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*Original Research*

# Effects of Light Stress Conditions on the Growth of *Rhododendron schlippenbachii* Saplings

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## Abstract

Light is a critical factor influencing the survival and growth of saplings. *Rhododendron schlippenbachii*, an ornamental species endemic to Changbai Mountain in China, has been classified as Near Threatened (NT) on the IUCN Red List of Threatened Species. However, the optimal light intensity for its growth remains unclear. To determine this, we conducted a comprehensive investigation into the adaptation mechanisms of morphological growth, diurnal variations in photosynthesis, chlorophyll fluorescence, physiological indicators, and stomatal ultrastructure of *Rhododendron schlippenbachii* saplings under four light intensities (full light: CK; 70% light: L1; 50% light: L2; 30% light: L3) over a continuous 90-day shading period. The results demonstrated that under L3, the leaf morphological growth of *Rhododendron schlippenbachii* saplings was significantly greater than that of other treatments. As shading duration increased, saplings in the full-light treatment group experienced complete mortality. The highest values for Fv/Fm, Fv/F0, and NPQ, as well as the peak chlorophyll content, were observed in saplings subjected to 70% shading. Conversely, the lowest concentrations of proline (PRO), malondialdehyde (MDA), and soluble protein (SP) were also recorded under this condition. Activities of catalase (CAT), superoxide dismutase (SOD), and peroxidase (POD) did not exhibit significant differences across various shading treatments. It was observed that the protective effect was significantly enhanced by antioxidant enzymes under 70% shade conditions; shading reduced osmoregulatory substances while increasing chlorophyll content. The stomatal length, width, conductivity, and net photosynthesis rate of the 30% light treatment surpassed those under full-light conditions after 60 days of shading. Consequently, this study demonstrated

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that a 70% shade treatment represents the optimal level of light radiation for the growth of *Rhododendron schlippenbachii* saplings.

**Keywords:** light intensity, growth, eco-physiological characteristics, stomatal ultrastructure, *Rhododendron schlippenbachii*

## Introduction

Plant development is regulated by light conditions [1]. Lighting is a crucial factor influencing plant growth [2]. Light intensity not only determines the photosynthetic rate of plants but also impacts their morphological characteristics and physiological adaptations [3]. Light provides energy for photosynthesis, thereby modulating plant growth, development, and morphogenesis [4]. Low-light conditions induce morphological and physiological changes in plants, such as thinner leaves, reduced leaf chlorophyll content, decreased nitrogen content, diminished photosynthetic system activity, and lower enzyme activity [5]. Plant leaves tend to become thinner and smaller as light intensity decreases [6]. For instance, studies on soybean plants have demonstrated that the total leaf area under shaded conditions was significantly reduced compared to that grown in full sunlight. Specifically, the areas of young, middle-aged, and old leaves were approximately 70-80% of those observed in plants exposed to full sunlight [7]. Variations in light intensity differentially influence physiological changes in plants [8, 9]. Alterations in physiological parameters associated with plant nutritive and reproductive growth can be observed under varying light intensities [7]. For instance, research has demonstrated that the photosynthetic rate and stomatal conductance of plants exhibit significant changes in response to different light conditions. While high light intensity generally results in an increased photosynthetic rate, excessively high light levels may induce photoinhibition, thereby potentially damaging the photosynthetic system [10, 11]. Compared to low-light conditions, high-light conditions resulted in significantly higher light-saturated photosynthetic rates ($P_{max}$), light compensation points (LCP), and light saturation points (LSP) in *Athyrium pachyphlebium* seedlings. Additionally, the non-photochemical quenching capacity (NPQ) in response to excess light was reduced under high-light conditions [12].

*Rhododendron schlippenbachii* is a garden plant species that is distributed in southern and southeastern Liaoning as well as Inner Mongolia in China, and occurs in Korea and Japan. This species has been classified as Near Threatened (NT) on the IUCN Red List of Threatened Species (IUCN) (http://www.iplant.cn/rep/prot/Rhododendron%20schlippenbachii). It possesses high ornamental value, characterized by its striking flower colors, which include orange, pink, red, purple, and blue [13]. Additionally, it is extensively utilized in the medical field. The anthocyanins present in *R. schlippenbachii* flowers have been documented to inhibit UV-induced inflammation and damage in liposomes [14], as well as exhibit significant antioxidant effects [15]. The leaves exhibit glucosidase inhibitory activity and represent a promising source of herbal medicine for the management of diabetes mellitus [16-18].

The light environment plays a crucial role in sapling regeneration and population dynamics. As a core ecological factor, it significantly influences the survival strategies and distribution patterns of *Rhododendron schlippenbachii*. In overly dense forests with limited light availability, seed germination and seedling establishment are severely restricted. Conversely, under excessively intense illumination, elevated temperatures, and increased drought stress in full-sun environments can lead to high seedling mortality. This species' highly specific light requirements result in a narrow ecological niche. Any disturbance to the forest structure of its natural habitat – whether leading to excessive shading or overexposure – can disrupt the delicate light balance essential for its survival, thereby impairing growth, inhibiting flowering, preventing successful regeneration, and ultimately contributing to population decline. This sensitivity underscores the importance of carefully selecting or simulating appropriate light conditions in both conservation efforts and artificial cultivation practices [19-22]. In this study, we simulated the light intensities of various habitats of *R. schlippenbachii* saplings using artificial shading. We investigated differences in morphology, ultrastructure, physiology, biochemistry, and photosynthesis under varying light intensities and shading durations. From the perspective of light environment adaptation, this study elucidates the growth strategies employed by plants to adapt to different light environments, providing a theoretical foundation for the utilization of *R. schlippenbachii* in landscape greening, configuration, and conservation. This research is of significant importance for the preservation of *Rhododendron* species and the development of green spaces in urban gardens.

## Materials and Methods

### Study Site

The research was conducted in Jiangnan Park, situated in Jilin City, Jilin Province, China. The park is geographically located within the coordinates of 125°40′E to 127°56′E longitude and 42°31′N to 44°40′N latitude. The local climate is characterized by an average annual temperature ranging between 3ºC and 5ºC. The soil properties include a pH level of 5.69 and an organic matter content of 28.45 g/kg.

These environmental factors delineated the conditions under which the study was carried out in Jiangnan Park.

## Experimental Design

The experiment primarily used three-year-old healthy saplings with uniform growth as the study subjects. The average height of the saplings was 37.28±6.45 cm (mean±standard deviation). Black nylon mesh was used to create four light intensity treatments: full light (CK), 70% light (L1), 50% light (L2), and 30% light (L3). Each treatment included 40 plants with 10 replicates. The experiment lasted 90 days, divided into 3 stages: 30 days (T1, July), 60 days (T2, August), and 90 days (T3, September). Photosynthetic parameters were measured using the CIRAS-III system (PP-SYSTEMS, USA). We then assessed changes in plant morphology, chlorophyll content, specific leaf weight, osmoregulatory substances, and antioxidant enzyme activities. Each experiment had 3 replicates.

## Morphological Indexes

Eight leaves from six saplings were randomly selected, and their leaf length, leaf width, and petiole dimensions were measured using a digital vernier caliper. At the conclusion of the experiment, the single leaf area was quantified with a portable leaf area meter. Subsequently, the leaves were dried in an electrically heated constant-temperature blast drying oven at 80ºC until they reached a constant weight, after which the dry mass was determined [23].

$$\text{Specific Leaf Weight (WSL)} = \frac{W_D}{A_L} \qquad (1)$$

## Photosynthetic Indicators

### *Photosynthetic Daily Variation*

The net photosynthetic rate (Pn), stomatal conductance (Gs), transpiration rate (Tr), and water use efficiency (WUE) of leaves were measured under controlled conditions. Measurements were conducted on 3 consecutive sunny days at 3 time points: 30 days of shading (T1, July), 60 days (T2, August), and 90 days (T3, September). Each measurement was replicated twice using leaves from identical treatments.

### *Photosynthetic Response Curve and $CO_2$ Response Curve*

Saplings were measured using a CIRAS-III portable photosynthesizer at 25ºC and 80% relative humidity. The light response curve was determined under 390 μmol mol$^{-1}$ $CO_2$, with PAR set at 2000 to 0 μmol m$^{-2}$ s$^{-1}$ in 200 μmol m$^{-2}$ s$^{-1}$ decrements. For $CO_2$ response curves, PAR was fixed at 1200 μmol m$^{-2}$ s$^{-1}$, and the $CO_2$ gradients were set to 390, 300, 250, 200, 150, 100, 50, 390, 450, 550, 650, 750, 850, 1000, and 1200 μmol mol$^{-1}$. Relevant parameters were subsequently calculated based on the modified rectangular hyperbolic model (MRHM).

### *Chlorophyll Fluorescence Content*

The CIRAS-III portable photosynthesizer was employed to measure relevant parameters. In the Fv/Fm mode, chlorophyll fluorescence characteristics under varying light intensities were assessed, including the initial fluorescence (Fo), maximum fluorescence (Fm), maximum photochemical quantum yield of PSII (Fv/Fm), and potential activity of PSII (Fv/Fo). Additionally, the effective quantum yield of photochemical energy conversion (Yield), photochemical quenching (qP), and non-photochemical quenching (NPQ) were measured. Light-adapted parameters such as initial fluorescence (Fo'), maximum fluorescence (Fm'), steady-state fluorescence (Fs), and maximum variable fluorescence (Fv') were also determined [24].

## Physiological and Biochemical Indexes

On the 30th, 60th, and 90th days of shading treatment, the chlorophyll content in the leaves of seedlings exposed to different light intensities was measured using the ethanol extraction method and spectrophotometric analysis. Chlorophyll A and B concentrations were determined at wavelengths of 665 nm and 649 nm, respectively, following established protocols [25, 26]. After 90 days, additional physiological indicators were assessed: malondialdehyde (MDA) via the TBARS assay, proline (PRO) using acid ninhydrin staining, soluble protein (SP) with Coomassie Brilliant Blue, catalase (CAT) by iodine titration, peroxidase (POD) through guaiacol colorimetry, and superoxide dismutase (SOD) using xanthine oxidase inhibition [27].

## Stomatal Ultrastructure

In August, during peak solar irradiance, we selected leaves from shaded plants showing pronounced diurnal changes in photosynthesis. From 8:00 to 16:00, we collected 1×1 cm leaf samples every 2 hours and fixed them immediately in FAA. After fixation, the samples were dehydrated, mounted, gold-coated, and examined under a Quanta200 environmental scanning electron microscope to observe stomatal structures and capture images.

## Statistical Data Analysis

Each treatment was conducted in triplicate, and the resulting data were presented as the mean±standard deviation. Significance was assessed using one-way ANOVA, followed by Duncan's multiple-range test for post hoc analysis. The statistical analysis was performed using SPSS 20.0, with statistical significance defined as $p<0.05$. Graphs were generated using Origin 2021 software.

## Results

### Effects of Light Intensities on Morphological Features of *R. schlippenbachii* Saplings

With the increase in shading duration, the leaf length, leaf width, and specific leaf weight of saplings under different shading intensities exhibited varying changes (Fig. 1). The growth trend of leaf length for CK, L1, and L2 initially decreased and subsequently increased, whereas the leaf length growth of L3 continued to decline (Fig. 1a)). The leaf width growth of CK and L2 showed a continuous decreasing trend, while that of L1 and L3 demonstrated a pattern of initial decrease followed by an increase, with L3 achieving the maximum leaf width growth (Fig. 1b)). In terms of specific leaf weight, no significant variation was observed for L1 and L3 (Fig. 1c)).

### The Impacts of Light Intensity on Photosynthetic Daily Variation of *R. schlippenbachii* Saplings

The extremes of the environmental factor photosynthetically active radiation (PAR) were observed at 10:00 a.m., 12:00 noon, 14:00, and 16:00 (Fig. 2a)). Daily variations in photosynthetic parameters, including net photosynthetic rate (Pn), stomatal conductance (Gs), transpiration rate (Tr), intercellular carbon dioxide concentration (Ci), and water use efficiency (WUE), exhibited significant increases or decreases (Fig. 2(b-f)). Net photosynthetic rate (Pn) exhibited distinct peaks or troughs in its curve between 10:00 and 14:00. In treatments T1 and T2, the net photosynthetic rate (Pn) of seedlings under varying shading conditions followed a unimodal curve, suggesting the absence of a midday depression in photosynthesis. In treatment T3, the net photosynthetic rate under CK and L3 conditions displayed a bimodal curve, indicating that the midday depression in photosynthesis began at 10:00 for CK and L3 treatments. Specifically, the peak values for CK and L3 occurred at 10:00 and 14:00, respectively. Stomatal conductance (Gs), transpiration rate (Tr), and net photosynthetic rate followed a similar pattern of change. Intercellular carbon dioxide concentration (Ci) exhibited distinct variations, with the lowest values consistently observed at 12:00 noon and 14:00 in all 4 shading treatments as shading duration increased. During the T1 and T2 periods, water use efficiency (WUE) reached its minimum at 12:00 noon, contrasting with the trends of Pn, Gs, and Tr. In the T3 period, WUE peaked at 14:00.

### Photosynthetic Response Curve and $CO_2$ Response Curve

With the increase in shading duration, the trends of changes in light response curves for T1, T2, and T3 saplings remained consistent (Fig. 3). Similarly, the trends of changes in carbon dioxide response curves also remained consistent (Fig. 4). Notably, the light response curves and carbon dioxide response curves of the L3 treatment were higher than those of the other 3 groups. We analyzed the parameters of light response curves (Table 1) and carbon dioxide response curves (Table 2) for saplings subjected to 90 days of shading.

The analysis of the light response curve parameters revealed that the dark respiration rate (Rd), maximum net photosynthetic rate ($A_{max}$), light saturation point (LSP), and light compensation point (LCP) in saplings subjected to four shading treatments did not exhibit significant differences (Table 1). However, the Apparent Quantum Yield (AQY) demonstrated significant variations, specifically between the control group (CK) and the shaded groups (L1, L2, L3). Furthermore, AQY exhibited an upward trend as light intensity decreased.

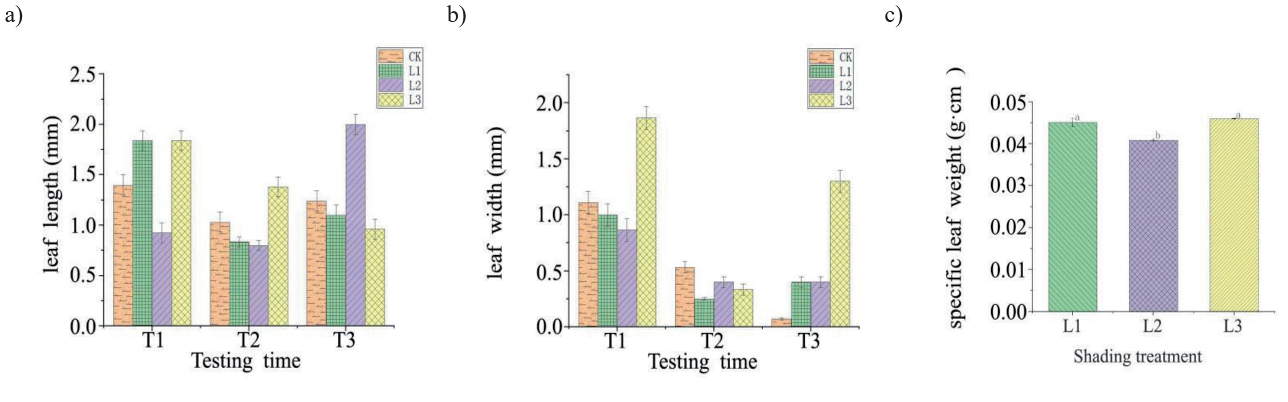

Fig. 1. Effect of light-regulation on Morphological Attributes of *R. schlippenbachii*. a) leaf length, b) leaf width, c) specific leaf weight. Treatment Conditions: CK (Full Light), L1 (70% Light), L2 (50% Light), L3 (30% Light); Shading Durations: T1 (30 Days), T2 (60 Days), T3 (90 Days). Data were subjected to a one-way ANOVA test. Different lowercase letters represent significant differences in light intensity at the 0.05 level. Bars indicate means±SE.

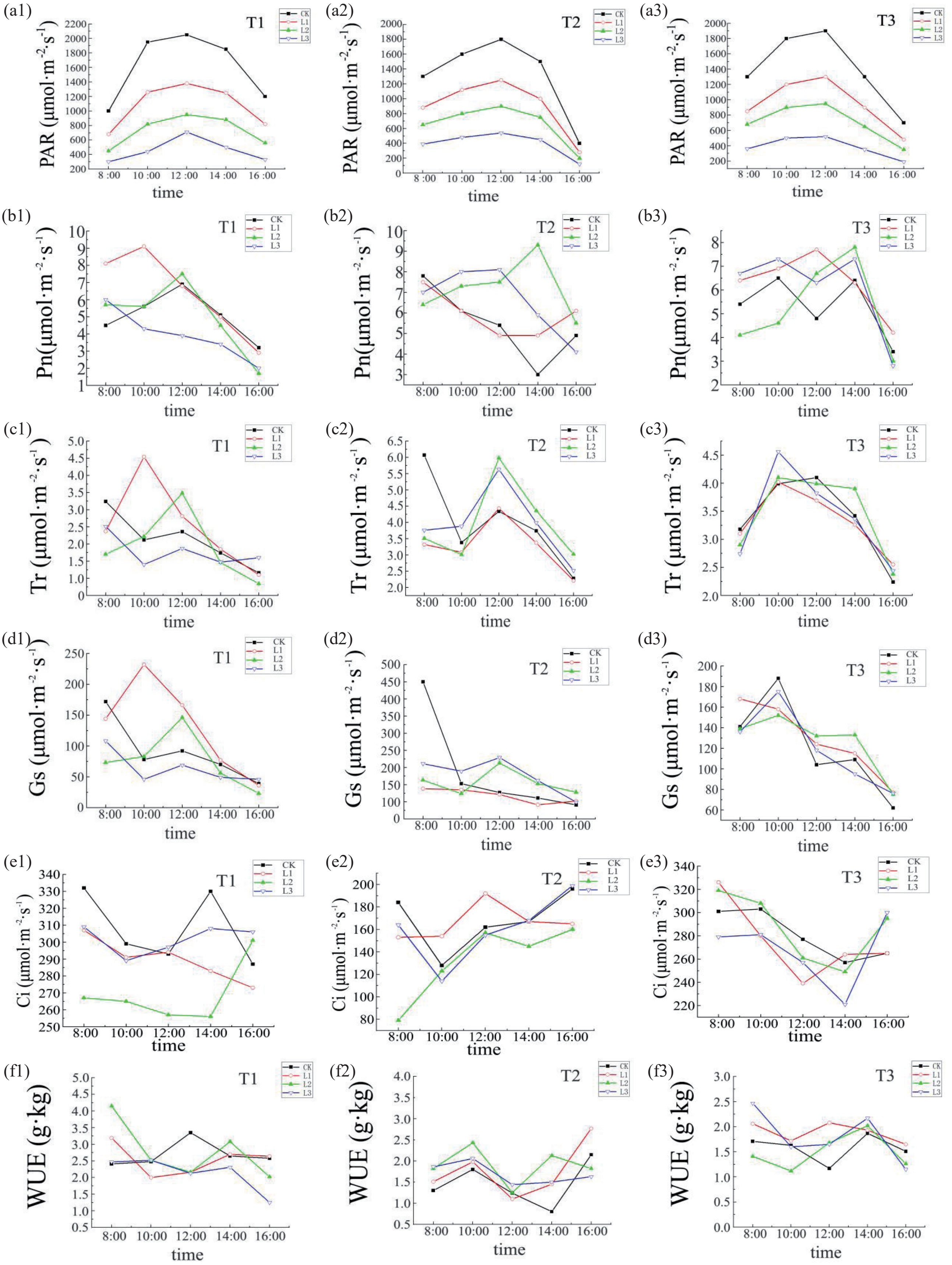

Fig. 2. Daily Variation of Photosynthesis in *R. schlippenbachii* saplings under four different light intensities: (a1-a3) Photosynthetically Active Radiation (PAR), (b1-b3) Diurnal Patterns of Net Photosynthesis ($P_n$), (c1-c3) Diurnal Patterns of Transpiration Rate ($T_r$), (d1-d3) Stomatal Conductance ($G_s$), (e1-e3) Intercellular $CO_2$ Concentration ($C_i$), and (f1-f3) Plant Water Use Efficiency (WUE = $P_n/G_s$). Treatment Conditions: CK (Full Light), L1 (70% Light), L2 (50% Light), L3 (30% Light); Shading Durations: T1 (30 Days), T2 (60 Days), T3 (90 Days).

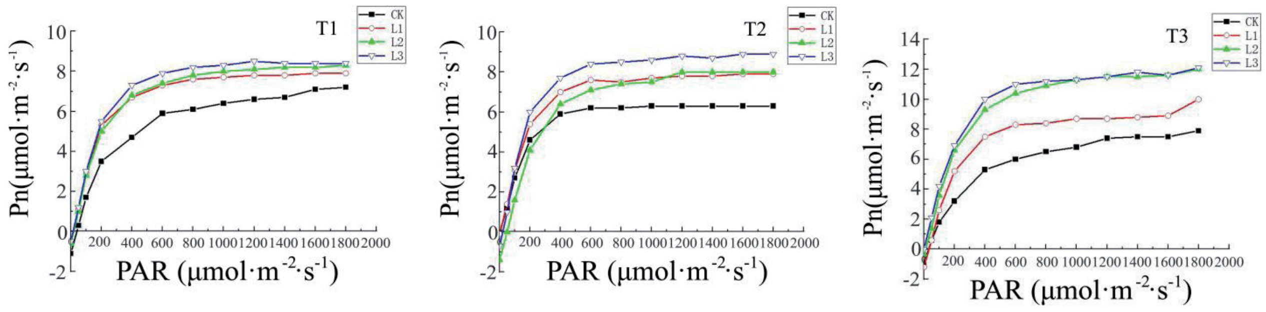

Fig. 3. Analysis of the Photosynthetic Response Curve. Treatment Conditions: CK (Full Light), L1 (70% Light), L2 (50% Light), L3 (30% Light); Shading Durations: T1 (30 Days), T2 (60 Days), T3 (90 Days).

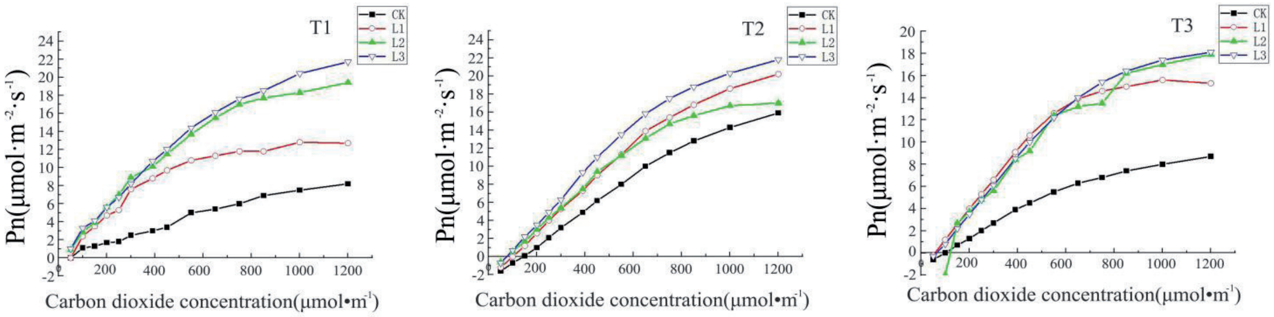

Fig. 4. Analysis of the $CO_2$ Response Curve. Treatment Conditions: CK (Full Light), L1 (70% Light), L2 (50% Light), L3 (30% Light); Shading Durations: T1 (30 Days), T2 (60 Days), T3 (90 Days).

The $CO_2$ response curves indicated that there were no statistically significant differences in photorespiration rate (Rp), $CO_2$ saturation point (CSP), and $CO_2$ compensation point (CCP) among the four shading treatments (Table 2). However, the maximum net photosynthetic rate ($A_{max}$) of the CK group was significantly different from that of the L2 and L3 groups. As light intensity decreased, the $A_{max}$ value exhibited an increasing trend, with the highest value observed under the L3 treatment, which increased by 87.74% compared to the CK group. The ranking of $A_{max}$ values across treatments was as follows: L3>L2>L1>CK.

## Chlorophyll Fluorescence Content

The fluorescence parameters Fv/Fm and NPQ in the sapling leaves did not exhibit significant changes ($p>0.05$) during T3 (in September), as shown in Table 3. The parameter Fv/Fm serves as an indicator of the plant's potential maximum photosynthetic capacity, reaching a value of 0.81 under the L3 treatment, which was higher than that observed in CK, L1, and L2 treatments. These findings suggest that heavy shading enhances the light-trapping efficiency of the PSII reaction center in leaves, whereas strong light conditions lead to inhibitory effects. NPQ reflects the plant's capacity to dissipate excess energy as heat under high light intensities. Compared

Table 1. Effects of different light intensities on photosynthetic parameters of saplings in T3.

| Treatment | $R_d$ ($\mu mol \cdot m^{-2} \cdot s^{-1}$) | $A_{max}$ ($\mu mol \cdot m^{-2} \cdot s^{-1}$) | LSP ($\mu mol \cdot m^{-2} \cdot s^{-1}$) | LCP ($\mu mol \cdot m^{-2} \cdot s^{-1}$) | AQY |
|---|---|---|---|---|---|
| CK | 0.79±0.51a | 7.65±1.17a | 8498.23±7795.1a | 21.68±14.69a | 0.03±0b |
| L1 | 0.89±0.58a | 8.36±0.76a | 1427.49±356.18a | 15.87±9.84a | 0.04±0a |
| L2 | 1.04±0.56a | 9.32±2.08a | 1419.07±71.21a | 22.21±15.35a | 0.04±0.01a |
| L3 | 0.64±0.43a | 9.75±1.8a | 1306.08±182.63a | 10.98±7.28a | 0.04±0a |

$R_d$: Dark respiration rate; Amax: The light-saturated photosynthetic rate; LSP: Light saturation point; LCP: Light compensation point; AQY: Apparent Quantum Yield. Treatment Conditions: CK (Full Light), L1 (70% Light), L2 (50% Light), L3 (30% Light). T3: 90 d of shading (in September). Small letters indicate significant differences under different light intensities ($p<0.05$).

Table 2. Effects of different $CO_2$ rate intensities on photosynthetic parameters of saplings in T3.

| Treatment | $R_p$ (μmol·m$^{-2}$·s$^{-1}$) | $A_{max}$ (μmol·m$^{-2}$·s$^{-1}$) | CSP (μmol·m$^{-2}$·s$^{-1}$) | CCP (μmol·m$^{-2}$·s$^{-1}$) |
|---|---|---|---|---|
| CK | 1.57±0.8a | 10.93±2.47b | 1262.44±49.68a | 86.21±35.32a |
| L1 | 2.42±0.24a | 16.2±2.17ab | 1223.33±66.42a | 71.39±15.73a |
| L2 | 3.09±1.63a | 19.8±1.69a | 2113.33±963.77a | 73.71±28.09a |
| L3 | 1.8±0.68a | 20.52±1.23a | 1113.33±61.73a | 55.97±21.03a |

$R_p$: Photorespiration rate; $A_{max}$: The light-saturated photosynthetic rate; CSP: $CO_2$ saturation point; CCP: $CO_2$ Compensation Point. Treatment Conditions: CK (Full Light), L1 (70% Light), L2 (50% Light), L3 (30% Light). T3: 90 d of shading (in September). Small letters indicate significant differences under different light intensities ($p<0.05$).

Table 3. Effects of different Chlorophyll fluorescence parameters on photosynthetic parameters of saplings in T3.

| Treatment | $F_v/F_m$ | $F_v/F_o$ | ETR | qP | NPQ |
|---|---|---|---|---|---|
| CK | 0.63±0.06a | 0.76±0.19b | 29.74±1.43b | 0.24±0.12b | 1.46±0.07a |
| L1 | 0.67±0.12a | 0.92±0.42ab | 66.28±14.61a | 0.7±0.14a | 1.48±0.39a |
| L2 | 0.72±0a | 1.06±0ab | 25.96±11.05b | 0.17±0.04b | 1.6±0.52a |
| L3 | 0.81±0.01a | 1.58±0.06a | 22.43±5.35b | 0.41±0.26ab | 1.84±0.41a |

PSII ($F_v/F_m$): Maximum photochemical efficiency; $F_v/F_o$: Potential photochemical efficiency; ETR: Electron transfer rate; qP: Photochemical quenching coefficient; NPQ: Non-photochemical quenching coefficient. Treatment Conditions: CK (Full Light), L1 (70% Light), L2 (50% Light), L3 (30% Light). T3: 90 d of shading (in September). Different lowercase letters represent significant differences ($p<0.05$).

with CK, L3 enhanced the photosynthetic activity of saplings. ETR exhibited an increasing trend followed by a decrease with increasing shading levels. qP demonstrated a trend of first increasing, then decreasing, and subsequently increasing again as shading increased.

Fv/Fo tended to increase with increasing shading and reached 1.58 under the L3 treatment, which was significantly higher than that of CK ($p<0.05$).

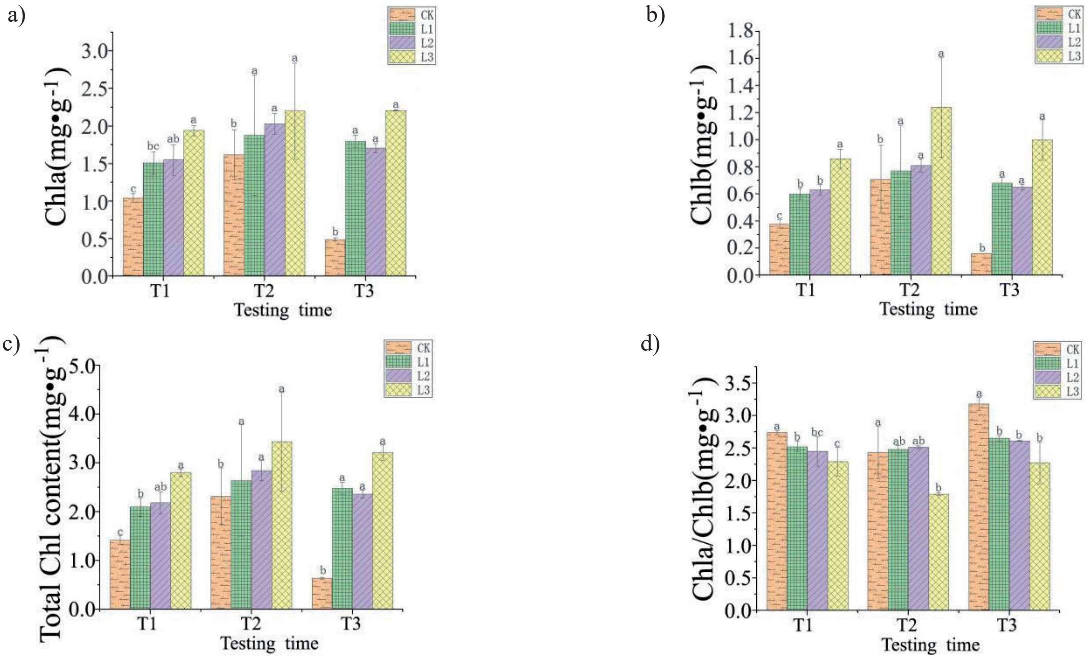

Fig. 5. Effect of light regulation on chlorophyll content. a) Chl a; b) Chl b; c) Chl a+b; d) Chl a/b. Treatment Conditions: CK (Full Light), L1 (70% Light), L2 (50% Light), L3 (30% Light); Shading Durations: T1 (30 Days), T2 (60 Days), T3 (90 Days).

## Chlorophyll Content

Fig. 5 indicates that chlorophyll content fluctuated with light intensity. Specifically, the chlorophyll a, chlorophyll b, and total chlorophyll levels in the L3 treatment were higher compared to those in the other 3 shading treatments. Additionally, chlorophyll a, chlorophyll b, and total chlorophyll exhibited a trend of initially increasing and subsequently decreasing as shading time progressed. Notably, the CK treatment demonstrated the highest chlorophyll a/b ratio.

## Physiological and Biochemical Indexes

We quantified the physiological parameters of the saplings after 90 days of shading treatment. By that time, the saplings in the CK group had perished due to their inability to acclimate to the environmental conditions. Consequently, our analysis focused solely on the physiological parameters of the three shaded treatment groups: L1, L2, and L3 (Fig. 6).

There were no significant differences in malondialdehyde (MDA) values among the shade-treated saplings L1, L2, and L3 ($p>0.05$). However, a decreasing trend was observed in MDA values, with concentrations of 28 $\mu\text{mol}\cdot\text{g}^{-1}$, 19.99 $\mu\text{mol}\cdot\text{g}^{-1}$, and 16.53 $\mu\text{mol}\cdot\text{g}^{-1}$ for L1, L2, and L3, respectively, indicating that the MDA content followed the order L1>L2>L3 (Fig. 6a)). A statistically significant difference ($p<0.05$) was found in proline (PRO) content between the L1 treatment and the L3 treatment. Proline concentrations exhibited a decreasing trend, with levels of 7.35 $\mu\text{g}\cdot\text{g}^{-1}$, 3.45 $\mu\text{g}\cdot\text{g}^{-1}$, and 0.55 $\mu\text{g}\cdot\text{g}^{-1}$ for L1, L2, and L3 treatments, respectively, confirming the order L1>L2>L3 (Fig. 6b)). Significant differences ($p<0.05$) were also observed in soluble protein (SP) content among the seedlings of groups L1, L2, and L3 under shading treatment. The SP concentrations demonstrated a decreasing trend, with values of 4.57 $\text{mg}\cdot\text{g}^{-1}$, 2.1 $\text{mg}\cdot\text{g}^{-1}$, and 1.06 $\text{mg}\cdot\text{g}^{-1}$ for L1, L2, and L3, respectively, further supporting the order L1>L2>L3. No significant differences were detected among other groups ($p>0.05$) (Fig. 6c)).

There were no statistically significant differences ($p>0.05$) in catalase (CAT) values among the three groups (L1, L2, and L3) under shading treatments. However, CAT activity demonstrated a trend of initially decreasing and subsequently increasing. The maximum activity was observed in group L3, with a mean value of (452.17±20.86) U/g. Furthermore, the catalase content in saplings followed the order L3>L1>L2 (Fig. 6d)). No statistically significant differences in peroxidase (POD) activity were detected among the shading treatment groups L1, L2, and L3 ($p>0.05$). POD activity exhibited a decreasing trend followed by an increasing trend. The highest POD activity was recorded in L1 (54±4.36 U/g), while the lowest activity was observed in L2 (46.5±5.01 U/g) (Fig. 6e)). The peroxidase content in saplings followed the order L1>L3>L2. No statistically significant differences ($p>0.05$) were observed in superoxide dismutase (SOD) values among seedlings L1, L2, and L3 under all three shading treatments. SOD activity demonstrated an increasing trend, with the highest activity recorded in L3 (874.44±138.9 U/g) and the lowest in L1 (746.44±88.87 U/g). The SOD content values followed the order L3>L2>L1(Fig. 6f)).

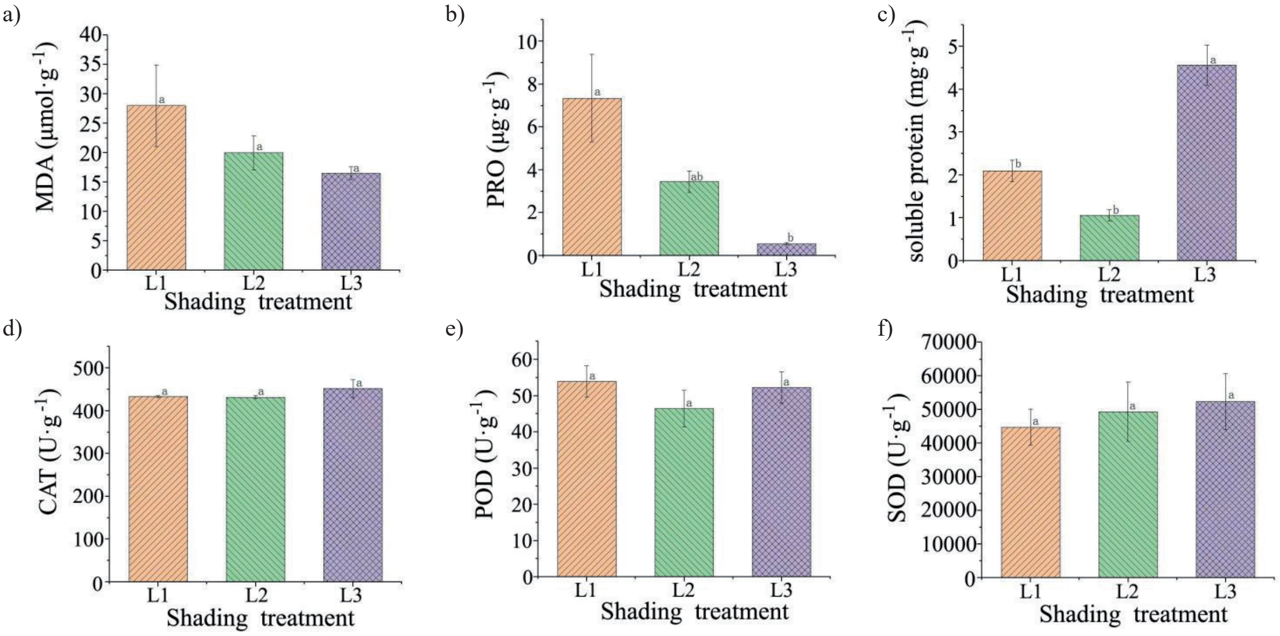

Fig. 6. Effect of light-regulation on physiology and biochemistry in T3. a) Malondialdehyde (MDA), b) Proline (PRO), c) Soluble protein (SP), d) Catalase (CAT) activity, e) Peroxidase (POD), f) Superoxide dismutase (SOD). Treatment Conditions: CK (Full Light), L1 (70% Light), L2 (50% Light), L3 (30% Light); Shading Durations: T1 (30 Days), T2 (60 Days), T3 (90 Days).

Table 4. Stomatal characteristics of sapling leaves.

| Time | CK | | L3 | |
|---|---|---|---|---|
| | Stomatal length (μm) | Stomatal width (μm) | Stomatal length (μm) | Stomatal width (μm) |
| 8:00 | 11.32 | 4.34 | 11.32 | 6.23 |
| 10:00 | 11.7 | 2.26 | 9.81 | 5.47 |
| 12:00 | 11.32 | 2.26 | 15.47 | 5.43 |
| 14:00 | 9.43 | 3.77 | 6.6 | 3.77 |
| 16:00 | 7.55 | 2.83 | 3.21 | 0.75 |

## Stomatal Ultrastructure

In this experiment, the leaves of saplings subjected to CK and L3 treatments during the T2 period were selected for observation of leaf stomatal ultrastructure. As shown in Figs 7 and 8, and Table 4, the stomatal conductance (Gs) of L3-treated saplings exhibited an increasing trend from 8:00 to 12:00, with Gs reaching its peak at 12:00. The maximum stomatal organ length was recorded as 15.47 μm, and the maximum stomatal organ width was 4.53 μm. Subsequently, Gs demonstrated a decreasing trend from 14:00 to 16:00. In contrast, the Gs of CK-treated seedlings showed a continuous decline, and by 14:00, the seedlings had entered the photosynthetic midday depression phase, during which both net photosynthetic rate (Pn) and Gs reached their minimum values.

## Relevance Analysis

Most of the saplings in the CK group exhibited damaged leaves; therefore, we focused our analysis on the physiological and biochemical parameters of saplings from L1, L2, and L3 at the T3 period (September). As depicted in Fig. 9, different shading treatments were significantly positively correlated ($p<0.01$) with specific leaf weight (SLW), while being significantly negatively correlated ($p<0.01$) with $CO_2$ saturation point (CSP), peroxidase (POD) activity, maximum net photosynthetic rate (Amax), photochemical quenching coefficient (qP), and other relevant parameters. Additionally, we investigated the relationships between antioxidant enzyme activities, chlorophyll content, and chlorophyll fluorescence parameters. Our findings revealed that peroxidase (POD) activity was significantly positively correlated ($p<0.05$) with non-photochemical quenching coefficient (NPQ), catalase (CAT) activity, malondialdehyde (MDA), proline (PRO), soluble protein (SP), and chlorophyll content. Furthermore, specific leaf weight (SLW) was significantly correlated ($p<0.05$) with soluble protein (SP) and malondialdehyde (MDA), while superoxide dismutase (SOD) activity exhibited a significant positive correlation ($p<0.01$).

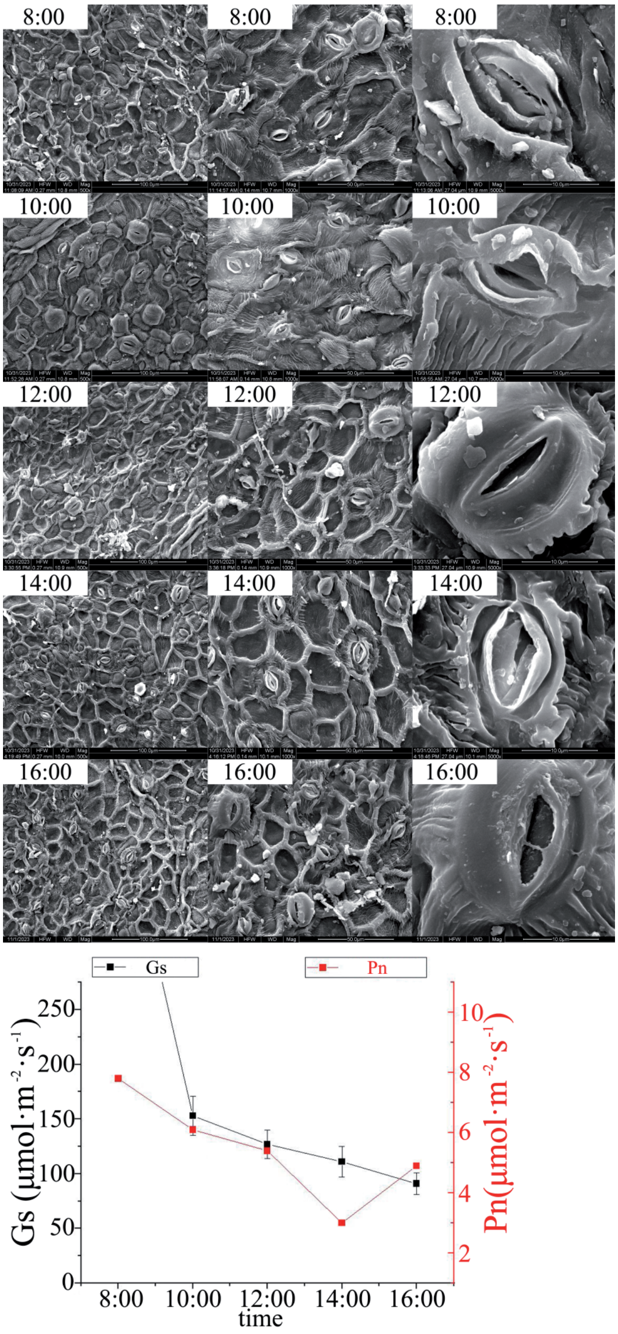

Fig. 7. Ultrastructure of Leaf Stomata, Stomatal Conductance, and Net Photosynthetic Rate under CK Conditions during the T2 Period.

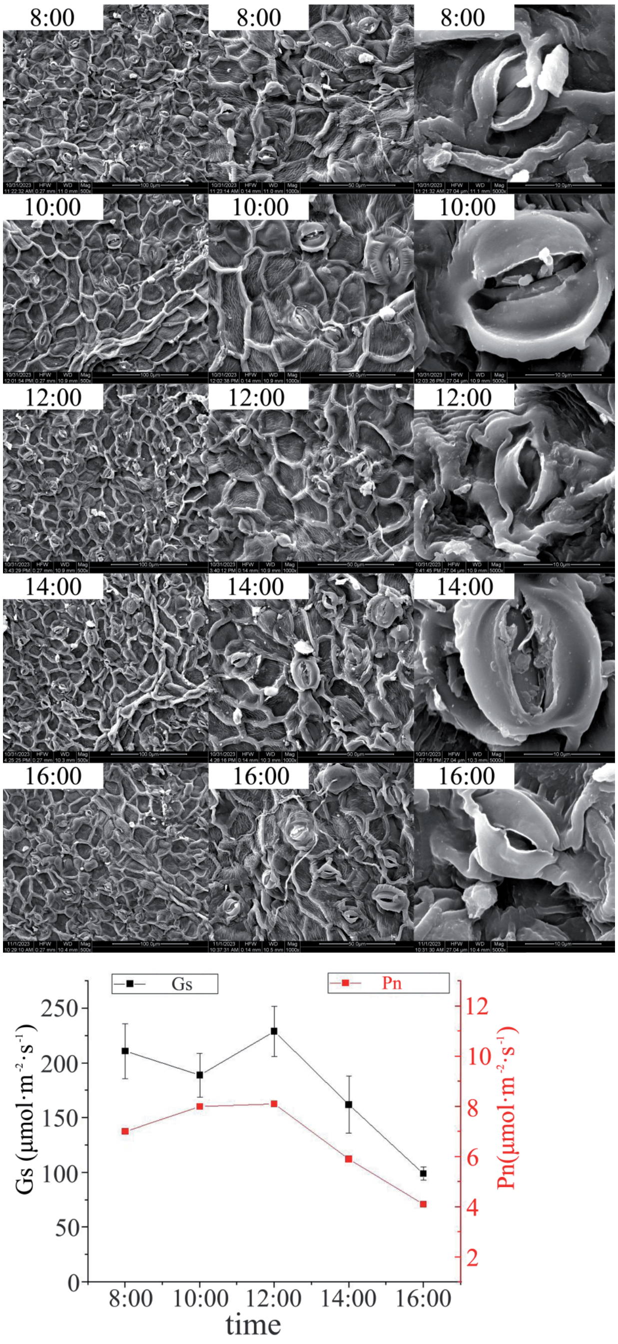

Fig. 8. Ultrastructure of Leaf Stomata, Stomatal Conductance, and Net Photosynthetic Rate under L3 Conditions during the T2 Period.

## Discussion

### Morphological Characteristics

The morphological characteristics of plant leaves directly reflect the processes of plant growth and development [28]. Additionally, leaf morphology serves as an indicator of a plant's ability to adapt to environmental conditions [29]. The saplings of *Rhododendron schlippenbachii* reduce the number of leaves per plant and adapt to full sunlight by decreasing leaf length, width, petiole length, and leaf thickness while increasing individual leaf area. These morphological adjustments indicate that full sunlight provides limited benefits for the growth of *Rhododendron schlippenbachii* saplings. Notably, *Rhododendron schlippenbachii* exhibits shade-tolerant characteristics, with plant architecture and leaf display likely optimized under the low-light conditions of the forest understory. With increasing shading, both leaf length and width of the saplings showed a progressively increasing trend, reaching their maximum values under the L3 treatment, with statistically significant differences. This suggests that plants increase leaf size under low-light conditions, thereby enhancing the overall photosynthetic capacity by maximizing the ratio of leaf area per unit biomass exposed to photons. Consequently, this improvement increases the light interception efficiency of the leaf, thus contributing to the enhancement of the plant's overall photosynthetic performance [30, 31].

### Photosynthetic Parameters

The peak net photosynthetic rate for saplings in each shade treatment group occurred between 8:00 and 14:00, coinciding with the period of stronger photosynthetically active radiation (PAR) during the day. The minimum values were consistently observed at 16:00, corresponding to the time when PAR was weaker. These findings suggest that the net photosynthetic rate of saplings is influenced by PAR [32-34]. Light intensity plays a critical role in photosynthesis; however, excessive light can damage the photosynthetic apparatus, thereby reducing photosynthetic efficiency and affecting the accumulation of photosynthetic products via stomatal conductance and transpiration rates [35-40]. The phenomenon of "photosynthetic midday depression" became more pronounced after 90 days of shading (in September). This occurrence under high light intensity at noon (12:00) is likely attributable to photoinhibition induced by intense midday light [41-43]. Shade treatments mitigated photoinhibition in plants, demonstrating their strong photosynthetic plasticity [44, 45]. Within a specific range, water use efficiency increases with rising light intensity due to enhanced photosynthetic activity, which enables greater production of organic matter [46-48]. At this stage, stomatal conductance increases within a reasonable range, facilitating the influx of carbon dioxide into the leaves while simultaneously maintaining control over water dissipation. This enables plants to utilize water more efficiently for the synthesis of organic compounds, thereby enhancing water use efficiency [49]. However, excessive light intensity may induce photoinhibition, which can compromise the photosynthetic system and result in reduced photosynthetic efficiency. Additionally, to mitigate potential damage from high temperatures and intense light, plants may excessively regulate their stomatal aperture, leading to significant closure.

| | Amax | CSP | SLW | POD | CAT | MDA | PRO | SP | SOD | Chl a+b | FvFm | NPQ | qP |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Amax | | | | | | | | | | | | | |
| CSP | 0.12 | | | | | | | | | | | | |
| SLW | -0.051 | -1.00 | | | | | | | | | | | |
| POD | -0.42 | -0.95 | 0.93 | | | | | | | | | | |
| CAT | 0.67 | -0.65 | 0.70 | 0.39 | | | | | | | | | |
| MDA | -1.00 | -0.13 | 0.059 | 0.42 | -0.67 | | | | | | | | |
| PRO | -0.99 | | -0.081 | 0.29 | -0.76 | 0.99 | | | | | | | |
| SP | 0.51 | -0.79 | 0.83 | 0.57 | 0.98 | -0.51 | -0.62 | | | | | | |
| SOD | 0.99 | | 0.054 | -0.32 | 0.75 | -0.99 | -1.00 | 0.60 | | | | | |
| Chl a+b | -0.93 | -0.47 | 0.41 | 0.72 | -0.36 | 0.94 | 0.88 | -0.17 | -0.89 | | | | |
| FvFm | 0.93 | -0.26 | 0.32 | -0.050 | 0.90 | -0.93 | -0.97 | 0.79 | 0.96 | -0.73 | | | |
| NPQ | 0.92 | -0.28 | 0.35 | -0.024 | 0.91 | -0.92 | -0.96 | 0.81 | 0.95 | -0.72 | 1.00 | | |
| qP | -0.71 | -0.78 | 0.74 | 0.93 | 0.038 | 0.72 | 0.62 | 0.24 | -0.64 | 0.92 | -0.40 | -0.38 | |

Fig. 9. Correlation analysis of physiological and biochemical indexes of saplings during the T3 Period. $A_{max}$: maximum net photosynthetic rate; CSP: carbon dioxide saturation point; SLW: specific leaf weight; POD: peroxidase; CAT: catalase; MDA: malondialdehyde; PRO: proline; SP: soluble protein; SOD: superoxide dismutase; Chl a+b: chlorophyll a+b; $F_v/F_m$: PSII primary light energy conversion efficiency; NPQ: non-photochemical quenching coefficient; qP: photochemical quenching coefficient; T3: 90d of shading.

This reduction in stomatal opening diminishes carbon dioxide uptake, thereby constraining photosynthesis and disrupting normal physiological metabolism, ultimately decreasing water utilization efficiency [50-54].

Carbon dioxide response curves serve as a critical tool for evaluating the efficiency of light reactions in plants. Plants can adjust their respiratory processes to adapt to varying light environments [55]. This study demonstrated that reduced light intensity decreases respiratory consumption in saplings, thereby promoting dry matter accumulation. Furthermore, the maximum net photosynthetic rate of saplings was higher under shaded conditions compared to full-light treatments, with the L3 treatment being most conducive to sapling growth [45]. A lower light compensation point signifies a plant's capacity to initiate organic matter accumulation for survival under weaker light intensities [56, 57]. Light compensation points typically range from 0-20 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for shade-tolerant species and 50-100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for sun-loving species. Under full-light and L1 treatments, the light compensation points of saplings fell between those of shade-tolerant and sun-loving species, whereas under L3 treatments, these points ranged from 0-20 $\mu mol \cdot m^{-2} \cdot s^{-1}$, indicating that saplings exhibit greater adaptability to 70% shaded environments [58].

## Chlorophyll Fluorescence

The light energy conversion efficiency (Fv/Fm) of maximal PSII serves as a critical indicator for assessing the capacity of PSII reaction centers to convert light energy [59]. Under normal conditions, the Fv/Fm value remains stable; however, under environmental stress, damage to the PSII reaction center leads to a significant decrease in the Fv/Fm value. Non-photochemical quenching (NPQ) functions as a self-protection mechanism in photosynthetic organs, enabling plants to dissipate excess light energy as heat, thereby preventing potential damage to these organs [60, 61]. In this study, saplings exhibited maximum values of Fv/Fm, Fv/Fo, and NPQ at L3 light intensity. These parameters decreased with increasing light intensity, reallocating more energy toward carbon accumulation in plant leaves and satisfying the demands of rapid seedling growth. Additionally, the lowest NPQ values were observed at CK light intensity, indicating that under appropriate light intensities, leaves require less energy dissipation via heat, thus promoting photochemical reactions [62-64].

## Physiological Property

The chlorophyll content level plays a crucial role in determining the intensity of photosynthesis and the accumulation of dry matter. In this study, it was observed that the concentrations of chlorophyll a, chlorophyll b, and total chlorophyll (a+b) in saplings increased as the degree of shading increased. Conversely, the chlorophyll a/b ratio decreased with higher levels of shading [65, 66].

The content of chlorophyll a, chlorophyll b, and total chlorophyll (a+b) reached their maximum values under the L3 treatment. Conversely, the contents of proline (PRO), malondialdehyde (MDA), and soluble protein (SP) were minimized under these conditions. In response to light stress, plants increase the levels of soluble proteins and free proline to maintain cellular stability and mitigate high-light-induced damage. This suggests that when subjected to adverse conditions, plants can adapt to unfavorable external environments through osmoregulatory substances such as proline, which plays a beneficial role in helping plants cope with environmental stress [67-69].

Saplings exhibited no significant differences in SOD, POD, and CAT activities with increasing shade intensity. However, the activities of CAT and POD in saplings generally displayed a trend of first decreasing and then increasing with light intensity. This phenomenon may be attributed to the fact that the plant's response to stress involves not only the antioxidant system but is also closely associated with other systemic and molecular response mechanisms within the plant. Furthermore, the SOD activities of all saplings increased with decreasing light intensity, suggesting that SOD active enzymes exhibit strong resistance to membrane lipid peroxidation damage following shading treatment [70].

### Stomatal Ultrastructure

Saplings grown under full-light conditions exhibit a decline in both stomatal conductance and net photosynthetic rate during the midday period. This phenomenon is primarily attributed to stomatal limitations that reduce the photosynthetic rate [71]. To minimize water loss in the high-light, midday environment, saplings decrease their stomatal aperture, which leads to reduced water use efficiency as an adaptation to environmental changes [35, 42]. Consequently, when cultivating these saplings, appropriate shading measures should be implemented to enhance their overall quality.

Stomatal pore density and aperture size are key determinants of stomatal conductance. Our results indicate that increased light intensity simultaneously reduces both the length and width of stomata. Under conditions of high light intensity and effective radiation, *Rhododendron schlippenbachii* saplings exhibit a reduction in stomatal aperture, which represents an adaptive mechanism to minimize water loss in response to environmental stress. Notably, under full sunlight exposure, both stomatal conductance and net photosynthetic rate reached their lowest values, primarily due to stomatal limitations. Given that stomatal transpiration inherently involves water loss, the observed decrease in stomatal porosity further supports the strategy employed by seedlings to conserve water under intense midday irradiance. Conversely, under the L3 treatment (i.e., 70% shading), stomatal conductance, as well as stomatal length and width, were significantly higher than those in the control group (CK) and peaked during periods of maximum photosynthetically active radiation. These findings suggest that a moderately shaded environment (70% shade) is optimal for the growth and physiological performance of *Rhododendron schlippenbachii* saplings [72-74].

## Conclusions

Leaf length and width increments of *Rhododendron schlippenbachii* saplings exhibited their maximum values under the 70% shade treatment. This suggests that, in low-light environments, the plant enhances its overall photosynthetic capacity by increasing leaf size to maximize the contact area per unit biomass with photons. As demonstrated in the experiment, the saplings under 70% shade exhibited the highest Fv/Fm ratio, net photosynthetic rate (Pn), and chlorophyll content, as well as the lowest malondialdehyde (MDA), proline (PRO), and soluble protein (SP) levels. Additionally, stomatal dimensions (length and width) and conductance were higher compared to those under full-light conditions. Consequently, the 70% shade treatment is optimal for the growth and development of *Rhododendron schlippenbachii* saplings. When cultivating these saplings, appropriate shading should be implemented to ensure their protection, thereby contributing to the conservation of this endangered species.

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## Conflict of Interest

The authors declare no conflict of interest.

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