

Its ecological adaptability is notable but conditional. *D. officinale* shows physiological flexibility in carbon assimilation, functioning as a facultative CAM plant in which the balance between C3 and CAM photosynthesis shifts with environmental conditions. Decreasing substrate water content induces a more typical CAM pattern, while rewatering promotes a return toward mixed C3-CAM behavior, indicating an adaptive response to intermittent water deficit common in epiphytic habitats. This plasticity supports survival under drought, heat, and nutrient limitation, but adaptation is not unlimited: karst forest cultivation often faces severe water shortage, slow growth, and low yield, and recent work shows that combined high temperature and drought stress can markedly impair morphology, antioxidative status, yield, and polysaccharide accumulation, with clear differences among germplasm types (Luo et al., 2024; Gao et al., 2026). Endophytic and mycorrhizal fungi are therefore not incidental associates but part of its adaptive strategy, because they can improve growth, drought tolerance, disease resistance, and overall stress resilience (Li et al., 2021).

## 2.2 Requirements for light, temperature, humidity, and substrate

The growth and quality formation of *D. officinale* depend strongly on coordinated regulation of light, temperature, humidity, and water status. Multiple studies identify light, temperature, and water as major environmental cues affecting photosynthesis, growth rate, and active-compound synthesis (Zhang et al., 2024). *D. officinale* is a photosensitive plant, and inappropriate shading leads to unstable yield and quality. Evidence from light-gradient experiments indicates that moderate light is preferable to either extreme: under 11 000 lx, plants achieved peak biomass, maximal bioactive compound yield, superior fresh-consumption quality, and lower oxidative stress, whereas excessive light increased antioxidant enzyme activity and structural carbohydrate accumulation but suppressed plant height and edible quality. Greenhouse trials likewise found that 50~70% shade improved growth and biomass, while red light favored biomass production and increased polysaccharide and alkaloid contents (Nguyen et al., 2023).

Temperature and humidity must also be controlled within a relatively narrow ecological window. *D. officinale* has strict climatic requirements, and quality-related components are significantly associated with ecological variables such as maximum and minimum relative humidity, maximum temperature, and sunshine duration (Yuan et al., 2020). Recent synthesis further suggests that breaking the coupling of high temperature and high humidity is important for preventing southern blight, highlighting that warm and moist conditions are beneficial only when they do not cross the threshold for disease outbreaks (Liu et al., 2025b). Substrate conditions are equally important because this species is epiphytic and requires a loose, breathable rooting environment rather than dense field soil (Ding et al., 2018). Pine bark-based substrates appear especially suitable: one study reported high flavonoid accumulation in pine bark substrate (Zhang et al., 2024), while greenhouse-grown plants in physiological experiments were maintained successfully in a mixed substrate of pine bark fractions, perlite, and composted sawdust. Nutrient supply also shapes quality traits, as potassium treatment significantly increased anthocyanin accumulation and flavonoid-related metabolic responses, indicating that substrate fertility management is part of quality-oriented cultivation rather than merely biomass production (Jia et al., 2022).

## 2.3 Environmental regulation under different cultivation modes

The two main artificial production pathways for *D. officinale* are facility cultivation and wild-simulated or semi-wild cultivation, and the environmental regulation logic of these systems differs fundamentally (Yang et al., 2026). Facility cultivation emphasizes controllability, using greenhouse structures and monitoring systems to stabilize light, humidity, substrate moisture, and temperature. In related greenhouse control work, real-time monitoring and intelligent prediction based on soil temperature, soil moisture, humidity, and light achieved prediction error below 2.5%, showing that facility systems can support precise microclimate management. Wild-simulated cultivation, by contrast, relies on shade, breathable substrates, open ecological planting (Ding et al., 2018). This mode places greater emphasis on matching the original habitat and maintaining ecological interactions, including microbial and fungal symbioses (Liu et al., 2025b).

These different regulatory strategies lead to different biological and quality outcomes. Greenhouse cultivation can increase production stability, but it also changes growth patterns relative to wild plants and shifts the dominant