# EFFECTS OF DIFFERENT SHADING CONDITIONS ON THE GROWTH, PHOTOSYNTHETIC CHARACTERISTICS AND LEAF STRUCTURE OF *FIRMIANA KWANGSIENSIS* SAPLINGS

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**Abstract.** To determine the optimal light environment for *Firmiana kwangsiensis* saplings, the growth characteristics and physiological traits of the saplings in environments shaded in different ways were compared with those in the full light environment as a control in this paper. The study revealed that *F. kwangsiensis* saplings showed significantly higher ground diameter, radiation area of the root, and fresh weight under 25% shading rate. The chlorophyll a, chlorophyll b, and total amount and ratio of both chlorophylls displayed a decreasing trend with the reduction of shading intensity. The photosynthetic physiological parameters, including maximum net photosynthetic rate ($P_{max}$) and net photosynthetic rate (Pn), etc. of *F. kwangsiensis* saplings under 25% shading condition were higher than that in other treatments. The density of stomata, palisade tissue, spongy tissue, and leaf thickness of leaves increased with higher light intensity. The leaves of saplings under full light condition displayed a "double-layer palisade tissue" structure with drought-resistant properties. The results of correlation analysis showed that photosynthetic physiological characteristics and leaf anatomical structure had the greatest influence on the growth of *F. kwangsiensis* saplings. In summary, *F. kwangsiensis* saplings thrive in shaded environments, with a 25% shading being particularly optimal for their growth. However, it is worth noting that this plant is vulnerable to drought stress, and as such, it is crucial to ensure proper water management when introducing and cultivating it.
**Keywords:** *Firmiana, chlorophyll, photosynthetic rate, stomata, palisade tissue, spongy tissue*

**Abbreviations:** AQY, apparent quantum yield; AW, aboveground part weight; CA, canopy; Chl (a/b), The ratio of chlorophyll a to chlorophyll b; Chl (a + b), The sum of chlorophyll a and chlorophyll b; Chl a, chlorophyll a; Chl b, chlorophyll b; $C_i$, intercellular $CO_2$ concentration; GD, ground diameter; $G_s$, stomatal conductance; LCP, light compensation point; LET, lower epidermal cell thickness; LSP, light saturation point; LT, leaf thickness; OS, Openness of stomata; PH, plant height; $P_{max}$, maximum net photosynthetic rate; $P_n$, net photosynthetic rate; PPT, palisade tissue thickness; PPT/SPT, ratio of palisade tissue to spongy tissue; RAR, radiation area of the root; RTR, root top ratio; SA, Stomatal area; SD, Stomatal density; SL, Stomatal length; SPT, spongy tissue thickness; SW, Stomatal width; $T_r$, transpiration rate; UET, upper epidermal cell thickness; UW, underground part weight

## Introduction

*Firmiana kwangsiensis* H. H. Hsue is a deciduous tree of the genus *Firmiana*, family Malvaceae. The State Council listed this species in the "National Key Wild Plant Protection List (the first batch)" in 1999, and designated it as a key wild plant under second class state protection (Lu and Luo, 2024). The species is indigenous to Guangxi province, China, and is solely found in the regions of limestone, spanning from central to southern Guangxi. The species thrives in areas with well-suited environmental conditions and relatively dense vegetation (Huang, et al., 2016). Additionally, the prolonged florescence period and the bright, golden yellow flowers with a slight red hue make *F. kwangsiensis* an optimal option for urban greening. Moreover, its straight tree


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shape, lightweight and soft wood, and resistance to cracking make it a high-quality material for crafting furniture and interior decor (Huang, et al., 2016). However, currently, the number of *F. kwangsiensis* is rapidly declining due to environmental destruction, pollution, deforestation, and other human activities. This has led to the near-extinction of wild forest resources. As a result, the plant has been classified as an extremely small population and has been upgraded to a national-level protected key plant in China in 2021. Therefore, as we endeavor to enhance the preservation of the extant germplasm resources, it will be imperative to devise effective strategies for the precise and effective cultivation of this species. This is unequivocally one of the pressing issues that must be addressed in the realm of seedling propagation of *F. kwangsiensis* in the future.

Currently, the primary research focus on *F. kwangsiensis* involves resource investigation (He and Lu, 2006), sowing, and seedling raising (Huang, et al., 2008; Fu, et al., 2010; Luo, et al., 2015a), genetic diversity (Dai, et al., 2013; Luo, et al., 2015b), among others. Additionally, research on photosynthetic characteristics is progressively advancing (Mao, et al., 2011). Mao et al. (2010) found that transpiration rate was the main factor affecting the net photosynthetic rate of *F. kwangsiensis* saplings. They suggested that the transpiration rate could be enhanced by increasing light transmittance and appropriate watering to ameliorate the net photosynthetic rate, thereby promoting seedling growth. Light is a key ecological factor influencing plant growth and development, playing a crucial role in plant morphogenesis and organic matter accumulation (Qiao et al., 2024). Research has noted differences in plant adaptation to light environments during different growth stages (Li, et al., 2020). *F. kwangsiensis* is a species adapted to sunlight. The adult plants occupy a single dominant position with a favorable light environment. However, only 23.6% of the total population consists of saplings, which renders the entire population unstable (Luo, et al., 2010). Lu et al. (2023) discovered that light significantly affects the regeneration of *F. kwangsiensis* in the wild by investigating light adaptability. The seedling growth necessitates adequate light. Nonetheless, the research only assessed the physiological metrics of seedlings in the early stage and did not scrutinize the morphogenesis of seedlings in the later stages. Therefore, based on prior research, this study examines growth conditions, photosynthetic features, and leaf anatomy of *F. kwangsiensis* saplings. Experimentation was conducted under varying degrees of shade intensity (75%, 50%, and 25%) with full light environment serving as the control (CK). Relationships between morphological characteristics and physiological indicators were explored. The aim was to identify the optimal light conditions for their cultivation and provide valuable insights into their growth under different light conditions. Our findings will support the scientific basis for introducing and cultivating *F. kwangsiensis* saplings.

## Experimental field condition and methods

### *Experimental field condition*

The experimental field is situated in the Guangxi Institute of Botany, Guilin, in southern China (25.28° N, 110.29° E). The climate of the field is characterized by a subtropical monsoon climate, with an annual temperature of 19°C. The average temperature in July rises up to 28.4°C, whereas in January it drops to 7.7°C. The absolute high temperature is 38°C, and the absolute low temperature is -5.5°C. There are frosty conditions in the winter months with a yearly frost period of 9-24 days.


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Annual rainfall is 1800 mm and the relative humidity is 78.0%. The soil has an acidic composition with a pH level of 6.0.

### *Material*

One-year-old seedlings of *F. kwangsiensis* exhibiting robust growth, devoid of plant diseases and insect pests, and with uniform seedling height and ground diameter were chosen. Each seedling was transplanted and grown in a 50 cm × 50 cm nutrient pot.

### *Methods*

#### *Different shade treatments*

The *F. kwangsiensis* saplings handpicked for the study were carefully transplanted into four experimental plots over a period of two months. In each experimental plot, the planting distance between individual seedlings was maintained at approximately 1 m. Each plot received uniform water management during the plantation. Depending on the seasonal moisture levels, irrigation was performed once or twice a week, with each plant receiving 1.0 liter of water per irrigation. This ensured that soil moisture remained at approximately 70% of the field capacity.

In April 2021, shading was applied to the plants; poorly growing ones were eliminated before the treatment. Each plot retained six healthy and thriving saplings of *F. kwangsiensis*. With full light and no shading treatment as the control group (CK), three shading treatments were established: L1 (shading rate of 75%), L2 (shading rate of 50%), and L3 (shading rate of 25%). During the culture period, other factors such as water and fertilizer management were kept consistent, so that the growth of *F. kwangsiensis* saplings under different treatments was only affected by the factor of light intensity.

#### *Measurement of plant height, canopy, ground diameter and other biomass.*

After two years of being grown in varying levels of shade, three plants from each treatment were selected at random. The biomass, including measurements such as plant height (PH), canopy (CA), were recorded using a scale. Additionally, the ground diameter (GD) of the seedlings, 20 cm from the soil mark, was measured using a vernier caliper. Once all measurements were taken, the entire plant was removed without compromising the root system. The radiation area of the root (RAR) was measured with a tape. After washing and drying the soil, it was separated into its above-ground and underground parts. Finally, weigh and record the aboveground part weight (AW) and underground part weight (UW).

#### *Determination of chlorophyll content*

After two years of implementing shading treatments, we selected five healthy and disease-free leaves for each treatment. We selected healthy, pest- and disease-free leaves from three randomly chosen plants in each treatment group. Taking care to avoid the main vein, we cut 1 cm × 1 cm sections of leaf tissue from each leaf, which were then sliced into filaments measuring approximately 5 mm in length and 2 mm in width. Next, we placed 0.2 g of the leaf tissue in a 20 mL centrifuge tube and added a chlorophyll extract comprising 95% ethanol and 80% acetone in equal parts. The leaf


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tissue was wrapped entirely in tin foil and stored devoid of light for 24 h. Once the tissue became completely bleached, it was removed from the tin foil and its extract was transferred into a 25 mL volumetric flask, which was later diluted. After thorough mixing, the chlorophyll solution was prepared. The levels of chlorophyll a and b were measured at wavelengths of 470 nm, 649 nm, 665 nm respectively, using a TU-1901 UV spectrophotometer (Beijng Puxi general instrument CO. Ltd., Beijng, China) with a chlorophyll extract solution as a reference. Chla and chlb contents in the leaves were determined following the method described by Pan et al. (2023).

*Determination of light response curve*

In August 2021, on a sunny day, three healthy leaves from the middle section were randomly selected for the determination of the light response curve using the LI-6400 portable photosynthesis instrument with an LED red and blue light source leaf chamber (Ye, et al., 2010). The leaves had undergone four months of shading treatment and were free from pests and diseases. PAR was set to light intensities of 0, 20, 50, 100, 200, 400, 800, 1000, 1200, 1400, and 1500 $\mu mol \cdot m^{-2} \cdot s^{-1}$, with three parallel results taken at each level. The concentration of carbon dioxide stood at 400 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Before taking measurements, the leaves were exposed to a light intensity of 1500 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for 20 min, and the measurements were taken between 10:00 am and 12:00 am. For each shading treatment, five plants were selected for measuring the light response curves.

*Determination of diurnal variation of photosynthesis*

After four months of shading treatment, net photosynthetic rate ($P_{n}$), transpiration rate ($T_{r}$), stomatal conductance ($G_{s}$) and intercellular $CO_2$ concentration ($C_{i}$) of *F. kwangsiensis* were measured using the transparent leaf chamber of the LI-6400 portable photosynthesis instrument on a sunny day in August 2021 (Ye, et al., 2010). Three leaves at the same position were measured for each plant. The measurement of diurnal variation is fully completed under the condition of natural light. The light intensity can reach 2000 $\mu mol \cdot m^{-2} \cdot s^{-1}$, the carbon dioxide concentration in the air is about 400 $\mu mol \cdot m^{-2} \cdot s^{-1}$, the maximum temperature is about 36°C and the maximum humidity is 87°C. The measurement time was 8:30-18:30, and the diurnal variation of photosynthesis was measured every 1.5 h. For each shading treatment, five plants were selected to measure the diurnal variations in photosynthesis.

*Stomatal structure and anatomical structure of leaves*

The stomatal characteristics and leaf anatomical structure of *F. kwangsiensis* under different shading conditions were investigated following the method described by Pan et al. (2024). After two years of shade treatment, four healthy leaves from the same position on *F. kwangsiensis* were selected for the determination of photosynthesis. The leaves were cut into 25 mm×25 mm small leaves along the transverse section, avoiding the main leaf vein, and five were randomly selected and immediately placed in 2.5% glutaraldehyde fixative for 30 min. The leaves were then gradient eluted with ethanol solutions of different concentrations (30, 50, 70, 80, 90, 100, 100%) for 15 min each, dried and gilded at the critical point. The upper epidermis, lower epidermis and stomata of the leaves were observed with a ZEISS EVO18 vacuum scanning microscope (Carl Zeiss AG, Oberkochen, Germany). Stomatal length (SL), Stomatal width (SW) and


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Stomatal density (SD) were measured using Axio Vision SE64 Rel.4.9.1 SEM software (Carl Zeiss AG, Oberkochen, Germany). Stomatal density (SD) = number of stomata in visual field/field area ($\mu m^2$); Stomatal area = $SL \cdot SW \cdot \pi/4$, $\pi = 3.14$. Openness of stomata (OS) = SW/SL. The mean values of 30 visual field statistical indicators were taken for each treatment.

Five small leaves of 25 mm×25 mm obtained in the previous step were randomly selected and placed in FAA fixative (70% ethanol: formalin: glacial acetic acid = 90: 5: 5) for fixation. Ethanol and xylene series dehydration, paraffin embedding, toluidine blue staining, neutral rubber sealing. The sections were observed and photographed under a light microscope, and the microscopic parameters were measured using the CaseViewer graphical analysis software (3DHISTECH Ltd., Budapest, Hungary). The measured parameters were: upper epidermal cell thickness (UET), lower epidermal cell thickness (LET), leaf thickness (LT), palisade tissue thickness (PT), sponge tissue thickness (ST), palisade tissue/sponge tissue thickness ratio (PT/ST). 30 visual fields were taken to measure the statistical parameters of each index.

### *Data analysis*

Excel 2019 software was used for preliminary statistics and data processing, and the T-test was performed using SPSS 23.0 software, and Duncan's multiple range test was applied to assess the significance of differences in growth and photosynthetic characteristics of *F. kwangsiensis* saplings under different shading treatments. The non-rectangular hyperbola correction model (Ye and Wang, 2009) in the photosynthetic calculation software was used to fit the light response curve, and Origin 8.5 software was used to generate the chlorophyll content in leaves under different shading conditions and heat map of correlation analysis between morphological characteristic index and physiological characteristic index.

## Result

### *Growth of F. kwangsiensis sapling under different shading conditions*

The growth of *F. kwangsiensis* saplings under different shade conditions is shown in *Table 1*. The six indices, including plant height, canopy and ground diameter, showed a trend of first increasing and then decreasing with the increase in light transmittance. The plant height and canopy of the plants under L2 treatment were significantly higher than those of the other three treatments ($P < 0.05$). Soil diameter, radiation area of the root and fresh weight of above-ground parts in L3 treatment were significantly higher than those in the other three treatments ($P < 0.05$). Among them, in terms of fresh weight of aboveground parts, L3 treatment group was 11.34 times, 1.36 times and 11.34 times of other treatment groups, respectively. In terms of fresh weight of underground parts, there was no significant difference between L3 and L2, but the two treatment groups were significantly higher than L1 and CK. Unlike the other indicators, the root-shoot ratio showed a trend of first increasing, then decreasing and then increasing with the decrease in shade. Under CK, the root-shoot ratio of the *F. kwangsiensis* saplings was the largest, and the root-shoot ratio of the L3 treatment group was the smallest. Based on the above growth data, it can be seen that the L3 treatment group (25% shade) is most conducive to the growth of *F. kwangsiensis* saplings.


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***Table 1.*** *Growth status of F. kwangsiensis sapling under different shading environments*

| Treatment | PH (m) | GD (m) | CA ($m^2$) | RAR ($m^2$) | AW (kg) | UW (kg) | RTR |
|---|---|---|---|---|---|---|---|
| L1 | 1.340±0.410 c | 0.016±0.006 c | 0.565±0.181 c | 0.067±0.013 c | 0.205±0.017 c | 0.200±0.127 b | 0.976±0.586 b |
| L2 | 3.1240±0.309 a | 0.055±0.007 b | 2.268±0.672 a | 0.958±0.093 b | 1.708±0.576 b | 1.688±0.488 a | 0.988±0.087 b |
| L3 | 2.895±0.144 b | 0.065±0.014 a | 1.370±0.192 b | 2.057±0.381 a | 2.325±0.286 a | 1.583±0.173 a | 0.681±0.034 c |
| CK | 1.28±0.108 c | 0.020±0.003 c | 0.062±0.023 c | 0.115±0.046 c | 0.205±0.021 c | 0.253±0.039 b | 1.223±0.116 a |

L1 is 75% shading treatment. L2 is 50% shading treatment. L3 is 25% shading treatment. CK was unshaded treatment. Different letters represented significant difference ($P < 0.05$). The same as follow

### *Chlorophyll content in leaves of F. kwangsiensis sapling under different shading conditions*

From *Figure 1*, the result showed that with the decrease of shading intensity, chlorophyll a, chlorophyll b and the total amount of two chlorophylls all showed a decreasing trend, but chlorophyll a decreased faster. The comparison between the treatment groups showed that the chlorophyll a, chlorophyll b and total chlorophyll contents in the leaves of the L1 treatment group were significantly higher than those of the other treatment groups ($P < 0.05$), and there was a significant difference compared with the other treatments ($P < 0.05$). In addition, it can be seen from *Figure 1* that with the decrease in shade intensity, Chla/b in the leaves of *F. kwangsiensis* saplings showed a trend of first decreasing and then increasing. The ratio of the L1 treatment group was the highest, and it was significantly higher than that of the other treatment groups ($P < 0.05$).

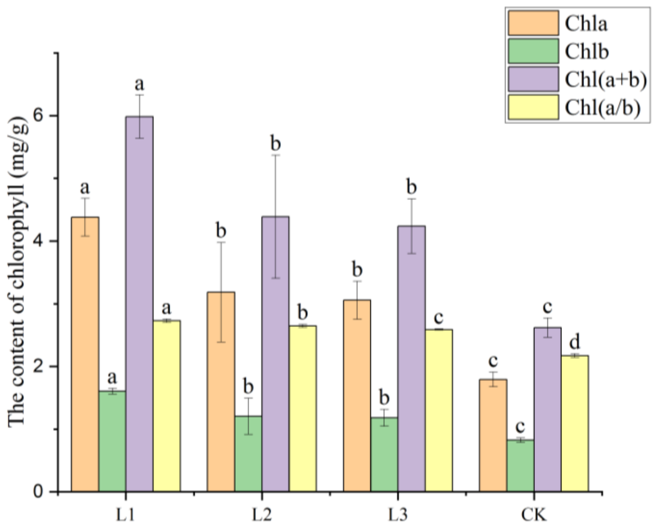


***Figure 1.*** *The content of Chlorophyll in leaves of F. kwangsiensis sapling under different shading. Different letters represented significant difference (P < 0.05). The same as follow. The error bars represent the standard deviation of each data set, illustrating the variability within each group*

### *Response of net photosynthetic rate to light intensity of F. kwangsiensis sapling under different shading conditions*

The net photosynthetic rate ($P_n$) under different shading conditions is shown in *Figure 2*. Under different conditions, the trend of change in $P_n$ with photosynthetically


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active radiation (PAR) was different. Under CK, when PAR was in the range of 0-200 μmol·m$^{-2}$·s$^{-1}$, $P_n$ increased linearly. After that, the increasing trend gradually slowed down and at 600 μmol·m$^{-2}$·s$^{-1}$, $P_n$ reached the maximum value of 3.361 μmol·m$^{-2}$·s$^{-1}$. After reaching the peak, $P_n$ gradually decreased with increasing PAR. Under L1, $P_n$ had the least tendency to change with PAR. When PAR was in the range of 0-150 μmol·m$^{-2}$·s$^{-1}$, $P_n$ increased linearly. Thereafter, the increasing trend slowed down and was increasing. The overall change trend of $P_n$ of *F. kwangsiensis* saplings in L2 and L3 treatment groups was higher than that of the other two treatments, and the change trend of $P_n$ in L2 treatment group was lower than that of L3 overall, and there were similarities and differences between the two trends. When PAR was in the range of 0-200 μmol·m$^{-2}$·s$^{-1}$, the $P_n$ of L2 and L3 increased linearly. After more than 200 μmol·m$^{-2}$·s$^{-1}$, the change trend of both slowed down, but the $P_n$ of L3 increased with the increase in PAR. The $P_n$ of L2 increased up to 1000 μmol·m$^{-2}$·s$^{-1}$ in PAR and its value showed a decreasing trend. The peak value of $P_n$ was 9.390 μmol·m$^{-2}$·s$^{-1}$. Overall, the magnitude of $P_n$ under different shading treatments was as follows: L3 > L2 > CK > L1.

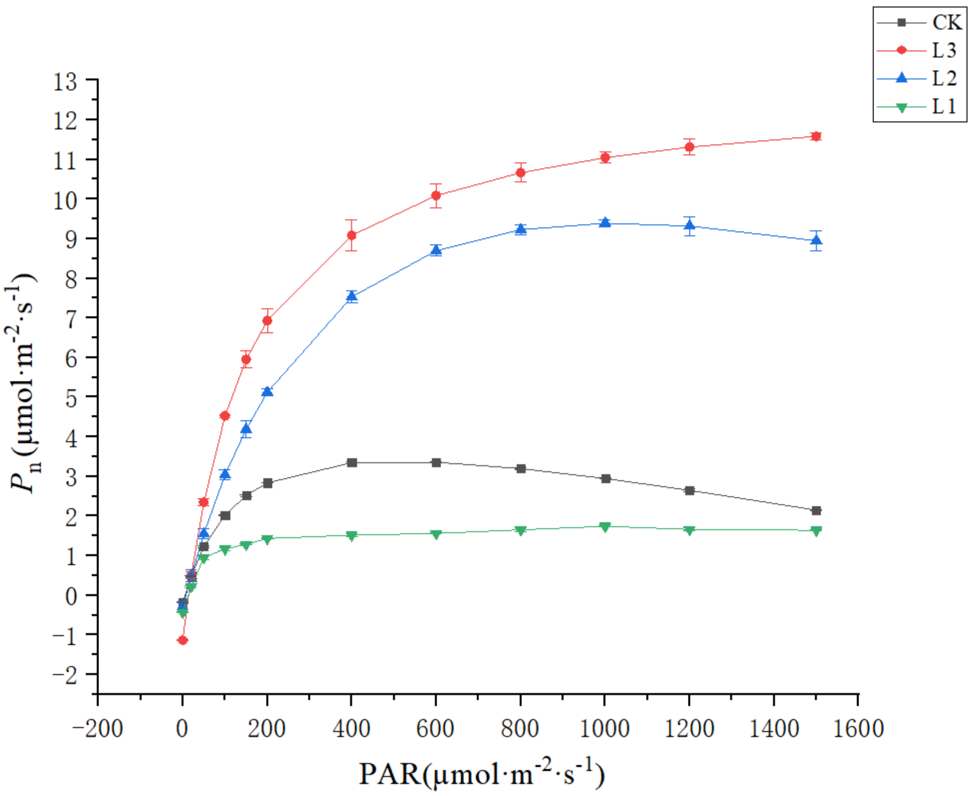


***Figure 2.*** *Response of photosynthetic rate ($P_n$) to photosynthetically active radiation (PAR) under different shade treatments in F. kwangsiensis saplings*

The photosynthetic parameters of *F. kwangsiensis* seedlings under different shading conditions are shown in *Table 2*. The maximum net photosynthetic rate ($P_{max}$), apparent quantum efficiency (AQY) and light compensation point (LCP) of L3 were significantly higher than those of the other three treatments, and the light saturation point (LSP) of L2 was significantly higher than that of the other three treatments. With increasing light transmittance, $P_{max}$ showed a tendency to first increase and then decrease. The


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maximum $P_{max}$ of L3 was 12.644 ± 0.482 μmol·m$^{-2}$·s$^{-1}$, and the $P_{max}$ of L1 treatment was the smallest. AQY, LSP, LCP and Pmax are the same with the increase in light transmittance, showing a trend of first increasing and then decreasing. Specifically, the AQY of L3 treatment group was the largest, which was 0.046 ± 0.04 μmol·m$^{-2}$·s$^{-1}$, and there was no significant difference in AQY between L1 and CK ($P > 0.05$). The LSP of L2 was the largest, which was 346.755 ± 5.761 μmol·m$^{-2}$·s$^{-1}$, and the LSP of L1 was the smallest. The maximum LSP of L3 was 13.235 ± 0.748 μmol·m$^{-2}$·s$^{-1}$ and the LSP of CK was the smallest.

***Table 2.*** *Photosynthetic parameters of leaves of F. kwangsiensis saplings under different shading treatments (unit: μmol·m$^{-2}$·s$^{-1}$)*

| Treatment | $P_{max}$ | AQY | LSP | LCP |
|---|---|---|---|---|
| L1 | 1.677 ± 0.039 d | 0.011 ± 0.003 c | 216.266 ± 2.532 c | 6.661 ± 0.535 c |
| L2 | 9.392 ± 0.482 b | 0.046 ± 0.004 a | 327.512 ± 2.076 b | 7.260 ± 0.108 b |
| L3 | 12.644 ± 0.193 a | 0.032 ± 0.004 b | 346.755 ± 5.761 a | 13.235 ± 0.748 a |
| CK | 3.387 ± 0.279 c | 0.015 ± 0.001 c | 199.079 ± 5.189 d | 5.047 ± 0.182 d |

***Diurnal variation of main photosynthetic parameters of F. kwangsiensis sapling under different shading conditions***

*Figure 3a* shows the diurnal variation of gas exchange parameters of *F. kwangsiensis* saplings under different shading conditions. It can be seen that changes of $P_n$ in *F. kwangsiensis* saplings are basically similar, all of them first increase, then peak, then decline, then increase again, reach second peak and finally decline again, all of them show a “bimodal” curve, but there are differences in peak time. In the four treatments, the strongest peak of $P_n$ occurred at 10:00. Under the different shading treatments, the phenomenon of “midday depression of photosynthesis” appeared in the *F. kwangsiensis* saplings. The daily average net photosynthetic rate was as follows: L3 > L2 > CK > L1 (*Table 3*). It was found that shading of 40% was most conducive to accumulating photosynthetic products. *Figure 3(b)* shows the transpiration rate of *F. kwangsiensis* saplings under different shading conditions. Under the different shading environments, the $T_r$ of *F. kwangsiensis* sapling showed a “bimodal” curve, showing a trend of increase-decrease-increase-decrease, and the strongest peak appeared at 10:00 a.m. The second peak of the other three treatments occurred around 2:30 pm, while the second peak of L1 occurred around 1:00 pm. In contrast to the other two treatments, the $T_r$ of CK and L1 was smaller. The trend of change was not obvious. The average value of $T_r$ on a daily basis was as follows: L3 > L2 > CK > L1 (*Table 3*).

From *Fig 3 (c)*, it can be seen that the $G_s$ under the four treatments all showed a “single peak” curve, which first increased and then decreased, and all peaks appeared at 10:00, indicating that the stomatal conductance was the largest and the stomatal opening degree was the highest. From the comparison of the four treatments, it was found that the diurnal variation of stomatal conductance of L2 and L3 treatment groups was similar and significantly higher than that of L1 and CK. The magnitude of $G_s$ was as follows: L3 > L2 > CK > L1 (*Table 3*). From *Fig 3 (d)* it can be seen that the $C_i$ of L1 and L2 showed a “W” type, first decreasing and then increasing, then decreasing again and finally increasing again. L3 and CK were “V” types. The daily average $C_i$ was as follows: L1 > L3 > L2 > CK.


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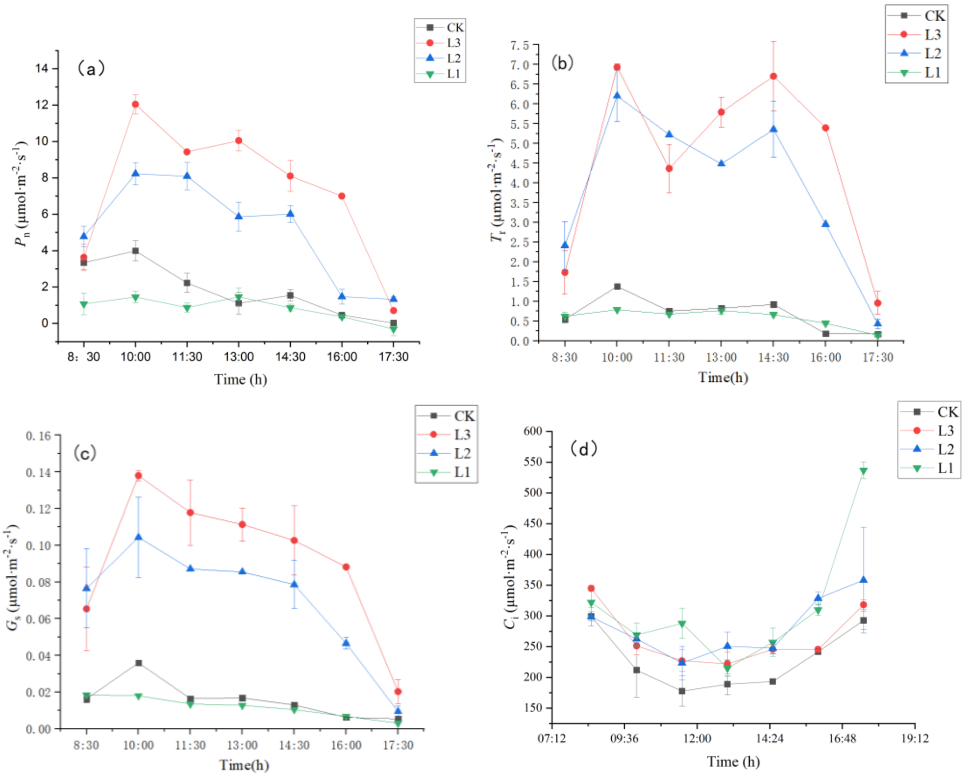


***Figure 3.*** *Daily variation of gas exchange parameters of F. kwangsiensis sapling under different shading treatments. a: Diurnal variation of Photosynthesis of F. kwangsiensis sapling under different shading conditions; b: Diurnal variation of Transpiration Rate of F. kwangsiensis sapling under different shading conditions; c: Diurnal variations of Stomatal Conductance F. kwangsiensis sapling under different shading conditions; d: Diurnal variation of intercellular $CO_2$ concentration of F. kwangsiensis sapling under different shading environments.*

***Table 3.*** *Daily average gas exchange parameters of F. kwangsiensis sapling under different shading treatments (unit: $\mu mol{\cdot}m^{-2}{\cdot}s^{-1}$)*

| Treatment | $P_n$ | $T_r$ | $G_s$ | $C_i$ |
|---|---|---|---|---|
| L1 | 0.823 ± 0.818 b | 0.587 ± 0.227 b | 0.012 ± 0.006 b | 313.112 ± 53.027 a |
| L2 | 5.108 ± 2.817 a | 3.866 ± 2.027 a | 0.070 ± 0.032 a | 252.089 ± 46.133 a |
| L3 | 7.334 ± 3.895 a | 4.555 ± 2.362 a | 0.092 ± 0.039 a | 264.848 ± 47.257 a |
| CK | 1.081 ± 1.367 b | 0.784 ± 0.428 b | 0.016 ± 0.010 b | 229.266 ± 74.937 a |

### *Stomatal and anatomical structure of leaves*

The stomatal structure of the leaves of *F. kwangsiensis* saplings under different shading conditions is shown in *Figure 4* and *Table 4*. The stomata of *F. kwangsiensis* sapling are mainly distributed on the back of the leaves. There are no subsidiary cells around the stomata. The guard cells are surrounded by several common epidermal cells which are irregular. With the increase in light intensity, the stomatal density of *F. kwangsiensis* saplings increased, and the stomatal density of saplings in CK treatment group was the highest, which was significantly higher than that in L1, L2 and L3


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treatment groups. The stomatal area of *F. kwangsiensis* saplings in CK treatment was significantly lower than that in other treatments. Among the four shade treatments, there was no significant difference in stomatal aperture.

It can be seen from *Figure 5* that the upper and lower epidermis of the leaves of the *F. kwangsiensis* saplings are composed of monolayer cells. Below the upper epidermis there are palisade and spongy tissues. In L1, the palisade and spongy tissues of the leaves were significantly stunted. The palisade tissue and spongy tissue of the leaves in L2 showed clear differentiation and cell development was better. When the light intensity was further increased, the leaves gradually showed double-layered palisade tissue. The leaves in CK had obvious double layer palisade tissue. The leaf anatomical structure parameters of *F. kwangsiensis* saplings under different shade conditions are shown in *Table 5*. Thickness of upper epidermis is higher than that of lower epidermis in all treatment groups. With increasing light intensity, the thickness of the upper and lower epidermis first decreased and then increased, whereas the thickness of the palisade tissue, the spongy tissue and the leaf always increased. The thickness of palisade tissue, spongy tissue and leaf was greatest in CK.

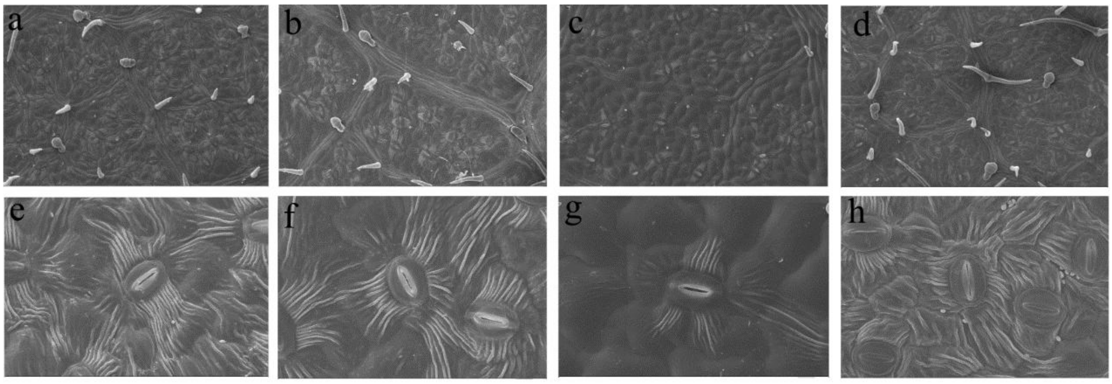


***Figure 4.*** *Stomatal structure of F. kwangsiensis saplings under different shading environments. a (200×) and e (1.00 K×) are the stomatal structure of leaves under L1; b (200×) and f (1.00 K×) correspond to L2; c (200×) and g (1.00 K×) correspond to L3; d (200×) and h (1.00 K×) correspond to CK*

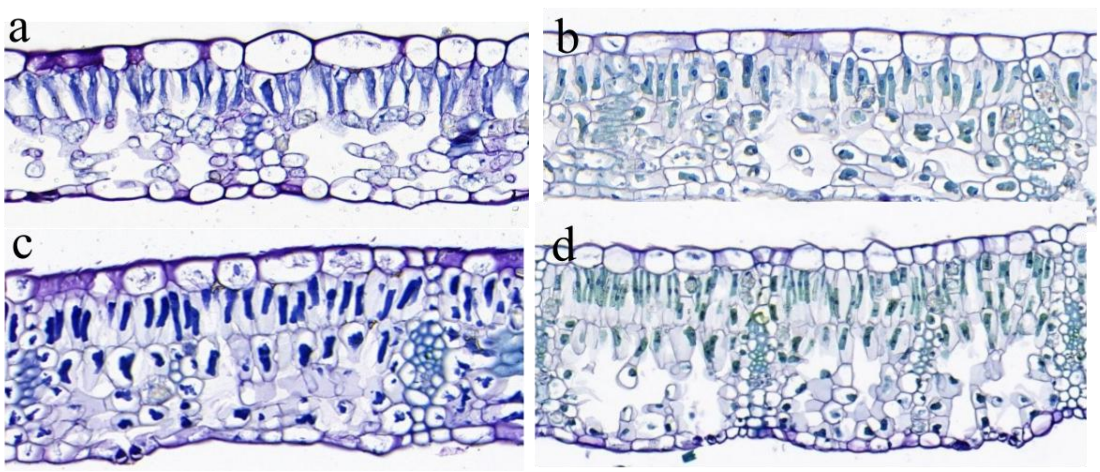


***Figure 5.*** *Leaf anatomical structure of F. kwangsiensis saplings under different shading treatments. a, b, c, d were the leaf anatomical structure under L1, L2, L3 and CK, respectively*


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***Table 4.** Stomatal parameters of F. kwangsiensis saplings leaves under varying shading conditions*

| Treatment | SD | SA (μm$^2$) | Openness of stomata (μm$^2$) |
|---|---|---|---|
| L1 | 241.966 ± 19.222 a | 259.216 ± 25.572 a | 0.611 ± 0.060 a |
| L2 | 136.8763 ± 9.388 b | 270.553 ± 25.832 a | 0.627 ± 0.063 a |
| L3 | 102.495 ± 14.534 c | 279.832 ± 31.666 a | 0.681 ± 0.063 a |
| CK | 219.261 ± 23.933 a | 230.005 ± 41.028 b | 0.716 ± 0.080 a |

***Table 5.** Leaf anatomical structure parameters of F. kwangsiensis saplings under varying shading conditions (unit: μm)*

| | UET | LET | PPT | SPT | LT | PPT/SPT |
|---|---|---|---|---|---|---|
| L1 | 20.918 ± 1.815 a | 14.036 ± 2.952 a,b | 32.527 ± 3.201 b | 44.609 ± 9.503 c | 104.157 ± 2.185 d | 0.729 ± 0.229 a |
| L2 | 16.371 ± 2.901 b | 9.600 ± 1.675 c | 32.707 ± 3.403 b | 45.679 ± 5.595 c | 112.291 ± 6.011 c | 0.716 ± 0.151 a |
| L3 | 20.312 ± 3.187 a | 12.824 ± 2.595 b,c | 33.176 ± 1.677 b | 69.976 ± 9.779 b | 136.288 ± 8.599 b | 0.484 ± 0.074 b |
| CK | 20.614 ± 3.153 a | 15.521 ± 4.257 a | 45.507 ± 5.382 a | 100.979 ± 11.170 a | 182.621 ± 6.055 a | 0.461 ± 0.108 b |

### *Correlation analysis*

*Figure 6* illustrates the heat map of correlation analysis between growth characteristics, chlorophyll content characteristics, photosynthetic characteristics and leaf structure characteristics of *F. kwangsiensis* saplings. Except RSR, other growth characteristics, such as PH, GD, Ch, and so on, were basically positively correlated with photosynthetic physiological parameters, and negatively correlated with SD, PPT and LT, while the correlation with chlorophyll content characteristics was not obvious。The parameters defining the chlorophyll content demonstrated negative correlations with PPT, SPT, LT, and others, but showed minimal correlations with the remaining parameters. Except for Ci, there were significant positive correlations between the parameters of photosynthetic characteristics, but there were more significant negative correlations between the photosynthetic parameters and leaf anatomical structures such as SD, LT and PPT. The correlation between the parameters of leaf anatomical structure was weak, but there was a significant positive correlation between PPT and LT.

## Discussion

When the light environment changes, plants tend to change their morphological structure to get more light, such as reducing branches and changing leaf shape (Paul and Bruce, 2023; Rehman, et al., 2024). We found that shading had a significant effect on plant height, soil diameter and canopy of *F. kwangsiensis* saplings. Under the 50% shade treatment, the plant height and canopy of the seedlings were significantly higher than those of the other treatment groups, while the radiation area of the root, ground diameter and fresh weight of the aboveground part were the highest under the 25% shade treatment. This indicates that moderate shade is beneficial for the growth and development of *F. kwangsiensis* seedlings. On the one hand, in the primary community, *F. kwangsiensis* saplings survive in the shade. On the other hand, because the mechanism of protection and utilization of excess light energy by saplings may not be perfect enough, excessive light will damage the tissue structure of leaves and inhibit the growth of plants (Zhang, et al., 2024). The study found that under full light, the *F.*


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*kwangsiensis* seedlings were pygmyism, and the leaves were withered and yellowed. To adapt to different light environments, the accumulation and distribution of biomass in different parts will also be different (Zhou, et al., 2023). In the low light environment, plants will place more biomass in the aerial part and increase the yield of photosynthetic products. In the high light environment, plants will increase the use of the underground part to obtain more water and nutrients (Daryaei et al., 2019). In this paper, this phenomenon was also found in the shade treatment of *F. kwangsiensis* saplings. Compared with the 50% shade treatment group, the *F. kwangsiensis* sapling put more organic matter into the roots to absorb more water and nutrients in the 75% shade environment. Mao et al. (2010) found that the main factor affecting the photosynthetic rate of *F. kwangsiensis* sapling was the transpiration rate, so sufficient water was of great importance to ensure normal development and growth of *F. kwangsiensis* sapling.

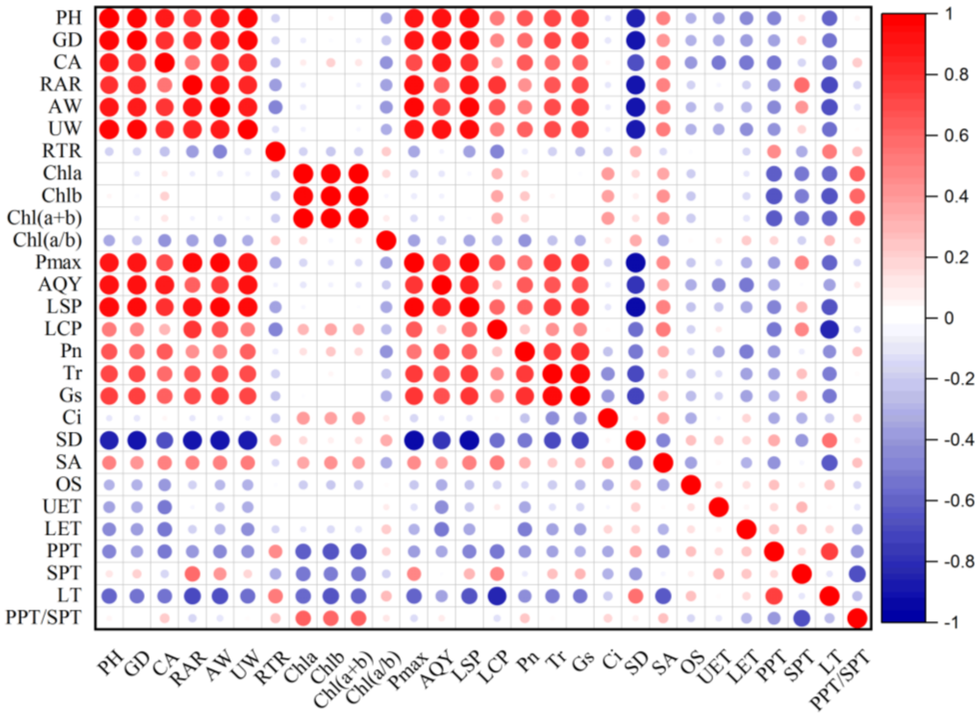


***Figure 6.*** *Heat map of correlation analysis between growth, photosynthetic physiology and leaf structure of F. kwangsiensis saplings*

In addition to the corresponding changes in morphological structure, there will also be corresponding changes in physiological characteristics. In order to adapt to different light environments, the content and proportion of chlorophyll in leaves will change as the light environment changes (Burgess, et al., 2023; Tsujimoto, et al., 2021). Some studies have found that chlorophyll a mainly absorbs the long wavelength part of red light, and its content may reflect the ability of leaves to use light energy, while chlorophyll b mainly absorbs blue and purple light, and its content and total chlorophyll reflect the ability to capture light (Cheng, et al., 2019). Therefore, when the plant is transferred from a high light environment to a low light environment, the reduction in light energy received will cause the plant to increase the total amount of chlorophyll, especially the chlorophyll b content, and improve the ability to capture the low light.


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Therefore, with the decrease in light, the contents of chlorophyll a, chlorophyll b and total chlorophyll increase, and the ratio of chlorophyll a/b also increases. This phenomenon was also found in the shading test of *Ilex asprella* (Cai, et al., 2020), *Cunninghamia lanceolata* (Tang, et al., 2023) and *Osmanthus fragrans* (Peng, et al., 2002). The same conclusion was reached in this study. This shows that the chlorophyll content and proportion in the leaves of *F. kwangsiensis* saplings changes accordingly to adapt to different light environments, which is one of its survival strategies. In addition, chlorophyll a/b is often used to assess the shade tolerance of plants. Some studies have suggested that if the ratio is greater than 3, it is a sun plant, and if it is less than 3, it is a shade plant with high shade tolerance (An et al., 2022; Simkin, et al., 2022). The results of this study showed that Chla/b in the leaves of *F. kwangsiensis* seedlings decreased with increasing light transmittance, but the ratio was less than 3. Furthermore, the field study also found that *F. kwangsiensis* saplings were mostly found on the scrub or lower part of the valley slope. In the lower part of the ecological community of the natural environment, the vegetation was dense, the light intensity was moderate, and the plants often had a high shade tolerance. Therefore, this paper believes that the *F. kwangsiensis* sapling has certain shade tolerance characteristics and moderate shade is conducive to its growth.

To further explore the appropriate light environment for *F. kwangsiensis* saplings, the photosynthetic characteristics under four shading treatments were studied and compared. The light response curve is of great importance for understanding the photochemical efficiency of plant photosynthesis (Caddell et al., 2023). LSP and LCP represent the upper and lower limits of the range of light energy available to plants, respectively, and their values can directly reflect the light demand characteristics (Song, et al., 2016). This study found that LSP and LCP of medium shade treatments (L2, L3) were significantly higher than those of full light treatments (CK) and heavy shade treatments (L1), indicating that under appropriate shade conditions, *F. kwangsiensis* saplings can increase use of weak light and strong light through reduced LCP and LSP, and maximize organic matter accumulation for its own growth and development. This is in agreement with the research results of Bai et al. (2017) on Rhododendron moulmainense seedlings. The AQY is also a commonly used method to measure the utilization of low levels of light in plants (Li, et al., 2021). This study found that AQY was greatest in 25% shade, which was 0.046, indicating that in this light environment, *F. kwangsiensis* saplings had the highest use efficiency of low light. Combined with $P_{max}$, LSP, LCP, AQY and other related parameters, this paper believes that under the light environment with 25% shading rate, the seedlings of *F. kwangsiensis* sapling have good adaptability to strong light and weak light, and the utilization rate of light energy is the highest.

In the natural environment, the photosynthetic rate of plants is affected not only by light radiation, but also by external factors such as temperature, humidity and internal and external factors such as stomatal conductance. Therefore, the diurnal variation curve of plant photosynthetic rate is not simple. In this study, it was found that the diurnal variation curve of photosynthesis of *F. kwangsiensis* saplings under different shading environments showed a “bimodal” type, with the phenomenon of midday depression of photosynthesis. However, unlike the results of the previous studies (Mao, et al., 2010), this study found that the overall photosynthetic rate of *F. kwangsiensis* saplings was lower under full light treatment. In this paper, the measurement time is July and the previous measurement time is October. There are large differences in light


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intensity, atmospheric temperature and humidity between these two periods. Due to the prolonged high temperature and high light stress in summer, the leaves of the plants are burned, which causes severe damage to the photosynthetic mechanism, thus limiting their photosynthetic capacity. Therefore, this paper suggests that this may be one of the reasons for the difference in diurnal variation of photosynthesis. This phenomenon was also observed in the study of *Rhodomyrtus tomentosa* (Yang, et al., 2022) and *Robinia pseudoacacia* L. (Liu, et al., 2020). The phenomenon of "midday depression of photosynthesis" is more common in subtropical regions. In comparison, it was found that the time of midday depression of photosynthesis in *F. kwangsiensis* saplings under four shading treatments was 10:00 a.m., but the overall trend of diurnal variation was different. Thus, this paper suggests that the causes of "midday depression of photosynthesis" may differ, leading to this phenomenon. Farquhar and Sharkey (1982) suggested that when $P_n$ decreased, $G_s$ and $C_i$ decreased and stomatal limitation was the main factor. When $G_s$ decreases and $C_i$ increases, non-stomatal limitation is dominant. Based on this reference, we found that under heavy shade (L1), non-stomatal factors caused the plant's "midday depression." The "midday depression" of the *F. kwangsiensis* saplings was the stomatal limiting factor in the L2, L3 and CK treatment groups.

Stomata are the main part of gas exchange and water transpiration between plants and the outside world. Stomatal density and stomatal aperture are closely related to physiological processes such as photosynthesis in plants (Cai, et al., 2016). In general, stomatal density and degree of stomatal opening decreased in the low light environment compared to the full light environment, which was related to the sufficient water, low light and low transpiration rate in this environment (Haworth et al., 2021). In this study, except for heavy shading (L1), the stomatal density of the two treatments with mild shading was lower compared to that of the group treated with full light., which was one of the adaptation methods of *F. kwangsiensis* saplings to low light environment. It was beneficial to control the content of free water in the leaves and maintain the water balance in the leaf system, which was of great importance to improve the water use efficiency.

Excessive stomatal density and openness will cause plants to lose too much water and inhibit plant growth. On the contrary, moderate shading can effectively control plant water loss, which is conducive to plant water storage (Ren, et al., 2015). This may be one of the reasons for the low photosynthetic efficiency of *F. kwangsiensis* saplings under full light. As the main photosensitive organ of plants and the main site of photosynthesis, the anatomical structure of leaves will also change adaptively with the changing light environment (Wyka, et al., 2022). Under high light conditions, plant leaves are small and thick. In low light conditions, plants tend to capture more light energy by increasing the leaf area, and the thickness of the leaf, palisade tissue and spongy tissue will also decrease (Puglielli, et al., 2015). To increase the absorption of reflected and diffuse light in the leaves, the cells inside the leaves also become looser (Karabourniotis et al., 2021; Yang, et al., 2022). In this study, the leaf structure of *F. kwangsiensis* saplings was also found to change to adapt to the low light environment. In the weak light environment, *F. kwangsiensis* saplings reduced the thickness of leaves and palisade tissues, which is similar to the adaptation of Phoebe bournei sapling to the light environment (An, et al., 2023). In addition to the effect of light environment on leaf thickness, water stress also affects leaf thickness (Wang, et al., 2021). The thicker the leaves, the better the plant's ability to store water, and the better the plant's ability to


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survive in arid environments (Soares, et al., 2023). Studies have found that multi-layered and dense palisade tissue and relatively underdeveloped spongy tissue are some of the main characteristics of xerophytes, which can increase the photosynthetic rate of plants and improve water transport capacity (Ren, et al., 2014). It is worth noting that this study found that in the full light environment, the leaves of the plant differentiated into double-layered palisade tissues and the thickness of sponge tissues were 126.36%, 121.06% and 44.30% higher than the other treatments, respectively, and it was speculated that the *F. kwangsiensis* saplings may be subjected to drought stress in the full light environment. In summary, we suggest that although the *F. kwangsiensis* saplings have a higher stomatal density under full light, they are more dependent on water and the transpiration of the plants is easily affected, which hinders the heat dissipation of the plants and is not conducive to the growth and development of the plants. Therefore, in breeding *F. kwangsiensis* saplings, we should pay attention to water and fertilizer management in addition to appropriately increasing light transmittance. However, the best water management technology for *F. kwangsiensis* saplings has not been clarified, which is worth further research.

After conducting a comparative analysis of the morphological and physiological features of distinct shade environments, this study concluded that the 25% shade environment was the most favorable for the growth of *F. kwangsiensis* saplings. Through the comparative analysis of the morphological and physiological characteristics of different shade environments, the paper concluded that 25% shade environment was the most favorable for the growth of *F. kwangsiensis* saplings. However, the correlation between the indicators was not obvious, so we further analyzed the correlation between each indicator. The variation in growth can be attributed to the differing photosynthetic characteristics. The photosynthetic characteristics index showed a significant and positive correlation with growth ($P < 0.001$), with Pmax, AQY, and LSP having the most notable impact on growth. The Pmax is indicative of the capacity of plants to harness intense light, whereas AQY reflects their ability to harness weak light. Consequently, *F. kwangsiensis* saplings must effectively harness both strong and weak light to attain optimal growth. Thus, a moderate shade is vital for the growth of these saplings. Leaf anatomy structure, in addition to photosynthetic characteristics, significantly influenced growth amount, and a negative correlation was observed between SD and growth amount. These findings imply that SD affects growth amount in both over-shaded and unshaded environments. Furthermore, a negative correlation existed between PPT and LT as well as the growth amount, while no correlation was found between the growth index and chlorophyll content. This suggests that in strong light conditions, *F. kwangsiensis* saplings can reduce the chlorophyll content in their leaves and increase the thickness of palisade tissue to prevent damage to the leaf structure from excessive light energy.

## Conclusion

The results of this study showed that *F. kwangsiensis* saplings possess some degree of shade tolerance, but can also adapt to a narrow range of light conditions. Under both insufficient and excessive light, the saplings exhibited stunted growth. A shading level of 25% was found to be optimal for their growth, as the saplings displayed favorable physiological indicators under these conditions. In this environment, the plants exhibited favorable physiological indicators. The heightened density and openness of


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stomata on the leaves within this environment could be a pivotal contributor to the elevated photosynthetic rate of flora. Under full light conditions, the plant showed stunted leaf growth and poor photosynthetic performance. The high stomatal density and double-layer palisade tissue suggest that the plant struggled to efficiently use water, making it vulnerable to water stress. The correlation analysis presented that modifying the photosynthetic physiological indexes such as Pmax, AQY, LSP and leaf structure such as SD, PPT, LT had the most significant impact on the growth rates of saplings under varying light environments. Excessive strong and weak light could also hinder the growth of the plants. Therefore, this study's conclusion is that *F. kwangsiensis* saplings exhibit shade-loving traits during the sapling stage and thrive in an environment with 25% shading. Appropriate shading surroundings and water management techniques must be chosen to optimize the development of *F. kwangsiensis* saplings when preserving, introducing, and cultivating saplings ex-situ. It is necessary to use physiological features when selecting the optimal growth conditions.

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**Conflicts of interests.** The authors declare no conflict of interests.

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