COMPARISON OF THE PHOTOSYNTHETIC PHYSIOLOGICAL CHARACTERISTICS AND LEAF MICROSTRUCTURES OF TWO NARROWLY DISTRIBUTED AND A WIDESPREAD SPECIES IN THE GESNERIACEAE FAMILY

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Abstract. The plants of the Gesneriaceae family have important ornamental value, however most narrowly distributed species have suffered severe damage to their wild resources and are at risk of extinction. This study aimed to compare the photosynthetic characteristics, photosynthetic pigment content, and leaf structure to explore the differences among two narrowly distributed species (*Oreocharis mileensis* and *Oreocharis cotinifolia*) and a relatively widespread species (*Primulina eburnea*) in the Gesneriaceae family, in China. The results revealed the followings: The maximum net photosynthetic rate (P_{max}), apparent quantum yield, light compensation point, light saturation point, potential maximum net photosynthetic rate, Chl(a + b) content, stomatal density (SD), leaf thickness (LT), and palisade tissue thickness (PTT) of *O. mileensis* and *O. cotinifolia* were significantly lower ($P < 0.05$) than those of *P. eburnea.* However, the CO_2 compensation point and CO_2 saturation point of *O. mileensis* and *O. cotinifolia* were higher than those of *P. eburnea.* The photosynthetic physiological characteristics of the narrowly distributed species, *O. mileensis* and *O. cotinifolia*, are lower than those of the widely distributed species, *P. eburnea*. The ability of narrowly distributed species *O. mileensis* and *O. cotinifolia* to adapt to the light environment and utilize light energy is relatively weak, which can be an important physiological cause of the narrow distribution.
Keywords: *Gesneriaceae, stomatal characteristics, photosynthetic characteristics, leaf anatomy, light response curse, chlorophyll*

Introduction

The Gesneriaceae family involves perennial herbaceous plants, with a predominantly distributed in the karst regions of China. As a crucial component of these karst ecosystems, Gesneriaceae plants exhibit significant ornamental value (Xu et al., 2017). *Oreocharis mileensis* and *Oreocharis cotinifolia* are Chinese endemic perennial herbaceous species within the Gesneriaceae family. *O. mileensis* is found in Guangxi, Yunnan, and Guizhou provinces, in China. It grows in forested areas near the limestone mountains at an elevation of approximately 1200 m sea level. It has a restricted geographical distribution and limited number of individuals in the wild (Xu et al., 2009; Yang et al., 2014). *O. cotinifolia* has an even more confined distribution, occurring solely within a narrow region of the Dayaoshan Nature Reserve in Jinxiu, Guangxi, in China.

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This species inhabits mountain forests or roadside woodlands at elevations of 800–1200 m above sea level. Due to its small population size, limited distribution area, and the adverse impacts of human activities, the population of *O. cotinifolia* has declined precipitously (Wang et al., 2008). Thus, both *O. mileensis* and *O. cotinifolia* have been categorized as endangered species on the Threatened Species List of China's Higher Plants (Qin et al., 2017), underscoring the urgent need for conservation efforts to safeguard these valuable plant resources. *Primulina eburnea*, a perennial herbaceous plant, that belongs to the Gesneriaceae family, inhabits limestone forests at elevations of 100–1500 m above sea level. This species grows in loose, fertile acidic or slightly acidic soils. It is more resistant to direct light and high temperatures and is widely distributed in Guangxi, Guizhou, Hunan, Hubei, Sichuan, and Zhejiang in China (Wang, et al., 2017). The distribution range of this species is larger than that of *O. mileensis* and *O. cotinifolia*.

As a fundamental environmental factor, light critically regulates both the growth patterns and spatial distribution of plant species (Boardman, 1977; Rozendaal et al., 2006; Kelly et al., 2008). Thus, investigating plant photoresponse mechanisms has remained a central theme in plant ecophysiology research (Rodríguez-López et al., 2014; Hudson et al., 2017; Violeta et al., 2020). Photosynthetic characteristics may predetermine and explain important ecological requirements of a plant species (Adamec, 1997; Chai et al., 2018). The interaction between the comprehensive survival ability of plants, such as their competitiveness and adaptability during growth process, and environmental factors can reveal the underlying internal regular governing plant growth and development (Niinemets, 1998; Zhang et al., 1999; Chen et al., 2023a). The strength of photosynthetic ability can reflect the competitive status and adaptability of plants in the population to a large extent (Liang et al., 2010). Photosynthetic, morphological, and growth responses to light environment can be useful measurements to determine favorable habitat conditions for the conservation of endangered species (Smith et al., 1993; Aleric and Kirkman, 2009; Lockhart et al., 2012; Zhou, 2017). It can judge the optimal light needed for its plant growth and choose the best place to cultivate it (Smith and Houpis, 2004; Lockhart et al., 2012; Wang et al., 2023).

Comparing the photosynthetic characteristics of endangered plants and their widely distributed relatives can better reveal the internal endangerment mechanism of endangered plants (Cui et al., 2016; Chai et al., 2015; Ou et al., 2023; Xu et al., 2024). Compared with closely related widespread species, endangered plants have lower photosynthetic rate, water use efficiency (Ge et al., 2003; Wei et al., 2008; Shi et al., 2012). For example, when compared with *Zygophyllum xanthoxylon*, *Tetraena mongolica* had lower a photosynthesis and water use efficiency, which demonstrates its weaker photosynthetic capability and lower adaptability to a drought prone environment (Shi et al., 2012). Photosynthetic capacity and adaptability of *Geodorum eulophioides* were poorer compared with *G. densiflorum* and *G. attenuatum*, which might be greatly related to its endangerment (Xu et al., 2024). In their comparative study of photosynthetic traits, Wei et al. (2008) demonstrated significant physiological divergence between the endangered *Camellia nitidissima* and its widespread congener *C. sinensis*. Their findings revealed that *C. nitidissima* exhibits shade-tolerant characteristics, whereas *C. sinensis* displays broad photoadaptation capacity, which may explain its extensive geographical distribution. Furthermore, the photosynthetic physiological characteristics of *Oreocharis esquirolii* are generally lower than those of two other species within the same genus, namely *O. elegantissima* and *O. duyunensis*. Additionally, its capacity to adapt to varying light environment and its efficiency in utilizing light energy are comparatively limited

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(Ou et al., 2023). These findings suggest that endangered plants are highly sensitive to their external environment, with relatively low survival and adaptability, as well as weaker photosynthetic capabilities. Thus, exploring the differences in photosynthetic characteristics and physiological structures between endangered plants and their widely distributed relatives is crucial for elucidating their mechanisms of endangerment and implementing appropriate conservation measures.

Compared with the widely distributed species of *P. eburnea*, the distribution range of endangered species *O. mileensis* and *O. cotinifolia* is relatively narrow, and there are certain differences in habitat. The reason for this difference may be related to the different demand and adaptability of light environment (Wei et al., 2008; Ou et al., 2023; Xu et al., 2024). Despite these three plants of the significant scientific value and their high demand due to their ornamental value, their eco-physiological responses to endangered and widespread species have not been studied. It is necessary to understand the differences in eco-physiological among these three plants. This knowledge will help develop effective conservation measures through appropriate shading treatments. Additionally, it will facilitate proper introduction and cultivation efforts for restoration. Thus, the main objective of this study of *O. mileensis*, *O. cotinifolia*, and *P. eburnea.* By comparing the photosynthetic characteristics and leaf structure of these three species in the Gesneriaceae family, it aims to provide a reference for elucidating the endangered mechanisms of *O. mileensis* and *O. cotinifolia*, and to offer theoretical support for the conservation and introduction cultivation of germplasm resources in this family. Our specific questions were: (1) whether the photosynthetic capacity of the endangered species *O. mileensis* and *O. cotinifolia* was lower than that of the widely distributed species *P. eburnea*? (2) If the photosynthetic capacity of *O. mileensis* and *O. cotinifolia* was lower than that of *P. eburnea*, whether it was related to the leaf structure and chlorophyll content?

Materials and methods

Study site

The experimental was conducted at the Guangxi Institute of Botany (25° 01'N, 110° 17'E; 178 above sea level) in Guilin, Guangxi, South China. The region is characterized by a subtropical monsoon climate. The mean annual temperature is approximately 19.12℃, with average temperature for the coldest month (January) and the hottest month (July) being 8.1℃ and 28.2℃, respectively; temperature extremes can reach up to 40 and drop as low as -6 ℃. Annual rainfall totals around 1890 mm, with about 73% occurring between April and August. The relative humidity averages at 78%, exhibiting distinct wet and dry seasons throughout the year. Average annual sunshine duration approximately 1487 h. The main tree species in the upper layer are *Elaeocarpus chinensis*, *Pinus massoniana*, and *Acer buergerianum*. The shade under the forest is 90%.

Plant materials

The test materials consisted of *O. mileensis*, *O. cotinifolia*, and *P. eburnea* (*Fig. 1*). They were planted in plastic pots with an inner diameter of 21 cm and a depth of 18 cm, with six pots for each species, and one plant was planted in each pot. The cultivation medium was a mixture of peat soil, humus soil, and fine sand, the volume ratio was 1:1:1. All the sample seedlings were consistently cared for with timely watering and regular weed removal throughout the entire experiment.

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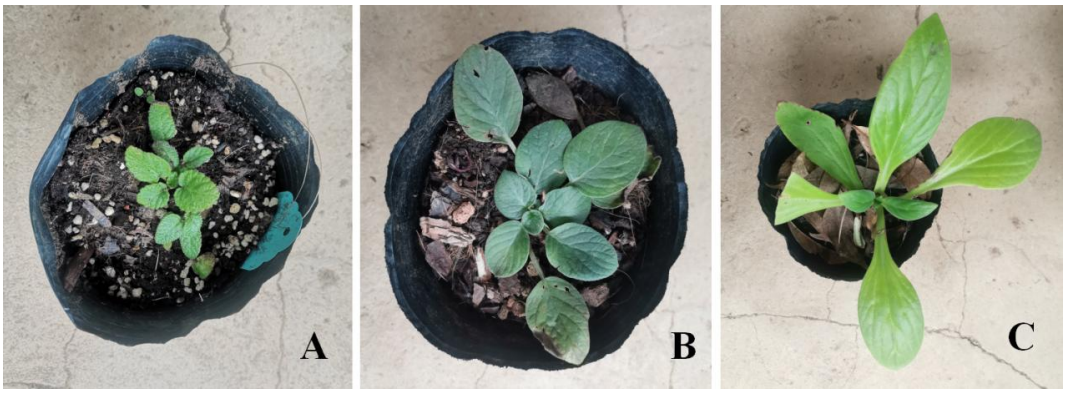

Figure 1. *Three species morphological characteristics. A: O. mileensis; B: O. cotinifolia; C: P. eburnean*

Methods

In August 2023, six plants of each species were selected from the experimental seedlings with a similar size and good growth, and healthy mature peripheral leaves with consistent growth were selected for the determination of the leaf epidermal structure, leaf anatomical structure, photosynthetic parameters, and photosynthetic pigment content.

Light response curves

Photosynthetic measurements were performed on fully expanded upper leaves of five individual plants per species (one leaf per plant) using a Li-6400XT portable photosynthesis system (Li-Cor Inc., Lincoln, NE, USA) on sunny days between 08:00 and 12:00 h. Prior to measurements, leaves were dark-adapted for 30 min and then illuminated with a red-blue light source at 400 $\mu mol \cdot m^{-2} \cdot s^{-1}$ to fully activate the photosynthetic apparatus. Open-flow gas exchange measurements were conducted under controlled conditions: flow rate of 500 $cm^3 \cdot min^{-1}$, leaf temperature of 28°C, and CO_2 concentration of 400 $\mu mol \cdot mol^{-1}$ (regulated by a CO_2 cylinder). A photosynthetic photon flux density (PPFD) series of 1500, 1200, 1000, 800, 600, 400, 200, 150, 100, 50, 20, and 0 $\mu mol \cdot m^{-2} \cdot s^{-1}$ was applied, with each irradiance level stabilized for 120 s before data acquisition. Light response curves were fitted using a modified rectangular hyperbola model (Ye, 2007; Wargent et al., 2011; Xu et al., 2013) to derive parameters including net photosynthesis (P_n), light saturation point (LSP), maximum photosynthetic rate (P_{max}), light compensation point (LCP), dark respiration rate (R_d), and apparent quantum yield (AQY).

CO_2 response curves

Leaf CO_2 response curve was measured using a Li-6400XT portable photosynthesis measurement system (*Li-Cor* Inc., Lincoln, NE, USA) between 08:00 and 12:00 h on fully expanded leaves. The airflow rate was set at 500 $cm^3 \cdot min^{-1}$, and the leaf temperature was 28°C. According to the light saturation point measured by light response curve, the fixed light intensity of *O. mileensis* and *O. cotinifolia* was set to 400 $\mu mol \cdot m^{-2} \cdot s^{-1}$, and the fixed light intensity of *P. eburnea* was set to 600 $\mu mol \cdot m^{-2} \cdot s^{-1}$. The CO_2 concentration gradients were set at 400, 300, 200, 150, 100, 50, 400, 400, 600, 800, 1000, 1200, 1500,

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and 2000 μmol·mol^{-1} (concentration controlled with CO_2 cylinders). The P_n at the different CO_2 concentrations was recorded automatically at a balance of 180 s per CO_2 concentration (Chai et al., 2015). Five plants were measured for each species, one leaf was measured per plant. The photosynthetic parameters were measured according to the calculation methods of Ye and Yu (2010), and the modified rectangular hyperbola model was used to fit the data. These included the net photosynthesis (P_n), atmospheric CO_2 concentration (C_a), photorespiration rate (R_p), CO_2 compensation point (CCP), CO_2 saturation point (CSP), the initial carboxylation efficiency (α), and the potential maximum net photosynthetic rate (A_{max}).

Photosynthetic pigments

Using a hole puncher, eight small round leaf discs, each with an area of 1 cm², were excised from the leaves previously utilized for photosynthesis measurements. These discs were subsequently fragmented and transferred into a 25 mL brown volumetric flask. The flask was filled to the mark with 95% ethanol to prepare the extract, which was then incubated in the dark for 24 h until complete decolorization of the leaf material occurred. The absorbance of the resulting extract was measured at wavelengths of 665 nm, 649 nm, and 470 nm, respectively. Five biological replicates were performed for each plant species. Chlorophyll a (Chl a), chlorophyll b (Chl b), total chlorophyll [Chl (a + b)], carotenoid (Car) contents, along with the Chl a/b ratio, were calculated according to the formulas described by Li (2000):

$$\text{ChIa} = 13.95A_{665} - 6.88A_{649} \quad \text{(Eq.1)}$$

$$\text{ChIb} = 24.96A_{649} - 7.32A_{665} \quad \text{(Eq.2)}$$

$$\text{Car} = (1000\ A_{470} - 2.05\text{ChIa} - 114.8\text{ChIb})/245 \quad \text{(Eq.3)}$$

Leaf epidermal characteristics

Mature functional leaves with good growth in the same direction as the photosynthetic test seedlings were selected, and the central part of the leaves from the leaf edge to the main vein was clipped, with an area of about 10 × 10 mm. Five plants were measured for each species. After sampling, the samples were immediately put into a 2.5% glutaraldehyde fixing solution, and they were brought back to the laboratory for ethanol step-by-step dehydration, critical point drying, and gold-plating. The upper epidermis, lower epidermis, and stomatal apparatus of the leaves were observed under a vacuum electron scanning electron microscope (ZEISS EVO18), and photos were taken. Each sample was randomly observed in 10 fields. The AxioVision SE64. Rel. 4.9.1 scanning electron microscope software was used to observe the stomatal apparatus length, stomatal apparatus width, stomatal density (SD) and single stomatal apparatus area (ISA).

Leaf anatomical structure

Leaf anatomy, paraffin sections were made according to Li (1980) and optimized appropriately. The leaves of the three species of Gesneriaceae were cut crosswise along the midvein, the pieces were 10 × 10 mm, and fixed with formalin acetic acid fixing solution (70% ethanol: formalin: acetic acid = 90:5:5). Then, they were dehydrated with

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ethanol and xylene, embedded in paraffin, stained with toluidine blue, and sealed with a neutral gum. The digital slice scanner was used for panoramic scanning, and the graphic analysis software CaseViewer 2.4 was used to measure the microscopic parameters. The measurement indexes were the leaf thickness (LT), upper epidermal cell thickness (UET), lower epidermal cell thickness, palisade tissue thickness (PTT), spongy tissue thickness (STT), and median catheter tissue diameter (MCTD), and PTT/STT was calculated. PTT/STT = palisade tissue thickness/sponge tissue thickness. Additionally, 10 fields of view were observed at random for each sample, and the parameters of each index were measured statistically.

Data analysis

The experimental data were analyzed using Microsoft Excel 2010 software, Origin 2015 software. One-way ANOVA was performed using SPSS 25.0 software, and multiple comparisons were conducted using the Duncan method. According to the method of Ye (2010), the photosynthetic parameters of the light response curve and CO_2 response curve were simulated and combined with the modified rectangular hyperbola model of the Photosynthesis Calculation 4.1.1 software.

Results

Light response parameters of the three Gesneriaceae species

Light response curve of the three Gesneriaceae species showed similar trend. With the increase in the photosynthetic photon flux density, the P_n increased rapidly, reached its maximum value, and then decreased slightly and remained basically stable (*Fig. 2*). The P_n of *O. mileensis* and *O. cotinifolia* was lower than that of *P. eburnea*. The P_{max} of *O. mileensis* and *O. cotinifolia* was 1.59 μmol·m^{-2}·s^{-1} and 1.73 μmol·m^{-2}·s^{-1}, respectively, which was significantly ($P < 0.05$) lower than that of *P. eburnea* (4.69 μmol·m^{-2}·s^{-1}). The AQY, LSP, LCP, and R_d of *O. mileensis* and *O. cotinifolia* were significantly lower than those of *P. eburnea* ($P < 0.05$) (*Table 1*).

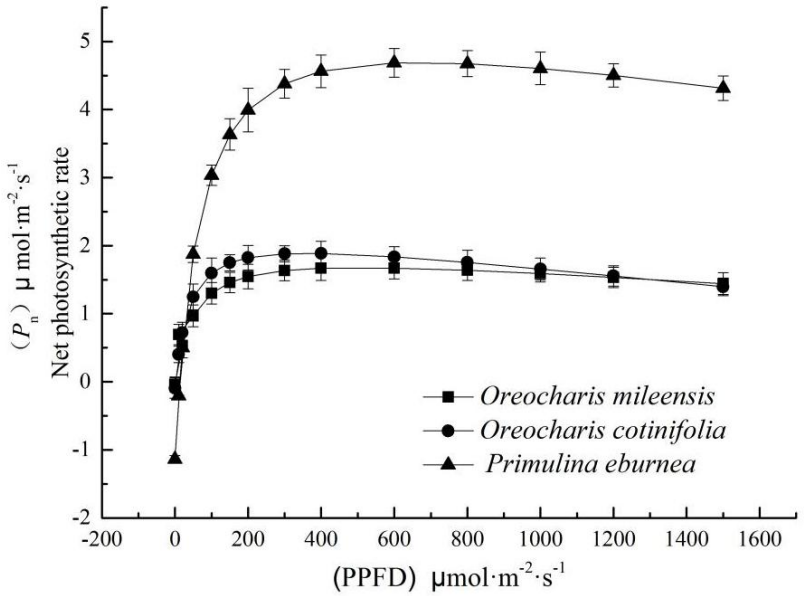

Figure 2. *Light response curves of three species of Gesneriaceae*

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Table 1. *Light response parameters of the leaves of the three species of Gesneriaceae*

Species	P_{max} (μmol·m^{-2}·s^{-1})	LSP (μmol·m^{-2}·s^{-1})	LCP (μmol·m^{-2}·s^{-1})	AQY (μmol·μmol^{-1})	R_d (μmol·m^{-2}·s^{-1})
O. mileensis	1.59 ± 0.21 b	411.05 ± 60.21 b	2.41 ± 0.12 b	0.039 ± 0.01 c	0.097 ± 0.02 b
O. cotinifolia	1.73 ± 0.19 b	361.67 ± 30.25 c	1.55 ± 0.10 c	0.062 ± 0.02 b	0.093 ± 0.02 b
P. eburnea	4.69 ± 0.51 a	666.87 ± 50.26 a	12.67 ± 1.52 a	0.107 ± 0.05 a	1.135 ± 0.08 a

Different lowercase letters in the same column indicate significant differences between the parameters ($P < 0.05$)

CO_2 response parameters of the three Gesneriaceae species

The CO_2 response curve of the three Gesneriaceae species showed similar trend. With the increase in the CO_2 concentration, the P_n of the leaves increased continuously and then increased slowly (*Fig. 3*). The P_n of *O. mileensis* and *O. cotinifolia* was lower than that of *P. eburnea*. The A_{max} of *O. mileensis* and *O. cotinifolia* was 3.896 μmol·m^{-2}·s^{-1} and 5.158 μmol·m^{-2}·s^{-1}, respectively, which was significantly ($P < 0.05$) lower than that of *P. eburnea* (10.724 μmol·m^{-2}·s^{-1}). The CCP and CSP of *O. mileensis* and *O. cotinifolia* were significantly higher ($P < 0.05$) than those of *P. eburnea*, while *α* and R_p were significantly lower ($P < 0.05$) than those of *P. eburnea* (*Table 2*).

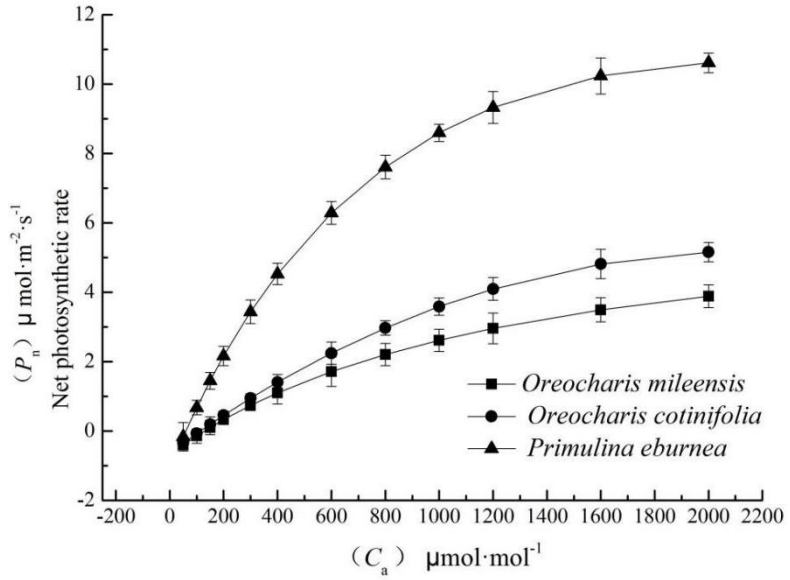

Figure 3. *CO_2 response curves of the leaves of the three species of Gesneriaceae. P_n, net photosynthetic rate; C_a, Atmospheric CO_2 concentration*

Table 2. *CO_2 response parameters of the leaves of three species of Gesneriaceae*

Species	A_{max} (μmol·m^{-2}·s^{-1})	CSP (μmol·mol^{-1})	CCP (μmol·mol^{-1})	α (μmol·m^{-2}·s^{-1})	R_p (μmol·m^{-2}·s^{-1})
O. mileensis	3.896±0.337 c	2684.51±107.683 a	136.076±24.481 a	0.0065±0.0012 b	0.743±0.130 b
O. cotinifolia	5.158±0.412 b	2154.69±148.763 b	112.542±30.375 a	0.0058±0.0023 b	0.597±0.117 b
P. eburnea	10.724±0.463 a	1905.52±60.825 c	60.936±5.570 b	0.0196±0.0026 a	1.121±0.071 a

Different lowercase letters in the same column indicate significant differences between the parameters ($P < 0.05$)

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Photosynthetic pigment content of the three species of Gesneriaceae

The Chla, Chlb, and Chl(a + b) contents of the leaves of *O. mileensis* and *O. cotinifolia* were significantly ($P < 0.05$) lower than those of *P. eburnea*. The Chla/b and Car of *O. cotinifolia* were significantly higher than those of *O. mileensis* and *P. eburnea*. ($P < 0.05$) (*Table 3*).

Table 3. *Photosynthetic pigment content in the leaves of the three species of Gesneriaceae*

Species	Chla ($mg \cdot dm^{-1}$)	Chlb ($mg \cdot dm^{-1}$)	Chl(a + b) ($mg \cdot dm^{-1}$)	Chla/b	Car ($mg \cdot dm^{-1}$)
O. mileensis	0.755 ± 0.011 b	0.648 ± 0.015 b	1.322 ± 0.139 b	1.412 ± 0.362 b	0.121 ± 0.019 b
O. cotinifolia	0.725 ± 0.089 b	0.369 ± 0.031 c	1.094 ± 0.119 b	1.958 ± 0.103 a	0.214 ± 0.011 a
P. eburnea	0.910 ± 0.064 a	0.875 ± 0.071 a	1.785 ± 0.074 a	1.050 ± 0.138 b	0.107 ± 0.011 b

Different lowercase letters in the same column indicate significant differences between the parameters ($P < 0.05$)

Leaf epidermal structure of the three species of Gesneriaceae

The upper and lower epidermis of the leaves of the three species of Gesneriaceae had superficial fur distribution, and the stomata were only distributed in the lower epidermis of the leaves (*Fig. 4*). There were significant ($P < 0.05$) differences in the stomatal apparatus length, stomatal apparatus width, and single stomatal apparatus area among the three species of Gesneriaceae, *O. mileensis* > *P. eburnea* > *O. cotinifolia*. The stomatal density of *O. mileensis* and *O. cotinifolia* was significantly lower ($P < 0.05$) than that of *P. eburnea* (*Table 4*).

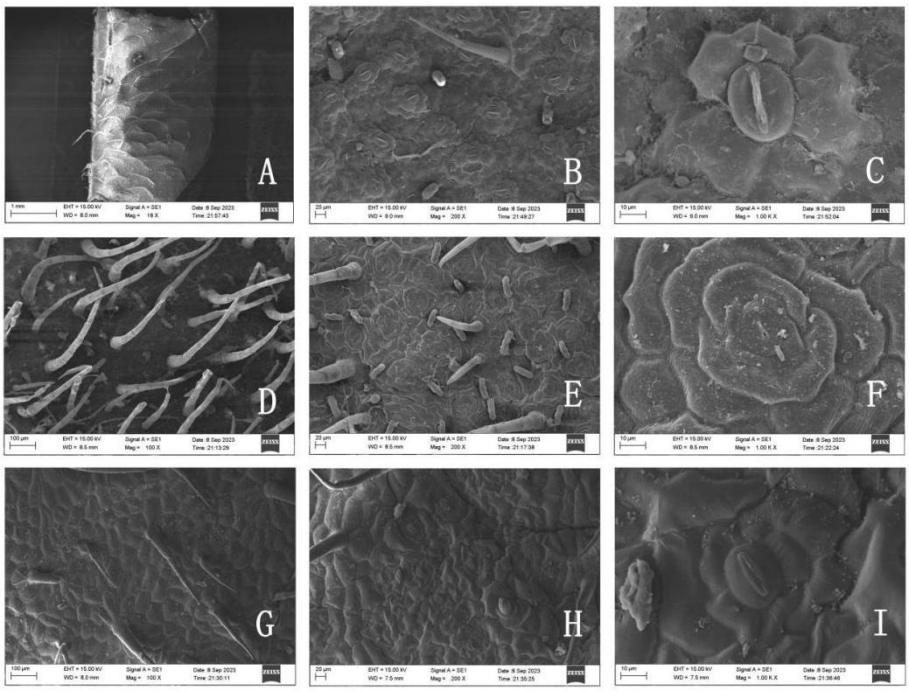

Figure 4. *Epidermal structure of the leaves of the three species of Gesneriaceae. A–C: Upper epidermis, lower epidermis, and stomata of Oreocharis mileensis; D–F: Upper epidermis, lower epidermis, and stomata of Oreocharis cotinifolia; G–I: Upper epidermis, lower epidermis, and stomata of Primulina eburnean*

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Table 4. *Leaf stomatal indices of the three species of Gesneriaceae*

Species	Stomatal apparatus width (μm)	Stomatal apparatus length (μm)	Stomatal apparatus area (μm^2)	STOMATAL density (individual·mm^{-2})
O. mileensis	26.45 ± 0.46 a	30.97 ± 0.49 a	643.06 ± 17.83 a	41.72 ± 3.35 b
O. cotinifolia	15.43 ± 0.27 c	21.25 ± 0.71 c	257.61 ± 12.76 c	48.79 ± 1.83 b
P. eburnea	20.85 ± 0.25 b	27.32 ± 0.39 b	477.30 ± 11.76 b	85.33 ± 4.99 a

Different lowercase letters in the same column indicate significant differences between the parameters ($P < 0.05$)

Leaf anatomical structure of the three species of Gesneriaceae

The leaf anatomical of the three species of Gesneriaceae was composed of the epidermis, mesophyll cells, and leaf veins. The mesophyll tissues were composed of palisade tissues and spongy tissues. The upper epidermis of *P. eburnea* had a thick cuticle, while the upper epidermis of *O. mileensis* and *O. cotinifolia* had no cuticle (*Fig. 5*). The LT, UET, PTT, STT, and MCTD were significantly ($P < 0.05$) lower than those of *P. eburnea*. The PTT/STT of *O. cotinifolia* was significantly lower ($P < 0.05$) than those of *O. mileensis* and *P. eburnea*. The PTT/STT size was *O. cotinifolia* < *P. eburnea* < *O. mileensis* (*Table 5*).

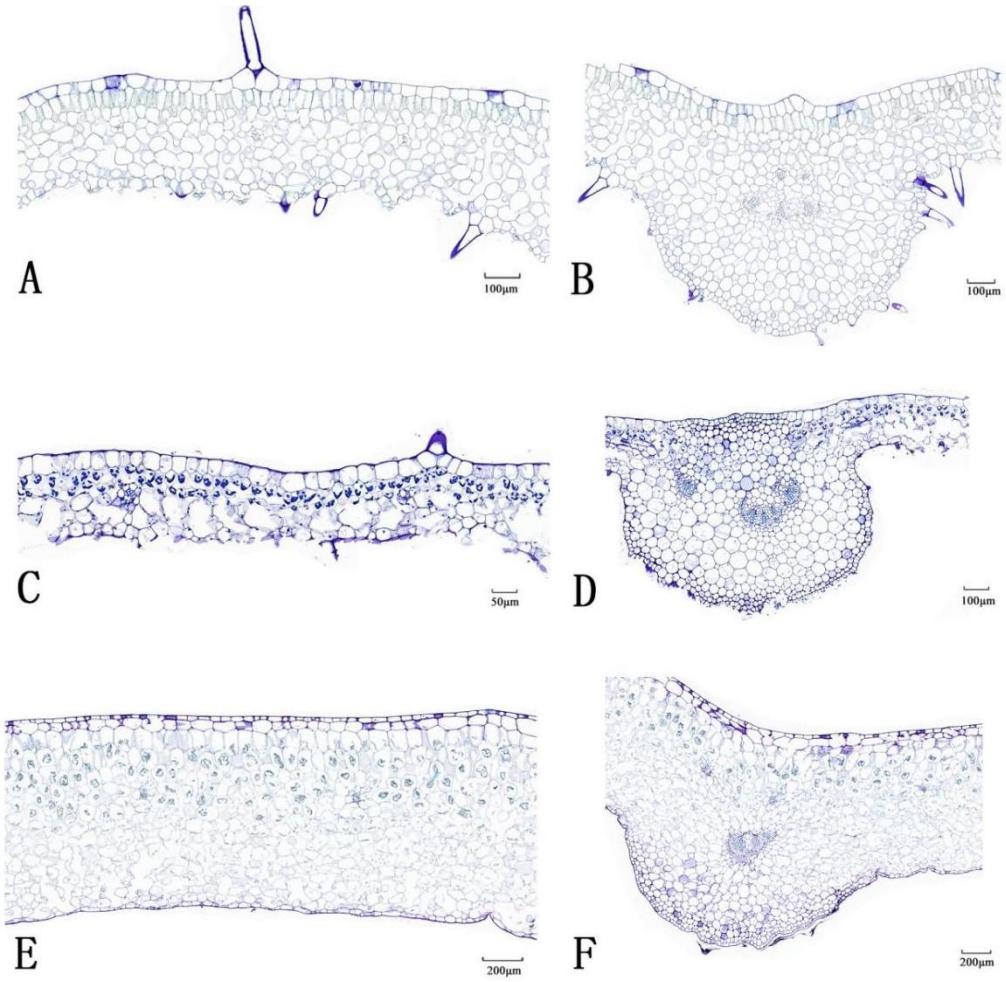

Figure 5. *Anatomical structure of the leaves of the three species of Gesneriaceae*

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Table 5. *Anatomical parameters of the leaves of the three species of Gesneriaceae*

Species	LT	UET	PTT	STT	PTT/STT	LET	MCTD
O. mileensis	339.91±18.97 b	41.38±5.13 b	108.06±15.52 b	162.31±18.78 b	0.678±0.141 a	33.86±7.94 a	10.46±2.00 b
O. cotinifolia	210.83±27.05 c	36.07±4.67 b	46.31±6.12 c	100.24±13.27 c	0.484±0.113 b	23.16±4.89 b	10.78±1.88 b
P. eburnea	914.01±63.89 a	50.91±7.46 a	305.21±40.66 a	505.39±41.65 a	0.606±0.079 a	28.24±3.11 ab	14.99±2.32 a

Different lowercase letters in the same column indicate significant differences between the parameters ($P < 0.05$)

Discussion

Photosynthetic characteristics

The P_{max} represents the potential maximum net photosynthetic efficiency of a plant, and the greater the P_{max}, the stronger the photosynthetic capacity of the plant (Chen et al., 2023b). Our results showed that the P_{max} of *O. mileensis* (1.59 μmol·m^{-2}·s^{-1}) and *O. cotinifolia* (1.73 μmol·m^{-2}·s^{-1}) was significantly ($P < 0.05$) lower than that of *P. eburnea* (4.69 μmol·m^{-2}·s^{-1}). Similar results were reported for three species of Gesneriaceae in China (Ou et al., 2023). The AQY reflects the utilization capacity of the plants in low light, and the higher the value, the stronger the light energy conversion efficiency of the leaves under low-light conditions (Han et al., 2010). The LSP and LCP reflect the utilization capacity of the plants in high light and low light, respectively (Shang et al., 2020). Our results showed that the AQY, LSP, and LCP of *O. mileensis* and *O. cotinifolia* were significantly ($P < 0.05$) lower than those of *P. eburnea*. This shows that the low light utilization capacity of *O. mileensis* and *O. cotinifolia* was weak and the range of light intensity adaptation was narrower than that of *P. eburnea*. Consistent results have been found for two Theaceae species in China (Chai et al., 2015).

Light and CO_2 are essential raw materials for plant photosynthesis, and they determine the growth and development of plants and are extremely important ecological factors (Russell et al., 2011; Tomimatsu et al., 2016; Guo et al., 2019). Our results showed that the P_n of the three Gesneriaceae species increased slowly when the C_a exceeded 800 μmol·mol^{-1}. It is speculated that this may be due to the change in the pH value in the cells caused by the excessive CO_2 concentration, which led to a decrease in the turgor pressure of the leaf guard cells and influenced stomatal opening, thus, inhibiting the growth of the P_n in the leaves (Terashima et al., 2011; Tholen et al., 2011). This may also be related to the photosynthetic capacity of the leaves being affected by the regeneration rate of ribulose 1, 5-diphosphate (Li et al., 2015). Similar results were reported in five *Hemiboea* species in China (Sun et al., 2010).

Our results showed that the A_{max} of *O. mileensis* (3.896 μmol·m^{-2}·s^{-1}) and *O. cotinifolia* (5.158 μmol·m^{-2}·s^{-1}) was significantly ($P < 0.05$) lower than that of *P. eburnea* (10.724 μmol·m^{-2}·s^{-1}). This indicated that the CO_2 utilization capacity of *O. mileensis* and *O. cotinifolia* was weak than of *P. eburnea*. Consistent results have been found in two Theaceae species (the endangered plant *Camellia pubipetala*: 7.37 μmol·m^{-2}·s^{-1} and the widely distributed related species *C. sinensis*: 19.78 μmol·m^{-2}·s^{-1}; Chai et al., 2015) and three *Geodorum* species (the endangered plant *Geodorum eulophioides*: 8.12 μmol·m^{-2}·s^{-1}, the widely distributed related species *Geodorum densiflorum*: 12.26 μmol·m^{-2}·s^{-1}, and *Geodorum attenuatum*: 10.27 μmol·m^{-2}·s^{-1}; Xu et al., 2024). It is generally believed that the α in the CO_2 response curve is positively correlated with the activity of ribulose 1, 5-diphosphate carboxylase (Fu et al., 2014; Sharkey, 2022). Our results supported that the α of *P. eburnea* was significantly higher than that of *O. mileensis* and *O. cotinifolia* ($P < 0.05$). This may be due to the higher enzyme activity of RuBPCase in *P. eburnea*,

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which can enhance the photosynthetic rate. Similar results were reported in *Gentiana macrophylla* in China (Fu et al., 2014). In this study, the CSP and CCP of *O. mileensis* and *O. cotinifolia* were significantly higher than that of *P. eburnea*, indicating that *O. mileensis* and *O. cotinifolia* have a strong ability to utilize high CO_2 concentrations and a weak ability to utilize low CO_2 concentrations in the external environment than of *P. eburnea*. Therefore, increasing the CO_2 concentration would be beneficial to the growth and development of *O. mileensis* and *O. cotinifolia*.

Field investigations found that the natural habitat communities of *O. mileensis* and *O. cotinifolia* have a shading rate of over 90%, mostly growing on rocks under the forest. They compete with other herbaceous plants for light, nutrients, and space. The adult plants grow well, but their regenerated seedlings are very rare, which may be related to the lighting conditions in their niche. Mo et al. (2012) also found similar results for *O. cotinifolia*. In comparison, the wild natural population of *P. eburnea* grows in limestone mountain forests or under the gully edge of the forest, and the shading rate is about 50%–90%; thus, it has adapted to a wide range of light.

Photosynthetic pigment content

Chlorophyll absorbs light energy in photosynthesis and chlorophyll contents is directly related to rate of photosynthesis (Mao et al., 2007). Our results showed that the contents of Chla, Chlb, and Chl(a + b) in *P. eburnea* were significantly ($P < 0.05$) higher than those in *O. mileensis* and *O. cotinifolia.* This is consistent with results that have been found in three *Geodorum* species in China (Xu et al., 2024).

Leaf structure characteristics

Our results showed that the upper and lower epidermal cells of the three Gesneriaceae plants all had superficial fur, and the stomata were only distributed in the lower epidermis of the leaves. This is not only conducive to resisting external biological invasion and various stressors (Hua et al., 2021; Hernandez et al., 2022), but is also beneficial for maintaining adequate water and reducing transpiration (Sam et al., 2000; Chen et al., 2018). Additionally, the leaf anatomy was composed of an epidermis, mesophyll cells, and leaf veins. Similar results were found in the study of the leaf structure of *O. cotinifolia* (Wang et al., 2014), *P. eburnea*, and *P. medica* (Ye et al., 2015).

Studies have shown that the higher the stomatal density of plants, the thicker the leaf and the palisade tissue, which results in stronger drought resistance ability and the ability to adapt to a strong light environment (Cao et al., 2016; Khan et al., 2023). Our results showed that the *O. mileensis* and *O. cotinifolia* stomatal density, leaf thickness, and palisade tissue thickness were smaller than of *P. eburnea*, indicating that their drought resistance and light adaptation ability of *O. mileensis* and *O. cotinifolia* were weaker than of *P. eburnea*. Similar results have been found in three *Geodorum* species in China (Xu et al., 2024).

The cuticle is the first line of defense against external stress and provides the functions of drought resistance, water retention, ultraviolet radiation resistance, and pest resistance (Liu et al., 2023). Our results showed that the upper epidermis of *P. eburnea* had a thick cuticle, and no cuticle was observed on the epidermis of *O. mileensis* and *O. cotinifolia*. Similar results were found in the study of the leaf structure of *O. cotinifolia* (Wang et al., 2014). This indicates that *O. mileensis* and *O. cotinifolia* have weaker stress resistance when compared with *P. eburnea*.

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The PTT/STT is a measurement of the development degree of the parenchyma tissue of the plant palisade tissue, which can reflect the ability of plants to adapt to drought environments. If the ratio is large, plants have a strong ability to resist cold and drought (Ennajeh et al., 2010; Zhao et al., 2020; Chang et al., 2022). In this study, the PTT/STT of *O. cotinifolia* was the smallest, indicating that the cold resistance and drought resistance of *O. cotinifolia* was small. The PTT/STT of *O. mileensis* was higher than that of *P. eburnea*, which may be related to the genetics of *O. mileensis. O. mileensis* is a recovery plant that can cope with drought by regulating the physiological mechanisms and has a certain drought tolerance. Sun et al. (2022) reported similar results for drought stress in *O. mileensis*.

However, we must acknowledge that this study has certain limitations. We only conducted experiments under cultivation conditions, which do not necessarily reflect the adaptability of the plants in nature environments.

Conclusions and prospects

Our results showed that the P_{max}, AQY, LCP, LSP, A_{max}, Chl(a + b) content, stomatal density, leaf thickness, and palisade tissue thickness of *O. mileensis* and *O. cotinifolia* were significantly ($P < 0.05$) lower than those of *P. eburnea*; however, the CCP and CSP were higher than those of *P. eburnea.* The SD, LT, PTT, and Chl(a + b) of the three species of plants in the Gesneriaceae family were significantly positively correlated with the P_{max} ($P < 0.01$). The findings showed that *O. mileensis* and *O. cotinifolia* have a narrow range of adaptation to light intensity, a low photosynthetic capacity, and a low CO_2 utilization capacity, which may be an important physiological reason for their narrow distribution. Therefore, appropriate shading is required for the ex-situ cultivation of *O. mileensis* and *O. cotinifolia,* and appropriate increases in CO_2 concentration could enhance photosynthesis to promote their growth. In ex-situ conservation, we suggest using shading treatment. The introduced *O. mileensis* and *O. cotinifolia* should be planted in a higher shade environment. In situ conservation, we recommend protecting the upper tree species and original habitats of these species, which will reduce survival competition with other herbaceous plants that grow under moderate light conditions.

Subsequent research can compare the photosynthetic physiological characteristics of endangered species and widely distributed wild natural and cultivated populations of the Gesneriaceae family, which will better reflect the adaptability of plants in constantly changing environments. Photosynthetic physiological experiments can be conducted under different shading conditions to explore the optimal growth environment for endangered species of the Gesneriaceae family. From the perspective of genomics, combined with conservation genetics and conservation genomics, we can elucidate the genetic differences between endangered and widely distributed species of the Gesneriaceae family. The research results can provide meaningful protection for endangered plants in the Gesneriaceae family.

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