have been reported to promote growth and active polysaccharide accumulation in *Dendrobium*, while nitrogen-fixing and stress-responsive genera such as *Devosia* are enriched in rhizocompartments and may support adaptation to nutrient-poor or stressful substrates (Xie et al., 2024). The practical implication is that precise greenhouse control of light, temperature, and moisture should be coordinated with substrate selection, root-zone aeration, and microbiome management, because sustainable improvement in *D. officinale* polysaccharide accumulation appears to emerge from this whole-plant environmental network rather than from single-factor optimization.

6 Mechanisms of Controlled-Environment Regulation of Polysaccharide Accumulation in *Dendrobium officinale*

6.1 Regulation of carbon supply for polysaccharide synthesis through photosynthesis

Photosynthesis is the primary upstream source of carbon for polysaccharide synthesis in *Dendrobium officinale*, and controlled environments regulate this source first by altering the plant's photosynthetic mode and then by changing total assimilate supply. *D. officinale* is a facultative CAM plant that can switch between CAM, C_3, and intermediate states depending on substrate moisture and light-dark regime, so environmental regulation changes not only photosynthetic rate but also the timing and pathway of carbon fixation (Zhang et al., 2014). Under natural weather variation, sunny days favor a typical CAM-like pattern, rainy days favor C_3-like daytime uptake, and cloudy days produce an intermediate pattern, indicating that light intensity, humidity, and temperature together determine whole-day CO_2 assimilation behavior. Controlled cultivation can exploit this plasticity: shortening the light-dark cycle to 4 h/4 h or 2 h/2 h improved photosynthetic apparatus status, shifted carbon fixation toward C_3 behavior, doubled daily net CO_2 exchange and biomass increase relative to 12 h/12 h, and increased soluble polysaccharide yield, especially under 2 h/2 h conditions (Cheng et al., 2019).

Carbon supply is further regulated by light and temperature effects on photosynthetic efficiency and by their downstream effects on carbohydrate metabolism. Developmental transcriptomics showed that changes in stem polysaccharide content are tightly associated with genes enriched in starch and sucrose metabolism, indicating that photosynthetic carbon enters a regulated source-to-sink pathway rather than passively accumulating (Yang et al., 2025). Seasonal transcriptomics similarly found that genes associated with sugar accumulation were enriched in photosynthesis and starch-sucrose metabolism, and identified hub genes that appear to stabilize sugar metabolism under low-temperature and drought conditions. Temperature studies show an important source-sink distinction: net photosynthesis and vegetative growth were highest around 30℃, but stem polysaccharide content was highest at 20℃, indicating that maximal carbon fixation does not necessarily produce maximal polysaccharide concentration because carbon partitioning also shifts with temperature. Consistent with this, carbon-nitrogen co-application improved photosynthetic pigments, net photosynthetic rate, carbon-metabolism enzyme activity, soluble sugars, and overall quality, showing that controlled environments increase polysaccharides partly by strengthening the upstream carbon source that feeds downstream biosynthesis (Yin et al., 2026).

6.2 Promotion of polysaccharide formation through sugar transport and metabolic enzyme activity

Once carbon is fixed, controlled-environment regulation promotes polysaccharide formation by controlling sugar transport, sucrose cleavage, precursor interconversion, and polymer assembly. Transcriptome analysis identified 430 glycosyltransferase genes and 89 cellulose synthase-related genes in *D. officinale*, establishing that polysaccharide formation depends on a large enzymatic network rather than a single biosynthetic step (Zhang et al., 2016). Developmental expression profiling further showed that polysaccharide-associated genes change across stem growth stages and that 15 key genes are positively correlated with water-soluble polysaccharide content (Yang et al., 2025). Sugar transporter regulation is now directly implicated in this process: comparative genomics and silencing experiments identified several *DoSWEET* genes as candidate regulators, and silencing six candidates reduced polysaccharide accumulation by 14~22%, with the strongest effects for *DoSWEET1, 8, 13, 17,* and *24*. Because these *SWEET* genes also contain abiotic-stress-responsive cis-elements and show stress-dependent expression, controlled environments likely regulate polysaccharide accumulation partly by changing sugar export, unloading, and redistribution between source and sink tissues.