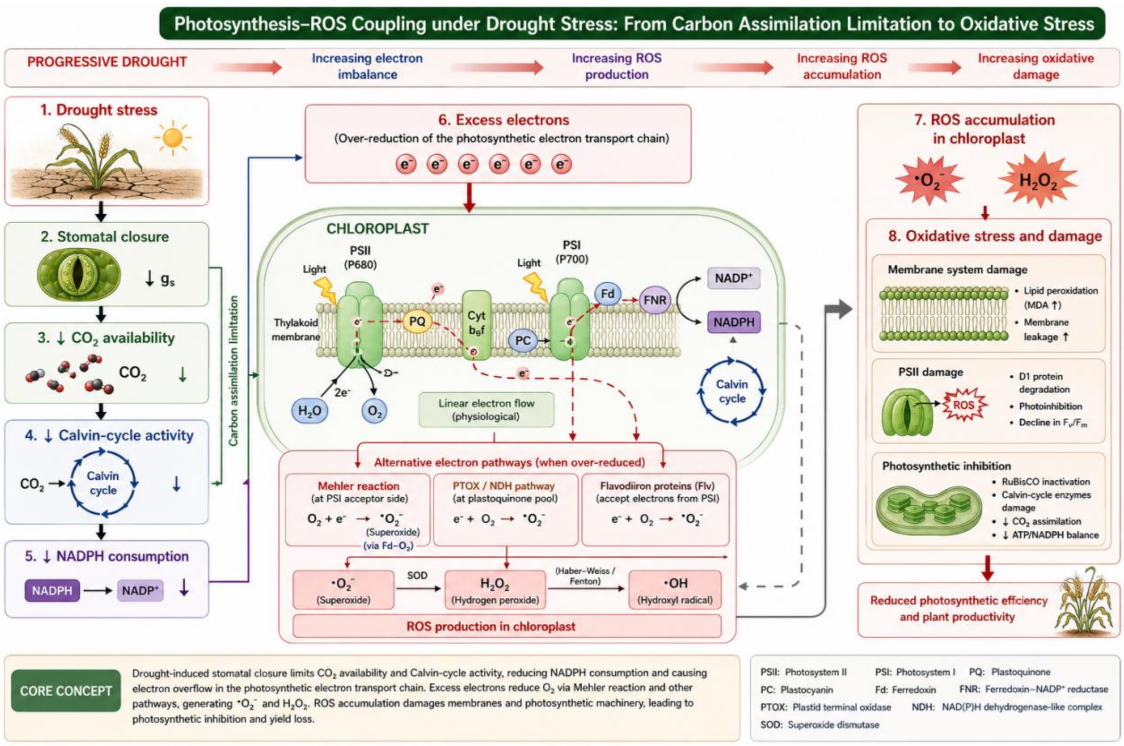

Figure 2 Coupling between drought-induced photosynthetic limitation, electron over-reduction, and reactive oxygen species generation in wheat leaves. Stomatal closure restricts CO_2 availability and decreases Calvin-cycle consumption of NADPH, thereby increasing the probability of electron over-reduction 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.