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Light intensity-mediated acclimation in *Dendrobium denneanum*: coordinated responses of growth, photosynthesis, leaf microstructure, and medicinal constituents

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Introduction: This study aimed to characterize light-acclimation responses of the endangered medicinal orchid *Dendrobium denneanum* and identify suitable light conditions for cultivation and *ex situ* conservation.

Methods: We examined growth, gas exchange, chlorophyll content, leaf microstructure, and medicinal constituent accumulation under three relative light intensities: 40%, 20%, and 8% of full natural light.

Results: The 20% treatment produced the greatest increments in plant height, crown width, basal stem diameter, leaf area, and leaf number, with particularly clear advantages in crown width, basal stem diameter, and leaf area. It also resulted in the highest daily average net photosynthetic rate, maximum net photosynthetic rate, and light saturation point, indicating that this light level was most favorable for vegetative growth and photosynthetic carbon assimilation under the tested cultivated conditions. Plants under 40% light showed lower photosynthetic performance than those under 20% light but higher performance than those under 8% light. This treatment was associated with the highest apparent quantum yield, thicker leaves and mesophyll, and greater stomatal density, width, and area, suggesting structural adjustment to relatively higher irradiance. Under 8% light, chlorophyll a, chlorophyll b, and total chlorophyll contents were highest, indicating shade acclimation, whereas growth increments, daily photosynthesis, maximum photosynthetic capacity, and light saturation point were reduced. Medicinal constituents showed contrasting responses to light intensity. Polysaccharide content increased with increasing light intensity and was highest under 40% light, whereas alcohol-soluble extract content decreased with increasing light intensity and was highest under 8% light.

Discussion: Therefore, the suitable light condition for *D. denneanum* depends on the cultivation objective: 20% relative light intensity favors vegetative growth and photosynthetic performance, 40% favors polysaccharide accumulation, and 8% favors alcohol-soluble extract accumulation. These results provide objective-specific guidance for sustainable cultivation and *ex situ* conservation of *D. denneanum*.

KEYWORDS

acclimation, *Dendrobium denneanum*, growth, leaf microstructure, light intensity, medicinal constituents, physiology

1 Introduction

Light availability is a fundamental environmental factor regulating plant morphology, photosynthetic capacity, and metabolic processes. Changes in light intensity can induce species-specific adjustments in structural traits and photosynthetic responses, thereby shaping plant acclimation to heterogeneous light environments (Sarropoulou et al., 2025). Photosynthetic carbon assimilation provides the carbon skeletons and metabolic energy required for plant growth; the carbohydrates produced through photosynthesis also serve as important precursors for the biosynthesis of specialized metabolites, including phenolics, flavonoids, terpenoids, and alkaloids (Yang et al., 2018). Insufficient light may restrict carbon assimilation and consequently limit plant growth and development (Zhao et al., 2012), whereas excessive irradiance can induce photoinhibition, impair the photosynthetic apparatus, and reduce photosynthetic efficiency (Sharma et al., 2023). Therefore, maintaining appropriate light conditions is essential for optimal plant growth and physiological performance.

With growing attention to biodiversity conservation, clarifying the light requirements of endangered plants has become increasingly important. Light availability strongly affects the survival, regeneration, and habitat suitability of rare species. For instance, *Pterocarpus indicus* seedlings tolerate shade through morphological and physiological adjustments despite reduced growth (Lee et al., 2023), while *Heptacodium miconioides* performs best under moderate light, with both insufficient and excessive light impairing photosynthesis and antioxidant activity (Liu et al., 2006). Studies of *Camellia nitidissima* have demonstrated that this species is shade-tolerant, with growth rates increasing as light intensity decreases (Chai et al., 2018). Importantly, the light conditions that favor vegetative growth may not coincide with those that promote the accumulation of medicinally important constituents. Therefore, identifying suitable light conditions for growth, physiology, and medicinal constituent accumulation is essential for the conservation and cultivation of endangered medicinal plants.

Epiphytic orchids often inhabit forest canopies or shaded understories where light availability is highly heterogeneous and frequently limited. Many shade-adapted epiphytic orchids therefore exhibit considerable photosynthetic and morphological plasticity, which helps them maintain carbon assimilation under fluctuating irradiance (Pires et al., 2012). More broadly, plants can adjust to variable light environments by modifying growth, morphology, physiology, and resource allocation, thereby maintaining performance under

changing irradiance conditions (Wei et al., 2024). Under low-light conditions, many species adjust by expanding leaf area (Pan and Guo, 2016), promoting stem elongation, and reallocating biomass among plant organs (Lockhart et al., 2012). Physiologically, plants may improve photosynthetic efficiency by modulating chlorophyll content (Li et al., 2025), apparent quantum yield (AQY) (Wang et al., 2024), and antioxidant activity, thereby promoting organic matter accumulation. From a biochemical perspective, plants can also regulate the synthesis of secondary metabolites such as flavonoids and triterpenoids to enhance antioxidant defenses and stress resistance under varying light regimes (Xu et al., 2020). Integrating morphological, physiological, anatomical, and biochemical analyses therefore provides a comprehensive framework for understanding how plants coordinate growth, photosynthetic function, leaf structure, and metabolite production under different light regimes.

Dendrobium denneanum is a typical epiphytic herbaceous orchid species (Lin et al., 2013). It is primarily distributed in the provinces of Yunnan, Guizhou, Guangxi, and Hainan in China, as well as in neighboring regions including India, Myanmar, and Thailand. The species commonly inhabits sparsely wooded mountainous areas and grows on tree trunks at elevations ranging from 600 to 2,500 m, where its growth is strongly affected by factors such as temperature, light availability, and substrate conditions (Jia et al., 2023). Owing to its brightly colored, fragrant flowers, *D. denneanum* also possesses high ornamental value (Fan et al., 2023). In addition, it is a highly valued traditional Chinese medicinal plant (Luo et al., 2011). Modern pharmacological studies have shown that its stems contain various bioactive compounds, including dendrobine, *Dendrobium* polysaccharides, and bibenzyl derivatives (Konhar et al., 2019), which exhibit diverse pharmacological activities, including anti-tumor, anti-aging, immunomodulatory, hypoglycemic, and anti-cataract effects. *Dendrobium* polysaccharides are primary metabolites derived from carbohydrate metabolism but are widely recognized as important medicinal constituents. The high economic and medicinal value of *D. denneanum* has led to excessive harvesting and a sharp decline in wild populations. As an epiphyte, its survival is highly dependent on stable environmental conditions. Human activities, including deforestation of mountainous forests and habitat fragmentation, have further accelerated the depletion of natural resources. Consequently, *D. denneanum* has been declared a national Class II protected wild species in China (National Forestry and Grassland Administration; Ministry of Agriculture and Rural Affairs, 2021). Past analyses of this species

have largely focused on medicinal compound extraction and the development of artificial cultivation techniques (Peng et al., 2024). Although (Wang et al., 2025) recently examined light-intensity responses in *D. denneanum*, the coordinated links among growth, photosynthetic performance, leaf microstructure, and medicinal constituent accumulation remain insufficiently understood. Such integrated studies are needed to clarify light-dependent acclimation responses and provide evidence-based guidance for cultivation and conservation.

Here, we evaluated the growth performance, photosynthetic physiology, leaf anatomical characteristics, and medicinal constituent accumulation of *D. denneanum* under three controlled light regimes. The specific objectives were (1) to identify the light conditions most suitable for vegetative growth and photosynthetic carbon assimilation, (2) to determine how light intensity influences the accumulation of different medicinal constituents, and (3) to characterize the integrated morphological, physiological, anatomical, and biochemical acclimation responses of *D. denneanum* across a light gradient.

2 Materials and methods

2.1 Study site

This study was conducted at the Guangxi Institute of Botany (25°11' N, 110°12' E; 178 m above sea level) in Guilin, Guangxi, China, which served as the *ex situ* cultivation site for all experimental plants. The region has a subtropical monsoon climate, with an annual mean temperature of 20.21 °C and monthly mean temperatures ranging from 9–28.4 °C. The recorded extreme temperatures ranged from −3.8 °C to 38.4 °C. Monthly mean temperatures ≥ 20 °C occur for approximately 6–7 months each year, and the annual accumulated temperature above 10 °C reaches 5,955.3 °C·d. The region receives an average annual precipitation of 1,854.8 mm, with approximately 73% of rainfall from April through August. Mean relative humidity is 78.0%, and the climate exhibits well-defined wet and dry seasons. The annual duration of sunshine is approximately 1,550 h, while frost days range from 9 to 24 per year, primarily occurring between December and February.

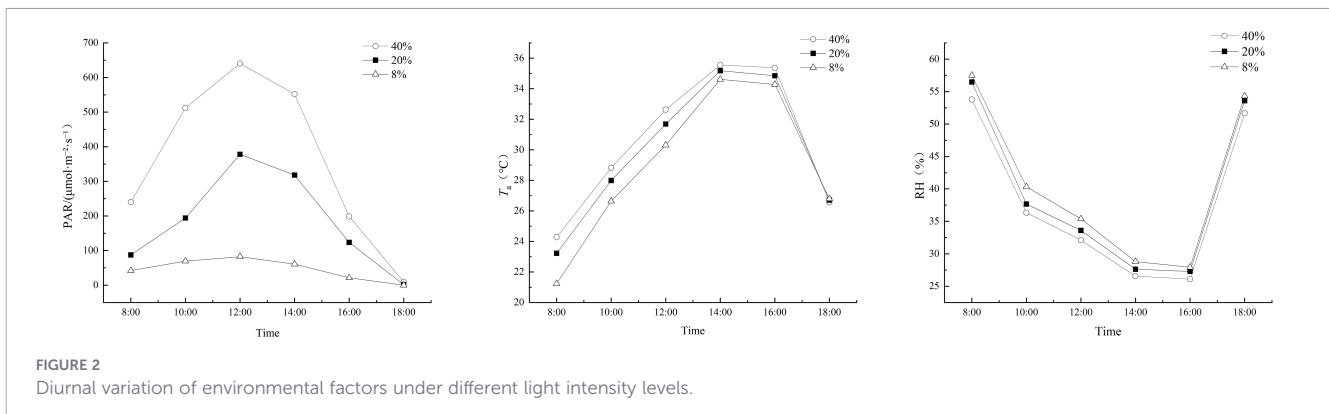
2.2 Materials and processing

Two-year-old *D. denneanum* plants were used as the experimental material. Three shading treatments were established using black nylon shade nets (Binzhou, Shandong, China) to create relative light intensities of 8%, 20%, and 40% of natural sunlight, corresponding to approximately 150–250, 350–500, and 700–900 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ photosynthetic photon flux density (PPFD), respectively, measured at plant canopy height under the shade nets at midday under clear-sky conditions. These light levels were selected to represent a practical shade gradient from deep shade to relatively open shade, which is broadly consistent with the heterogeneous light environments experienced by epiphytic orchids in forest habitats. Thus, the three treatments allowed us to evaluate the growth and physiological responses of *D. denneanum* under

different shade conditions. Individual plants were cultivated in plastic pots (15 cm high and 13 cm diameter) containing a 3:1:1 (v/v/v) mixture of bark, coconut coir, and perlite. Before the experiment, plants were acclimated for one month under 8% relative light intensity to minimize transplant shock and standardize initial growth conditions. In total, 30 plants (10 per treatment) were randomly assigned to the three shading treatments and placed under the corresponding shelters in early May. For subsequent measurements, three healthy and uniformly growing plants were selected from each treatment as independent biological replicates, with individual plants treated as the replicate unit. Throughout the experimental period, consistent irrigation and fertilization practices were applied across all treatments. Plants were irrigated according to substrate moisture conditions, typically two to three times per week, to maintain adequate moisture. A balanced water-soluble fertilizer (N–P–K = 20–20–20, approximately 1 g·L^{−1}) was applied every two weeks, and pest and disease control was conducted regularly to maintain plant health. The shade nets used in this experiment were made of black nylon and were used to establish different relative light intensity treatments. Because spectral composition was not measured, the treatments were interpreted primarily in terms of relative light intensity. After five months of treatment, representative plants grown under the three light conditions were photographed (Figure 1). Photosynthetic and physiological measurements were then conducted. Subsequently, leaf and pseudobulb samples were collected for analyses of leaf microstructure, chlorophyll content, and medicinal constituent contents. In addition, diurnal changes in photosynthetically active radiation (PAR), relative humidity (RH), and air temperature (*T*_a) were monitored from 08:00 to 18:00 on a representative clear day during the physiological measurement period under each shading condition (Figure 2). These measurements were conducted to characterize the microenvironmental conditions of the three shading shelters during data collection and to compare the relative differences among treatments.



FIGURE 1
Representative plants of *D. denneanum* grown under three relative light intensities (8%, 20%, and 40%) after five months of treatment.



2.3 Methods

2.3.1 Growth parameters

All growth parameters were measured on current-year shoots of three independent replicate plants per treatment, with one plant representing one biological replicate. At the initiation of the experiment, 30 plants were randomly selected to measure initial plant height (18.30 ± 1.77 cm), initial basal stem diameter (5.37 ± 0.70 mm), and initial crown diameter (15.13 ± 0.68 cm). One-way ANOVA showed no significant differences among the treatments ($P > 0.05$), confirming the uniformity of the initial plant material. Final measurements were taken after five months of treatment, and growth increments were calculated as the difference between the final and initial measurements for each parameter. The assessed parameters included plant height, basal stem diameter, crown width, leaf number, and leaf area. Measurement procedures were as follows: (1) plant height was determined using a steel measuring tape (precision 1 mm) positioned vertically from the plant base to the highest growth point; (2) basal stem diameter (BSD) was assessed 1 cm above the substrate surface using a digital caliper (0.01 mm accuracy); (3) crown width (CW) was calculated by measuring the maximum horizontal spread of the plant in two perpendicular directions and averaging the two values; (4) leaf number was obtained by manually counting all healthy, completely expanded leaves on each plant; and (5) leaf area (LA) was quantified using a LI-3100C leaf area meter, with mature leaves selected for scanning. All measurements were performed with plants in their natural, undisturbed growth posture.

2.3.2 Parameters of gas exchange

Gas exchange parameters were determined in early October on clear days using a portable Li-6400XT photosynthesis system (LI-COR, USA). The three biological replicate plants selected from each treatment were used for gas exchange analysis.

Diurnal changes in photosynthetic activity were recorded at 2-h intervals between 08:00 and 18:00 (Beijing time). For each sampled leaf, three measurements were taken and averaged. The measured gas exchange parameters included net photosynthetic rate (P_n), stomatal conductance (G_s), transpiration rate (T_r), and intercellular CO_2 concentration (C_i). The daily average net photosynthetic rate (DAP) was calculated as the mean of P_n values measured at all time

points throughout the day. Three biological replicates were included for each treatment.

2.3.3 Photosynthetic light-response curves

The Li-6400XT system was used to generate photosynthetic light-response curves. Measurements were conducted on mature, completely expanded leaves from the three independent biological replicate plants in each treatment, with one leaf measured per plant. Prior to formal measurements, preliminary tests were conducted to identify the approximate light saturation point (LSP) and to confirm that the selected PPFD range covered the saturation and post-saturation phases. Leaves were then preconditioned for 30 min under saturating light provided by the instrument's internal red and blue light sources to ensure full induction of the photosynthetic apparatus. Measurements were carried out on clear mornings between 08:30 and 11:30. During data acquisition, airflow was maintained at $500 \text{ mL} \cdot \text{min}^{-1}$, leaf temperature was regulated between 26 and 28 °C, and CO_2 concentration was maintained at $400 \mu\text{mol} \cdot \text{mol}^{-1}$. A series of PPFD levels ($1,500, 1,200, 1,000, 800, 600, 400, 200, 150, 100, 50, 20, 10$, and $0 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) was applied sequentially from high to low. Gas-exchange parameters were recorded after a stabilization period of approximately 3 min at each light level.

2.3.4 Chlorophyll content analysis

Mature, healthy leaves from the mid-upper plant sections were collected from three biological replicate plants per treatment for chlorophyll extraction, ensuring consistency with the gas exchange assays. The leaf samples were chopped and extracted in 95% ethanol for 24 h in the dark. Absorbances at 665 nm and 649 nm were read using a PerkinElmer Lambda 35 UV-Vis spectrophotometer (USA), with 95% ethanol serving as the blank. Concentrations of chlorophyll a (Chl a), chlorophyll b (Chl b), total chlorophyll (Chl), and the Chl a/Chl b ratio were determined using published formulae (Lichtenthaler and Wellburn, 1983).

2.3.5 Measurement of leaf microstructure

Leaves previously used for photosynthetic measurements were chosen for anatomical analysis. Each treatment included three biological replicates, with one leaf sampled per plant to maintain consistency in orientation and developmental stage. Leaf segments

(5 × 5 mm) close to the midrib were excised before immediate fixation in formaldehyde-acetic acid-ethanol (FAA) for 24 h and subsequent dehydration in a graded ethanol gradient (2 h per concentration), cleared in xylene, paraffin-embedded, sectioned (8 μm), stained with toluidine blue, and mounted in neutral balsam before evaluation and imaging under light microscopy. Leaf and mesophyll thicknesses from 10 random fields were assessed using Case Viewer.

For epidermal structure analysis, samples were collected from the same three biological replicate plants in each treatment. Samples (4 × 4 mm) were cut from leaves, avoiding the main vein. The material was fixed (2.5% glutaraldehyde in 0.1 mol·L⁻¹ phosphate buffer [pH 7.2], 24 h, 4 °C) and dehydrated in an ethanol gradient (30%, 50%, 70%, 90%, and 100%), with 30 min per step, before drying and subsequent gold sputter-coating for 90 s. The adaxial and abaxial surfaces of the leaves in five random fields were evaluated and imaged under scanning electron microscopy (Zeiss EVO18). Stomatal densities and major/minor axis lengths were determined using Image-Pro Plus 6.0. Stomatal area (SA) was computed with the elliptical formula (Equation 1):

$$S = \pi ab/4, \quad (1)$$

where a and b are the lengths of the major and minor axes, respectively. For each leaf, measurements from multiple fields were averaged before statistical analysis.

2.3.6 Quantification of medicinal constituents

To determine the concentrations of medicinal constituents, stem samples of *D. denneanum* were collected from each light treatment, with three biological replicates per group. Well-developed, one-year-old pseudobulbs were selected, thoroughly rinsed with distilled water, and dried at 60 °C. The dried material was finely ground, sieved (60-mesh), and kept in a desiccator until analysis. The alcohol-soluble extract (ASE) content was quantified using the cold maceration method specified in the Pharmacopoeia of the People's Republic of China, using 95% ethanol as the extraction solvent. ASE content was determined from the difference in sample mass before and after extraction (Chinese Pharmacopoeia Commission, 2020). Polysaccharides were extracted in hot water followed by precipitation with 95% ethanol. The total polysaccharide content was determined using the phenol-sulfuric acid colorimetric method at 490 nm. A glucose standard curve was established using standard solutions with concentrations ranging from 0 to 100 μg mL⁻¹, and good linearity was achieved ($R^2 > 0.99$). Each treatment included three biological replicates. All analyses of medicinal constituents were conducted by a certified third-party laboratory (Guangxi Yipu Testing Technology Co., Ltd.) following standard protocols.

2.3.7 Data processing

Fitting of the photosynthetic light-response curves was performed using the following modified version of the rectangular hyperbola model (Ye et al., 2013) (Equation 2):

$$P_n(I) = \alpha \frac{1 - \beta I}{1 + \gamma I} I - R_d \quad (2)$$

Where α is the initial slope, β and γ are coefficients, I denotes the photosynthetic photon flux density (PPFD), and R_d corresponds to the dark respiration rate. Details of the light-response curve fitting procedure are provided in Supplementary Material, the goodness-of-fit of the model was evaluated using the coefficient of determination (R^2). High R^2 values indicate that the model adequately describes the response of net photosynthetic rate to light intensity.

The apparent quantum yield (AQY) was determined by the slope of the linear section of the curve with PPFD values < 100 μmol·m⁻²·s⁻¹. The maximum net photosynthetic rate (P_{max}), light saturation point (LSP), and light compensation point (LCP) were derived as follows (Equations 3–5):

$$P_{max} = \alpha \left(\frac{\sqrt{(\beta + \gamma)} - \sqrt{\beta}}{\gamma} \right)^2 - R_d \quad (3)$$

$$LSP = \frac{\sqrt{(\beta + \gamma)/\beta} - 1}{\gamma} \quad (4)$$

$$LCP = \frac{-(\gamma R_d - \alpha) - \sqrt{(\gamma R_d - \alpha)^2 - 4\alpha\beta R_d}}{2\alpha\beta} \quad (5)$$

All data were organized and preprocessed with WPS Spreadsheets 2025. Statistical analyses were performed using SPSS 27. Prior to analysis, all data were tested for normality and homogeneity of variance. One-way ANOVA followed by Duncan's multiple range test was used to evaluate differences among treatments at a significance level of $P < 0.05$. Pearson correlation coefficients among growth traits, photosynthetic parameters, chlorophyll content, leaf microstructural characteristics, and medicinal constituent concentrations were calculated using data from individual biological replicates across all three treatments ($n = 9$). Data are presented as mean ± standard error (SE). Figures were generated using Origin 2025.

3 Results

3.1 Influence of light intensity on *D. denneanum* growth

Growth increments of *D. denneanum* under varying light levels are summarized in Table 1. Plants cultivated under 20% light demonstrated the greatest increases in CW, BSD, and LA, markedly higher than those under 40% and 8% light. Increases in plant height (PH) and leaf number (NOL) were also greatest at 20% light intensity, with PH and LA being significantly greater than values recorded under 8% light conditions. Overall, the growth increments indicated that 20% relative light intensity provided the most favorable conditions for vegetative growth, while *D. denneanum* still maintained a degree of tolerance to both higher (40%) and lower (8%) light environments.

TABLE 1 Growth increments of *D. denneanum* under varying relative light intensity conditions.

Relative intensity (%)	PH (cm)	CW (cm)	BSD (mm)	LA (cm ²)	NOL
40	10.73 ± 0.45 a	9.73 ± 1.35 b	1.50 ± 0.11 b	1.66 ± 0.08 b	3.67 ± 0.58 a
20	10.93 ± 1.12 a	12.50 ± 0.52 a	3.04 ± 0.32 a	3.04 ± 0.32 a	4.33 ± 0.58 a
8	7.63 ± 1.42 b	9.55 ± 0.10 b	0.95 ± 0.14 c	1.09 ± 0.14 c	3.33 ± 0.58 a

Different lowercase letters in a given column indicate significant differences ($P < 0.05$); Error bars represent mean $\pm$ standard error (SE) ($n=3$). PH: Plant height increment; CW: Canopy width increment; BSD: Basal stem diameter increment; LA: Leaf area increment; NOL: Number of leaves increment, The increments represent the increases in each growth parameter during the experimental treatment period.

3.2 Influence of light intensity on diurnal variations in *D. denneanum* gas exchange parameters

Under all light treatments, the P_n of *D. denneanum* followed a clear unimodal diurnal pattern, reaching peak values at approximately 10:00 (Figure 3A). The daily average net photosynthetic rate (DAP) differed significantly among treatments, following the order: 20% ($1.020 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) > 40% ($0.930 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) > 8% ($0.316 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) ($P < 0.05$). This indicates that plants cultivated under 20% light showed the strongest capacity for photosynthetic carbon assimilation.

Stomatal conductance (G_s) under all treatments initially increased during the morning and then declined, with peak values observed at 10:00 (Figure 3B). The mean daily G_s was highest under 20% light intensity. Transpiration rate (T_r) also displayed a unimodal diurnal trend (Figure 3C), peaking at 10:00 under 20% and 8% light treatments, whereas the peak under 40% light occurred later, at 12:00. Inter-cellular

CO_2 concentration (C_i) exhibited a U-shaped diurnal pattern across all treatments (Figure 3D). Except at 08:00, C_i values under 40% and 8% light intensities were consistently higher than those under 20% light intensity, and these differences were statistically significant at certain time points ($P < 0.05$).

3.3 Effects of light intensity on *D. denneanum* photosynthetic light-response curves

Photosynthetic light-response curves of *D. denneanum* exhibited similar overall trends across treatments, although pronounced differences in P_n magnitude were observed (Figure 4). When photosynthetically active radiation (PAR) was $< 200 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, P_n rose rapidly as light intensity increased in all treatments. At higher PAR levels, P_n gradually declined, with the onset of decline occurring at approximately $700 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ under 20% light, $500 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ under 40% light, and $300 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ under 8% light.

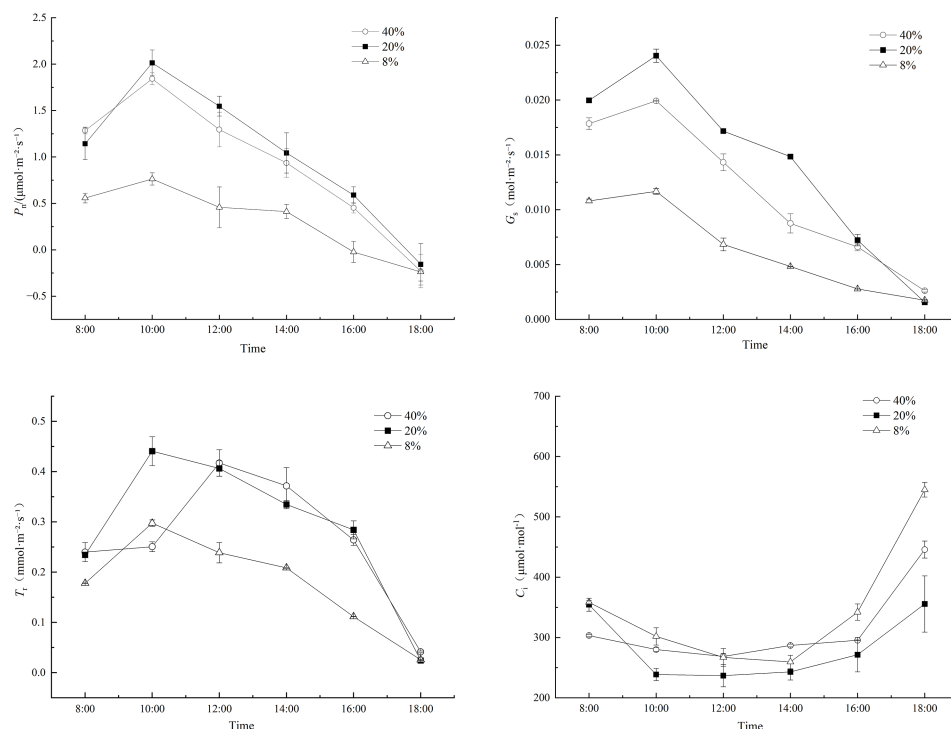
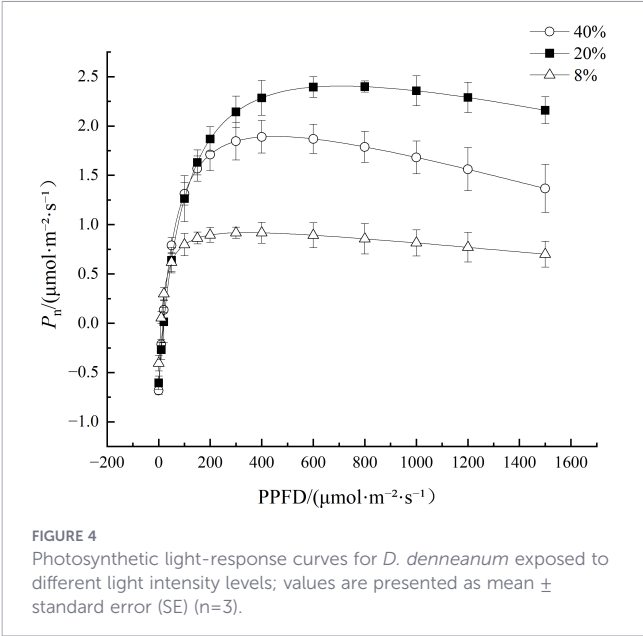


FIGURE 3

Diurnal variations of gas exchange parameters in *D. denneanum* exposed to different light intensity levels. A: net photosynthetic rate (P_n); B: stomatal conductance (G_s); C: transpiration rate (T_r); D: intercellular CO_2 concentration (C_i); values are presented as mean $\pm$ standard error (SE) ($n=3$).



The maximum net photosynthetic rate ($P_{\max}$) of *D. denneanum* was significantly higher under 20% light than under the other two light treatments ($P < 0.05$), indicating that 20% light supported the greatest maximum photosynthetic capacity. Compared with the 20% treatment, $P_{\max}$ decreased by 21.16% and 74.01% under 40% and 8% light, respectively. The light saturation point (LSP) also reached its highest value under 20% light, suggesting that plants under this treatment had a broader capacity to utilize increasing irradiance before reaching saturation. In contrast, apparent quantum yield (AQY) and dark respiration rate (R_d) increased with increasing growth light intensity and were highest under 40% light. The light compensation point (LCP) showed the same treatment order as LSP, with the maximum value observed under 20% light and the minimum under 8% light (Table 2).

3.4 Influence of light intensity on *D. denneanum* chlorophyll contents

Chl a, Chl b, and total Chl contents rose substantially as the light declined (Figure 5), with the highest values observed under 8% light and the lowest values under 40% light. The three light treatments differed significantly for these pigment parameters ($P < 0.05$), indicating enhanced chlorophyll accumulation under lower irradiance. In contrast, the Chl a/Chl b ratio was significantly higher under 20% light than under either 40% or 8% light ($P < 0.05$), suggesting differences in pigment composition among irradiance treatments.

3.5 Influence of light intensity on *D. denneanum* leaf microstructural features

3.5.1 Leaf anatomical structure

Leaves of *D. denneanum* consisted of upper and lower epidermal layers, mesophyll tissue, and vascular bundles. Microscopic observations showed that the mesophyll lacked clear differentiation into palisade and spongy tissues, and the vascular bundle sheath did not form a ring-like “Kranz” arrangement with surrounding mesophyll cells (Figure 6). Leaf thickness (LT) increased significantly with rising light intensity. Plants grown under 40% light had the greatest LT (297.93 μm), followed by those under 20% (286.50 μm) and 8% light (272.03 μm), with significant differences among all treatments ($P < 0.05$; Table 3). Mesophyll thickness (MT) showed a similar numerical trend (40% > 20% > 8%), but the differences among treatments were not statistically significant ($P > 0.05$). Upper epidermal thickness (UET) reached its maximum value under 20% light (38.00 μm), followed by 8% light (33.47 μm) and 40% light (29.70 μm), with significant differences among all treatments ($P < 0.05$). In contrast, lower epidermal thickness (LET) showed no significant differences among the three light treatments ($P > 0.05$; Table 3).

3.5.2 Leaf stomatal characteristics

Stomatal observations were conducted on both adaxial and abaxial leaf surfaces, and stomata were found only on the abaxial (lower) surface, indicating that the leaves of *D. denneanum* are hypostomatic (Figure 7). Stomatal density (SD) varied significantly across light treatments ($P < 0.05$), following the pattern: 40% > 20% > 8% light intensity (Table 4). The area of individual stomata (SA) under 40% light was significantly larger than that under 8% light. Stomatal width (SW) reached its highest value at 40% light (2.87 μm), which was markedly greater than values measured under 20% and 8% light. In contrast, stomatal length (SL) was comparable among these treatments ($P > 0.05$).

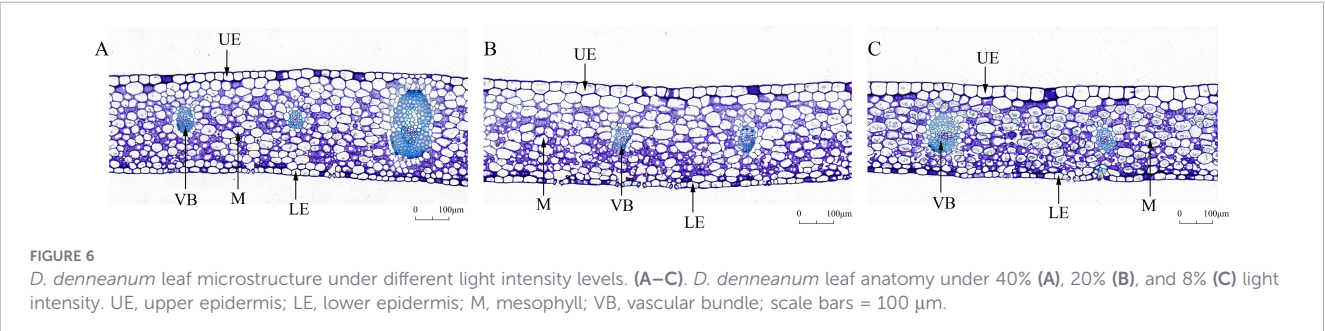
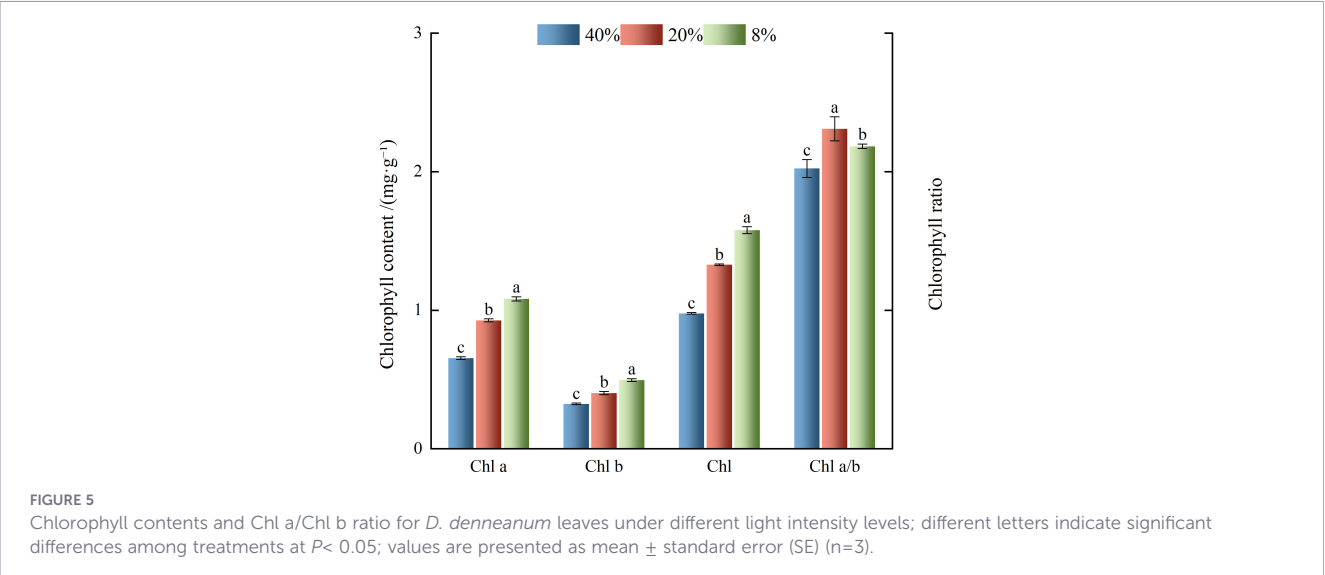
3.6 Influence of light intensities on medicinal constituents

Light intensity had marked effects on the accumulation of medicinal constituents in *D. denneanum* (Table 5). Polysaccharide (PS) content increased significantly with increasing light intensity, reaching its highest level under the 40% light treatment, which was substantially higher than that under the 8% treatment ($P < 0.05$). In contrast, alcohol-soluble extract (ASE) content showed the opposite

TABLE 2 *D. denneanum* photosynthetic parameters associated with varying levels of light intensity.

Relative intensity (%)	AQY (mol·mol ⁻¹)	$P_{\max}$ (μmol·m ⁻² ·s ⁻¹)	LSP (μmol·m ⁻² ·s ⁻¹)	LCP (μmol·m ⁻² ·s ⁻¹)	R_d (μmol·m ⁻² ·s ⁻¹)	R ²
40	0.055 $\pm$ 0.004 a	1.896 $\pm$ 0.164 b	455.12 $\pm$ 15.85 b	15.855 $\pm$ 0.371 b	0.681 $\pm$ 0.040 a	0.9862 $\pm$ 0.001
20	0.036 $\pm$ 0.001 b	2.405 $\pm$ 0.267 a	711.35 $\pm$ 5.80 a	18.805 $\pm$ 1.570 a	0.577 $\pm$ 0.059 b	0.9727 $\pm$ 0.017
8	0.025 $\pm$ 0.007 c	0.625 $\pm$ 0.170 c	283.081 $\pm$ 7.93 c	5.607 $\pm$ 0.994 c	0.121 $\pm$ 0.037 c	0.9526 $\pm$ 0.031

Different lowercase letters within a column indicate significant differences ($P < 0.05$); Values are presented as mean $\pm$ standard error (SE) (n = 3). AQY, apparent quantum yield; $P_{\max}$, maximum net photosynthetic rate; LSP, light saturation point; LCP, light compensation point; R_d , dark respiration rate; R², coefficient of determination.



trend, decreasing significantly as light intensity increased. Plants grown under 8% light accumulated the highest ASE content, which was markedly greater than that measured under 40% light. These contrasting patterns indicate that light intensity differentially affected polysaccharide accumulation and total alcohol-soluble extract content in *D. denneanum*.

3.7 Correlation analyses

Pearson correlation analysis using individual biological replicates across all three treatments ($n = 9$) showed significant associations among growth traits, photosynthetic parameters, chlorophyll content, leaf microstructural traits, and medicinal constituents (Figure 8). Among growth traits, BSD was positively correlated with LSP ($P < 0.001$), $P_{\max}$, LCP, and DAP ($P < 0.01$); CW was positively correlated with LSP ($P < 0.05$); and PH was positively

correlated with $P_{\max}$ ($P < 0.05$). Total Chl content was negatively correlated with LCP and DAP ($P < 0.001$) and with $P_{\max}$ ($P < 0.01$). Among leaf microstructural traits, LT was positively correlated with $P_{\max}$ ($P < 0.05$), while SD was positively correlated with AQY ($P < 0.001$), LCP and DAP ($P < 0.01$), and $P_{\max}$ ($P < 0.05$). For medicinal constituents, PS content was positively correlated with AQY ($P < 0.05$), whereas ASE content was negatively correlated with LCP, DAP, and SD ($P < 0.001$), as well as with AQY, $P_{\max}$, and SA ($P < 0.01$). These correlations suggest coordinated trait variation in *D. denneanum* across light treatments.

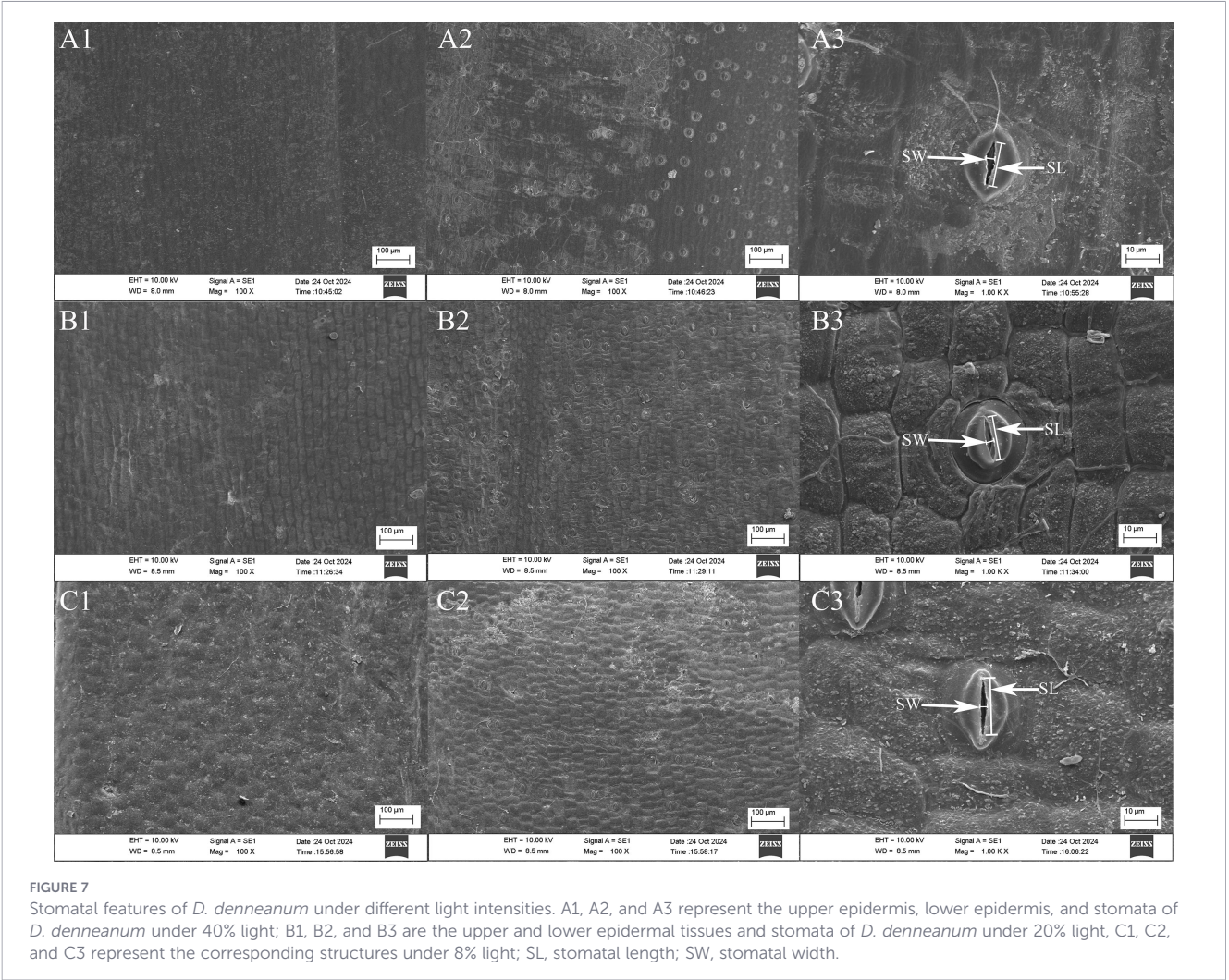
4 Discussion

Light availability is an important environmental factor influencing plant growth and photosynthetic performance (Munoz-Salas

TABLE 3 Leaf anatomical parameters of *D. denneanum* under different light intensity levels.

Relative intensity (%)	LT (μm)	MT (μm)	UET (μm)	LET (μm)
40	297.93 ± 4.41 a	251.90 ± 3.63 a	29.70 ± 1.84 c	17.07 ± 1.25 a
20	286.50 ± 2.18 b	246.60 ± 9.72 a	38.00 ± 1.61 a	17.23 ± 1.36 a
8	272.03 ± 6.92 c	238.87 ± 5.48 a	33.47 ± 1.69 b	17.03 ± 2.15 a

Different lowercase letters within a column represent significant differences ($P < 0.05$); Values are presented as mean ± standard error (SE) ($n = 3$). LT, leaf thickness; MT, mesophyll thickness; UET, upper epidermis thickness; LET, lower epidermis thickness.



et al., 2025). Insufficient irradiance can limit photosynthesis and reduce net carbon assimilation, thereby constraining plant development, whereas excessive light may damage the photosynthetic apparatus and impair physiological function (Tang et al., 2015; Yamori, 2016). In the present study, plants grown under 20% relative light intensity exhibited the most favorable vegetative growth, as reflected by greater increases in CW, BSD, and LA compared with the other light treatments. Contrary to the commonly observed shade-induced elongation response, exposure to relatively low light intensity (8%) did not significantly increase plant height, possibly because insufficient light energy limited photosynthate production for elongation growth and organ development. Under relatively higher light intensity (40%), plants maintained relatively high plant height, but overall growth performance was

lower than that under 20% light, which may be related to increased energy allocation to photoprotection rather than growth. Similar responses have been reported in many shade-tolerant or understory species, in which intermediate irradiance promotes more balanced growth performance (Poorter et al., 2009). Thus, moderate light availability may support coordinated growth and structural development in *D. denneanum* (Khan et al., 2025). Collectively, these findings highlight the sensitivity of *D. denneanum* to changes in light intensity and suggest that differences in growth performance may be closely linked to coordinated changes in photosynthetic capacity, morphology, and anatomical structure under different light conditions (Gommers et al., 2013).

The photosynthetic rate reflects the capacity of plants to convert absorbed light energy into organic compounds through carbon

TABLE 4 *D. denneanum* stomatal characteristics under varying light conditions.

Relative intensity (%)	SD (ind·mm ⁻²)	SL (µm)	SW (µm)	SA (µm ²)
40	167.33 ± 2.97 a	14.69 ± 0.59 a	2.87 ± 0.15 a	33.10 ± 0.69 a
20	133.10 ± 12.24 b	16.81 ± 1.02 a	2.35 ± 0.08 b	30.98 ± 1.42 ab
8	69.88 ± 6.93 c	15.97 ± 1.46 a	2.24 ± 0.11 b	28.05 ± 2.46 b

Different lowercase letters in the same column represent significant differences ($P < 0.05$); Values are presented as mean ± standard error (SE) (n = 3). SD, stomatal density; SL, stomatal length; SW, stomatal width; SA, stomatal area.

TABLE 5 Medicinal constituents content in *D. denneanum* under different light intensity levels.

Relative intensity (%)	Polysaccharides (%)	Alcohol-soluble extracts (%)
40	18.1 ± 0.8 a	14.6 ± 0.8 b
20	17.0 ± 0.9 ab	15.2 ± 0.3 ab
8	16.2 ± 0.4 b	19.4 ± 0.7 a

Different lowercase letters in the same column correspond to significant differences ($P < 0.05$); Values are presented as mean ± standard error (SE) ($n = 3$).

assimilation (Li et al., 2023b). In the present study, the diurnal variation in net photosynthetic rate (P_n) of *D. denneanum* exhibited a typical unimodal pattern, a response widely reported in shade-adapted plant species under relatively stable environmental conditions (Yamori et al., 2020). The daily average net photosynthetic rate and maximum net photosynthetic rate (P_{max}) both reached their highest values under the 20% light treatment, while the highest LSP under this treatment indicated a greater capacity to utilize increasing irradiance before light saturation. Further analysis showed relatively low LSP and LCP values across treatments, which are characteristic of shade-adapted species (Zhang et al., 2022). By contrast, AQY was highest under 40% light and lowest under 8% light, indicating that low-irradiance light-use efficiency did not follow the same pattern as P_{max} or daily photosynthesis. The low AQY under 8% light suggests that deep shading did not improve low-light-use efficiency under the tested conditions and may have limited carbon assimilation (Liu et al., 2023). Overall, although *D. denneanum* showed relatively modest photosynthetic potential, with P_n values generally below $2.5 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, the 20% light treatment provided the most favorable conditions for daily

carbon assimilation and maximum photosynthetic capacity. These results suggest that *D. denneanum* is physiologically adapted to intermediate-light environments and has limited tolerance to both relatively high and extremely low irradiance, consistent with the view that moderate shading can help shade-tolerant plants maintain stable physiological performance (Yan et al., 2025). Variations in photosynthetic performance among light treatments are likely associated with changes in the composition and concentration of photosynthetic pigments, which in turn influence plant morphology and function (Pappert et al., 2025). Chlorophyll plays a central role in light harvesting and is strongly affected by shading conditions (Tang et al., 2022). Shade-tolerant plants, or shade-acclimated leaves, typically exhibit a low Chl a/b ratio, often below 3, reflecting a relatively higher proportion of Chl b associated with light-harvesting capacity under low-light conditions (Lichtenthaler et al., 1981). Here, the Chl a/b ratio of *D. denneanum* consistently remained below 3 across treatments, which is consistent with characteristics commonly observed in shade-adapted species and aligns with the observed photosynthetic responses. Total chlorophyll content increased as light intensity

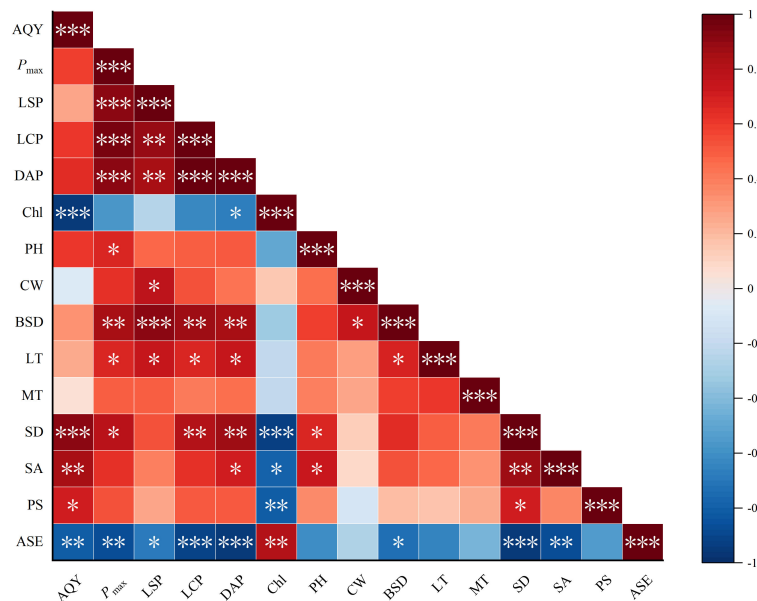


FIGURE 8 Heatmap illustrating correlations among chlorophyll content, growth traits, leaf microstructural parameters, medicinal constituents, and photosynthetic characteristics of *D. denneanum* under different light intensity levels using individual biological replicates from all treatments ($n = 9$). $*P < 0.05$; $**P < 0.01$; $***P < 0.001$. AQY, apparent quantum yield; P_{max} , maximum net photosynthetic rate; LSP, light saturation point; LCP, light compensation point; DAP, daily average net photosynthetic rate; Chl, total chlorophyll; PH, plant height; CW, canopy width increment; BSD, basal stem diameter increment; LT, Leaf thickness; MT, Mesophyll thickness; SD, stomatal density; SA, stomatal area; PS, polysaccharides; ASE, alcohol-soluble extracts.

decreased, with the highest values observed under 8% light. However, higher chlorophyll accumulation did not translate into greater photosynthetic carbon assimilation, as plants under 8% light showed the lowest $P_{\max}$, DAP, and AQY. This indicates that pigment accumulation under deep shade was insufficient to offset the limitation of low irradiance on photosynthetic performance. The significant negative correlations between total chlorophyll content and both LCP and DAP may therefore reflect coordinated trait variation across light treatments rather than a direct positive effect of chlorophyll accumulation on photosynthetic capacity. These findings indicate that increased light availability, such as that following canopy opening, may affect the physiological performance of *D. denneanum*. However, field studies under natural canopy gradients are still needed to determine whether similar responses occur in wild populations.

Leaves are among the most environmentally responsive and morphologically plastic plant organs, and their anatomical traits often vary with surrounding environmental conditions (Niinemets and Valladares, 2004; Guo et al., 2019). In this study, epidermal thickness was greatest under the 20% light intensity treatment, a trait that can reduce transpirational water loss and improve water-use efficiency (Guo et al., 2017). In contrast, leaves developed under 8% light intensity were thinner, which may reflect a shade-acclimation response that facilitates light capture under limited irradiance. However, this structural adjustment was insufficient to offset the strong limitation of deep shade on carbon assimilation, as indicated by the lower $P_{\max}$, DAP, and AQY under the 8% treatment. Previous studies have reported that mesophyll cells in *Dendrobium* species often lack clear differentiation into palisade and spongy tissues, forming relatively uniform parenchymatous tissue. In the present study, *D. denneanum* exhibited the same anatomical pattern, and no Kranz anatomy was observed. Such a homogeneous mesophyll structure is commonly observed in shade-adapted understory plants and may facilitate internal light distribution under low-light environments, suggesting that this trait may be associated with acclimation to shaded habitats (Rindiyastuti et al., 2018).

Stomatal density and stomatal aperture are critical determinants of stomatal conductance and gas exchange (Fanourakis et al., 2015). Similar light-dependent physiological responses have also been reported in other *Dendrobium* species. For example, light conditions have been shown to influence photosynthetic behavior, carbon metabolism, growth performance, and medicinal constituent accumulation in *Dendrobium* species, suggesting that light-dependent acclimation is a common feature in this genus, although the specific responses of stomatal traits, photosynthetic regulation, and metabolite allocation may differ among species (Cheng et al., 2019). In many plant species, stomatal density tends to decline as light intensity increases (Xiong et al., 2022). However, the present study revealed that both stomatal density and individual stomatal area in *D. denneanum* increased at higher levels of light. This atypical response may be associated with species-specific stomatal development under different light intensities. Under relatively

higher light conditions, increased stomatal density and stomatal area may enhance the potential capacity for CO_2 diffusion and transpiration regulation, thereby supporting gas exchange under stronger irradiance. It is possible that this response is linked to the species' high water requirements, suggesting that water limitation, including frequent drought events in its native habitat, may be an important factor contributing to its endangerment. Under such conditions, increased stomatal development may facilitate gas exchange, but this adjustment may also intensify water loss under high irradiance, thereby increasing physiological constraints on plant growth (Mano et al., 2020). The reduced stomatal density observed under the 8% light treatment may be related to developmental regulation under low-light conditions, leading to decreased stomatal formation. This reduction in stomatal density may lower stomatal conductance, potentially limiting CO_2 diffusion into the leaf and indirectly affecting net photosynthetic rate. Such coordinated responses are consistent with light-mediated developmental responses reported in previous studies (Li et al., 2021). The significant positive correlation between stomatal density and AQY across light treatments further suggests that stomatal traits may be associated with photosynthetic efficiency in *D. denneanum*.

Accumulation of polysaccharides is widely regarded as an important physiological strategy enabling plants to tolerate unfavorable environmental conditions (Li et al., 2023a). In this study, polysaccharide content increased with rising light intensity and reached its highest value under 40% light, whereas total alcohol-soluble extract content showed the opposite trend and was highest under 8% light. These contrasting responses indicate that the light conditions favorable for medicinal constituent accumulation differ from those favorable for vegetative growth and photosynthetic performance. Specifically, 20% light was most suitable for growth and photosynthetic performance, whereas 40% light favored polysaccharide accumulation and 8% light favored total alcohol-soluble extract accumulation. This pattern may be associated with changes in carbon allocation under different light regimes, with relatively higher light promoting assimilate supply for polysaccharide accumulation and lower light increasing the proportion of ethanol-soluble extractable constituents. Because alcohol-soluble extract content represents a total ethanol-soluble fraction, this response should not be interpreted as direct evidence for changes in specific compound classes, such as flavonoids, alkaloids, or bibenzyls. Exposure to higher light levels may impose physiological stress on *D. denneanum* and was associated with increased polysaccharide accumulation (Shi et al., 2022; Xu et al., 2024). Polysaccharides may be involved in metabolic responses under different light conditions (Fu et al., 2021). Conversely, under low-light conditions, total alcohol-soluble extract content increased markedly. Similar responses have been reported in other medicinal species, including *Bletilla striata* (Zhu et al., 2024) and *Carapichea ipecacuanha* (Moll Hüther et al., 2024), suggesting that extractable medicinal constituents may respond sensitively to light availability. Furthermore, the negative correlations between alcohol-soluble extract content and photosynthetic parameters such as $P_{\max}$ and AQY suggest an

association between photosynthetic performance and total ethanol-soluble extract accumulation in *D. denneanum* under different light regimes.

The limited number and range of light intensity treatments (8%, 20%, and 40% of full sunlight) may restrict the precision of conclusions regarding light acclimation. Future studies should consider expanding the light intensity range to include both lower and higher irradiance levels for a more comprehensive understanding.

5 Conclusions

This study demonstrates that varying light intensities affect growth, photosynthetic physiology, leaf microstructure, and medicinal constituent accumulation in *D. denneanum*, and reveals associations among these traits. Among the tested treatments, 20% relative light intensity provided the most favorable conditions for vegetative growth and photosynthetic performance. However, the optimal light condition for medicinal constituent accumulation varied with the target constituent, with relatively higher light favoring polysaccharide accumulation and lower light favoring alcohol-soluble extract accumulation. *D. denneanum* exhibits considerable phenotypic and physiological plasticity, enabling it to respond to changing light environments through coordinated adjustments in morphology, anatomy, and metabolism. These findings provide a useful reference for cultivation and *ex situ* conservation, suggesting that intermediate shade may promote vegetative growth and photosynthetic performance, whereas light regimes can be adjusted according to the target medicinal constituents. For *in situ* conservation, maintaining relatively stable canopy light conditions may help preserve suitable habitats for *D. denneanum*, although further field validation in natural populations is needed.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Author contributions

LW: Conceptualization, Data curation, Writing – original draft, Software, Visualization. ZY: Data curation, Visualization, Validation, Writing – review & editing. LP: Conceptualization, Validation, Supervision, Writing – review & editing. YW: Writing – review & editing, Software. ZC: Writing – review & editing, Validation. YL: Writing – review & editing, Formal analysis. QJ: Supervision, Writing – review & editing. XW: Writing – review & editing, Resources. SC: Conceptualization, Writing – review & editing, Funding acquisition. DZ: Writing – review & editing, Project administration.

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fphgy.2026.1806831/full#supplementary-material>

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