

the control level under moderate stress, while cyclical water-deficit studies indicate that controlled reduction of water supply can improve tolerance and post-stress performance (Gogoláková and Paganová, 2020). These findings suggest that moderate drought can trigger a conservative water-use strategy that improves instantaneous efficiency even while overall growth remains constrained.

However, improved water use efficiency under drought does not necessarily indicate superior productivity, because severe stress eventually restricts both water loss and photosynthetic carbon gain. In *Chrysanthemum* seedlings, exogenous melatonin increased transpiration, net photosynthesis, and stomatal conductance while also attenuating declines in relative water content, indicating that higher efficiency under mitigation can arise from better coordination between hydration and carbon assimilation rather than from extreme stomatal restriction alone (Luo et al., 2023). Likewise, drought-tolerant *Chrysanthemum* types maintain photosynthesis with less water-status disruption than sensitive ones, implying that the most favorable drought response is not simply low water use, but balanced water conservation with sustained metabolic activity (Zhang et al., 2022).

5 Molecular and Biochemical Mechanisms Regulating Drought Adaptation

5.1 Hormonal regulation of drought responses

Abscisic acid is the central hormonal signal regulating drought adaptation in *Chrysanthemum*, primarily by coordinating stomatal behavior, water conservation, and downstream stress-responsive gene expression. In *Chrysanthemum*, ABA treatment maintains higher leaf water content under water deficit by reducing transpiration through stomatal closure, while broader mechanistic work identifies ABA as the core signal that activates guard-cell drought responses through receptor-mediated signaling cascades that control stomatal movement (Hsu et al., 2020). This role is consistent with the general view that ABA is not only a physiological regulator of drought avoidance, but also a transcriptional signal that links water deficit perception to biochemical and molecular defense programs (Ali et al., 2020; Aslam et al., 2022).

Hormonal regulation in *Chrysanthemum* also depends on crosstalk between ABA and other phytohormones rather than on ABA alone. Exogenous melatonin under drought decreases endogenous ABA, jasmonate, and ethylene while increasing auxin, gibberellin, salicylic acid, and cytokinin levels, indicating that improved drought tolerance can result from a rebalanced hormonal network rather than from uniformly elevated ABA signaling (Parwez et al., 2022; Luo et al., 2023). At the gene-regulatory level, this network includes ABA-responsive transcriptional modules, because CmBBX19 interacts with the master ABA signaling component CmABF3 and suppresses ABA-dependent downstream genes, thereby negatively affecting *Chrysanthemum* drought tolerance (Xu et al., 2020).

5.2 Gene expression and molecular regulation of photosynthetic responses

Drought adaptation in *Chrysanthemum* involves large-scale transcriptional reprogramming that affects both protective stress pathways and photosynthesis-related metabolism. Genome-wide expression profiling under dehydration identified 8,558 responsive transcripts, including hundreds of transcription factors and protein kinases, and showed that drought alters hormone response, amino acid metabolism, secondary metabolism, and light- and photoperiod-related pathways. Proteomic evidence further indicates that drought changes the abundance of proteins associated with stress response, physiological transport, gene regulation, and secondary metabolism, alongside declines in photosynthesis, PSII yield, and stomatal conductance (Sahithi et al., 2020).

Several transcription factor families now appear central to the molecular regulation of *Chrysanthemum* drought responses that indirectly stabilize photosynthetic performance. *Chrysanthemum* and related germplasm studies have identified drought-responsive bZIP, MYB, and NAC candidates, including 28 bZIP family members in *C. mongolicum*, 51 stress-related MYB candidates in *C. nankingense*, and NAC subfamily genes involved in drought-responsive growth regulation (Ai et al., 2023). Functional evidence is stronger for some regulators than others: *CmbZIP9* overexpression increases stress-related gene expression and antioxidant enzyme activity under drought, whereas *CmbHLH112* overexpression elevates ABA levels, antioxidant defenses, and proline accumulation, together supporting photosynthetic tissues by reducing oxidative damage and water loss (Wang et al., 2024; Huang et al., 2026).