

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