

Responses of Growth, Photosynthetic Physiology, Leaf Microstructural Properties, and Bioactive Compounds of *Dendrobium fimbriatum*, an Epiphytic Orchid, to Different Light Intensities

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Abstract

Light is a critical ecological factor influencing growth, development, and physiological regulation in epiphytic orchids. To elucidate the adaptive strategies of *Dendrobium fimbriatum* under different light environments, plants were subjected to three natural light intensity treatments (40%, 20%, and 8% of full sunlight). Growth traits, photosynthetic physiological parameters, leaf microstructural properties, and bioactive compound contents were measured to comprehensively evaluate the response patterns of this species along a light gradient. The results demonstrated that *D. fimbriatum* does not rely on adjustments of a single trait to cope with changes in light availability; instead, it maintains carbon balance and functional stability through coordinated regulation across growth, physiological, structural, and metabolic levels. Under moderate light conditions (20% light intensity), a high degree of coordination among traits was observed, enabling plants to sustain relatively high photosynthetic efficiency while effectively controlling respiratory consumption and metabolic costs, thereby maintaining elevated carbon assimilation capacity and growth performance. In contrast, under low or relatively high light conditions, plants adopted distinct adjustment pathways to cope with light stress, characterized by enhanced light-use efficiency under low light and strengthened photoprotection and defensive metabolic investment under higher light. These findings indicate that *D. fimbriatum* can flexibly adjust its growth and physiological strategies in response to changes in light conditions, allowing adaptation to the heterogeneous understory light environment. From the perspective of coordinated multi-trait responses, this study reveals the light adaptation pattern of *D. fimbriatum*, providing experimental evidence for a deeper understanding of the ecological adaptation mechanisms of epiphytic orchids and offering a theoretical basis for optimizing artificial cultivation practices and light management strategies for this species.

Introduction

Light is one of the most important regulatory factors governing photosynthesis, morphological development, carbon balance, and ecological adaptation in plants. Its intensity, spectral composition, and spatiotemporal variability directly determine light-use efficiency and survival strategies (Givnish, 1988). A large body of research has demonstrated that plant responses to light gradients involve multilevel regulation, including changes in key parameters such as photosynthetic pigment content, PSII quantum efficiency, non-photochemical quenching (NPQ), maximum net photosynthetic rate (P_{max}), light compensation point (LCP), and light saturation point (LSP) (Boardman, 1977; Demmig-Adams & Adams, 1992; Lambers & Oliveira, 2019). Under low-light conditions, plants typically exhibit classic shade-adaptation traits, including increased chlorophyll content, reduced LCP, expanded individual leaf area, and decreased leaf thickness. These adjustments enhance the capacity to capture limited light energy (Terashima et al., 2006; Walters, 2005). In contrast, high light may induce photoinhibition, leading to PSII damage and reactive oxygen species accumulation, while simultaneously activating photoprotective mechanisms such as thylakoid membrane reorganization, chlorophyll degradation, and enhanced NPQ (Long et al., 2003; Huang et al., 2019). In addition, light availability profoundly influences leaf anatomical

and microstructural properties, including mesophyll cell density, palisade tissue development, adaxial and abaxial epidermal thickness, as well as stomatal density and stomatal size (Hetherington & Woodward, 2003; Rindyastuti et al., 2018). Together, these coordinated physiological and structural adjustments constitute the basis of plant adaptation to different light environments. Therefore, investigating plant response mechanisms along light gradients is essential for understanding their ecological adaptation strategies.

Epiphytic plants inhabit forest canopies, tree trunks, or branches, where the light environment is highly heterogeneous. This heterogeneity arises from shading, sunflecks, and rapid fluctuations in irradiance caused by canopy disturbance, creating an exceptionally challenging habitat (Valladares et al., 2008). Within such highly variable light niches, epiphytes generally develop more sensitive and highly plastic light-acclimation strategies than terrestrial plants (Zotz, 1999). These strategies include increasing chlorophyll content, adjusting the chlorophyll a/b ratio, modifying chloroplast ultrastructure, enhancing PSII activity, and strengthening NPQ to mitigate transient high-light stress (Murchie & Lawson, 2013; Miller et al., 2017). Structural adaptation is also pronounced in epiphytic plants. Under low-light conditions, they tend to form thinner leaves, lower mesophyll density, and larger stomatal areas, thereby facilitating light penetration and CO₂ diffusion (Terashima et al., 2006; Zhang et al., 2018). Conversely, in high-light environments such as upper trunks or forest edges, epiphytes often exhibit increased leaf thickness, well-developed palisade tissues, and thickened epidermal layers, which reduce radiation damage and improve water-use efficiency (Franks & Beerling, 2009; Poorter et al., 2009). Because the roots and leaf surfaces of epiphytes are directly exposed to the external environment, their light-acclimation strategies are closely coupled with stomatal regulation. Stomatal density and morphology frequently adjust in response to light conditions to balance transpirational water loss and CO₂ assimilation (Hetherington & Woodward, 2003). The integrated effects of these physiological and structural regulatory mechanisms enable epiphytic plants to successfully establish in complex and fluctuating light environments. However, light-adaptation traits vary substantially among different genera and ecological types of epiphytes, highlighting the need for more targeted experimental studies focusing on specific taxonomic groups.

The genus *Dendrobium* (Orchidaceae) represents a group of exceptionally high economic value and is widely distributed in forests of Southeast Asia and southern China. Most *Dendrobium* species are typical epiphytes and exhibit pronounced sensitivity to changes in light availability (Hou et al., 2017). Previous studies have demonstrated that light intensity strongly influences growth and development, photosynthetic characteristics, antioxidant metabolism, and the accumulation of bioactive compounds in *Dendrobium* species, including polysaccharides, phenolic compounds, and flavonoids (Wu et al., 2014; Wang et al., 2025). For example, under moderate shading conditions, both *D. officinale* and *D. nobile* exhibit higher light-use efficiency and increased bioactive compound contents, whereas excessive irradiance often induces photoinhibition and reduces photosynthetic capacity (Zhang et al., 2014; Yang et al., 2022). However, substantial interspecific variation exists in light-acclimation strategies within the genus *Dendrobium*, which is closely associated with differences in microhabitat types, epiphytic

positions, leaf microstructural properties, and physiological regulation strategies. *D. fimbriatum* is an important species within the genus and is commonly distributed along forest edges, stream valleys, and the middle to lower portions of tree trunks. The light environment of its natural habitats is characterized by pronounced gradients and temporal instability, which may have driven the evolution of unique light-adaptation strategies. The Chinese Pharmacopoeia (Chinese Pharmacopoeia Commission, 2020) lists several *Dendrobium* species, including *D. fimbriatum*, as traditional medicinal materials, indicating their officially recognized medicinal value. The major bioactive constituents of *Dendrobium* species include polysaccharides, phenolics, flavonoids, and alkaloids, which confer diverse pharmacological activities such as immunomodulatory and antioxidant effects. At present, research on *D. fimbriatum* has mainly focused on germplasm resources, habitat distribution, and partial analyses of bioactive compounds. In contrast, systematic and quantitative investigations of its growth, photosynthetic physiology, leaf microstructural properties, and bioactive compound accumulation across light gradients remain limited. Moreover, comparing the light-adaptation characteristics of *D. fimbriatum* with those of other *Dendrobium* species reported in the literature may help to identify potential commonalities and species-specific differences. Therefore, studies on the light adaptation of *D. fimbriatum* are not only of theoretical significance but also of practical importance for artificial cultivation, commercial production, and conservation-oriented utilization.

To address these knowledge gaps, the present study systematically investigated the coordinated responses of photosynthetic performance, leaf microstructural properties, and bioactive compound accumulation in *D. fimbriatum* under different light intensities. The novelty of this study is reflected in three main aspects. First, by simulating its natural understory habitat, a light-intensity gradient spanning shade to semi-shade conditions was established, and the dynamic relationships between photosynthesis and irradiance were used to comprehensively analyze the coordinated responses of photosynthetic parameters and non-photosynthetic traits under different light regimes, providing new evidence for light-adaptation mechanisms in epiphytic orchids. Second, quantitative microstructural analyses were conducted to reveal the plasticity of leaf microstructure in response to changes in light intensity. Finally, by quantifying major bioactive compounds, including polysaccharides and ethanol-soluble extractives, this study elucidated the regulatory effects of light intensity on bioactive compound accumulation and revealed trade-offs in the allocation of photosynthetically derived carbon between growth and secondary metabolism. By clarifying these coordinated response mechanisms, the present study provides a scientific basis and quantifiable regulatory parameters for biomimetic cultivation and medicinal quality optimization of *D. fimbriatum*.

Methods

Study site and plant materials

The experiment was conducted in 2023 at the Guangxi Institute of Botany, Yanshan District, Guilin City, Guangxi Zhuang Autonomous Region, China (25°01' N, 110°17' E). The study area is located at an altitude of approximately 180 m and is characterized by a subtropical monsoon climate. The mean

annual air temperature is 18.8°C, with an average temperature of 8.3°C in the coldest month (January) and 28.3°C in the hottest month (July). The annual precipitation ranges from 1900 to 2000 mm, more than 70% of which occurs between April and August. The mean annual relative humidity is approximately 78%, and the average annual sunshine duration is about 1,500 h.

Healthy two-year-old plants of *D. fimbriatum* were used as experimental materials. Shade structures were constructed using black nylon shading nets to regulate natural light intensity and establish three target light levels corresponding to 40%, 20%, and 8% of full sunlight. Individual plants were grown separately in plastic pots with a diameter of 13 cm and a depth of 15 cm. The cultivation substrate consisted of a homogeneous mixture of bark, coconut coir, and perlite at a volume ratio of 3:1:1. Prior to the formal treatments, all seedlings (10 plants per treatment) were acclimated under 8% light intensity for one month. In early May, plants were transferred to their respective shading treatments and cultivated under standardized irrigation and fertilization management. After five months of light treatments, when morphological traits in each treatment group had stabilized, photosynthetic and physiological parameters were measured. Subsequently, leaves and pseudobulbs were harvested for analyses of chlorophyll content, leaf microstructural properties, and bioactive compound contents.

Measurement of growth indicators

To evaluate the growth responses of *D. fimbriatum* to different light environments, morphological traits were measured at the beginning of the experiment (early May) and at the end of the experiment (early October). Growth performance was quantified based on the increment values of plant height, stem diameter, and canopy length. Plant height and canopy length were measured using a measuring tape, while basal stem diameter was determined with a digital vernier caliper. Leaf expansion was assessed by scanning individual leaves and calculating single-leaf area using professional image analysis software. The number of newly emerged leaves was continuously recorded throughout the experimental period to quantify leaf production. All measurements were conducted with four replicates per treatment.

Measurement of diurnal variation in net photosynthetic rate

Net photosynthetic rate (P_n) was measured under natural environmental conditions using a LI-6400XT portable photosynthesis system (LI-COR, USA). Measurements were conducted in early October on clear days, from 08:00 to 18:00, at 2 h intervals. At each time point, three consecutive readings were recorded and averaged for subsequent analyses. Simultaneously, photosynthetically active radiation (PAR), ambient air temperature (T_a), and relative humidity (RH) were recorded under each light treatment (Fig. 1).

Measurement of light response curve

Light-response curves were determined using a LI-6400 portable photosynthesis system (LI-COR, USA). For each treatment, four plants were randomly selected, and one fully expanded mature leaves from the middle to upper portions of each plants was used for measurements. Prior to data collection, leaves

were pre-acclimated for 20 min under a photosynthetically active radiation (PAR) of $500 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ provided by the built-in red–blue LED light source to ensure that photosynthesis reached a steady state. Measurements were conducted under open gas-exchange conditions with a flow rate of 0.5 L min^{-1} . Leaf temperature was maintained at 28°C , and the CO_2 concentration was controlled at $400 \mu\text{mol mol}^{-1}$ using a CO_2 cylinder. The PAR gradient was set sequentially from high to low as follows: 1,500, 1,200, 1,000, 800, 600, 400, 300, 200, 150, 100, 50, 20, 10, and $0 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. All measurements were performed on clear days between 08:00 and 11:00, with each light level maintained for 120–180 s. Based on the light-response curve data, maximum net photosynthetic rate (P_{max}), apparent quantum yield (AQY), light saturation point (LSP), light compensation point (LCP), and dark respiration rate (R_d) were calculated.

Measurement of chlorophyll

After completion of the photosynthetic measurements, fresh leaf samples (0.2 g) were collected from individual plants. The leaves were finely cut and extracted with 95% ethanol for 24 h at 4°C in darkness. Absorbance values at 665 nm (A_{665}) and 649 nm (A_{649}) were measured using a PerkinElmer Lambda 35 UV–visible spectrophotometer (USA). Each treatment consisted of four biological replicates, with one plant per replicate. Chlorophyll a and b concentrations were calculated according to the equations $\text{Chl a} = 13.95 \times A_{665} - 6.88 \times A_{649}$ and $\text{Chl b} = 24.96 \times A_{649} - 7.32 \times A_{665}$, respectively. Total chlorophyll content was expressed on a fresh weight basis ($\text{mg}\cdot\text{g}^{-1} \text{ FW}$) and calculated as $\text{Chl} = (\text{C} \times \text{V} \times \text{N}) / \text{W}$, where C represents pigment concentration ($\text{mg}\cdot\text{L}^{-1}$), V is the extraction volume (mL), N is the dilution factor, and W is the fresh weight of leaf tissue (g).

Measurement of leaf microstructural

Leaf anatomical structure was examined using leaves collected from *D. fimbriatum* plants after completion of photosynthetic measurements. For each treatment, one leaf per plant was sampled from four plants, ensuring consistency in orientation and maturity with those used for photosynthetic measurements. After sampling, leaves were cut into small segments ($5 \text{ mm} \times 5 \text{ mm}$) along the midrib direction and immediately fixed in FAA solution (formaldehyde–acetic acid–ethanol) for 24 h. The fixed samples were dehydrated through a graded ethanol series, with each step lasting 2 h, followed by clearing with xylene and paraffin embedding. Embedded samples were sectioned into continuous slices with a thickness of $8 \mu\text{m}$ using a rotary microtome. Sections were stained with toluidine blue, mounted with neutral balsam, and then observed and photographed under a light microscope. Leaf thickness, mesophyll thickness, and other microstructural parameters were quantified using CaseViewer image analysis software, with measurements taken from 10 randomly selected fields of view per sample.

Leaf epidermal characteristics were also analyzed using leaves collected after photosynthetic measurements. For each treatment, one healthy, fully expanded mature leaf was sampled from each of four plants. Leaf segments ($4 \text{ mm} \times 4 \text{ mm}$) were excised along the vein direction and fixed in 2.5% glutaraldehyde prepared in 0.1 mol L^{-1} phosphate buffer (pH 7.2) at 4°C for 24 h. Samples were then dehydrated through a graded ethanol series of 30%, 50%, 70%, 90%, and 100%, with each step lasting 30

min. After dehydration, samples were dried using a critical point dryer and sputter-coated with gold for 90 s. The adaxial and abaxial epidermal structures were observed using a scanning electron microscope (ZEISS EVO18), and five randomly selected fields of view per sample were photographed. Stomatal characteristics were analyzed using Image-Pro Plus 6.0 software, including stomatal density (number of stomata per unit leaf area), stomatal length (major axis), and stomatal width (minor axis). Individual stomatal area was calculated assuming an elliptical shape according to the formula $S = \pi ab/4$, where a and b represent the lengths of the major and minor axes, respectively.

Measurement of bioactive compounds

To quantitatively analyze bioactive compounds, pseudobulbs of *D. fimbriatum* were collected, dried to constant weight in a drying oven at 60°C, and then ground into fine powder for chemical analyses. The content of ethanol-soluble extractives was determined using a cold maceration method. This procedure was adapted from the Chinese Pharmacopoeia (Chinese Pharmacopoeia Commission, 2020) with modifications based on Xing et al. (2013). Ethanol at an appropriate concentration was used as the extraction solvent, and the extractive yield was calculated based on the mass difference of samples before and after extraction. Polysaccharide content was determined using a hot extraction method, followed by quantification using the phenol–sulfuric acid assay. Absorbance was measured at a specific wavelength, and a calibration curve was established using glucose as the standard. Four replicates were conducted for each treatment.

Data analyses

Light response curves were fitted using a modified rectangular hyperbola model (Ruan et al., 2022):

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

where α is the initial slope of the light response curve, β and γ are coefficients, I is the photosynthetic photon flux density (PPFD), and R_d is the dark respiration rate.

AQY was calculated as the slope of the linear regression portion of the curve where PPFD < 100 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. $P_{\max}$, LSP, and LCP were derived from the following equations:

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

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

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

Raw data were organized and preprocessed using Microsoft Excel 2019. Statistical analyses were performed using SPSS Statistics 27. One-way analysis of variance (ANOVA) was applied to evaluate the effects of different light treatments on each parameter, and when significant differences were detected ($p < 0.05$), Duncan's multiple range test was conducted to compare means among treatments. Pearson's bivariate correlation analysis was used to examine the relationships among photosynthetic physiological parameters, leaf microstructural properties, and bioactive compound contents. Graphical visualization and curve fitting were performed using Origin 2021 software.

Results

Growth responses

Significant differences in growth performance of *D. fimbriatum* were observed among the different light treatments across multiple traits (Table 1). Overall, plants grown under 40% light intensity exhibited significantly lower values for most growth parameters compared with those under 20% light intensity, although these values were generally higher than those observed under 8% light intensity. Specifically, increments in plant height (PH), canopy width (CW), and leaf area (LA) under 40% light were all significantly lower than those under 20% light, indicating that relatively high light intensity imposed certain constraints on overall plant growth. Plants exposed to 20% light intensity showed the most favorable performance in key indicators reflecting biomass accumulation. Both canopy width (CW) and basal stem diameter (BSD) reached their highest values under this treatment and were significantly greater than those under the other light regimes, suggesting that moderate light conditions were more conducive to lateral growth and the development of structural tissues. In contrast, under 8% light intensity, PH increment was significantly higher than that under 40% light, whereas increments in BSD and LA were markedly reduced. These results indicate that under low-light conditions, plants tend to enhance vertical elongation to improve light acquisition, while structural growth and leaf area expansion are constrained (Fig. 2).

Table 1
Growth increment of *D. fimbriatum* under different light intensities.

Relative intensity (%)	PH(cm)	CW(cm)	BSD(mm)	LA(cm)	NOL
40	1.583 ± 0.055 ^c	4.020 ± 0.087 ^b	1.36 ± 0.050 ^b	0.800 ± 0.033 ^b	4.33 ± 0.58 ^b
20	4.203 ± 0.137 ^a	5.040 ± 0.115 ^a	1.927 ± 0.067 ^a	2.003 ± 0.085 ^a	6.67 ± 0.58 ^a
8	3.383 ± 0.138 ^b	2.020 ± 0.091 ^c	0.450 ± 0.031 ^c	0.703 ± 0.037 ^b	3.67 ± 0.58 ^b

Diurnal Variation in Net Photosynthetic Rate

The diurnal variation in net photosynthetic rate (P_n) of *D. fimbriatum* under different light intensities is shown in Fig. 3. Under the 40% light treatment, P_n exhibited a typical unimodal pattern, increasing from 08:00 and maintaining relatively high values between 10:00 and 12:00 ($1.367\text{--}1.451\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), followed by a continuous decline without a pronounced secondary peak. A similar diurnal trend was observed under the 20% light treatment; however, this treatment exhibited the highest daily mean net photosynthetic rate. P_n increased rapidly after 08:00, reached its maximum at 10:00, and then decreased sharply between 12:00 and 14:00, followed by a sustained decline during the remaining measurement period. In contrast, plants grown under 8% light intensity showed a markedly lower P_n throughout the day, with both peak and daily mean values being the lowest among all treatments. Quantitative analysis indicated that the daily photosynthetic assimilation (DPA) ranked as follows: 20% light intensity ($1.005\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) > 40% light intensity ($0.857\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) > 8% light intensity ($0.323\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), suggesting that moderate light conditions were most favorable for maintaining higher photosynthetic carbon assimilation in *D. fimbriatum*.

Light response curves

With increasing light intensity, the parameters derived from light response curves exhibited pronounced differences among treatments (Fig. 4). Under the 40% light treatment, the $P_{\max}$ was $2.005\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, while the LSP ($427.79\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), LCP ($8.88\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), and R_d ($0.471\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) were the highest among all treatments. Under the 20% light treatment, $P_{\max}$ reached $3.340\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, which was significantly higher than that observed under the other light conditions. Meanwhile, the AQY was $0.076\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, indicating that plants grown under moderate light maintained both a strong capacity for low-light utilization and high photosynthetic potential. In addition, the LSP and LCP under this treatment were $390.43\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and $4.209\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively. In contrast, under the 8% light treatment, $P_{\max}$ decreased to $1.164\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, and the LSP ($250.82\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), LCP ($2.666\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), and R_d ($0.471\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) were the lowest among all treatments.

$2 \cdot s^{-1}$), and R_d ($0.182 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) were all the lowest among treatments. However, AQY remained relatively high ($0.078 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$), suggesting an enhanced efficiency of light energy utilization under low-light conditions (Table 2).

Table 2
Light response curves parameters of *D. fimbriatum* under different light intensities.

Relative intensity (%)	AQY ($\text{mol} \cdot \text{mol}^{-1}$)	P_{max} ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)	LSP ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)	LCP ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)	R_d ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)
40	0.061 ± 0.005^b	2.047 ± 0.167^b	420.52 ± 38.65^b	9.359 ± 0.950^a	0.472 ± 0.002^a
20	0.094 ± 0.007^a	2.493 ± 0.214^a	483.85 ± 48.06^a	7.237 ± 0.363^b	$0.535 \pm .038^a$
8	0.070 ± 0.007^{ab}	1.279 ± 0.142^c	302.15 ± 33.23^c	6.288 ± 0.790^b	0.322 ± 0.025^b

Chlorophyll content

The effects of different light intensities on leaf chlorophyll content in *D. fimbriatum* are shown in Fig. 5. Overall, the contents of chlorophyll a (Chl a), chlorophyll b (Chl b), and total chlorophyll increased significantly with decreasing light intensity. Among the treatments, plants grown under 8% light exhibited the highest levels of Chl a, Chl b, and total chlorophyll, all of which were significantly higher than those observed under 20% and 40% light conditions. This pattern indicates that under low-light conditions, *D. fimbriatum* enhances chlorophyll synthesis and accumulation to improve light-harvesting capacity and adapt to reduced irradiance. In contrast, the lowest chlorophyll contents were observed under the 40% light treatment, which may be associated with a downregulation of chlorophyll accumulation under relatively high light conditions to limit excess light absorption and mitigate the risk of photoinhibition. The chlorophyll a/b ratio was significantly higher under the 20% light treatment than under the 8% and 40% light treatments, suggesting that under moderate light conditions, plants optimize the relative proportions of different chlorophyll components to improve the structural organization of the photosynthetic apparatus and enhance photosynthetic efficiency.

Leaf anatomical characteristics

The leaf anatomical traits of *D. fimbriatum* showed significant differences under different light intensity treatments (Table 3; Fig. 6). Under 40% relative light intensity, both leaf thickness (LT) and mesophyll thickness (MT) remained at relatively high levels, indicating a well-developed photosynthetic structural configuration. At 20% light intensity, LT was comparable to that under 40% light; however, the thickness of the upper epidermis (UET) and lower epidermis (LET) increased significantly, suggesting adaptive modification of epidermal tissues under moderate light conditions. When light intensity was further

reduced to 8%, LT and MT decreased markedly, accompanied by a reduction in UET and LET, resulting in a simplified leaf anatomical structure. These results indicate that *D. fimbriatum* adjusts its leaf anatomical traits along the light gradient, reflecting pronounced structural plasticity in response to varying light environments.

Table 3
Leaf anatomical parameters of *D. fimbriatum* under different light intensities.

Relative intensity (%)	LT (μm)	MT (μm)	UET (μm)	LET (μm)
40	273.30 ± 5.48 ^a	170.67 ± 6.31 ^a	72.13 ± 3.99 ^{ab}	30.50 ± 2.27 ^b
20	278.27 ± 3.41 ^a	157.30 ± 1.25 ^b	81.50 ± 3.68 ^a	39.47 ± 0.45 ^a
8	215.10 ± 10.16 ^b	123.97 ± 4.07 ^c	61.70 ± 8.56 ^b	29.43 ± 2.43 ^b

Leaf epidermal characteristics

Stomatal characteristics also showed significant variation in response to different light intensities (Fig. 7). Under 40% light intensity, stomatal density was highest, whereas the area of individual stomata was the smallest. In contrast, plants grown under 8% light intensity exhibited a significantly lower stomatal density (SD) but a markedly larger stomatal area (SA). Stomatal density and stomatal area under 20% light intensity were intermediate between those observed under 40% and 8% light conditions. No significant differences were detected in stomatal length (SL) among the three light treatments (Table 4); however, stomatal width (SW) increased significantly under low-light conditions. These results indicate that higher light availability enhances gas exchange capacity by increasing stomatal density while reducing individual stomatal size, whereas low-light conditions favor an alternative strategy characterized by reduced stomatal density and enlarged stomatal size to cope with light limitation.

Table 4
Leaf epidermal parameters of *D. fimbriatum* under different light intensities.

Relative intensity (%)	SD (ind.mm ⁻²)	SL (μm)	SW (μm)	SA (pores·mm ⁻²)
40	75.79 ± 4.10 ^a	19.44 ± 2.99 ^a	2.89 ± 0.32 ^b	43.89 ± 6.57 ^c
20	63.29 ± 4.75 ^b	19.99 ± 3.06 ^a	3.74 ± 0.24 ^b	62.44 ± 6.89 ^b
8	29.34 ± 1.87 ^c	21.27 ± 1.49 ^a	5.59 ± 1.27 ^a	88.63 ± 9.84 ^a

Bioactive Compounds

Different light intensity treatments significantly affected the contents of bioactive compounds in *D. fimbriatum* (Table 5). Overall, both polysaccharide (PS) and alcohol-soluble extract (ASE) contents exhibited similar response patterns along the light intensity gradient. The highest levels of these two components were observed under 40% light intensity, intermediate values occurred under 20% light intensity, and the lowest contents were detected under 8% light intensity.

Table 5
Bioactive compounds contents of *D. fimbriatum* under different light intensities.

Relative intensity (%)	Polysaccharide(%)	Alcohol-Soluble Extract(%)
40	15.4 ± 1.7 ^a	15.8 ± 1.4 ^a
20	13.5 ± 1.3 ^{ab}	14.2 ± 1.3 ^{ab}
8	11.1 ± 0.5 ^b	12.6 ± 1.1 ^b

Correlation analysis

Correlation analysis (Fig. 8) revealed significant associations among plant growth traits, leaf microstructural properties, bioactive compounds, and photosynthetic parameters. Regarding growth traits, crown width (CW) and basal stem diameter (BSD) were significantly and positively correlated with P_{max} , LSP, and DPA ($p < 0.05$). In contrast, plant height increment (PH) showed a significant positive correlation with AQY ($p < 0.05$) and a significant negative correlation with the LCP ($p < 0.05$). With respect to chlorophyll traits, total chlorophyll content (Chl) was significantly positively correlated with AQY ($p < 0.05$) but negatively correlated with LSP, LCP, and DPA ($p < 0.05$). The Chl a/b exhibited significant positive correlations with P_{max} , LSP, and DPA ($p < 0.05$). In terms of leaf structural traits, LT, MT, and SD were significantly and positively correlated with LSP, LCP, and DPA ($p < 0.05$), whereas SA showed significant negative correlations with these parameters ($p < 0.05$). Furthermore, the contents of PS and ASE exhibited varying degrees of positive correlations with LSP, LCP, and DPA, but both were significantly negatively correlated with AQY ($p < 0.05$).

Discussion

Growth responses

Light availability is a key ecological factor shaping the growth strategies of epiphytic orchids, which typically inhabit forest canopies where seasonal and microscale environmental conditions fluctuate markedly, making their growth highly dependent on light. In the present study, *D. fimbriatum* exhibited pronounced growth acclimation responses under different light intensities, with overall growth performance being optimal under 20% relative light intensity. Under this condition, increments in PH, CW,

and NOL were significantly higher than those under the other light treatments, indicating that moderate light availability strongly promotes vegetative growth. Such moderate irradiance likely supports sufficient photosynthetic carbon assimilation while avoiding excessive metabolic costs associated with photoprotective mechanisms, thereby improving carbon allocation efficiency and maintaining a balance between photosynthesis and respiration (Lichtenthaler et al., 2007). Similar growth patterns under moderate light conditions have been reported in other epiphytic orchids, including *D. officinale* (Sun et al., 2015), *Phalaenopsis* spp. (Paradiso & De Pascale, 2014), and *Cattleya* spp. (Ramos et al., 2024). In contrast, under 8% light intensity, although PH increment was relatively high, CW and BSD growth were significantly constrained, suggesting that assimilate allocation was preferentially directed toward shoot elongation to enhance light capture, a typical shade-avoidance strategy observed under low-light environments (Franklin, 2008; Gommers et al., 2013). Comparable elongation-oriented growth responses have been documented in orchid species such as *Isotria medeoloides* (Whigham et al., 2021) and *Cattleya walkeriana* (Rodrigues et al., 2013), and are considered effective survival strategies under diffuse understory light conditions. Under 40% light intensity, *D. fimbriatum* exhibited relatively reduced growth, particularly in PH and leaf LA increments, indicating that excessive irradiance may impose metabolic costs and shift resource allocation toward photoprotective and defensive processes rather than biomass accumulation (Niyogi, 1999; Li et al., 2009). Overall, *D. fimbriatum* displayed a clear growth response along the light intensity gradient, with optimal growth and balanced resource allocation under 20% light intensity, whereas growth strategies under 8% and 40% light intensities shifted toward shade-avoidance and defense-oriented modes, respectively (Guo et al., 2025; Wang et al., 2025).

Photosynthetic characteristics

The photosynthetic performance of *D. fimbriatum* exhibited a clear adaptive gradient in response to light intensity, indicating that this species can strategically regulate its carbon assimilation capacity under different irradiance conditions. The highest DPA rate was observed under the 20% light treatment, characterized by a rapid increase in photosynthetic rate in the morning, the formation of a pronounced peak, and a moderate midday decline while maintaining relatively high values throughout the afternoon, reflecting strong diurnal stability of carbon assimilation. Such diurnal patterns are commonly reported in epiphytic orchids (Silvera et al., 2009) and are generally considered to represent an effective balance between light-driven carbon gain and photoprotective regulation. The transient midday depression of photosynthesis observed here does not simply indicate stress, but rather reflects an important photophysiological adjustment that prevents excessive excitation energy accumulation under high irradiance, thereby reducing the risk of photoinhibition and enabling sustained carbon assimilation over the daily cycle (Ruban et al., 2016; Michelberger et al., 2025). This regulatory feature was particularly evident under the 20% light treatment, where neither persistent photoinhibition nor a marked decline in carbon assimilation occurred, suggesting that this irradiance level may be close to the photosynthetic optimum for *D. fimbriatum*. Under the 40% light treatment, although the LSP was relatively high, the $P_{\max}$ did not increase accordingly, and the R_d was elevated, indicating that under higher irradiance *D. fimbriatum* does not enhance photosynthetic potential to achieve greater carbon gain but instead incurs

higher respiratory and photoprotective costs. Previous studies have shown that excessive light can increase respiratory consumption, promote reactive oxygen species accumulation, and activate photoprotective pathways such as non-photochemical quenching (Sharma et al., 2023), and because epiphytic plants are frequently exposed to transient high-light conditions caused by canopy gaps and sunflecks, they often rely on dynamic photoprotective mechanisms to cope with rapid fluctuations in irradiance (Coubier & Pierik, 2019), albeit at the expense of carbon assimilation efficiency, which is consistent with the constrained net photosynthetic performance observed under the 40% light treatment in this study. In contrast, the 8% light treatment was characterized by a relatively high AQY together with low LCP and $P_{\max}$, indicating that *D. fimbriatum* can maintain a positive carbon balance under low-light conditions but has limited capacity to increase photosynthetic rates as irradiance increases. Shade tolerance in orchids is commonly associated with conservative carbon-use strategies that reduce metabolic costs while enhancing photon-use efficiency to cope with prolonged low-light environments (Cameron et al., 2009; Zhang et al., 2024); however, the inherently low photosynthetically active radiation under such conditions restricts overall carbon accumulation, which in this study was reflected by significantly constrained growth and biomass accumulation under the 8% light treatment. Overall, *D. fimbriatum* exhibited optimal integrated photosynthetic performance under the 20% light treatment, where carbon assimilation could be maintained at relatively high levels throughout the day while photoinhibition risk and respiratory costs remained comparatively low, a pattern also reported in *D. officinale* (Zhang et al., 2014), *Cymbidium* orchids (Kim et al., 2015), and other epiphytic orchids, suggesting that moderate light intensity represents a key ecological condition for efficient carbon assimilation in epiphytic orchids.

Chlorophyll characteristics

Changes in chlorophyll composition under different light conditions reflect the fine-scale trade-off between light harvesting and photoprotection in *D. fimbriatum*. The present results showed that chlorophyll a, chlorophyll b, and total chlorophyll contents increased significantly with decreasing light intensity, reaching the highest levels under 8% light and the lowest levels under 40% light, whereas the chlorophyll a/b ratio was significantly higher under 20% light than under either 8% or 40% light conditions. The pronounced increase in total chlorophyll content under 8% light represents a typical shade-adaptive response, whereby plants compensate for limited photon availability by increasing investment in light-harvesting pigments. This strategy is consistent with the well-documented responses of shade-tolerant species growing under low irradiance, where enhanced pigment accumulation expands light absorption capacity and improves photon capture efficiency per unit light (Valladares & Niinemets, 2008; Jin et al., 2016). In particular, the relative increase in chlorophyll b contributes to the enlargement of the light-harvesting antenna and broadens the absorption spectrum toward diffuse and low-intensity light, a trait that is especially advantageous for epiphytic orchids inhabiting shaded forest understories and lower trunk strata (De la Rosa-Manzano et al., 2015; Yang et al., 2021). In contrast, under 40% light intensity, total chlorophyll content was markedly reduced, indicating that *D. fimbriatum* downregulated pigment levels under relatively high irradiance to limit excessive energy input and alleviate excitation pressure on PSII. Previous studies have shown that high-light environments often promote chlorophyll

degradation and activate the xanthophyll cycle, thereby restricting light harvesting and enhancing non-photochemical energy dissipation (Barták et al., 2004; Shomali et al., 2023). The reduction in chlorophyll content observed under 40% light in this study is consistent with the increased respiratory costs and lower net photosynthetic efficiency reported for this treatment, suggesting a shift toward defensive regulation rather than enhanced carbon gain. Notably, a distinct pigment adjustment strategy was observed under 20% light intensity: although total chlorophyll content was relatively low, the chlorophyll a/b ratio was significantly elevated. This pattern indicates that under moderate light conditions, *D. fimbriatum* does not rely on increasing pigment abundance to enhance light capture, but instead optimizes pigment composition to improve the balance between reaction centers and light-harvesting antennae. A higher chlorophyll a/b ratio generally reflects a reduced antenna size and a higher proportion of reaction centers, which favors efficient electron transport and carbon assimilation when light supply is sufficient but does not induce photoinhibition. Similar pigment allocation strategies have been reported in several epiphytic orchids, including *Phalaenopsis* and *Dendrobium* species grown under moderate irradiance, where improvements in photosynthetic performance are achieved primarily through optimization of pigment composition and photosystem structure rather than increases in total chlorophyll content (Ceusters et al., 2019; Kim et al., 2025). This adaptive strategy is likely closely linked to the ecological background of epiphytic orchids, which naturally experience dynamic sunfleck environments in forest margins and lower canopy layers.

Leaf microstructural

The anatomical and epidermal responses of *D. fimbriatum* leaves to varying light intensities further demonstrate the structural plasticity that enables adaptation to different light environments. In this study, LT, MT, and epidermal thickness were higher under 40% and 20% light conditions than under 8% light, indicating that higher irradiance promotes the development of leaf tissue thickness. Thicker leaves and mesophyll layers enhance internal light scattering, extend photon path length within the leaf, and facilitate CO₂ diffusion to photosynthetic tissues (Niinemets, 1999; Dosanjós et al., 2024; Retta et al., 2024). The increased epidermal thickness under high-light conditions may provide mechanical support and improve desiccation tolerance, which is especially advantageous for epiphytic orchids exposed to variable microclimates on trunks and within the canopy. In contrast, reduced LT and MT under 8% light minimizes construction costs while maintaining sufficient light interception under low irradiance (Terashima et al., 2011; Tholen et al., 2012).

Stomatal traits also varied with light intensity, reflecting differential gas exchange demands. Under 40% light, SD was highest while SA was smallest, a configuration that enhances the responsiveness and control of leaf gas exchange while minimizing water loss under high evaporative demand (Casson & Gray, 2008; Casson & Hetherington, 2010). Conversely, under 8% light, lower SD combined with larger SA likely facilitates CO₂ uptake, particularly when carbon assimilation is primarily limited by irradiance rather than stomatal conductance (Flexas et al., 2004). Intermediate values observed under 20% light suggest that this irradiance represents an optimal stomatal structural state, where anatomical investment and stomatal regulation support efficient photosynthesis without incurring excessive structural or protective

costs. Together, these anatomical and stomatal adjustments indicate that *D. fimbriatum* maintains carbon balance and water-use efficiency through coordinated modifications in leaf structure and stomatal patterning, enabling adaptation to fluctuating light conditions characteristic of epiphytic habitats.

Bioactive Compound Responses

The contents of bioactive compounds in *D. fimbriatum* were highly sensitive to changes in light intensity. As relative irradiance increased from 8% to 40%, both PS and ASE levels exhibited an upward trend, reaching their maximum under 40% light, with 20% light yielding intermediate levels and 8% light the lowest. This pattern indicates that under low-light conditions, the limited supply of photosynthetic carbon restricts the synthesis of polysaccharides and alcohol-soluble secondary metabolites, whereas increased irradiance enhances net carbon assimilation, providing more carbon and energy for bioactive compound production. Interestingly, although plant growth under 40% light was lower than under 20% light, the accumulation of polysaccharides and alcohol-soluble extracts was higher, suggesting that high irradiance may redirect part of the photosynthetic carbon toward storage or defense-related metabolic pathways to mitigate potential photoinhibition and oxidative stress. This growth–metabolism allocation trade-off demonstrates that *D. fimbriatum* under high-light conditions prioritizes the accumulation of bioactive compounds while maintaining basic growth, whereas under the optimal 20% light condition, carbon allocation favors biomass formation.

Correlation Analysis

The correlation heatmap revealed multiple significant linkages between photosynthetic parameters and growth, leaf microstructural properties, and bioactive compound contents in *D. fimbriatum*. Leaf anatomical features exerted a strong influence on photosynthetic performance, as evidenced by the significant positive correlations between LT and key photosynthetic indicators ($P_{\max}$ and AQY), suggesting that structural optimization enhances photosynthetic capacity. Under low-light conditions, such as 8% irradiance, structural modifications in the leaf likely facilitate light capture, providing sufficient energy to support growth, as reflected by increased PH and CW. SD also exhibited strong positive correlations with $P_{\max}$, LCP, LSP, and DPA, indicating that higher SD may improve CO₂ uptake and gas exchange efficiency, thereby enhancing overall photosynthetic performance. Additionally, the relationships between bioactive compounds, including PS and ASE, and photosynthetic parameters suggest that under higher irradiance (e.g., 40% light), the accumulation of secondary metabolites is positively associated with enhanced $P_{\max}$ and DPA, likely reflecting the plant's allocation of carbon toward storage and defense-related metabolic pathways under high-light conditions. These results collectively indicate that *D. fimbriatum* coordinates anatomical, physiological, and metabolic traits to optimize carbon assimilation and growth across variable light environments.

Conclusions

Integration of growth, photosynthetic physiology, leaf microstructure, and bioactive compound under different light intensities indicates that *D. fimbriatum* exhibits pronounced adaptive responses through the coordinated regulation of multiple hierarchical traits. Among the three light treatments, plants under 20% irradiance showed significant increases in PH, CW, BSD, and LA, while maintaining relatively high net photosynthetic rates and light-use efficiency. Chl composition and photosystem parameter configurations were also well-coordinated, suggesting that this light level supports a balanced state between carbon assimilation capacity, resource allocation, and metabolic costs. In contrast, under 8% irradiance, plants displayed typical shade-adaptive traits, including increased Chl content, lowered LCP, and enhanced AQY to improve light capture under limiting conditions; although PH was prominent, maximum net photosynthetic rates and overall carbon accumulation were restricted, and the contents of PS and ASE were comparatively low, indicating that low-light environments primarily sustain basic carbon balance while limiting further growth and secondary metabolite investment. Under 40% irradiance, Chl content decreased and R_d increased, while LT and SD were elevated, reflecting a regulatory strategy focused on reducing light capture and enhancing photoprotection. Simultaneously, PS and ASE extract contents were significantly higher, suggesting preferential allocation of photosynthates toward storage or defense-related metabolic pathways rather than growth. Overall, *D. fimbriatum* does not rely on a single trait to respond to varying light conditions; rather, it maintains carbon balance and functional stability through the coordinated adjustment of growth, physiological performance, structural traits, and metabolic allocation, with the greatest trait coordination observed under 20% irradiance.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Availability of data and materials

All data generated or analyzed during this study are included in this published article.

Competing Interests

The authors declare no conflicts of interest.

Clinical trial number

Not applicable.

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Authors contributions

Conceptualization, Z.Y., S.C. and L.P.; data curation, Z.Y. and L.W.; formal analysis, L.P.; investigation, L.W.; methodology, Z.C. and J.T.; software, L.W. and Z.Y.; supervision, J.T., Y.W., Z.D. and X.W.; writing—original draft, T.D.; writing—review and editing, Z.Y. and S.C. All authors have read and agreed to the published version of the manuscript.

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Not applicable.

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Figures

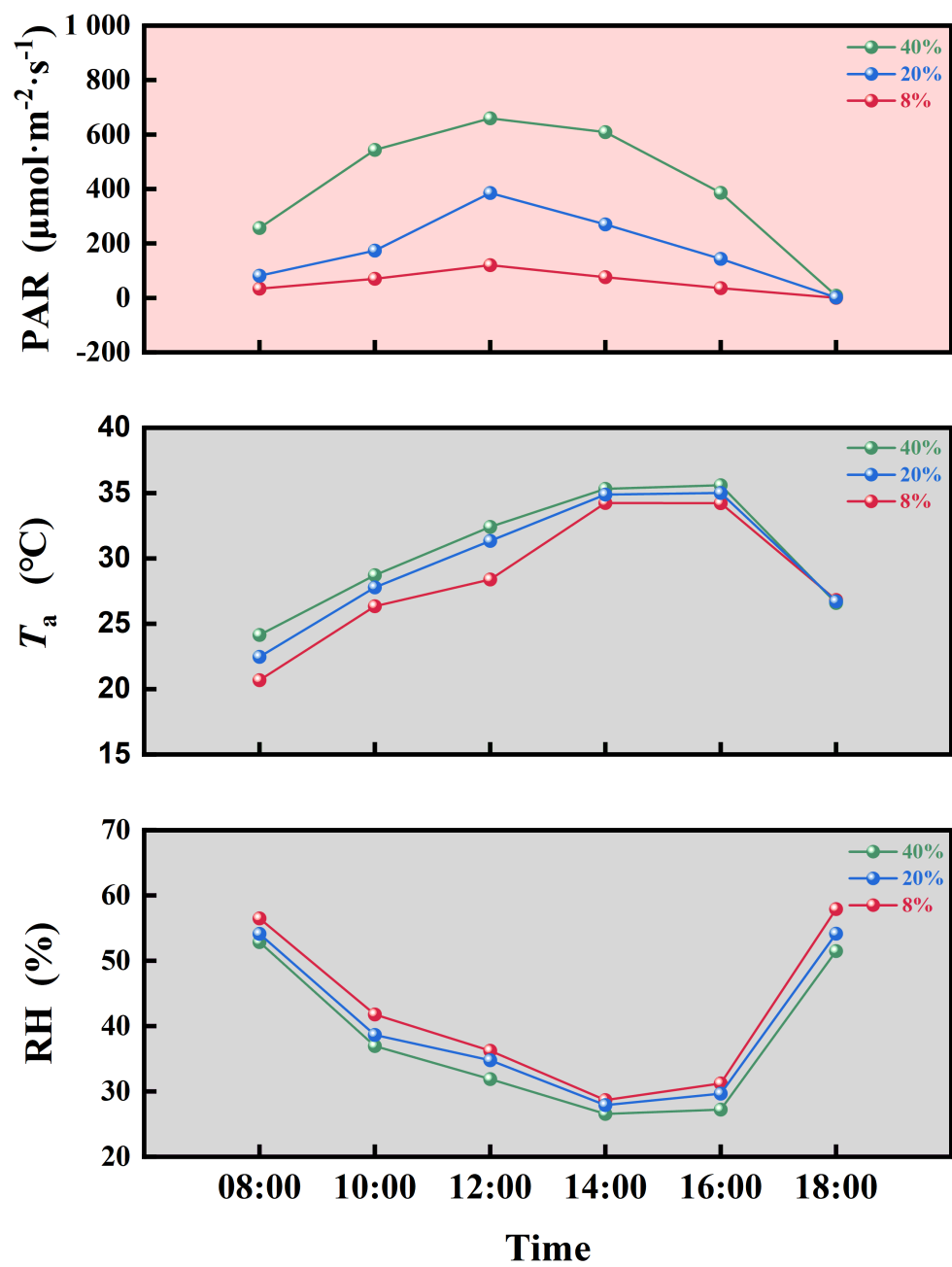


Figure 1

Diurnal variation curves of environmental factors

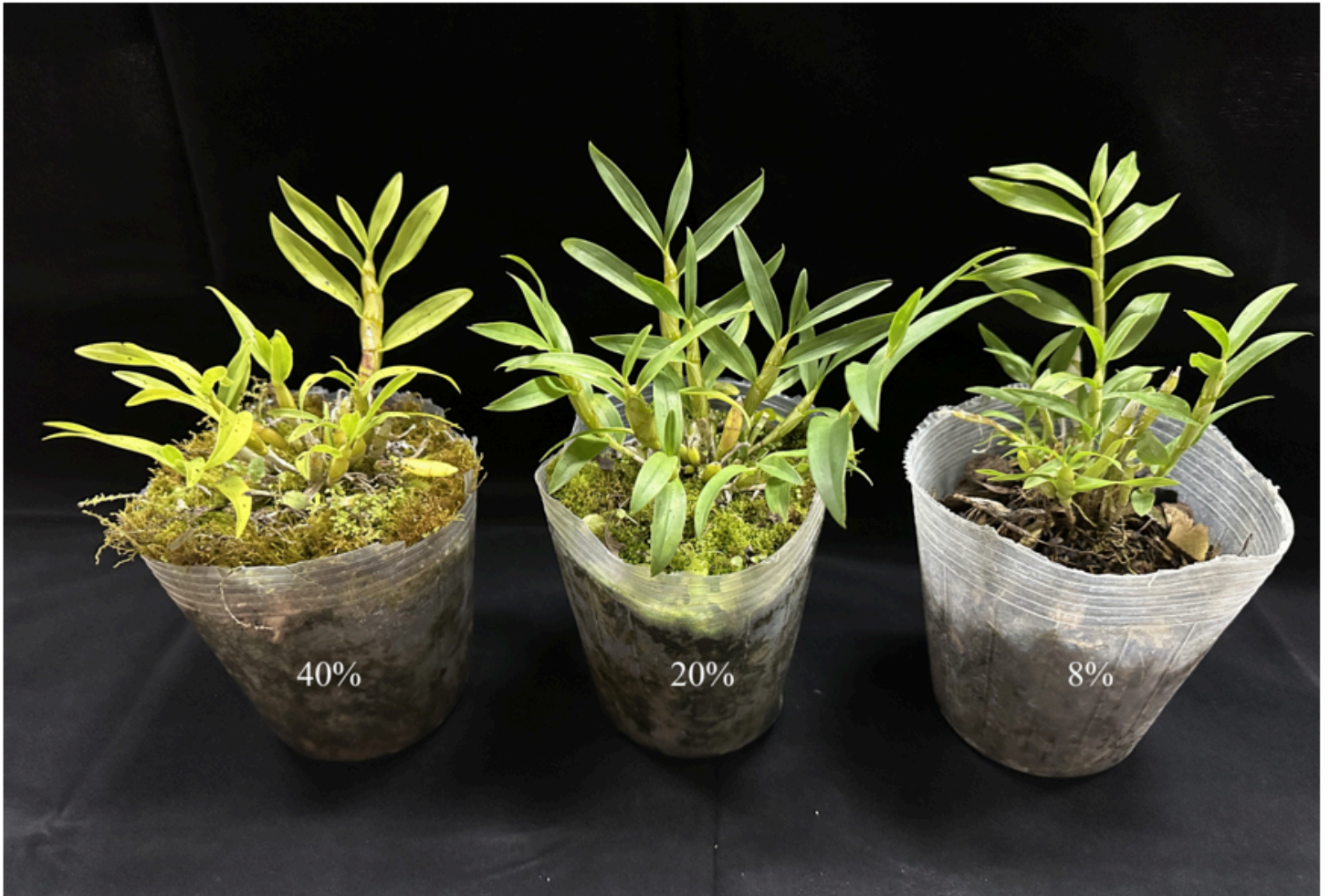


Figure 2

Representative images of *D.fimbriatum* under different light intensities (40%, 20%, and 8%).

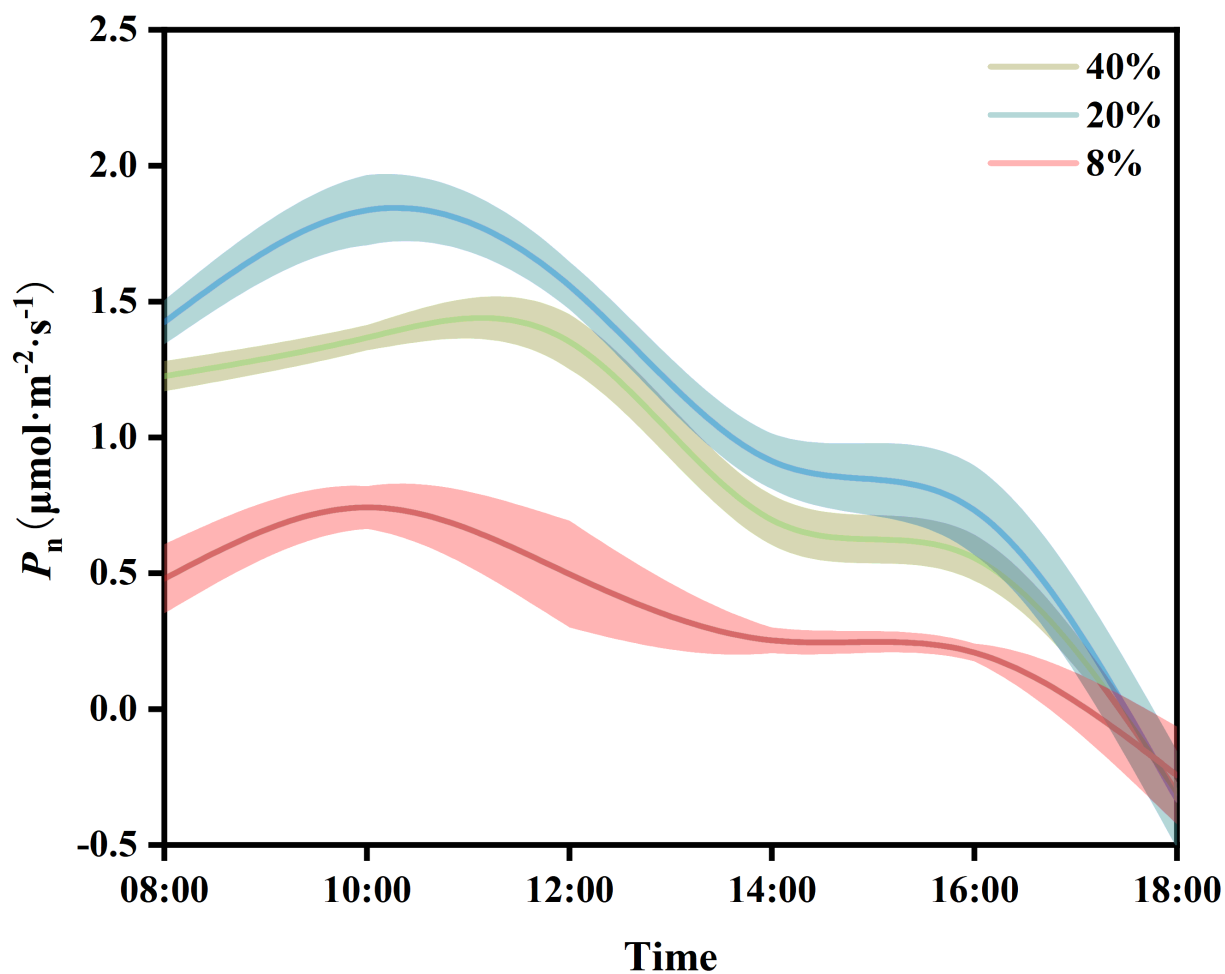


Figure 3

Diurnal variation response curves of photosynthesis in *D. fimbriatum* under different light intensities. Note: In the figure, the blue, green, and red curves represent the diurnal variation of net photosynthetic rate (P_n) under 20%, 40%, and 8% of full sunlight, respectively. Shaded areas indicate the standard error (SE).

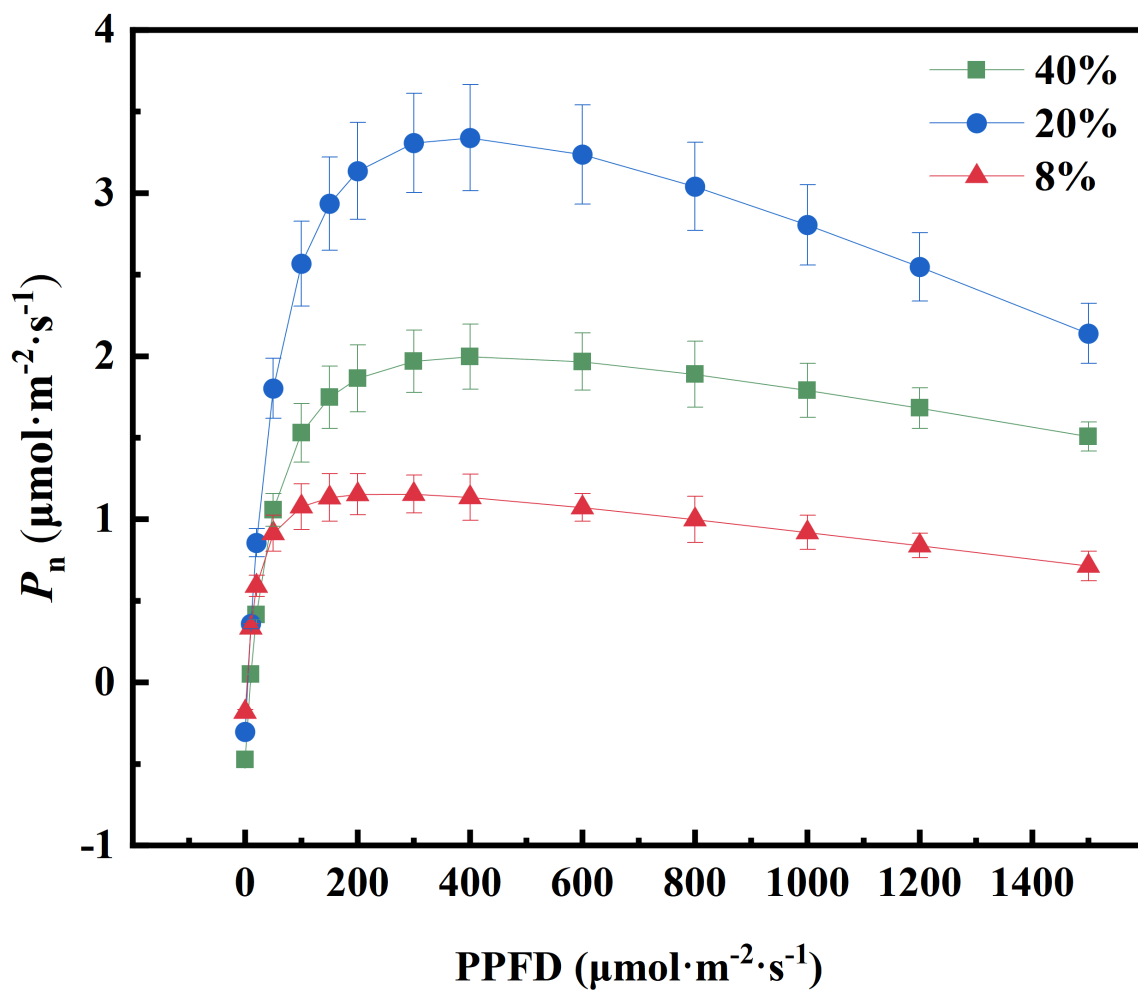


Figure 4

Light response curves of *D.fimbriatum* under different light intensities.

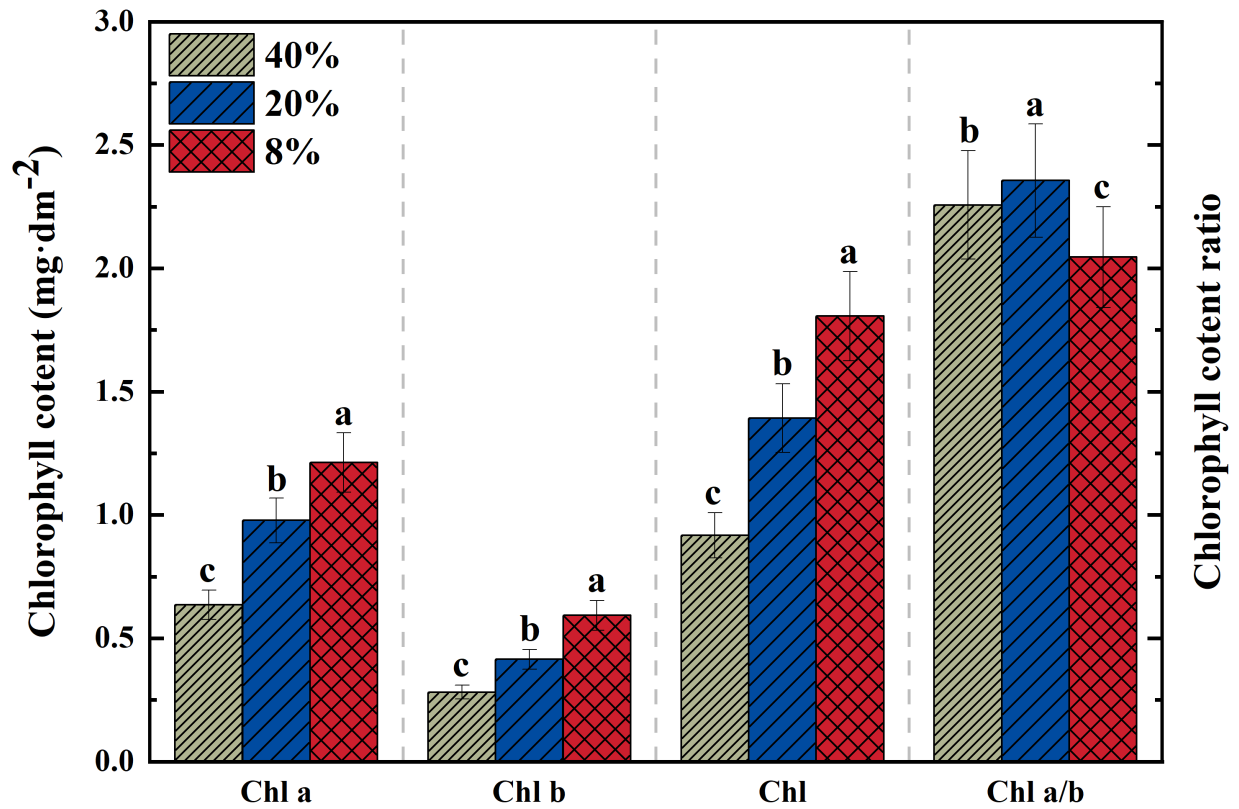


Figure 5

Chlorophyll content and ratio of *D. fimbriatum* under different light intensities. Note: Different lowercase letters above the bars indicate significant differences among light treatments at $p < 0.05$ according to Duncan's multiple range test.

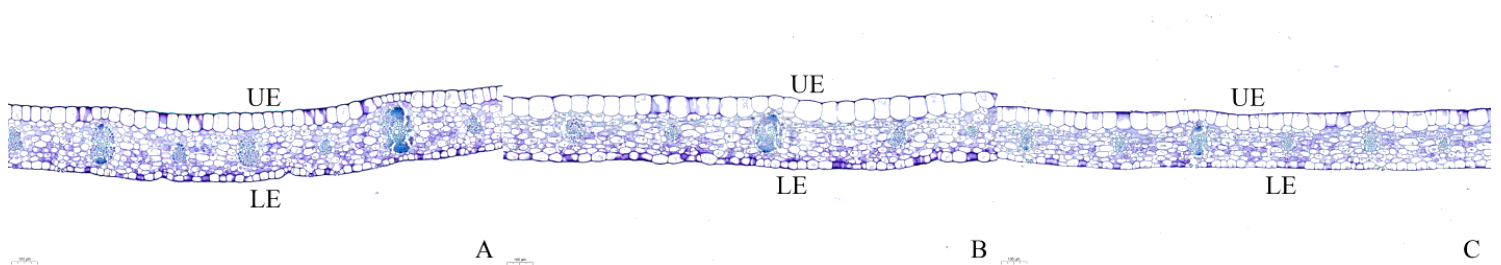


Figure 6

Leaf anatomical characteristics of *D. fimbriatum* under different light intensities. Note: Leaf anatomical characteristics of *D. fimbriatum* under different light intensities. Panels **A–C** represent leaf anatomical structures under 40%, 20%, and 8% light intensity, respectively. **UE** indicates the upper epidermis, and **LE** indicates the lower epidermis.

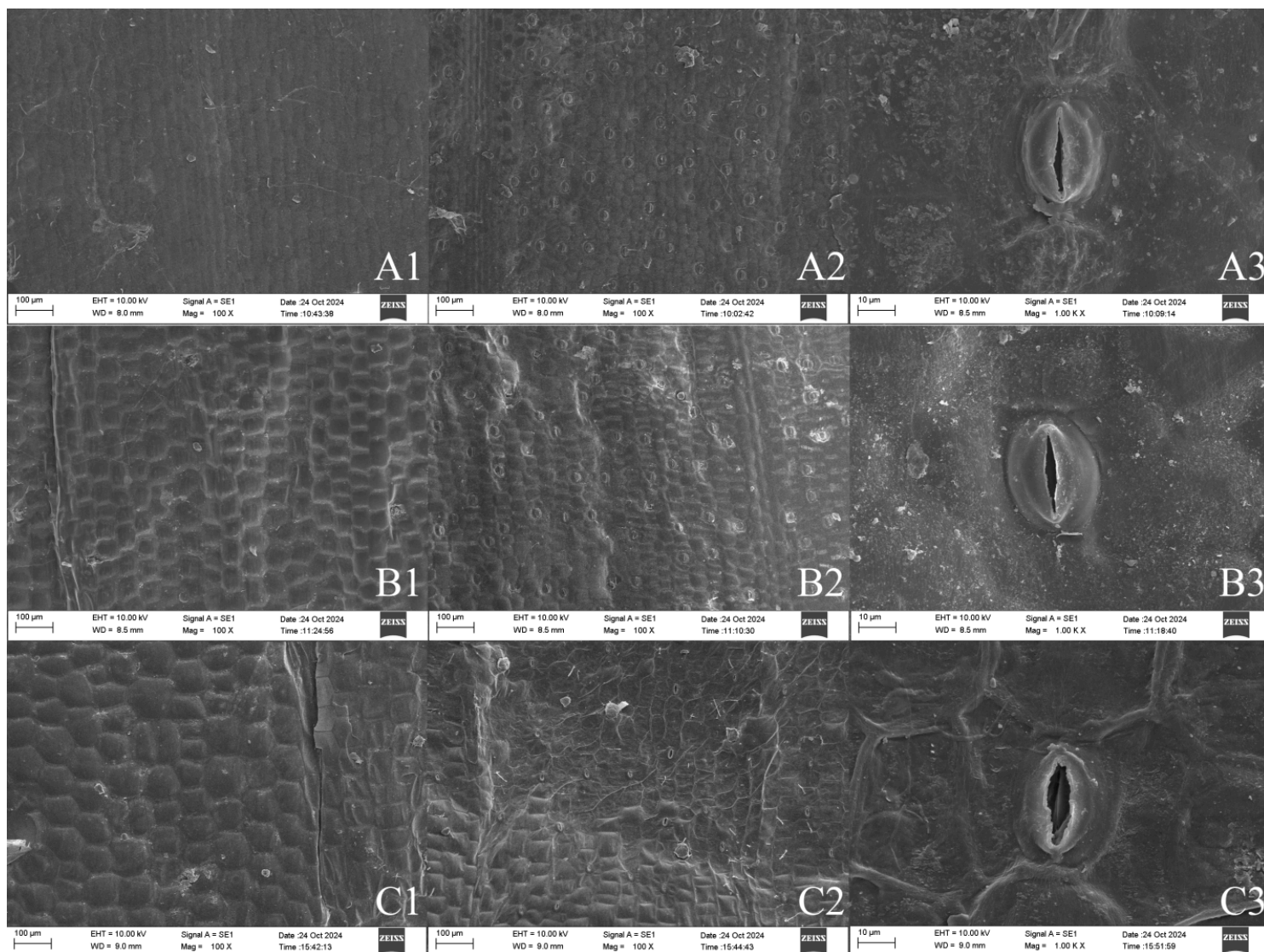


Figure 7

Leaf epidermal characteristics of *D. fimbriatum* under different light intensities. Note: **A1**, **A2**, and **A3** show the adaxial epidermis, abaxial epidermis, and abaxial stomata of *D. fimbriatum* under 40% light intensity, respectively; **B1**, **B2**, and **B3** display the corresponding structures under 20% light intensity; **C1**, **C2**, and **C3** represent those under 8% light intensity.

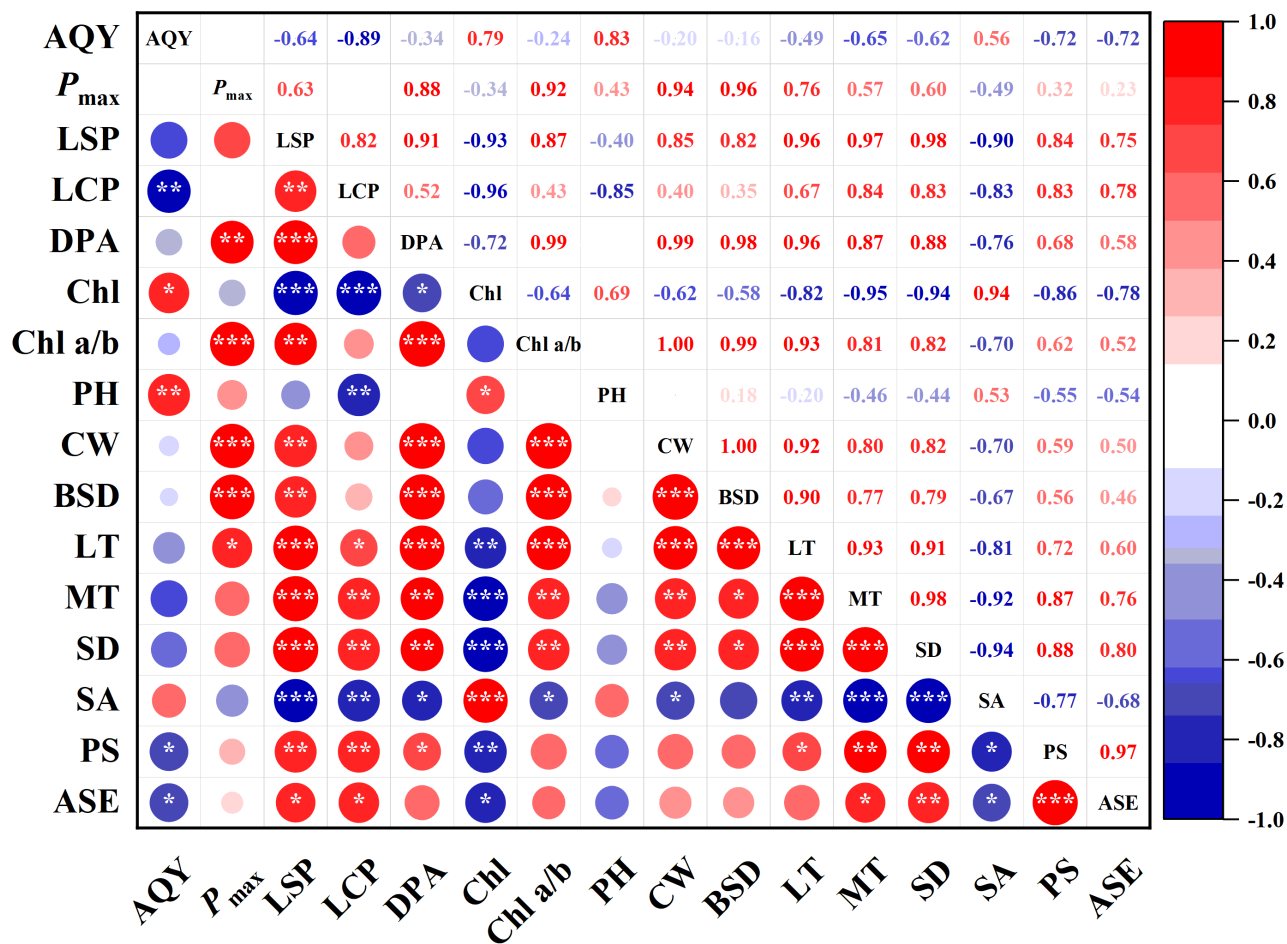


Figure 8

Correlation heatmap between growth parameters, photosynthetic parameters, leaf microstructure, and bioactive compounds of *D. fimbriatum* under different light intensities. Note: The color intensity reflects the strength of the correlations (−1 to +1), with red indicating positive correlations and blue indicating negative correlations. Greater color saturation corresponds to stronger correlation coefficients. Statistical significance is denoted as * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$.