mesophyll cells, leading to lower net photosynthetic rate. Under prolonged drought stress, chloroplast structure may be damaged, photosystem II electron transport may be inhibited, and reactive oxygen species may accumulate, causing premature leaf senescence.

Li et al. (2023) studied the effects of warming and drought stress on the coupling relationship between photosynthesis and transpiration in winter wheat on the North China Plain. Drought first reduced water loss by decreasing stomatal conductance. However, with increasing stress intensity, the decline in photosynthesis was no longer caused only by stomatal limitation, but also by downregulation of photosynthetic metabolism. In other words, mild water deficit may temporarily improve water use efficiency, but long-term or severe drought disrupts carbon-water coupling, turning water saving into yield reduction. Therefore, severe water deficit should be avoided during jointing, flowering, and early grain filling stages because photosynthetic capacity during these periods directly affects grain number and thousand-kernel weight.

During grain filling, the flag leaf is the major source of assimilates in late growth stages, and the duration of its photosynthetic activity directly affects grain fullness. Naseer et al. (2024) used the winter wheat cultivar "Xinong 979" in the dry farming region of the Loess Plateau to study the combined effects of drought and weak light during grain filling. Treatments included irrigation levels of 100%, 75%, 50%, and 25%, along with different shading durations. As irrigation decreased and shading time increased, net photosynthetic rate, transpiration rate, stomatal conductance, and intercellular CO_2 concentration all declined significantly. Under the treatment of 12 days of shading combined with the lowest irrigation level, photosynthetic gas exchange parameters showed the greatest decline. At the same time, chlorophyll fluorescence parameters Fv/Fm, qP, and quantum yield also decreased, indicating damage to PSII reaction centers (Figure 1). Drought and shading together reduced spike number, thousand-kernel weight, and grain yield, indicating that the grain filling stage is not simply a period where "less water is acceptable," but rather a critical window when the photosynthetic system of winter wheat requires strong protection.

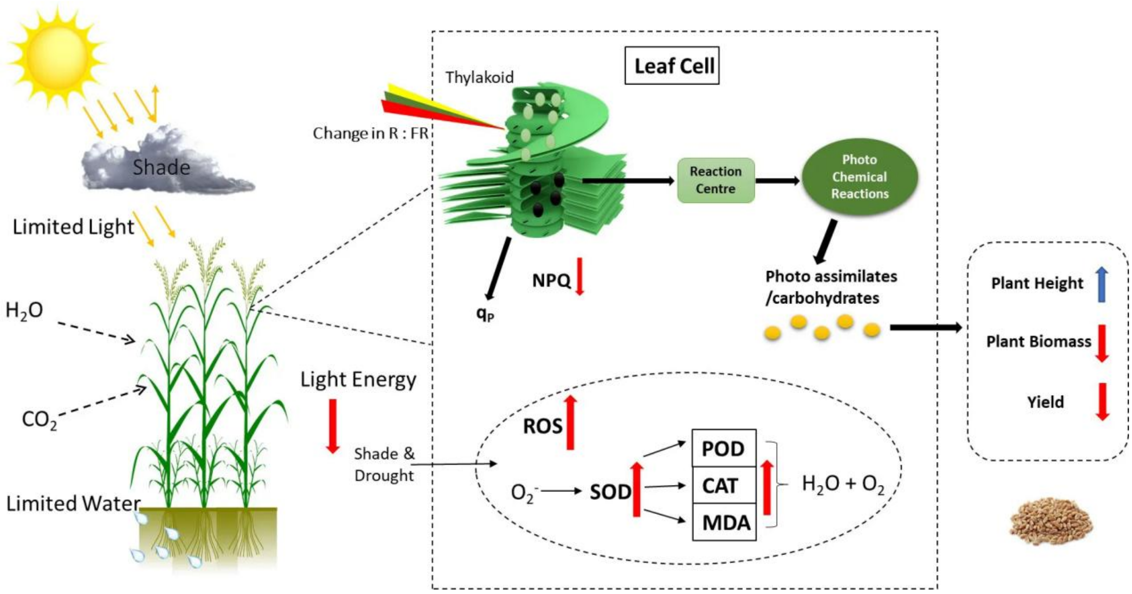

Figure 1 The comprehensive model of physiological metabolism regulation in winter wheat plants under drought and shading stress. Changing the light environment and drought conditions regulate the photosynthetic activity, photochemical efficacy, and antioxidant enzyme activities to adapt the environmental stress. The distribution and regulation of photo-assimilates affect the agronomic characteristics, and yield of winter wheat plants (Adopted from Naseer et al., 2024)

3.3 Water stress memory and adaptation mechanisms

Winter wheat has a certain capacity to adapt to water stress. Because the growth period is relatively long, winter wheat often experiences multiple stress events, including mild drought at the seedling stage, water fluctuations during regreening, spring drought after jointing, and hot dry wind during grain filling. If mild stress at early stages activates adaptive mechanisms, drought tolerance at later stages may be improved.