

equally effective under all fertility levels. Under medium and low fertility conditions, moderate deficit irrigation improved WUE and partial factor productivity of nitrogen while maintaining or increasing grain yield. However, under high fertility conditions, regulated deficit irrigation could reduce grain yield or weaken nitrogen use efficiency.

5 Breeding and Genetic Improvement of Water-Saving Wheat

5.1 Drought-resistant germplasm resources

Drought resistance in wheat is not controlled by a single trait. It is determined by multiple characteristics together, including root water uptake ability, leaf water retention, stomatal regulation, osmotic adjustment, antioxidant capacity, early maturity for drought escape, and grain filling stability. In recent years, more attention has been paid to landraces, wild relatives, synthetic hexaploid wheat, and core germplasm resources preserved by international breeding institutions. Many countries and international gene banks have conserved a large number of wheat landraces and wild materials. During long-term natural selection and farmer selection, these materials gradually developed adaptation to drought, poor soils, heat stress, and other adverse environments (Khadka et al., 2020).

Common wheat experienced a genetic bottleneck during domestication and modern breeding. Some allelic variations related to drought resistance, deep rooting, and stress adaptation may have been weakened or lost. Synthetic hexaploid wheat is usually developed by crossing tetraploid durum wheat with D-genome donors such as *Aegilops tauschii*, followed by chromosome doubling. This approach allows favorable alleles from wild relatives to be reintroduced into the genetic background of common wheat. Rosyara et al. (2019) analyzed the genetic contribution of synthetic hexaploid wheat to CIMMYT spring bread wheat breeding materials and found that synthetic-derived lines had already entered the international wheat improvement system.

Mokhtari et al. (2022) evaluated 184 synthetic hexaploid wheat-derived lines under both normal irrigation and water stress conditions over two years. Large genetic variation was observed in agronomic traits such as plant height, heading date, spike traits, thousand-kernel weight, and grain yield. Under water stress, grain yield significantly decreased, but the degree of reduction differed greatly among genotypes, indicating that synthetic hexaploid derivatives contain valuable materials for drought improvement. Mokhtari et al. (2024) further screened drought-tolerant types from 91 synthetic hexaploid wheat lines. Under water stress, significant differences were observed in relative water content, leaf area index, photosynthetic pigments, proline accumulation, antioxidant enzyme activity, and malondialdehyde content. Some synthetic hexaploid materials maintained relatively high grain yield, higher leaf relative water content, and lower membrane lipid peroxidation under drought conditions.

5.2 Key genes related to drought resistance

Drought resistance in wheat involves many biological processes, including root development, water absorption, stomatal regulation, ABA signaling, reactive oxygen species scavenging, osmotic adjustment, and photosynthetic stability. In arid and semi-arid wheat-growing regions, water in the topsoil evaporates quickly, while deeper soil layers often still contain available moisture. Therefore, wheat lines with deeper root systems and higher deep-root density usually show more stable performance from stem elongation to grain filling stages.

When soil moisture decreases, ABA levels in roots and leaves increase. This induces stomatal closure to reduce transpiration and water loss, while also activating antioxidant systems, osmotic adjustment, and stress-response gene expression. Mega et al. (2019) showed that enhancing ABA receptor function could regulate water-use efficiency and drought resistance in wheat. They developed wheat materials overexpressing ABA receptors and found that total water consumption was reduced, while biomass production and grain yield per unit water increased. Mao et al. (2022) reported that wheat lines overexpressing TaPYL1-1B exhibited higher ABA sensitivity, stronger photosynthetic capacity, and higher water-use efficiency. Under water-deficit conditions, these lines showed improved drought tolerance and maintained grain yield. More importantly, the study identified a favorable allelic variation, TaPYL1-1Bn-442, in the promoter region of TaPYL1-1B. This variation contains a MYB recognition site that can be regulated by TaMYB70, thereby enhancing TaPYL1-1B expression in drought-tolerant genotypes (Figure 3).