

5.3 Metabolic regulation under water deficit conditions

Metabolic adjustment under drought centers on osmoprotection, antioxidant defense, and maintenance of carbon and energy balance. In *Chrysanthemum*, melatonin treatment increases soluble sugars, soluble proteins, and antioxidant enzyme activities under drought, while transcriptomic analyses show that dehydration significantly affects pathways related to sugars, amino acids, lipids, hormones, and secondary metabolites (Luo et al., 2023). This pattern matches broader drought biology, in which osmotic adjustment depends on the accumulation of compatible solutes such as soluble sugars, proteins, and proline to maintain cell turgor and protect macromolecular structures under low water potential (Ozturk et al., 2020; Pamungkas et al., 2022).

Reactive oxygen species metabolism is another key biochemical layer of drought adaptation because water deficit disrupts the balance between light absorption and carbon assimilation. Drought commonly increases ROS and membrane lipid peroxidation, but tolerant plants counter this through stronger enzymatic scavenging and osmotic buffering; in *Chrysanthemum* relatives, ABA accumulation promotes proline and trehalose biosynthesis, activates SOD and POD, and supports water retention, while broader redox signaling studies show that ABA-induced stomatal closure is reinforced by ROS-dependent signaling loops (Yang et al., 2020; Ge et al., 2026). More specifically, evidence across plant systems suggests that soluble sugars can contribute more strongly than proline to osmotic adjustment in some drought contexts, which is relevant for interpreting *Chrysanthemum* responses where sugar metabolism repeatedly emerges as a major regulated pathway (Gurrieri et al., 2020).

6 Case Study: Comprehensive Evaluation of Photosynthesis and Water Use Characteristics of *Chrysanthemum morifolium* under Different Drought Intensities

6.1 Experimental design and physiological measurements

A comprehensive evaluation of drought effects in *Chrysanthemum morifolium* is best built on graded water-deficit treatments that capture both intensity and duration effects. Existing *Chrysanthemum* studies have used several complementary designs, including pot experiments with defined soil water contents for moderate and severe drought, and irrigation-withholding trials followed by rewatering to assess stress progression and recovery. These approaches are useful because they separate immediate drought injury from reversible acclimation and make it possible to compare tolerant and sensitive cultivars under the same decline in water availability.

Physiological measurements in such case studies should integrate gas exchange, water status, pigments, and stress-defense traits rather than relying on photosynthesis alone. *Chrysanthemum* screening experiments under hydroponic PEG stress and pot culture drought have measured chlorophyll content, carotenoids, relative water content, membrane stability index, canopy temperature depression, chlorophyll fluorescence, biomass, and reproductive traits, while proteophysiological studies additionally included leaf water potential and stress markers to depict tolerance level (Figure 2) (Sahithi et al., 2020). Together, these variables provide a multidimensional framework for evaluating how drought intensity alters both carbon assimilation and whole-plant water relations.

6.2 Dynamic responses of photosynthesis and water use efficiency under drought stress

As drought intensifies, *Chrysanthemum* leaves show a characteristic sequence of declining photosynthetic activity. Across cultivar-based experiments, net photosynthetic rate, stomatal conductance, and transpiration rate all decrease with increasing stress, and these reductions appear earlier and more strongly in drought-sensitive cultivars than in tolerant ones. This pattern indicates that the dynamic response is not only a function of drought severity, but also of genotype-specific capacity to maintain stomatal regulation and leaf physiological stability.

Water use efficiency often increases during mild to moderate drought, but this does not indicate unchanged photosynthetic performance. In ground-cover *Chrysanthemum*, water use efficiency rose with drought intensity and reached 1.34 times the control under moderate stress, while repeated water-regime studies showed that monitored cyclical deficit can improve tolerance and support rapid recovery after drying (Gogoláková and Paganová, 2020). At the same time, the shift in intercellular CO₂ from an initial decrease to a later increase under stronger drought supports the view that responses move from mainly stomatal limitation toward combined stomatal and non-stomatal inhibition as stress deepens.