tighter hydraulic constraints on leaf function. Across genotypes, the magnitude of these changes depends on their capacity to preserve hydration through osmotic regulation, elastic adjustment, and sustained water transport, rather than through simple dehydration avoidance alone. In drought-tolerant wheat, maintenance of higher relative water content and leaf water potential is often associated with better xylem exudation, stronger membrane stability, and improved chlorophyll retention under stress (Akter et al., 2023).

The physiological basis of these water-relation differences lies in the coordination between osmotic adjustment and hydraulic behavior. Resistant wheat genotypes commonly accumulate soluble sugars and other osmolytes that lower osmotic potential, improve soil water uptake, and help preserve cell function under declining soil moisture. By contrast, increasing water deficit causes sharper declines in relative water content, water potential, and membrane stability in susceptible materials, showing that inadequate adjustment accelerates dehydration injury. Leaf structural and anatomical integrity also matters, because maintaining functional leaf hydraulic properties and internal diffusion pathways helps sustain photosynthetic capacity as drought progresses (Yang et al., 2026). For this reason, traits such as relative water content, excised leaf water retention, relative water loss, leaf rolling, and waxiness are widely treated as practical indicators of drought tolerance in wheat.

2.2 Stomatal regulation and transpiration responses

Stomatal regulation is one of the earliest and most decisive responses of wheat leaves to drought stress because it directly controls both carbon dioxide influx and transpirational water loss. As soil dries, stomatal conductance usually declines before many other gas-exchange traits, and this reduction lowers transpiration and leaf cooling while progressively constraining photosynthesis (Pflüger et al., 2024). Experimental evidence further shows that stomatal conductance in wheat is positively linked with leaf water potential and hydraulic conductance, but negatively associated with abscisic acid accumulation and, under severe stress, with altered stomatal traits such as density and pore area. Thus, stomatal behavior reflects not only passive water loss control but also active integration of hydraulic and hormonal signals across stress intensities.

Wheat does not rely on a single stomatal strategy under drought. Under mild stress or early drying, some genotypes maintain relatively high conductance and behave more anisohydrically, allowing continued carbon assimilation despite falling hydraulic conductance. With increasing drought severity, however, stomata shift toward a more conservative, isohydric pattern, reducing transpiration to protect leaf water status and hydraulic safety. Genotypic differences are important in this transition: drought-tolerant lines can delay full stomatal closure during reproductive stress, whereas sensitive lines often close stomata earlier and enter a passive survival mode sooner (Onyemaobi et al., 2021). In parallel, structural stomatal traits contribute to performance, since smaller or more numerous stomata, depending on genetic background, can support faster regulation and improved transpiration efficiency under drought.

2.3 Water use efficiency and drought adaptation

Water use efficiency in wheat under drought is shaped by the balance between conserving water and sustaining assimilation. Moderate restriction of stomatal opening often increases instantaneous or integral water use efficiency because transpiration declines faster than photosynthesis, even though absolute carbon gain may still be reduced. Drought-resistant cultivars tend to achieve this balance more effectively, showing lower lifetime water consumption or transpiration together with better maintenance of productive photosynthesis under stress. This trade-off is central to wheat adaptation, since excessive water saving can protect tissues but penalize biomass accumulation, whereas insufficient control accelerates dehydration and oxidative damage. As a result, drought adaptation depends on optimizing, rather than maximizing, stomatal restriction and tissue hydration (Franco-Navarro et al., 2025).

At the whole-plant level, improved water use efficiency emerges from the integration of stomatal behavior, root water acquisition, osmotic adjustment, and management context. Deficit irrigation imposed at suitable growth stages can raise wheat water use efficiency, especially when stress is moderated and rewatering occurs after sensitive periods such as heading. Management interventions can also enhance efficiency: combining deficit irrigation with soil amendments improved water use efficiency in pot experiments, indicating that agronomic