

PHOTOSYNTHETIC CHARACTERISTICS OF *LARIX GMELINII* SEEDLINGS UNDER DIFFERENT LIGHT INTENSITY

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Abstract. To explore the effects of different light intensities on the physiological growth of *Larix gmelinii* seedlings, this study assessed three height grades of *L. gmelinii* seedlings (≤ 0.5 –1, 0.5–1, and 1–3 m) under the following treatments: full light (control), 65% NS (natural sunshine), 35% NS, and 10% NS. After treatment, photosynthetic pigment content, light response curve, CO₂ response curve, Chlorophyll Fluorescence and Diurnal Variations in Photosynthesis were assessed. Shading increased the photosynthetic pigment contents of *L. gmelinii* seedlings and young trees and played a positive role in the adaptation of *L. gmelinii* seedlings and young trees to low-light environments. The maximum net photosynthetic rate, maximum carboxylation rate, maximum photoelectron transmission rate, and utilization efficiency of acetone phosphate of *L. gmelinii* (1–3 m) considerably increased under the 65% NS treatment, showed the strongest photoinhibition resistance and a high proportion of the open PSII reaction center. The best shade treatment for young *L. gmelinii* trees at 1–3 m was 65% NS, which indicates that this treatment can improve the photosynthetic capacity of young *L. gmelinii* trees. However, for the growth of smaller *L. gmelinii* seedlings, an environment with greater light intensity is more suitable.

Keywords: chlorophyll, *Larix gmelinii*, light environment, photosynthetic parameters, saplings

Introduction

Light is the main ecological factor underlying plant growth and produces environmental signals that affect plant development (Zhang et al., 2014; Yang et al., 2021). Plants adjust and adapt to the external environment through photoreceptors and other pathways. When light conditions are limited, plants exhibit a series of photosynthetic physiological responses to improve their competitive and survival abilities (Farquhar et al., 1982; Richardson et al., 2002). Shading affects normal photosynthesis in plants, restricts leaf carbon assimilation, reduces carbohydrate content, and affects normal plant growth (Deng et al., 2022; Dai et al., 2022). When plants are shaded, they undergo physiological and morphological changes to adapt to weak light environments, such as reduction in leaf respiration rate, increase in chlorophyll b content, decrease in chlorophyll a/b content, and increase in short-wavelength light energy absorption (Chen et al., 2010; Liang et al., 2017).

Xing'an larch (*L. gmelinii*) is a tree species belonging to the *Pinaceae* family and *Larix* genus. It is a sun plant that is mainly distributed in the cold temperate mountainous areas of the Daxing'anling Mountain region in China and thus represents an important component species of the cold temperate coniferous forests of this region.

Moreover, it has a high economic value and plays an important role in maintaining ecosystem balance and conserving water resources. A number of recent studies on *L. gmelinii* have focused on its photosynthetic characteristics. For example, Zhu et al. (2015) studied the photosynthetic characteristics of *L. gmelinii* seedlings under different artificial thinning intensities by measuring the photosynthesis of a natural forest after the artificial treatment regimen and found that the light conditions of *L. gmelinii* seedlings at the felled sample site were improved and the net photosynthetic rate (P_n), transpiration rate (T_r), and stomatal conductance (G_s) were higher relative to those at the control sample site. Quan et al. (2015) studied the photosynthetic characteristics and related factors of six provenances of *L. gmelinii* and found that the improved leaf photosynthetic characteristics of *L. gmelinii* and correlation with the environment were the result of the combined effects of phenotypic domestication and genetic adaptation (Zhao et al., 2008). These results are mainly based on analyses of the growth of *L. gmelinii* at the stand level under changes in the light intensity; however, limited research has focused on changes in the physiological photosynthetic indicators of *L. gmelinii* at the seedling stage under different shading treatments, therefore, it should be highlighted whether the *L. gmelinii* have better or worse adaptation ability to shading. The seedling stage is a weak link in the plant growth and development cycle and regeneration process, and the responses of plants of different heights to shading must be further analyzed by dividing them according to different height levels (Laing et al., 2019; Liu et al., 2022; Wu et al., 2022). This study focused on the photosynthetic response characteristics of *L. gmelinii* seedlings at different height levels under different shading treatments and explored the suitable light environment for the growth of *L. gmelinii* seedlings, thereby providing a theoretical basis for forest management and artificial strategies to promote the natural regeneration of *L. gmelinii*.

Materials and Methods

Overview of the Study Area

The experimental area is located in the Chaocha Forestry Farm, Da Hinggan Ling, Inner Mongolia (120°30'–121°3'E, 50°49'–50°51'N). The elevation ranges from 800 to 1116 m, the soil type is brown coniferous forest soil, and there are large areas of marsh wetlands and continuous permafrost. The study area has a cold temperate continental monsoon climate and an annual average temperature of -5 °C, extreme high temperature of 40 °C, extreme low temperature of -50 °C, In winter (with an average temperature of <10 °C), it can last for 9 months, while in summer (with an average temperature of >22 °C), it does not exceed 1 month. The frost-free period is 80 days. annual average precipitation of 450–550 mm, relative humidity of 66%, and potential evapotranspiration of 800–1200 mm (Zhou, 2011).

Experimental Site and Experimental Design

The experimental site was surveyed before the experiment, and a *L. gmelinii* forest with consistent topography, slope, and elevation was selected. A randomized block design (four treatments × three replications) was used to establish 12 sample plots of similar forest density (20 m × 20 m). A black nylon net was used to construct a shading shed, and a lux meter (TES-1330A, Shenzhen Yeguan Instrument Equipment, Shenzhen, China) was used to measure the light transmittance of the shading net. Four shading

treatments were set up as follows: 100% natural sunlight (100% NS, control), one layer of shading net (65% NS), two layers of shading net (35% NS), and three layers of shading net (10% NS). *L. gmelinii* trees at heights of 1–3 (including 3 m), 0.5–1 (including 1 m), and ≤ 0.5 m was selected as the research objects, and three leaves were selected for each height level to measure their chlorophyll content, chlorophyll fluorescence, and daily changes in photosynthesis. One sample tree was selected for each height level (Table 1) to measure the light response curve and CO₂ response curve, and the changes in their photosynthetic characteristics were studied. Shading started on June 1, 2020, and ended on August 30, 2020. Light response curves and daily changes in photosynthesis were observed twice in early (1–15) and late (16–31) August, with each observation lasting 6 days. Light response curves were measured for 2 days, daily changes in photosynthesis were measured for 1 day, and daily changes in chlorophyll fluorescence were measured for 1 day.

Measurement of Photosynthesis

The light response curve measurements were performed on two clear and slightly cloudy days in early and late August. A LI-6400XT portable CO₂/H₂O infrared analyzer (LI-COR, Lincoln, NE, USA) was used to measure the gas exchange process and environmental factors of the coniferous trees. The leaf chamber temperature was set to 25 °C, the humidity was approximately 50%, and the flow rate was 500 μmol^{-1} . During the measurements, leaves on the sunny side of the upper canopy of each shade treatment at different tree heights were selected. The measurement process was induced by applying a saturating light intensity, and the photosynthetic rate was measured after stabilization. The photosynthetic photon flux density gradient during the light response curve measurement was set to 2000, 1500, 1200, 1000, 800, 600, 400, 200, 150, 100, 50, and 0 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$, and CO₂ concentration was set to 400 $\mu\text{mol CO}_2 \text{ mol}^{-1}$. The light response curve was fitted using the non-linear equation proposed by Prado and Demoraes (Prado and Moraes, 1997):

$$P_n = P_{\max} (1 - e^{-k * (PAR - LCP)}) \quad (\text{Eq.1})$$

where K is a constant, and PAR refers to photosynthetically active radiation measurements. In addition, the output parameters included the maximum P_n per unit area ($P_{n\max}$, $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$), P_n ($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$), light compensation point (L_{CP} , $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$), and light saturation point (L_{sp}). Linear regression is performed using PPFD and P_n below 200 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ as the horizontal and vertical coordinates, respectively. The slope of the regression line and its intercept from the horizontal axis are the apparent quantum yield (AQY, $\text{nmol } \mu\text{mol}^{-1}$) and dark respiration rate (R_a) (Quan and Wang, 2015).

The CO₂ response curve was measured using a LI-6400XT portable CO₂/H₂O infrared gas analyzer (LI-COR, Lincoln, NE, USA) and a 6400–02B red/blue light source chamber (LI-COR), in which the gas exchange and corresponding environmental factors were measured in needle leaves. The settings were the same as for the light response curve measurement. During the CO₂ response curve measurement, the CO₂ concentration gradient was set as follows: 400, 200, 150, 100, 50, 25, 400, 400, 600, 800, 1200, 1500, 1800, and 2000 $\mu\text{mol CO}_2 \text{ mol}^{-1}$, with a saturating light intensity of 1500 $\mu\text{mol photons m}^{-2} \cdot \text{s}^{-1}$. The CO₂ response curve was fitted using the following model.

Table 1. Basic parameters of the sampled trees

Height	1– 3 m				0.5–1 m				≤0.5 m			
Degree of shading	Tree height(m)	Ground diameter (cm)	Clear length (m)	crown diameter (m)	Tree height(m)	Ground diameter (cm)	Clear length (m)	crown diameter (m)	Tree height(m)	Ground diameter (cm)	Clear length (m)	crown diameter (m)
65% NS	1.5	1.66	0.35	0.56×0.86	1	1.05	0.19	0.25×0.3	0.25	0.33	0.06	0.12×0.12
	2.7	2.61	1.3	1×0.6	0.6	1.09	11.1	0.35×0.3	0.4	1.4	0.15	0.4×0.25
	1.8	1.94	0.55	0.5×0.64	0.8	1.32	0.23	0.38×0.45	0.4	0.89	0.25	0.24×0.15
35% NS	1.6	2.22	0.32	0.48×0.99	0.6	0.98	0.21	0.27×0.32	0.3	0.56	0.08	0.12×0.24
	2.5	2.76	1.3	0.8×0.9	0.7	1.42	0.35	0.3×0.35	0.25	0.74	0.03	0.1×0.24
	2.7	2.81	0.6	0.7×0.58	1	1.33	0.3	0.49×0.45	0.35	0.81	0.2	0.08×0.25
10% NS	1.5	1.7	0.3	0.55×0.6	0.75	0.81	0.29	0.35×0.45	0.5	1.48	0.23	0.3×0.3
	3	2.15	1	0.6×1	0.6	0.75	0.12	0.3×0.29	0.2	0.61	0.05	0.23×0.22
	2.9	1.94	0.77	0.4×0.7	0.8	0.78	0.37	0.4×0.3	0.3	0.79	0.14	0.18×0.16
CK	1.2	2.29	0.3	0.49×0.46	0.85	1.69	0.28	0.4×0.4	0.25	0.57	0.1	0.2×0.2
	2.7	3.07	0.5	0.72×0.8	0.7	1.61	0.2	0.37×0.35	0.4	1.11	0.12	0.15×0.2
	1.5	1.82	0.35	0.46×0.51	0.9	1.41	0.12	0.57×0.3	0.5	1.38	0.1	0.3×0.3

$$P_n = \min(W_c, W_j, W_t) \times (1 - \Gamma^* / C_i) - R_a \quad (\text{Eq.2})$$

where W_c , W_j , and W_t represent the potential CO_2 assimilation rates supported by the Rubisco activity, RuBP regeneration rate, and organic phosphate regeneration, respectively; Γ^* is the CO_2 compensation point; and C_i is the intercellular CO_2 concentration. The mathematical expressions for W_c , W_j , and W_t are as follows Equations 3,4,5,6 (Liu et al., 2007):

$$W_c = \frac{V_{\max} \bullet C_i}{C_i + K_c(1 + O / K_o)} \quad (\text{Eq.3})$$

$$W_j = \frac{J \bullet C_i}{4.5C_i + 10.5\Gamma^*} \quad (\text{Eq.4})$$

$$W_t = \frac{3TUP}{\left(1 - \frac{\Gamma^*}{C_i}\right)} \quad (\text{Eq.5})$$

$$J = f(J_{\max}) \quad (\text{Eq.6})$$

where $V_{\max}$ ($\mu\text{mol} \cdot (\text{m}^2 \cdot \text{s}^{-1})$) is the maximum Rubisco carboxylation rate per unit area; $J_{\max}$ ($\mu\text{mol} \cdot (\text{m}^2 \cdot \text{s}^{-1})$) is the maximum electron transport rate per unit area; K_c and K_o are the Michaelis-Menten constants for CO_2 and O_2 , respectively; O is the intercellular O_2 concentration; and TPU ($\mu\text{mol} \cdot (\text{m}^2 \cdot \text{s}^{-1})$) is the rate of utilization of photosynthetic product glyceraldehyde-3-phosphate per unit area. By inputting the values and related parameters obtained from the CO_2 curve measurement into the equation, $V_{\max}$, $J_{\max}$, and TPU can be calculated.

As the needle leaves used for photosynthesis measurement were not fully occupying the leaf chamber during the light and CO_2 response curve measurement, they were scanned to create images. The leaf area was then calculated in Photoshop using the ratio of pixels to area. In this study, the photosynthetic parameters were calculated using the leaf area on one side of the leaf.

Measurement of Diurnal Variations in Photosynthesis

Diurnal variations in photosynthesis in the *L. gmelinii* trees were measured on a sunny day in early and late August using a LI-6400XT portable photosynthesis system (LI-COR) under natural light (Figure 1). Measurements were taken in 2 h intervals from 7:00 am to 5:00 pm. Leaves similar in terms of growth and location were selected for the measurements, and three clusters of trees were measured for each shading treatment, with one cluster of leaves measured per tree and three repetitions performed. The measured indicators included the P_n , intercellular CO_2 concentration (C_i), G_s , and T_r .

Measurement of Chlorophyll and Soluble Sugar Contents

In July, three leaves with the same orientation from each shading treatment were selected, and the V(ethanol): V(acetone) = 1:1 extraction method was used to extract

chlorophyll (a and b) and soluble sugars (Gao, 2006). The absorption values at the wavelengths of 470, 645, and 663 nm were measured using a UV spectrophotometer (Alpha-1860 UV spectrophotometer, Shanghai spectral element instrument, Shanghai, China) (Tang et al., 2019). The formulae for calculating chlorophyll a (Chla), chlorophyll b (Chlb), total chlorophyll (CT), and soluble sugar (CCar) contents are as follows Equations 7,8,9,10:

$$Chla = 1272 \times A_{663} - 259 \times A_{645} \quad (\text{Eq.7})$$

$$Chlb = 2288 \times A_{645} - 467 \times A_{663} \quad (\text{Eq.8})$$

$$CT = Chla + Chlb \quad (\text{Eq.9})$$

$$CCar = (1000 \times A_{470} - 3.27 \times Chla - 104 \times Chlb) / 229 \quad (\text{Eq.10})$$

where A_{663} , A_{645} , and A_{470} represent the absorbance values at wavelengths of 663, 645, and 470 nm, respectively.



Figure 1. LI-6400XT Clustered Leaf Chamber for Measuring Diurnal Changes in Photosynthesis

Measurement of Chlorophyll Fluorescence

On a sunny day each month from June to August, dark adaptation was realized using a dedicated dark-adapted leaf clip for 30 min before measuring the fluorescence parameters of young seedlings of *L. gmelinii* Under different shading treatments using a FluorCam fluorescence imaging system from 7:00 am to 5:00 pm at 2 h intervals. The measured parameters included the actual quantum yield (Y), maximum photochemical efficiency (F_v/F_m) or initial conversion efficiency of PSII, non-photochemical quenching coefficient (NPQ), and photochemical quenching coefficient (qP).

Data analyses were reported as the mean $\pm$ standard deviation (SD). One-way analysis of variance (ANOVA) combined with the Tukey test was applied to determine the differences between sampling sites. ANOVA was performed using SPSS Statistics version 21 (IBM Corp, Armonk, NY, USA), with p values ≤ 0.05 considered statistically significant. The light response curve and CO_2 response curve have been fitted using R's "plantecophys" and "minpack.lm" software packages (4.0.4), and the light response curve and CO_2 response curve have been generated using R's "ggplot2" software package (4.0.4). The bar chart and daily change curve have been generated using SigmaPlot.

Results and Analysis

Effects of Shading on Photosynthetic Pigments in *L. gmelinii*

Shading had a significant effect on the photosynthetic pigments in young seedlings of *L. gmelinii* (Figure 2), and moderate shading resulted in an increasing trend of photosynthetic pigment content. For the 1–3 m seedlings, the maximum values for Chla, Chlb, CT, and Chla/b contents were achieved under 65% NS. For the 0.5–1 m and ≤ 0.5 m seedlings, the highest contents of Chla, Chlb, and CT were achieved under the 35% NS treatment, the highest content of Chla/b was achieved under the CK treatment, and significant differences were not observed among treatments. The soluble sugar content of the three different height groups of *L. gmelinii* was the highest under CK treatment. For the 1–3 m seedlings, significant differences in soluble sugar content were observed between the CK and 35% NS and 10% NS treatments; for the 0.5–1 m seedlings, a significant difference was observed between the CK and 35% NS treatments; and for the ≤ 0.5 m seedlings, significant differences were observed between the CK and 65% NS and 10% NS treatments.

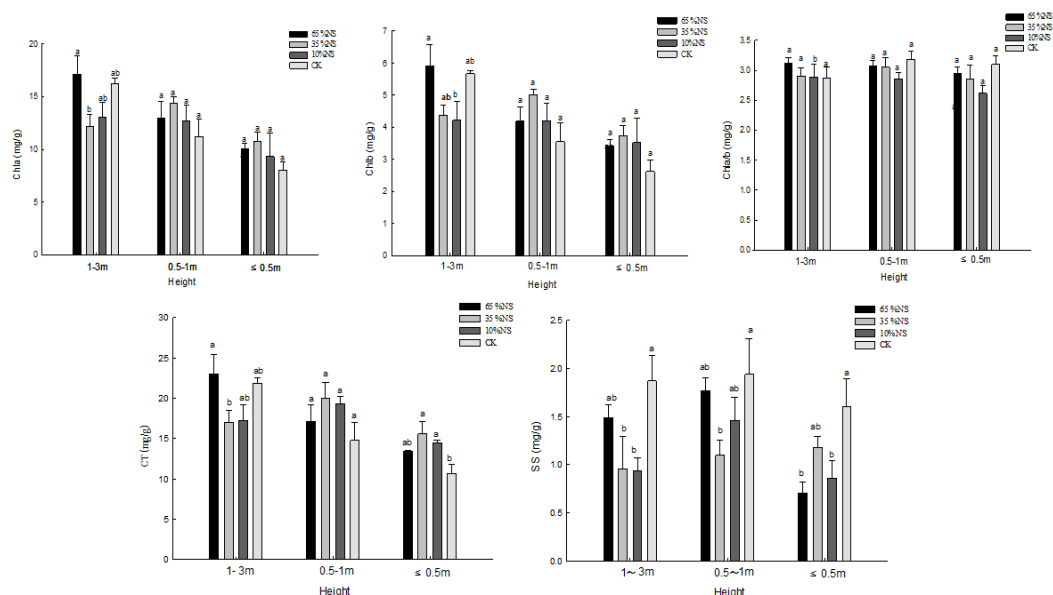


Figure 2. Changes in the contents of photosynthetic pigments of *Larix gmelinii* under different shading treatments. Data are expressed as Mean $\pm$ SD, 3 replicates per sample. For each fraction, means in bars followed by a different letter are significantly different ($P < 0.05$, one-way ANOVA followed by Tukey's test)

Effects of Shading on the Photosynthetic Characteristics of *L. gmelinii*

The initial light intensity in the photosynthetic light response curves of *L. gmelinii* seedlings and saplings showed a linear increasing trend under all treatments within the range of 0–500 $\mu\text{mol}\cdot(\text{m}^2\cdot\text{s}^{-1})$. As photosynthetic active radiation gradually increased, the net photosynthetic rate of *L. gmelinii* seedlings and saplings under all shading treatments gradually increased and then tended to stabilize when the photosynthetic active radiation reached approximately 1400 $\mu\text{mol}\cdot(\text{m}^2\cdot\text{s}^{-1})$ (Figure 3). The shading treatments significantly affected the CO_2 response curves, with P_n slowly increasing as C_i increased within the range of 0–300 $\mu\text{mol}\cdot(\text{m}^2\cdot\text{s}^{-1})$, rapidly increasing within 300–900 $\mu\text{mol}\cdot(\text{m}^2\cdot\text{s}^{-1})$, and then tending to stabilize at 900 $\mu\text{mol}\cdot\text{m}^2\cdot\text{s}^{-1}$ and not showing further increase with an increase in C_i (Figure 3). The shading treatment significantly increased the photosynthetic parameters of the leaves of 1–3 m *L. gmelinii* (Table 2). The $P_{n\text{max}}$, $V_{c\text{max}}$, J_{max} , and TPU of the 1–3 m *L. gmelinii* were all highest under 65% NS treatment and the lowest under 10% NS treatment, and the differences between treatments were significant. The $P_{n\text{max}}$, $V_{c\text{max}}$, J_{max} , and TPU of the 0.5–1 m and ≤ 0.5 m seedlings were all highest under the CK treatment, and the differences between treatments were significant. Under the four shading treatments at the three tree heights, the L_{sp} and L_{cp} were highest under the CK treatment.

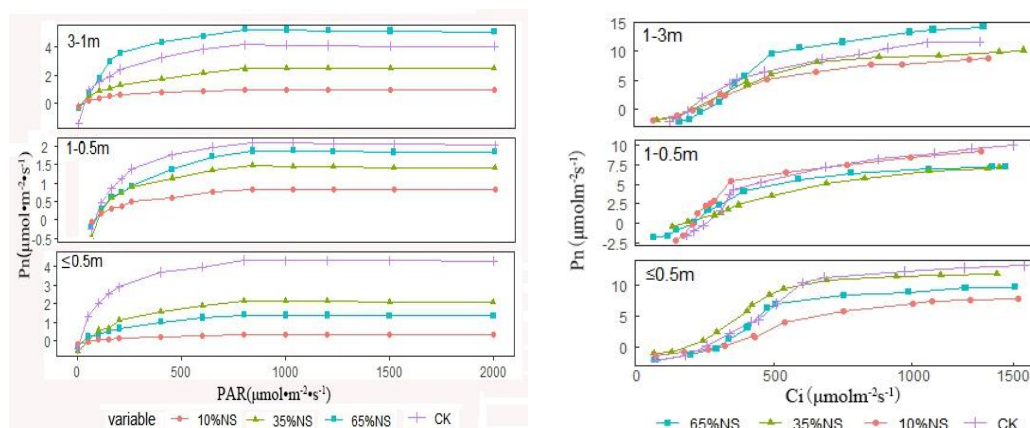


Figure 3. Changes in the photosynthetic light response curve and photosynthetic CO_2 response curve of *Larix gmelinii* under different shading treatments

Effect of Shading on Diurnal Variations in Photosynthesis in *L. gmelinii*

Diurnal Variation in the P_n

The diurnal variation in the P_n in *L. gmelinii* seedlings and young trees within the three height levels and four shading treatments showed a bimodal curve pattern (Figure 4). The peaks of P_n occurred at approximately 9:00 am and 3:00 pm, with the maximum value at 9:00 am and the minimum value after 5:00 pm. For the 1–3 m, *L. gmelinii* young trees, the highest P_n values were observed under the 65% NS treatment, followed by the CK, 35% NS, and 10% NS treatments. The CK treatment resulted in the highest P_n values for the 0.5–1 m and ≤ 0.5 m seedlings. The bimodal curve pattern of P_n in *L. gmelinii* seedlings and young trees at all three height levels was likely associated with the midday high light intensity causing stomatal closure, which resulted the reduced photosynthetic rate and occurrence of the "midday depression" phenomenon.

Table 2. Photosynthetic light response and photosynthetic CO₂ response parameters of *Larix gmelinii* under different shading treatments

Height	Treatment	P _{max} /μmol·m ⁻² ·s ⁻¹	L _{sp} /μmol·m ⁻² ·s ⁻¹	L _{cp} /μmol·m ⁻² ·s ⁻¹	J _{max} /μmol·m ⁻² ·s ⁻¹	V _{cmax} /μmol·m ⁻² ·s ⁻¹	TPU/μmol·m ⁻² ·s ⁻¹
1 – 3 m	65%NS	(5.19±0.71)a	(1528.48±4.62)b	(25.76±0.06)b	(29.26±0.23)a	(41.04±0.30)a	(7.54±0.03)a
	35%NS	(2.49±0.59)c	(1527.07±22.63)c	(15.30±0.09)c	(16.70±0.087)c	(22.33±0.46)c	(4.49±0.025)c
	10%NS	(0.97±0.68)d	(1171.40±15.35)d	(12.79±0.57)d	(16.08±0.37) d	(19.86±0.40)d	(4.01±0.053)b
	CK	(4.09±0.66)b	(1686.59±25.71)a	(32.39±0.23)a	(23.65±0.058)b	(27.78±0.38)b	(5.43±0.00034)b
0.5 – 1 m	65%NS	(1.89±0.76)b	(1394.35±5.89)b	(20.10±0.57)b	(15.22 ±0.37)c	(16.41±0.31)ab	(3.91±0.04)b
	35%NS	(1.45±0.59)c	(1339.60±5.16)c	(15.34±0.13)c	(27.52±0.03)b	(15.17±0.30)ab	(3.25±0.03)c
	10%NS	(0.82±0.04)d	(1173.49±7.56)d	(9.8±0.03)d	(11.20±0.13) d	(38.31±0.078)b	(3.21±0.03)d
	CK	(2.09±0.09)a	(1445.82±1.56)a	(23.87±0.03)a	(33.28±0.03)a	(38.50±0.55)a	(8.16±0.02)a
≤0.5 m	65%NS	(2.13±0.09)b	(1376.34±3.154)b	(38.28±0.04)a	(12.88±0.04)c	(15.59±0.331)c	(3.44±0.012)c
	35%NS	(1.48±0.08)d	(1336.71±22.78)c	(35.18±0.01)c	(18.20±0.01)b	(32.74±0.500)a	(4.91±0.045)b
	10%NS	(0.34±0.04)a	(1206.16±34.58)d	(19.82±0.04)b	(12.77±4.58)d	(14.17±0.317)b	(2.75±0.021)d
	CK	(4.33±0.28)c	(1500.30±5.48)a	(47.07±4.58)a	(27.56±0.04)a	(30.35±1.207)b	(5.26±0.007)a

Data are expressed as Mean ± SD, 3 replicates per sample. Means in each column followed by a different letter are significantly different P < 0.05, one-way ANOVA followed by Tukey's test) differences. The above significance is only the significance of the high category

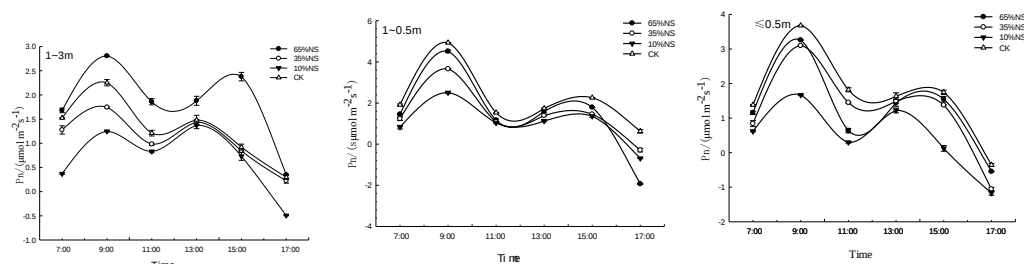


Figure 4. Diurnal variation in the net photosynthetic rate (P_n) of *Larix gmelinii* under different shading treatments

Diurnal Variation in the T_r

Under different light conditions, the diurnal variation in the T_r for *L. gmelinii* seedlings with different heights showed a bimodal curve (Figure 5). For the 1–3, 0.5–1, and ≤ 0.5 m groups, the T_r was lower at 7:00 am and increased with time, reaching a peak at 9:00 am under all shading treatments; however, a significant decreasing trend was observed at 11:00 am, with the T_r exhibiting a bimodal pattern at 9:00 am and 3:00 pm and reaching the maximum value at approximately 10:00 am and the minimum value after 5:00 pm. The T_r of the 1–3 m seedlings decreased in the order of 65% NS > CK > 35% NS > 10% NS, while that of the 0.5–1 m and ≤ 0.5 m seedlings decreased in the order CK > 65% NS > 35% NS > 10% NS.

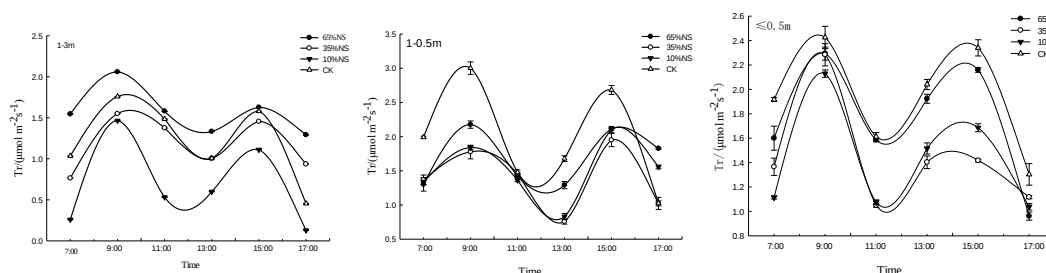


Figure 5. Diurnal variation in the transpiration rate (T_r) of *Larix gmelinii* under different shading treatments

Daily Variation in the G_s

The daily variation in the G_s in *L. gmelinii* seedlings at different height levels under different light conditions showed a bimodal curve (Figure 6). The first peak for the 1–3 m seedlings appeared at approximately 9:00 am, and the second peak appeared at approximately 1:00 pm, with the maximum value occurring at the first peak. For the 0.5–1 and ≤ 0.5 m seedlings, the first peak appeared at approximately 9:00 am, while the second peak appeared at approximately 3:00 pm, with the maximum value occurring at the first peak. For the 1–3 m seedlings, the G_s decreased in the order trend 65% NS > 10% NS > 35% NS > CK, whereas for the 0.5–1 m and ≤ 0.5 m seedlings, the trend was CK > 65% NS > 35% NS > 10% NS.

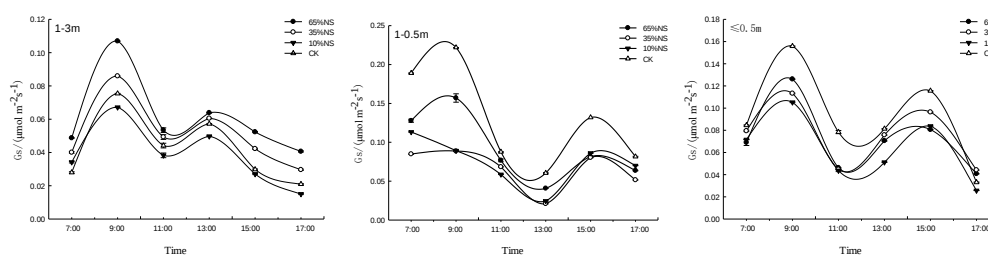


Figure 6. Diurnal variation in the stomatal conductance (G_s) of *Larix gmelinii* under different shading treatments

Daily Variation in the C_i

Under different light conditions, the daily variation in the C_i in young and small *L. gmelinii* saplings at different heights showed "W"-shaped and "V"-shaped curves (Figure 7). For *L. gmelinii* saplings with heights of 1–3, 0.5–1, and ≤ 0.5 m, the C_i was higher in the morning and evening. The C_i of saplings with heights of 1–3 m showed a decreasing trend of 10% NS > 35% NS > CK > 65% NS, while that of saplings with heights of 0.5–1 and ≤ 0.5 m showed a trend of 10% NS > 35% NS > 65% NS > CK.

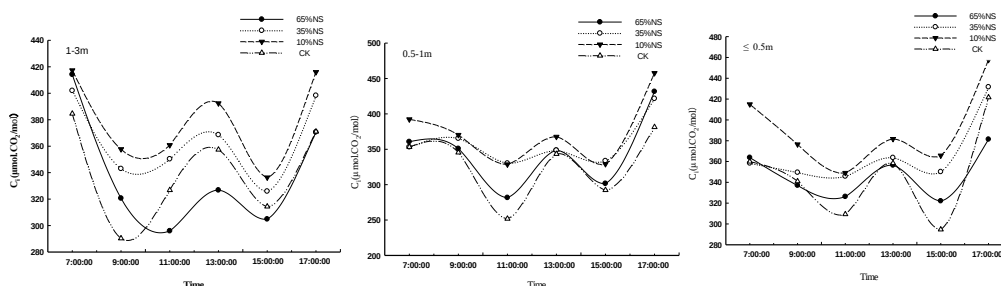


Figure 7. Diurnal variation in the intercellular CO_2 concentrations (C_i) of *Larix gmelinii* under different shading treatments

Effects of Shading on Chlorophyll Fluorescence Parameters in *Larix gmelinii*

Daily Variation in the Actual Photosynthetic Quantum Yield (Y)

The first peak of Y in saplings with heights of 1–3 m appeared at approximately 1:00 pm, with a secondary peak at approximately 9:00 am (Figure 8). The maximum value was observed at the first peak. The first peak of Y in saplings with heights of 0.5–1 and ≤ 0.5 m appeared at approximately 9:00 am, with a secondary peak at approximately 1:00 pm. The maximum value occurred at the first peak. The daily variation in the Y in saplings with heights of 1–3 m showed a decreasing trend of CK > 65% NS > 35% NS > 10% NS, while that for saplings with heights of 0.5–1 and ≤ 0.5 m showed trends of CK > 65% NS > 35% NS > 10% NS and 65% NS > 35% NS > CK > 10% NS, respectively.

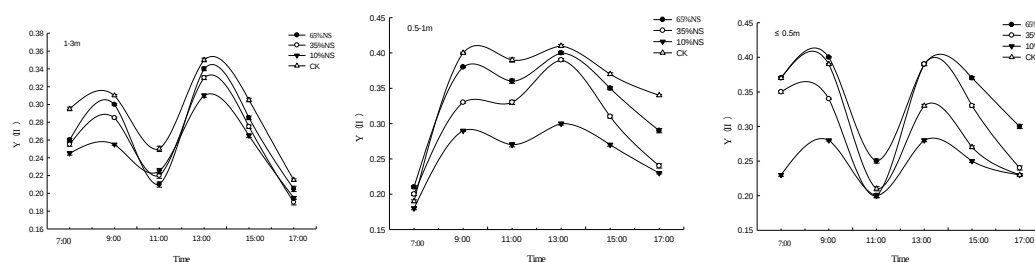


Figure 8. Daily variation in the actual light quantum yield (Y) of *Larix gmelinii* under different shading treatments

Diurnal Variation in the Maximum Quantum Efficiency of Photosystem II (F_v/F_m)

The diurnal variation trend of F_v/F_m for the young seedlings of different tree heights of *L. gmelinii* was a bimodal curve (Figure 9). For young trees with heights of 1–3 m, the first and second peaks appeared at approximately 11:00 am and 3:00 pm, respectively, with the minimum value occurring at 1:00 pm under both the CK and 65% NS treatments. For seedlings with heights of 0.5–1 and ≤ 0.5 m, the first peak appeared at approximately 9:00 am, the second peak appeared at approximately 3:00 pm, and the minimum value occurred at 11:00 am. The diurnal variation in the F_v/F_m in the 1–3 m *L. gmelinii* seedlings showed a decreasing trend of 65% NS > CK > 35% NS > 10% NS, while that in the 0.5–1 and ≤ 0.5 m seedlings showed a trend of CK > 65% NS > 35% NS > 10% NS.

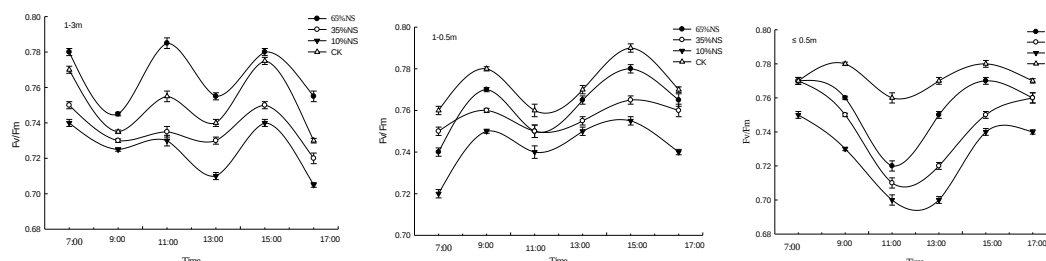


Figure 9. Diurnal variation in the maximum light quantum efficiency (F_v/F_m) of *Larix gmelinii* under different shading treatments

Diurnal Variation in the Non-Photochemical Quenching (NPQ) Coefficient

Under different light conditions, the diurnal variation in the NPQ in young and small seedlings of *L. gmelinii* showed an "M" shaped curve (Figure 10). For *L. gmelinii* trees with heights of 1–3, 0.5–1, and ≤ 0.5 m, the NPQ values were lower in the morning and evening. The diurnal variation in the NPQ in the 1–3 m seedlings decreased in the order 65% NS > CK (100% natural sunlight > 35% NS > 10% NS. For the 0.5–1 m seedling, the order was CK > 65% NS > 35% NS > 10% NS, while for the ≤ 0.5 m seedlings, the order was CK > 35% NS > 65% NS > 10% NS.

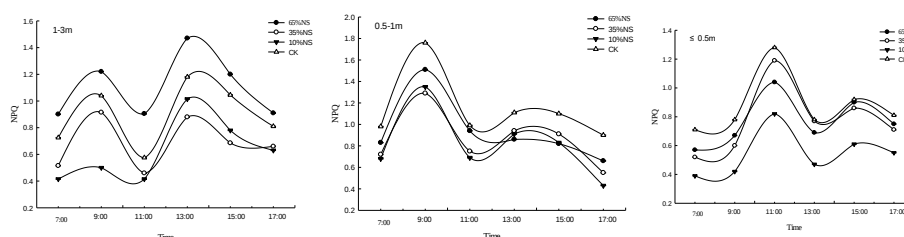


Figure 10. Daily variation in the non-photochemical quenching coefficient (NPQ) of *Larix gmelinii* under different shading treatments

Diurnal Variation in the Photochemical Quenching Coefficient (qP)

Under the same shading treatment, the diurnal variation in the qP for different heights of young *L. gmelinii* trees showed a "M"-shaped curve and an inverted "V"-shaped curve (Figure 11). The peak values for the 1–3 m tall young trees appeared at approximately 9:00 am and 1:00 pm, with the maximum value at 9:00 am and the minimum value after 5:00 pm. The peak values for the 0.5–1 m tall seedlings appeared at approximately 11:00 am and 3:00 pm, with the maximum value at 11:00 am. The peak value for seedlings ≤ 0.5 m appeared at approximately 11:00 am, with the minimum value after 5:00 pm. The diurnal variation in the qP for the 1–3 m saplings decreased in the order 65% NS > CK > 10% NS > 35% NS. The diurnal variation in the qP for the 0.5–1 and ≤ 0.5 m seedlings decreased in the order CK > 65% NS > 35% NS > 10% NS.

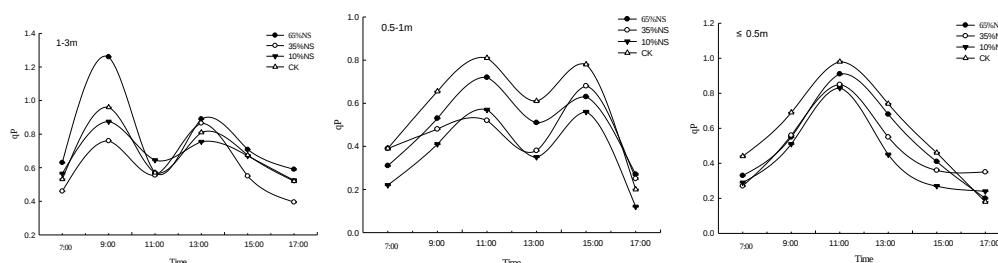


Figure 11. Diurnal variation of chemical quenching coefficient (qP) of *Larix gmelinii* under different shading treatments

Discussion

Plants selectively absorb light in different wavelength bands, with Chla having a longer absorption band in the red-light region and Chlb having a wider absorption band in the blue-violet light region (Luo et al., 2021; Ren et al., 2022). Therefore, as the ratio of Chla/b changes, plants are able to utilize blue-violet light more efficiently, which enhances their ability to survive in low-light environments (Wu et al., 2022; Yuan et al., 2022). The Chla, Chlb, and CT of 1–3 m young trees reached their maximum value under the 65% NS treatment because the leaves of the plants increased their ability to absorb and convert the light energy in weak light environments, thus promoting photosynthesis and dry matter accumulation. This research result is similar to that for other plants, such as *Phoebe bournei*, *Quercus acutissima*, and *Robinia pseudoacacia* (Xu et al., 2010). As the light intensity decreased, the Chla/b content of the 0.5–1 m and

≤ 0.5 m seedlings decreased first and then increased, with maximum values achieved under the 35% NS treatment; moreover, significant differences were not observed between treatments, which indicated that shading did not improve the weak light-utilization ability of the 0.5–1 and ≤ 0.5 m seedlings. In this study, as the shading intensity increased, the soluble sugar content of the 1–3, 0.5–1, and ≤ 0.5 m *L. gmelinii* seedlings gradually decreased, indicating that *L. gmelinii* seedlings are more conducive to soluble sugar accumulation under full light conditions. Thus, excessive shading can lead to severe damage to chloroplasts and a weakened photosynthetic ability of plants.

The light response curve is of great significance for describing the plant photosynthetic efficiency (Sharkey et al., 2007; Zhao et al., 2022). Shading significantly increased the P_{nmax} of the 1–3 m young tree leaves, which reached the maximum value at 65% transmittance and slowed down physiological damage and reduced light inhibition. The P_{nmax} of the 0.5–1 and ≤ 0.5 m seedlings began to decline at 65% transmittance. Excessive shading resulted in a severe lack of light for plants, which led to the consumption of a large amount of energy for capturing light, thus causing a decrease in the net photosynthetic rate. Low L_{CP} and L_{SP} can help plants maximize the use of low photon flux under weak light conditions (Murchie and Niyogi, 2011). The L_{CP} and L_{SP} of the larches at three height levels under the four shading treatments were lower than those under the CK treatment. This result indicates that the L_{SP} is reached earlier under shading conditions, at which point plant photosynthesis is stronger and organic matter accumulation is facilitated, thus meeting the needs of normal growth under shading conditions. Plant leaf V_{cmax} is the maximum carboxylation reaction rate catalyzed by Rubisco during plant photosynthesis, and it corresponds to the maximum number of moles ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) of CO_2 fixed by the plant leaf per unit area per unit time, which is an important parameter for expressing plant photosynthetic capacity (Wang et al., 2017; Peng et al., 2022). The V_{cmax} of the 1–3 m young trees reached a maximum under the 65% NS treatment, which indicated that these trees had a strong ability to utilize low concentrations of CO_2 . However, the 0.5–1 and ≤ 0.5 m seedlings expended greater energy to perform photosynthesis at higher CO_2 concentrations. The TPU of the 1–3 m young trees reached a maximum value under the 65% NS treatment and showed a decreasing trend with increasing and decreasing shading intensities, thus indicating that moderate shading considerably improves ecological adaptability. Moreover, the maximum TPU values for the 0.5–1 and ≤ 0.5 m seedlings were observed under the CK treatment, indicating that these trees showed good ecological adaptability. However, the photophosphorylation process was inhibited under severe shading of 10% NS. In this study, 1–3 m young trees showed good performance at 65% transmittance, which may be due to the following three reasons: first, this study did not investigate the underground litter layer, and the litter fungi may have stimulated the growth of young trees under shading conditions; second, climatic factors such as precipitation and temperature may have had an effect; third, the experiment was performed in August when growth was vigorous, which may have influenced the experimental results.

Under stress conditions, the photosynthesis of plants is affected by both stomatal and non-stomatal limiting factors. When the P_n decreases, the C_i and G_s decrease simultaneously, which indicates that photosynthesis is limited by stomatal factors (Xia et al., 2021). However, when the P_n decreases while C_i increases, photosynthesis is limited by non-stomatal factors. This study found that in the three height classes of *L. gmelinii* under four shading treatments, the P_n was negatively correlated with the C_i , suggesting that the decrease in the P_n was limited by non-stomatal factors. Under the

10% NS treatment, the P_n , G_s , and T_r values were significantly lower than those observed under other treatments, indicating that the photosynthesis of *L. gmelinii* was strongly affected by high-intensity shading conditions. The daily changes in the T_r and P_n in the three height classes under the four shading treatments were similar and showed consistent peak changes, which was due to the regulation of stomatal conductance. The maximum T_r of the *L. gmelinii* seedlings and young trees occurred under full sunlight (100% NS) and decreased as the shading intensity increased, indicating that under other environmental conditions, the stronger the light, the greater the transpiration water consumption. Water consumption was highest under full sunlight and lowest under the 10% NS treatment.

L. gmelinii trees from all the three height levels experienced a period of growth from 7:00 am to 9:00 am, followed by a decline in growth from 9:00 am and then a recovery from 11:00 am. This may be due to the weaker light intensity in the morning, which allowed the plants to absorb the light energy more efficiently for photosynthesis. As light intensity and temperature increased, the plants experienced light inhibition, which restricted electron transfer in the PSII reaction center and lowered the PSII electron transfer Y , resulting in a decrease in the photosynthetic efficiency of PSII. This finding is consistent with the research results of Zhou et al. (2019) and Zhang et al. (2020). The F_v/F_m values of the three *L. gmelinii* tree groups were all low during midday, indicating that photosynthesis activity was inhibited under strong light conditions. After 1:00 pm, the F_v/F_m values gradually increased, indicating that the damage to the PSII reaction center in the young *L. gmelinii* seedlings and trees was reversible and that the photosynthetic organs were not damaged. As light intensity and temperature decreased, the functions of photosynthetic organs were restored. The midday NPQ values of all the three types of trees under all four shading treatments decreased, possibly due to excessive light intensity at midday, which reduced the number of open PSII centers in the *L. gmelinii* trees; moreover, most of the absorbed light energy was dissipated as heat, which reduced the amount of light energy available for photosynthetic electron transfer. This indicates that *L. gmelinii* trees can adapt to high-light environments by dissipating excess light energy as heat to protect the photosynthetic apparatus. The reduced response of qP reduction under shading was lowest for the 1–3 m seedlings under the 65% NS treatment, indicating a higher proportion of open PSII reaction centers and higher efficiency of light energy conversion and electron transfer activity. However, for the 0.5–1 and ≤ 0.5 m seedlings, the reduction in the qP increased gradually with increasing shading degree, and the light energy conversion efficiency and electron transfer activity were highest under the CK treatment. The light characteristics of seedlings with heights of ≤ 0.5 and 0.5–1 m were not clearly evident from the study results, which was possibly due to the different height groups in the experimental design. Therefore, to find a suitable shading range for the growth of *L. gmelinii* seedlings, it is necessary to further divide seedlings with heights below 0.5 m into different levels and explore the responses of smaller *L. gmelinii* seedlings to different light conditions. Due to the large number of measurement samples, it takes two days each to measure the light response curve and the CO_2 response curve. The possible differences between these two days are also one of the reasons why the light and characteristics of seedlings ≤ 0.5 m and 0.5–1 m are not obvious.

Conclusion

In summary, the quality score of photosynthetic pigments and photosynthetic and fluorescence parameters that affect the photosynthetic characteristics of *L. gmelinii* were comprehensively considered. Results showed that the decline in the P_n of young and small *L. gmelinii* exposed to four different shading treatments was inhibited by non-stomatal limiting factors. Meanwhile, young, and small *L. gmelinii* could adapt to strong light environments by dissipating excess light energy as heat, the damage to the PSII reaction center was reversible, and photosynthetic organ functions could be restored as the light intensity and temperature decrease. The 1–3 m young and small *L. gmelinii* under the 65% NS treatment showed improved light energy absorption and conversion, increased photosynthesis, and dry matter accumulation, enhanced weak-light utilization, reduced light inhibition, and high light energy conversion efficiency and electron transfer activity. However, for seedlings at 0.5–1 and ≤ 0.5 m, excessive shading led to damage to the photosynthetic mechanism of young and small *L. gmelinii* and hence they were not able to grow normally. It is speculated that the optimal growth of seedlings of this size may occur in environments with better light conditions. Taken together, these findings provide a theoretical basis for forest management and artificial strategies to promote the natural regeneration of *L. gmelinii* which has a high economic value.

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