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Effects of Drought Stress on Photosynthesis and Water Use Characteristics of *Chrysanthemum morifolium*

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Abstract *Chrysanthemum morifolium* is an important medicinal and ornamental crop with high economic value; however, its growth and productivity are increasingly threatened by drought stress caused by climate change and limited water availability. Drought stress directly affects plant water balance, photosynthetic performance, carbon assimilation, and water use efficiency, thereby limiting biomass accumulation and flower yield formation. This review systematically summarizes the effects of drought stress on photosynthesis and water use characteristics of *C. morifolium*, with emphasis on physiological, biochemical, and molecular regulation mechanisms. Under drought conditions, reduced soil moisture availability induces declines in leaf relative water content, stomatal conductance, transpiration rate, and net photosynthetic rate, resulting from both stomatal limitation and non-stomatal inhibition. Meanwhile, drought stress alters chlorophyll metabolism, damages photosystem II activity, and affects electron transport efficiency, leading to reduced light energy conversion capacity and carbon fixation efficiency. To cope with water deficiency, *C. morifolium* plants employ multiple adaptive strategies, including stomatal regulation, osmotic adjustment through accumulation of proline and soluble sugars, enhancement of antioxidant defense systems, and modulation of drought-responsive gene expression. Changes in water use efficiency reflect the trade-off between carbon gain and water conservation, providing important indicators for evaluating drought adaptation. A case study approach is presented to analyze the dynamic responses of photosynthetic parameters and water use traits under different drought intensities, identifying key physiological indicators associated with drought tolerance. Furthermore, this review discusses practical strategies for improving drought resilience, including optimized irrigation management, application of soil amendments and biostimulants, and development of drought-tolerant cultivars through molecular breeding. Future integration of multi-omics technologies, high-throughput phenotyping, and intelligent irrigation systems will provide new approaches for enhancing water-saving production and sustainable cultivation of *Chrysanthemum morifolium* under increasingly variable climatic conditions.

Keywords *Chrysanthemum morifolium*; Drought stress; Photosynthetic characteristics; Water use efficiency; Drought adaptation mechanisms

1 Introduction

Chrysanthemum morifolium is a globally important horticultural crop with substantial ornamental, economic, ecological, and medicinal value. As one of the world's leading ornamental flowers and among the most valuable cut flowers in international floriculture, *Chrysanthemum* supports commercial production as cut flowers, potted plants, and landscape ornamentals across diverse cultivation systems (Luo et al., 2023). Beyond its ornamental role, *C. morifolium* has long been used as a medicinal and food-homology plant in East Asia, where its dried capitula and related products are valued in traditional medicine, tea, and functional foods because of their rich flavonoids, phenolic acids, volatile oils, polysaccharides, and other bioactive compounds (Hao et al., 2022; Liu et al., 2024). This dual-use identity means that stable *Chrysanthemum* production is important not only for the flower industry, but also for the sustained supply of plant material with nutritional and pharmacological relevance. As a result, environmental stresses that reduce biomass, flowering quality, or phytochemical accumulation can diminish both commercial value and downstream medicinal utility.

Among abiotic constraints, drought is one of the most serious factors limiting *Chrysanthemum* growth, production, and market performance. Studies consistently show that water deficit reduces plant growth and flower yield,

restricts planting area and geographical distribution, and lowers ornamental quality by impairing water relations and developmental performance (Xu et al., 2020). In commercial production systems, drought can also delay marketability and reduce profitability, while physiological symptoms commonly include dehydration, wilting, membrane damage, and suppressed gas exchange, indicating that *Chrysanthemum* is highly sensitive to inadequate water supply (Gogoláková and Paganová, 2020; Huang et al., 2026). More broadly, drought acts as a complex whole-plant stress that disrupts transpiration, photosynthesis, respiration, and cellular homeostasis, so its effects extend beyond visible growth inhibition to fundamental metabolic processes that determine survival and productivity. This is especially important under current climate trends, because increasing drought frequency and severity are likely to intensify water limitation during nursery, field, and postharvest phases of *Chrysanthemum* production.

Research on drought-induced photosynthetic regulation in *Chrysanthemum* has shown that photosynthesis is among the earliest and most sensitive processes affected by water deficit. Under drought conditions, net photosynthetic rate, stomatal conductance, transpiration rate, chlorophyll concentration, chlorophyll fluorescence, and PSII performance decline, with stronger or earlier reductions typically observed in drought-sensitive cultivars, indicating that both stomatal limitation and damage to the photosynthetic apparatus contribute to performance loss (Sahithi et al., 2020). At the same time, comparative physiological studies indicate that cultivar differences in drought tolerance are associated with variation in leaf structure, antioxidant capacity, and maintenance of photosynthetic function, while water-regime experiments show that reduced water availability significantly depresses stomatal conductance, transpiration, and photosynthesis and can alter intercellular CO₂ dynamics (Gogoláková and Paganová, 2020). These findings have established a useful physiological framework for understanding how drought reshapes carbon assimilation and water use in *Chrysanthemum*, and they also highlight the close coupling between leaf water status, oxidative stress, and photosynthetic stability.

Recent work has expanded this framework from whole-plant physiology to molecular and regulatory mechanisms, but important knowledge gaps remain. Drought-response studies in *Chrysanthemum* have identified genes and pathways related to ABA signaling, stomatal adjustment, cuticle formation, ROS detoxification, and stress-responsive transcriptional regulation, while genome-wide and transcriptomic analyses have emphasized that drought tolerance is a complex multigenic trait whose causal architecture remains incompletely resolved (Yang et al., 2020). Likewise, dehydration transcriptomics has shown large-scale reprogramming of hormone signaling, metabolism, and protective pathways, yet the integration of these molecular responses with dynamic changes in photosynthesis and water use efficiency under different drought intensities is still insufficiently characterized. In particular, more work is needed to link gas-exchange traits, chlorophyll fluorescence, leaf water status, and biochemical protection systems into a unified model of drought adaptation in *C. morifolium*. Therefore, examining the effects of drought stress on photosynthesis and water use characteristics is necessary for clarifying the physiological basis of drought injury and for supporting the breeding and cultivation of more water-efficient, drought-resilient *Chrysanthemum* cultivars.

2 Physiological Responses of *Chrysanthemum morifolium* to Drought Stress

2.1 Effects of drought stress on plant growth and biomass accumulation

Drought stress consistently suppresses vegetative growth and biomass accumulation in *Chrysanthemum*. Comparative physiological studies show that water deficit reduces biomass, flower development, transpiration, stomatal conductance, and photosynthetic performance, while cultivar-specific responses indicate that tolerant genotypes maintain growth better than sensitive ones under the same drought regime (Sahithi et al., 2020). This inhibitory effect is also evident at the production level, where drought decreases leaf increment, leaf area, and total biomass, although some cultivars partially compensate by increasing the root-to-shoot ratio to improve soil water use (Gogoláková and Paganová, 2020).

Growth reduction under drought is closely associated with impaired water status and declining physiological quality. Across diverse *Chrysanthemum* genotypes, relative water content, membrane stability, chlorophyll traits, fluorescence, and biomass are strongly correlated under stress, indicating that biomass loss reflects coordinated

disruption of hydration, membrane integrity, and carbon assimilation (Namita et al., 2025). Repeated osmotic stress experiments further show that initial drought episodes can inhibit microshoot growth more strongly than subsequent moderate stress, whereas severe repeated stress causes cumulative growth inhibition, suggesting that biomass responses depend on both stress intensity and stress history.

2.2 Morphological and anatomical adaptations to water deficit

Chrysanthemum responds to water deficit through structural adjustments that reduce transpirational water loss and improve dehydration avoidance. In a cultivar comparison, the drought-tolerant ‘Nannong Xuefeng’ developed denser trichomes, lower stomatal density, and much greater leaf wax deposition than the sensitive ‘Nannong Jingyan’, whereas transgenic evidence showed that enhanced drought resistance is likewise associated with reduced stomatal opening and a thicker epidermal cuticle (Wang et al., 2021). These traits fit the broader pattern of drought adaptation in leaves, where smaller effective evaporative surfaces, altered stomatal traits, and thicker cuticular barriers limit water loss while sustaining leaf function under drying conditions (Yavas et al., 2023).

The drought response of *Chrysanthemum* leaf morphology is also shaped by the growth environment and by long-term water relations rather than by acute soil drying alone. Plants grown under low vapor pressure deficit developed larger stomata and higher stomatal density, but their leaves lost water more rapidly during subsequent desiccation because stomatal closure was less effective, showing that preconditioning can alter later drought sensitivity. At the whole-plant level, drought commonly reduces leaf area and can shift biomass allocation toward roots, and these morphological changes are considered adaptive because they lower evaporative demand and improve water acquisition relative to shoot demand (Gogoláková and Paganová, 2020).

2.3 Osmotic regulation and antioxidant defense under drought conditions

Osmotic adjustment is a central component of *Chrysanthemum* drought tolerance. Under water deficit, *Chrysanthemum* commonly accumulates proline, soluble proteins, and soluble sugars to maintain cell turgor, and tolerant materials generally show stronger or more stable osmoprotective responses than sensitive ones (Zhang et al., 2022). Experimental mitigation studies support this interpretation, showing that exogenous melatonin increases soluble sugars and soluble protein under drought, while robinin plus chitosan promotes the accumulation of carbohydrates, proline, K^+ , and Ca^{2+} to sustain osmotic balance and turgor pressure (Elansary et al., 2020; Luo et al., 2023).

Antioxidant defense is equally important because drought-induced dehydration promotes reactive oxygen species accumulation, membrane lipid peroxidation, and loss of cellular stability. In *Chrysanthemum*, drought-sensitive plants accumulate more superoxide radicals and malondialdehyde, whereas tolerant genotypes or stress-alleviated plants maintain higher activities of SOD, POD, CAT, and APX, thereby limiting oxidative damage (Huang et al., 2026). Gene-level evidence is consistent with these physiological patterns: drought tolerance increases when ABA- and ROS-related defense pathways are activated, as shown by higher antioxidant enzyme activity in CmWRKY10-overexpressing lines and stronger proline accumulation and ROS-scavenging capacity in CmBBX22-repressed plants.

3 Effects of Drought Stress on Photosynthetic Characteristics of *Chrysanthemum* Leaves

3.1 Changes in photosynthetic pigments and light capture capacity

Drought stress generally weakens pigment accumulation and leaf light-harvesting capacity in *Chrysanthemum morifolium*, although the magnitude depends on stress severity and genotype. In *Chrysanthemum*, chlorophyll concentration declines as soil water content falls, and these decreases appear earlier and more strongly in drought-sensitive cultivars than in tolerant ones; multivariate screening across diverse spray *Chrysanthemum* genotypes similarly identifies chlorophyll a, chlorophyll b, total chlorophyll, carotenoids, and chlorophyll fluorescence as core drought-response traits linked to biomass and reproductive performance.

The physiological significance of these pigment changes is that reduced chlorophyll lowers the capacity for light absorption, while altered carotenoid dynamics help buffer stress-induced excess excitation. Ground-cover

Chrysanthemum showed a slight chlorophyll increase under light drought but a decline under moderate and heavy drought, indicating a threshold response rather than a simple monotonic loss, whereas broader pigment research shows that chlorophyll content and the chlorophyll a/b ratio directly influence antenna size, light distribution, and the balance between efficient capture and photodamage avoidance (Figure 1) (Simkin et al., 2022).

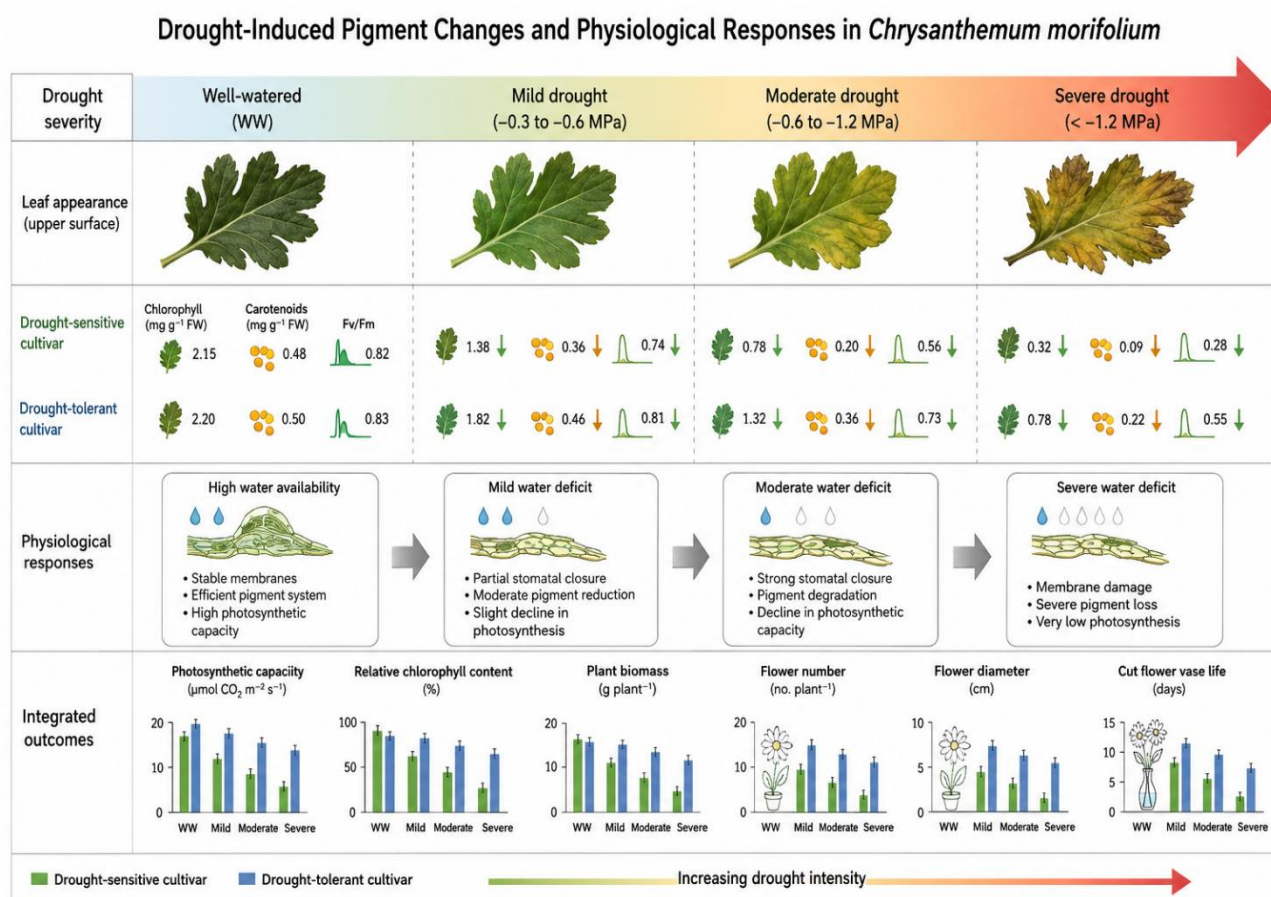


Figure 1 Phenotypic and physiological responses of *Chrysanthemum morifolium* leaves under progressive drought stress

3.2 Effects of drought stress on gas exchange parameters

Drought stress consistently suppresses the major gas-exchange parameters of *Chrysanthemum* leaves, especially net photosynthetic rate, stomatal conductance, and transpiration rate. In *Chrysanthemum* seedlings exposed to PEG-induced drought, net photosynthetic rate, stomatal conductance, and transpiration rate all decreased significantly while intercellular CO₂ concentration increased, and similar patterns were observed in ground-cover *Chrysanthemum*, where light drought reduced intercellular CO₂ but heavy drought increased it by 30.6% (Luo et al., 2023).

These patterns indicate a transition from stomatal limitation under milder drought to stronger non-stomatal limitation as stress intensifies. General drought physiology supports this interpretation: when leaf water status remains relatively higher, declines in photosynthesis track parallel declines in stomatal conductance and intercellular CO₂, but under more severe water deficit photosynthesis continues to fall even as intercellular CO₂ rises, implying biochemical impairment beyond stomatal closure; *Chrysanthemum*-focused analysis likewise notes that stomatal closure is typically the main determinant under mild to moderate drought, although metabolic damage becomes increasingly important as stress deepens (Gogoláková and Paganová, 2020).

3.3 Regulation of photosynthetic electron transport and carbon fixation

Beyond gas exchange, drought stress disrupts the photochemical machinery that supports electron transport and carbon assimilation in *Chrysanthemum* leaves. Comparative work in *Chrysanthemum* shows declines in PSII yield

and chlorophyll fluorescence under drought, with earlier and stronger reductions in sensitive cultivars, while severe drought in other model systems causes disassembly of PSII supercomplexes, degradation of the PSII core, and reduced operative quantum efficiency, indicating that the light reactions themselves become structurally and functionally compromised (Sahithi et al., 2020; Hu et al., 2023).

As photochemical efficiency declines, plants appear to increase protective energy dissipation and reroute electron flow, but these defenses are only partly effective under stronger stress. Drought studies across species show that PSII electron transport declines, non-photochemical quenching rises to relieve excitation pressure, and cyclic electron flow around PSI is activated to generate proton motive force and protect both photosystems; however, prolonged or severe stress also impairs carbon fixation by limiting ATP supply, RuBP regeneration, and Rubisco-related assimilation capacity, which helps explain why photosynthesis remains depressed even after stomatal effects are no longer the dominant constraint.

4 Water Relations and Water Use Characteristics under Drought Stress

4.1 Changes in plant water status and hydraulic regulation

Drought stress directly impairs plant water status in *Chrysanthemum morifolium*, primarily through a mismatch between water uptake and transpirational demand. Physiological studies show that reduced soil moisture lowers leaf water potential and relative water content, and varietal comparisons indicate that drought-tolerant materials maintain hydration more effectively than sensitive ones under stress (Sahithi et al., 2020; Zhang et al., 2022). This pattern is consistent with broader *Chrysanthemum* experiments showing that leaf relative water content declines progressively as drought intensifies, making tissue hydration one of the clearest indicators of water deficit severity and tolerance differences among cultivars (Luo et al., 2023).

Hydraulic regulation under drought depends strongly on stomatal control and epidermal barriers that limit water loss from leaves. In *Chrysanthemum*, transgenic and physiological evidence shows that reduced stomatal opening and thicker cuticles slow water loss, while exogenous ABA rapidly decreases stomatal conductance and delays wilting, indicating that hormonal and structural regulation act together to stabilize plant water balance during dehydration (Wang et al., 2021). Substrate-drying studies further show that more drought-tolerant cultivars conserve water by closing stomata earlier and retaining more water in the growing medium, suggesting that hydraulic regulation in *Chrysanthemum* is not only a leaf trait but also a whole-plant water conservation strategy.

4.2 Effects of drought stress on transpiration and water consumption patterns

Drought stress consistently suppresses transpiration in *Chrysanthemum*, and this response is closely tied to reduced stomatal conductance. Under reduced water availability, *Chrysanthemum* plants show marked declines in transpiration rate, while comparative cultivar studies confirm that transpiration decreases earlier and more strongly in drought-sensitive genotypes than in tolerant ones (Gogoláková and Paganová, 2020). Pot studies also show that both transpiration and stomatal conductance decrease as drought severity increases, and that tolerant cultivars maintain relatively higher gas exchange capacity under the same stress level.

Water consumption patterns in *Chrysanthemum* are shaped not only by soil drying but also by organ-specific and environmental controls on water loss. In cut *Chrysanthemum*, leaf transpiration decreases during desiccation because of stomatal closure, whereas stems and flowers show little active regulation, and leaf transpiration strongly predicts whole-cut-flower water loss (Fanourakis et al., 2021). Long-term growth under low vapor pressure deficit also alters later drought behavior: plants formed larger, denser stomata and then lost water faster during desiccation, showing that prior humidity conditions can modify subsequent transpiration control and wilting risk.

4.3 Water use efficiency responses to drought stress

Water use efficiency in *Chrysanthemum* generally increases under moderate drought because transpiration declines proportionally more than carbon assimilation during the early phase of stress. Ground-cover *Chrysanthemum* showed a progressive increase in water use efficiency with increasing drought, reaching 1.34-fold

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

Abscissic 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).

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.

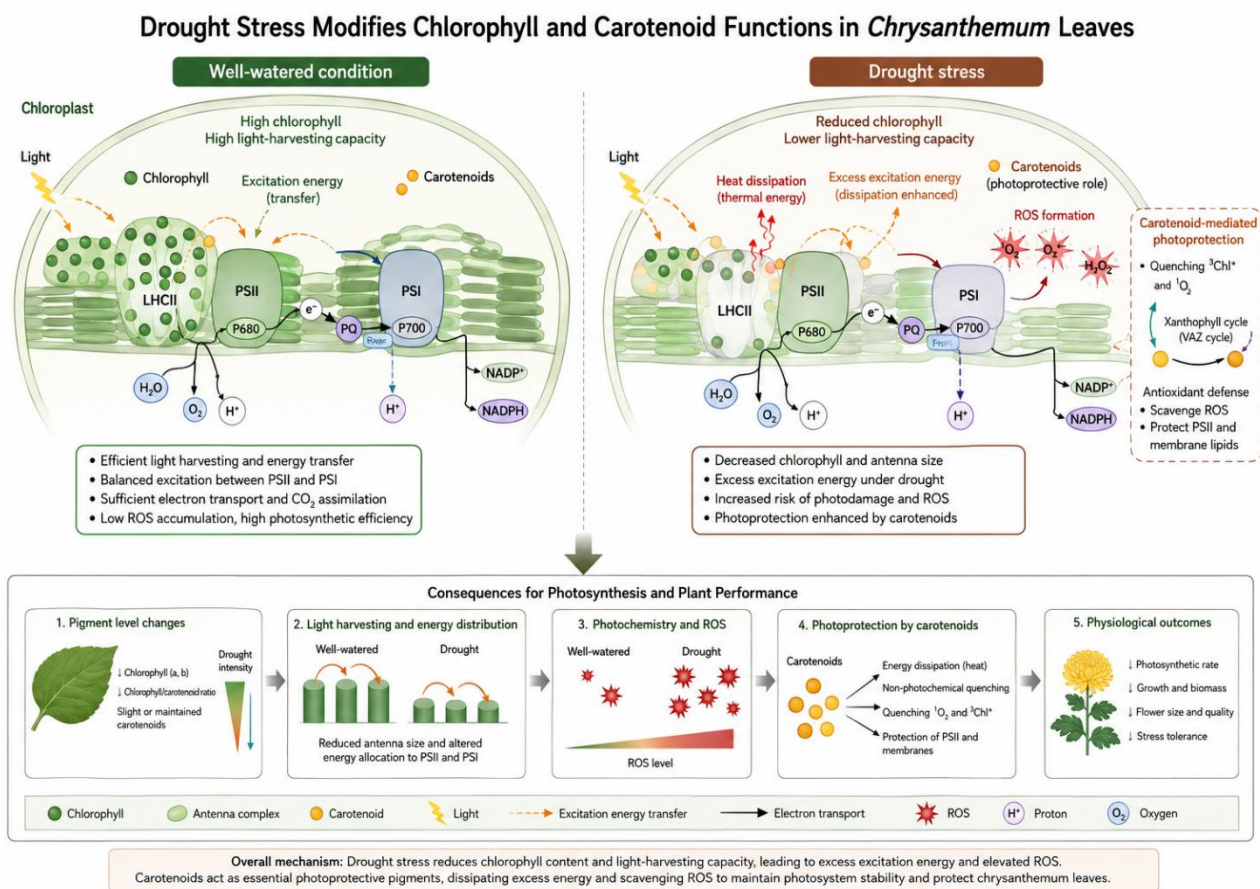


Figure 2 Mechanistic model of drought-induced regulation of chlorophyll and carotenoid functions in *Chrysanthemum morifolium*

6.3 Identification of key physiological indicators for drought adaptation

The most robust physiological indicators for drought adaptation in *Chrysanthemum* are traits that jointly reflect hydration status, photosynthetic integrity, and cellular protection. Multivariate analyses in standard and spray *Chrysanthemum* identified relative water content, membrane stability index, chlorophyll a and b, total chlorophyll, carotenoids, and chlorophyll fluorescence as major contributors to drought-related phenotypic variation and as practical selection indices for tolerant genotypes (Namita et al., 2025). These traits are especially useful because they integrate both functional performance and accumulated damage across different stress environments.

Biochemical indicators further refine this evaluation by distinguishing plants that merely endure dehydration from those that actively maintain homeostasis. Tea *Chrysanthemum* studies showed that increasing drought raised malondialdehyde, proline, and soluble protein while reducing growth and gas exchange, whereas comparative species analysis found that the more tolerant *Chrysanthemum* type maintained better water status, stronger antioxidant enzyme activity, less membrane damage, and less compromised photosynthesis (Zhang et al., 2022). Taken together, a comprehensive case-study assessment should prioritize relative water content, chlorophyll fluorescence, gas-exchange traits, membrane injury indices, and antioxidant or osmotic markers as the key physiological indicators of drought adaptation.

7 Agronomic Strategies for Improving Drought Tolerance and Water Use Efficiency in *Chrysanthemum* Production

7.1 Optimized irrigation management under water-limited conditions

Optimized irrigation management in *Chrysanthemum* production should aim to conserve water without causing irreversible drought injury. Regulated and sustained deficit irrigation are already recognized in ornamental crops as practical tools for controlling growth, hardening plants, and increasing water use efficiency, provided the strategy is adjusted to species-specific tolerance thresholds. In *Chrysanthemum* specifically, irrigation scheduling

and water input level strongly affect yield and efficiency, with field evidence showing that an intermediate irrigation regime of 0.75 Epan produced the highest water use efficiency among tested treatments under semi-arid conditions (Gouthami et al., 2025).

This optimization must also consider substrate and root-zone water dynamics rather than irrigation amount alone. Simulation-based work under protected cultivation showed that a 1.0 lph emitter combined with a 48-hour interval maintained optimal root-zone moisture while limiting deep percolation, indicating that irrigation design can improve water-use efficiency by keeping water available where *Chrysanthemum* roots can use it most effectively. At the same time, excessive deficit remains risky, because garland *Chrysanthemum* exposed to strong water restriction showed leaf chlorosis, reduced fresh and dry mass, and visible drought injury, whereas a moderate deficit treatment was more compatible with maintaining yield while improving efficiency (Chang et al., 2021).

7.2 Application of biostimulants and soil improvement measures

Among biostimulant approaches, exogenous melatonin has the clearest direct evidence for improving *Chrysanthemum* drought tolerance. Under PEG-induced drought, melatonin increased net photosynthesis, transpiration, and stomatal conductance, while also reducing the decline in chlorophyll and relative water content, indicating better coordination between water status and photosynthetic performance under stress. Melatonin also enhanced osmotic adjustment and antioxidant defense by increasing soluble sugars, soluble proteins, and antioxidant enzyme activities, which helps explain its protective effect on seedling vigor under water deficit (Luo et al., 2023).

Brassinolide and rhizosphere-oriented measures provide additional routes for stress mitigation and soil-related improvement. In *Chrysanthemum*, brassinolide treatment increased relative water content, net photosynthetic rate, chlorophyll fluorescence, Rubisco activity, and enzymes of the ascorbate-glutathione cycle, while reducing hydrogen peroxide accumulation, especially under drought conditions (Yang et al., 2020). Beyond plant growth regulators, review evidence indicates that *Chrysanthemum* production can also benefit from biological soil improvement, including rhizosphere inoculation strategies and beneficial microorganisms such as *Pseudomonas putida*, which have shown potential to improve plant growth and flowering and may support more resilient production systems.

7.3 Breeding and biotechnology approaches for drought-resistant *Chrysanthemum*

Breeding drought-resistant *Chrysanthemum* remains a high priority because drought tolerance is a complex trait controlled by many genes and strongly influenced by the species' polyploid and heterozygous genome. Transcriptome profiling under dehydration identified thousands of responsive transcripts, including transcription factors and kinases, and these datasets have been proposed as candidate-gene and marker resources for future breeding of drought-tolerant cultivars. More recent reviews likewise conclude that conventional breeding now needs to be integrated with marker-assisted selection, transgenic methods, genome editing, and multi-omics approaches to accelerate stress-tolerance improvement in *Chrysanthemum*.

Functional genetics and association mapping now provide more direct routes to cultivar improvement. Several drought-related regulators have already been characterized in *Chrysanthemum*, including CmSCL4 and CmR1MYB1, which synergistically enhance drought tolerance through ABA-responsive signaling, showing that targeted manipulation of signaling genes can improve stress adaptation (Zhang et al., 2022). At the population level, GWAS and integrative mapping studies identified favorable alleles, elite donor cultivars, and co-localized loci linked to drought tolerance, providing practical pre-breeding materials and genetic markers for developing cultivars with stronger drought resistance and more efficient water use (Lu et al., 2025).

8 Conclusions and Future Perspectives

Drought stress consistently depresses core photosynthetic processes in *Chrysanthemum* leaves, including net photosynthetic rate, stomatal conductance, transpiration, chlorophyll content, and PSII-related performance, and these declines become stronger as soil water deficit intensifies. Across graded drought treatments, intercellular CO₂ commonly decreases at earlier or milder stress and then rises under more severe stress, indicating a transition

from primarily stomatal limitation to combined stomatal and non-stomatal inhibition of photosynthesis. Water relations are impaired in parallel with photosynthesis, because declining leaf hydration, reduced water uptake relative to transpiration demand, and membrane injury all constrain physiological stability under drought. Even so, *Chrysanthemum* shows meaningful adaptive variation: tolerant genotypes or related species maintain better water status, less membrane damage, stronger antioxidative protection, and less compromised photosynthesis than sensitive materials.

For sustainable *Chrysanthemum* production, the main implication is that water-saving management should reduce unnecessary irrigation while avoiding severe stress that causes visible quality loss, depressed growth, and lower marketability. Moderate or monitored deficit appears more useful than uncontrolled drying, because *Chrysanthemum* can recover rapidly from cyclical water shortage and, in some systems, moderate deficit improves adaptation and post-production performance. Production strategies should also combine irrigation control with physiological protection and genotype choice. Exogenous melatonin and brassinolide both improved relative water content, photosynthetic performance, antioxidant capacity, and biochemical homeostasis under drought, while grafting onto *Artemisia annua* helped maintain gas exchange, photosynthesis-related gene expression, and Rubisco activity. At the cultivar level, multivariate screening now supports the use of chlorophyll traits, relative water content, membrane stability, canopy temperature depression, fluorescence, biomass, and reproductive traits as practical indicators for selecting drought-resilient production materials.

Future research should move from single-trait descriptions toward integrated multi-omics and phenomics frameworks that connect drought physiology with underlying genes, proteins, metabolites, and high-throughput phenotypes across developmental stages and environments. This need is especially pressing in *Chrysanthemum* because current omics applications remain relatively early, full-genome resources are still limiting, and large-population phenotyping under environmental variation remains one of the major bottlenecks for breeding progress. A second priority is to translate genetic discovery into usable breeding tools for drought-tolerant cultivars with stable photosynthesis and efficient water use. Association mapping, multi-locus GWAS, and integrative linkage mapping have already identified favorable alleles, pre-bred tolerant cultivars, colocalized loci, and validated candidate genes, but these resources still need functional validation and deployment in cultivar development. More broadly, future experiments should compare mild, moderate, and severe drought with rewatering phases, because stress intensity-dependent designs are better suited to linking dynamic physiological responses with transcriptomic regulation and to defining agronomically useful tolerance rather than survival alone.

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Conflict of Interest Disclosure

The author affirms that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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