



# Eco-physiological characteristics of *Tetracentron sinense* Oliv. saplings in response to different light intensities

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**Abstract** The regeneration of *Tetracentron sinense* Oliv. is poor in the understory and in open areas due to the characteristics of natural regeneration of the species on forest edges and in gaps. It is unclear whether different light intensities in various habitats affect eco-physiological characteristics of saplings and their natural regeneration. In this study, the light intensity in *T. sinense* habitats was simulated by artificial shading (L1: 100% NS (natural sunlight) in the open; L2: 50% NS in a forest gap or edge; L3: 10% NS in understory) to investigate differences in morphology, leaf structure, physiology, and photosynthesis of 2-year-old saplings, and to analyze the mechanism of light intensity on sapling establishment. Significant differences were observed

in morphology (including leaf area, and specific leaf area) under different light intensities. Compared to L1 and L3, chloroplast structure in L2 was intact. With increasing time, superoxide dismutase (SOD) and catalase (CAT) activities in L2 became gradually higher than under the other light intensities, while malondialdehyde (MDA) content was opposite. Shading decreased osmoregulation substance contents of leaves but increased chlorophyll. The results suggest that light intensities significantly affect the eco-physiological characteristics of *T. sinense* saplings and they would respond most favorably at intermediate levels of light by optimizing eco-physiological characteristics. Therefore, 50% natural sunlight should be created to promote saplings establishment and population recovery of *T. sinense* during in situ conservation, including sowing mature seeds in forest edges or gaps and providing appropriate shade protection for seedlings and saplings in the open.

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**Keywords** Chloroplast ultrastructure · Eco-physiological characteristics · Light intensities · Sapling establishment · *Tetracentron sinense* Oliv

## Introduction

Natural regeneration of seed plants refers to the process of mature seed dispersal to sapling establishment, including seed dispersal to suitable habitats, seed germination, and seedling survival and growth (Wiegand et al. 2009; Li et al. 2011). However, not all seeds being dispersed have the same fate, and most seeds cannot complete the sapling stage because of regeneration restrictions (Schupp et al. 2002; Swamy et al. 2011). Factors affecting the natural regeneration of plant populations include light, water, soil, intra- and inter-specific competition and predators (Li et al. 2011),

among which light is a crucial environmental factor affecting reproduction, growth and regeneration (Downum et al. 1992; De-Wit et al. 2016; Zhang et al. 2017; Chen et al. 2019). Generally, intense light may adversely affect plants. For example, plants exhibit photoinhibition under supersaturated light (Zhang et al. 2019b). At the same time, plants may adapt to different light environments by adjusting their morphological characteristics and physiological responses. Knowledge of these mechanisms can help reveal species adaptabilities to different light conditions (Guo et al. 2013; Wu et al. 2017).

*Tetracentron sinense* Oliv., a tall deciduous tree in the Trochodendraceae family, is a relic plant of ancient origin and is mainly distributed in central and southwest China (Li et al. 2021a). Because of the absence of vessel elements, it is of considerable scientific importance to study the systematic origin and evolution of ancient flora and angiosperms (Ren et al. 2007; Gan et al. 2013). *T. sinense* habitats have been over-logged because of the species value as an ornamental, use in furniture making and in medicine, resulting in poor regeneration (Wang et al. 2006; Shi et al. 2017). Thus, it has been listed as a national second-class key protected endangered plant ([http://www.gov.cn/zhengce/zhengceku/2021-09/09/content\\_5636409.htm](http://www.gov.cn/zhengce/zhengceku/2021-09/09/content_5636409.htm)) and listed in Appendix III of CITES (<https://cites.org/eng/app/appendices.php>). Studies have shown that *T. sinense* regenerates well at forest edges or in vegetation gaps, but regeneration is poor in understories and open spaces (Chen et al. 2008; Lu et al. 2020). Saplings are highly sensitive to changes in environmental factors, which may be attributed to limited resources such as light (Zhang et al. 2019b). It is unclear whether different light intensities in different habitats of *T. sinense* affect saplings eco-physiological characteristics, thereby affecting establishment.

In this study, light intensities of different habitats of *T. sinense* saplings were simulated using artificial shading. Differences in morphology, ultrastructure, physiology, biochemistry, and photosynthesis under different light intensities or in different shading times were investigated. The specific question of this study is: At what light intensity will *T. sinense* saplings respond most favorably, and what is the eco-physiological basis for their response to light? It is speculated that, as characteristics of natural regeneration in forest edge and gap, *T. sinense* saplings would respond most favorably at intermediate light levels by optimizing eco-physiological characteristics.

## Materials and methods

### Study site

The study was located in the Meigu Dafengding National Nature Reserve (103° 11' E–103° 29' E, 28° 51' N–28° 48'

N), Sichuan Province, China. The Reserve has a humid mid-subtropical monsoon climate with an average annual rainfall of approximately 1100 mm and relative humidity of approximately 80%. Annual average temperature is 9.6 °C (Lu et al. 2020). The study was carried out in a shelter at the Longwo Protection Station at an altitude of 2000 m.

### Plant materials

The experimental materials were healthy 2-year-old *T. sinense* saplings with uniform features and robust growth (base diameter: 0.8–1.0 cm; height: 1–1.2 m). In mid-April 2019, they were transplanted into nutrient pots for conventional water and fertilizer management (ind. pot<sup>-1</sup>). The substrate was soil from a *T. sinense* habitat.

### Experimental design

Shading was carried out three months after transplanting. According to Ellsworth et al. (2004) and Chai et al. (2018), light intensities in the open, forest gap or edge, and understory were simulated by covering the saplings with black shade netting. Three levels of light intensity were set: L1, 100% NS (natural sunlight), representing the open area; L2, 50% NS representing the forest gap or edge; and L3, 10% NS representing the understory. The levels of light were achieved by suspending the shade netting with different apertures above and around the site. No shade netting, 8-needle and 12-needle netting represented, respectively, 100%, 50% and 10% NS. Twenty-five saplings per treatment were used. The same water and fertilizer management was carried out throughout the experiment, and the shading experiment lasted for 60 d.

### Determination of morphological indexes

At the start and end of the experiment, five saplings/treatment were randomly selected for measuring height ( $H1$  and  $H2$ ) and basal diameter ( $D1$  and  $D2$ ); variations in height ( $\Delta H$ ) and basal diameter ( $\Delta D$ ) were calculated by Eqs. 1–2:

$$\Delta H = H2 - H1 \quad (1)$$

$$\Delta D = D2 - D1 \quad (2)$$

At the end of the experiment, five saplings/treatment were randomly selected for biomass measurement. Roots and above-ground parts were washed with tap water, and roots, stems and leaves were separated and stored in envelopes. Dry weights were obtained according to Fan et al. (2021) and root/shoot ratios were calculated by Eq. 3:

$$\text{root/shoot ratio} = \text{underground biomass/aboveground biomass} \quad (3)$$

Similarly, five saplings/treatment were randomly selected for identifying leaf morphological indexes at the end of the experiment. Mature and healthy functional leaves (the 3rd–5th leaves from the tip) of each sapling were collected and leaf length ( $LL$ ), width ( $LW$ ), area ( $LA$ ) and mass ( $LM$ ) were measured (Li et al. 2021b; Tang et al. 2022). Specific leaf area ( $SLA$ ) was (Eq. 4):

$$SLA = LA/LM \quad (4)$$

### Leaf ultrastructure

On the 20th, 40th and 60th d of the shading experiment, three healthy, functional leaves (the 3rd–5th leaves from the tip) from three healthy saplings with similar growth per treatment for each were collected from each treatment. Ultrathin 60–100 nm sections were prepared using an EM UC7 ultramicrotome (Leica, Germany). The sections were double stained with uranium acetate and lead citrate, observed and photographed under a transmission electron microscope (Tecnai G2 20 TWIN, USA) (Xu et al. 2008; Ren et al. 2016a; Qi et al. 2020).

### Physiological and biochemical indexes

On the 20th, 40th and 60th d of the experiment, three healthy, mature functional leaves (the 3rd–5th leaves from the tip) per individual (five/treatment) were collected at 8:00 am to measure the physiological and biochemical indices (Zhang et al. 2020; Peng et al. 2021). After sampling, the leaves were placed in an ice bucket and brought to the laboratory for storage at  $-80\text{ }^{\circ}\text{C}$ . Levels of peroxidase (POD), catalase (CAT), superoxide dismutase (SOD) activities, soluble sugar (SS), soluble protein (SP), free proline (PRO), malondialdehyde (MDA) and chlorophyll contents were measured with commercially available assay kits (Suzhou Grace Biotechnology Company, Suzhou, China).

### Photosynthetic characteristics

On sunny days before the end of the shade treatment, three healthy, mature functional leaves (the 3rd–5th leaves from the tip) from three saplings per treatment with similar growth were measured for light response using the Li-6400XT portable photosynthesis system (Li-COR, Lincoln, NE, USA). The light response was measured in triplicate 8:30–11:30 am at the following photosynthetic photon flux densities ( $PPFD$ ): 2000, 1800, 1600, 1400, 1200, 1000, 800, 600, 400, 200, 100, 50, 20, 10 and  $0\text{ }\mu\text{mol m}^{-2}\text{ s}^{-1}$ . The controls were: leaf chamber temperature was  $23\text{--}26\text{ }^{\circ}\text{C}$ ,  $\text{CO}_2$  concentration in the reference room was  $400\text{ }\mu\text{mol mol}^{-1}$ , and the airflow rate was  $500\text{ }\mu\text{mol s}^{-1}$ . Leaves were induced

with a light intensity of  $800\text{ }\mu\text{mol m}^{-2}\text{ s}^{-1}$  for 15 min before measurement. The following photosynthetic physiological parameters were recorded: net photosynthetic rate ( $P_n$ ), intercellular carbon dioxide concentration ( $C_i$ ), transpiration rate ( $T_r$ ), and stomatal conductance ( $G_s$ ).

Instantaneous water use efficiency ( $WUE$ ) and instantaneous light energy use efficiency ( $LUE$ ) were calculated based on the photosynthetic parameters (Long et al. 1993; Nijs et al. 1997). The maximum photosynthetic rate ( $P_{nmax}$ ), apparent quantum yield ( $AQY$ ), dark respiration rate ( $R_d$ ), light saturation point ( $LSP$ ) and light compensation point ( $LCP$ ) were determined using a light response curve (Ye 2007; Ye et al. 2008; Fan et al. 2021).

### Data statistical and analysis

Excel 2019 was used for data statistics, Origin 2018, Graph-Pad Prism 8 and Adobe Illustrator 2022 for plotting, and a one-way ANOVA test in IBM SPSS Statistics 23.0 used to analyze the significant differences of various indexes under different light intensities or at different treatment times. When the data conformed to the homogeneity of variance ( $P > 0.05$ ), Duncan's t-test was selected for the multiple comparative analysis. When the data did not meet the homogeneity of variance ( $P < 0.05$ ), Dunnett's T3 test was selected for the multiple comparative analysis.

## Results

### Effects of light intensities on morphological features of *T. sinense* saplings

Different light intensities had different effects on the morphology of *T. sinense* saplings. There were no significant differences in  $\Delta H$  and root/shoot ratios among the light intensities. The  $\Delta D$  in L1 was significantly greater than in L3. The  $LA$  in L2 was greater than in L1 and L3, whereas the  $SLA$  in L2 and L3 was significantly greater than in L1 (Table 1). Growth was poor in L1, with few, yellowish leaves (Fig. 1a). Sapling growth was best in L2, with numerous green leaves (Fig. 1b). Growth was moderate in L3, with a moderate number of dark green leaves (Fig. 1c).

### Effect of different light intensities on leaf ultrastructure

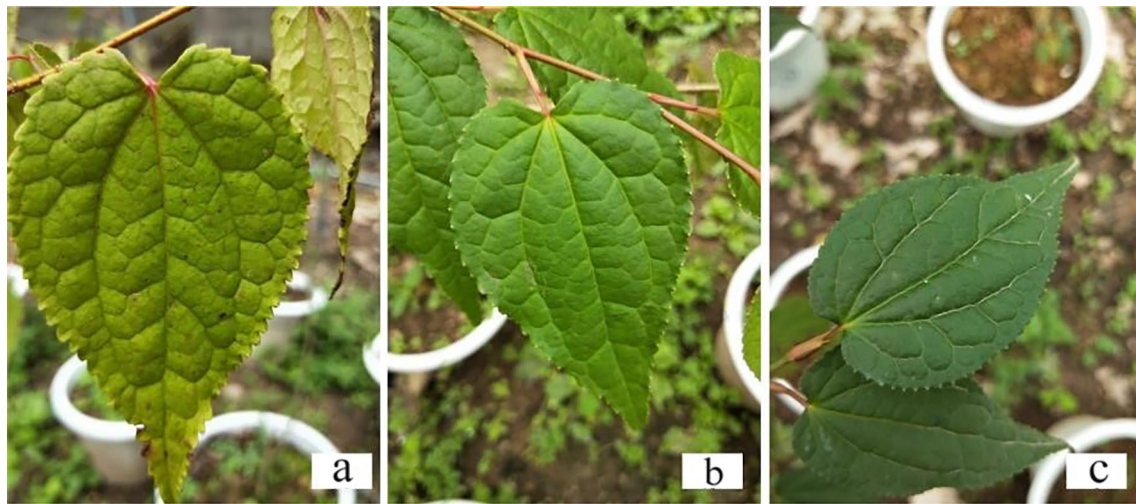
#### Day 20 of the treatment

Chloroplast structure under the three light conditions was relatively good. Compared with L1 and L2, the number of chloroplasts and starch granules in L3 was less and the stromal lamellar space larger. There were more osmiophilic granules in chloroplasts of L1 and L3 than in L2 (Fig. 2).

**Table 1** Morphological indexes of *T. sinense* saplings under different light intensities

Treatment	$\Delta H$ (cm)	$\Delta D$ (mm)	Root/shoot	LA (cm <sup>2</sup> )	SLA (cm <sup>2</sup> g <sup>-1</sup> )
L1	0.20 ± 0.07 <sup>a</sup>	1.09 ± 0.19 <sup>a</sup>	0.43 ± 0.09 <sup>a</sup>	13.09 ± 0.47 <sup>b</sup>	151.71 ± 2.47 <sup>b</sup>
L2	0.30 ± 0.09 <sup>a</sup>	0.67 ± 0.18 <sup>a, b</sup>	0.36 ± 0.03 <sup>a</sup>	16.49 ± 1.00 <sup>a</sup>	186.14 ± 5.90 <sup>a</sup>
L3	0.10 ± 0.00 <sup>a</sup>	0.41 ± 0.09 <sup>b</sup>	0.34 ± 0.04 <sup>a</sup>	13.56 ± 0.54 <sup>b</sup>	207.82 ± 8.41 <sup>a</sup>

One-way analysis of variance (ANOVA); Different lowercase letters represent significant differences in light intensity at 0.05 level



**Fig. 1** Morphological features of *T. sinense* saplings in different light intensities on the 60th d. **a:** L1 (100% NS); **b:** L2 (50% NS); **c:** L3 (10% NS)

#### Day 40 of the treatment

The chloroplasts in L2 were spindle-shaped and well-structured with intact membranes, containing smaller and fewer starch grains, fewer osmiophilic granules, and more grana with tightly arranged lamellae compared to those of L1 and L3. Chloroplasts in L1 and L3 were ellipsoidal or spherically shaped. The chloroplast still had a large number of starch granules under strong light, while the number of starch granules decreased significantly under weak light. Both strong and weak light intensity lead to a large number of osmiophilic granules in chloroplasts (Fig. 3).

#### Day 60 of the treatment

After a long shading treatment, only chloroplast morphology in L2 was intact, containing a few small starch grains, few osmiophilic granules, and a large number of grana with tightly arranged lamellae. The chloroplast structures were impaired under both strong and weak light conditions, the number of grana decreased, the gap of stroma lamellae was large, and many osmiophilic granules were contained in the chloroplast. Compared with L2, chloroplasts in L1 contained

numerous large starch grains; chloroplasts in L3 were less numerous (Fig. 4).

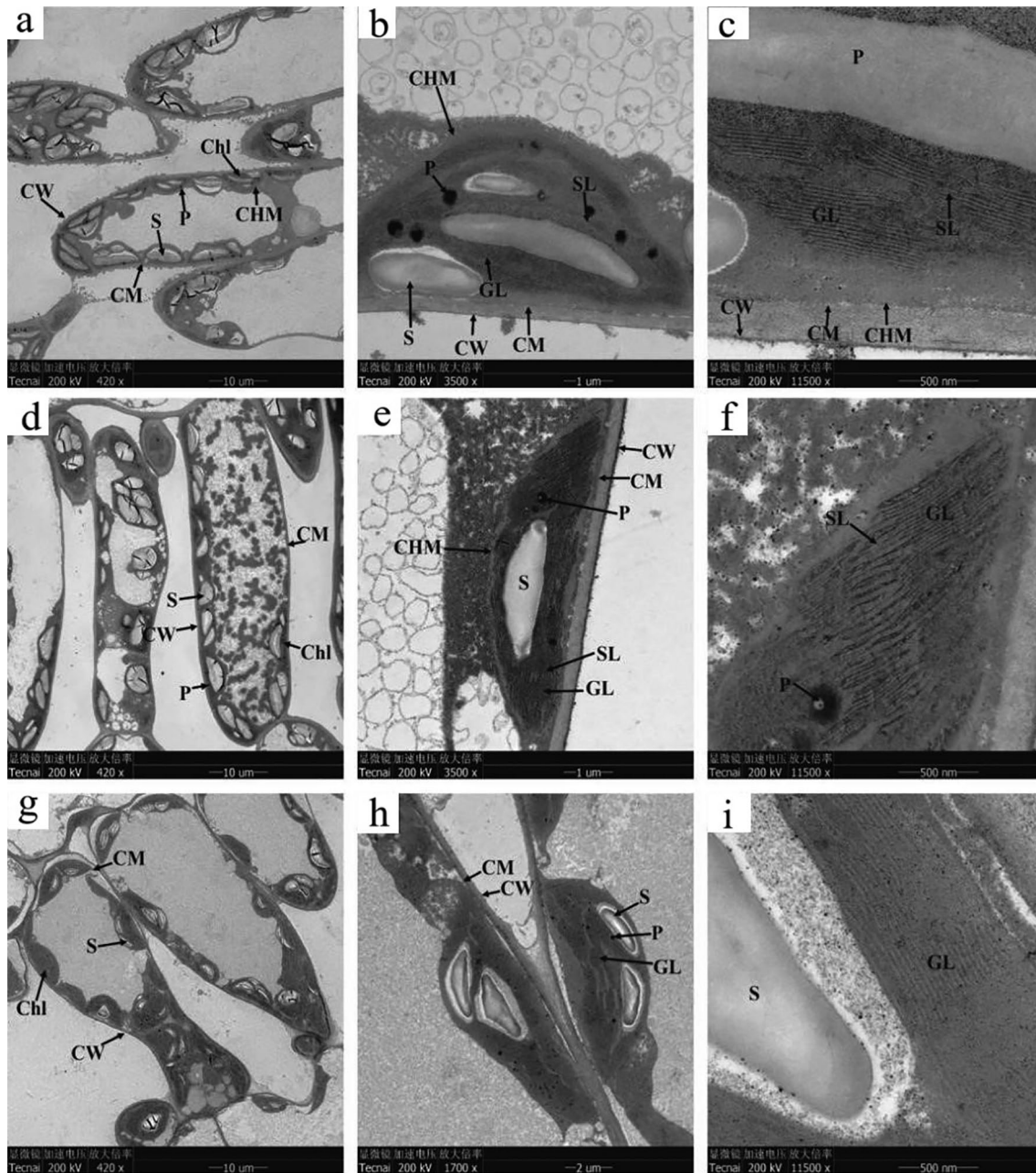
#### Effect of different light intensities on leaf physiology, biochemistry

##### Malondialdehyde content

With the increase in treatment time, MDA content in L2 leaves remained basically unchanged. By the 20th d, MDA levels in L1 leaves were significantly lower than in L2 and L3 leaves. After 40 d and 60 d of shading, MDA in L2 was significantly lower than that in L1 and L3 leaves (Fig. 5a).

##### Superoxide dismutase activity

With the increase in treatment time, SOD activity first increased and then decreased in L1 leaves but gradually increased in L2 and L3 leaves. With decreasing light intensity, SOD activity decreased gradually during the first 20 d, while first increasing and then decreasing on the 40th and 60th d. SOD activity in L1 leaves was at a moderate level during the experiment, but in L2 leaves, it gradually rose to a high level. (Fig. 5b).



**Fig. 2** Chloroplast ultrastructure observed in the leaves on the 20th d. **a–c:** L1 (100% NS); **d–f:** L2 (50% NS); **g–i:** L3 (10% NS). Abbreviations: CW Cell wall; CM Cell membrane; Chl Chloro-

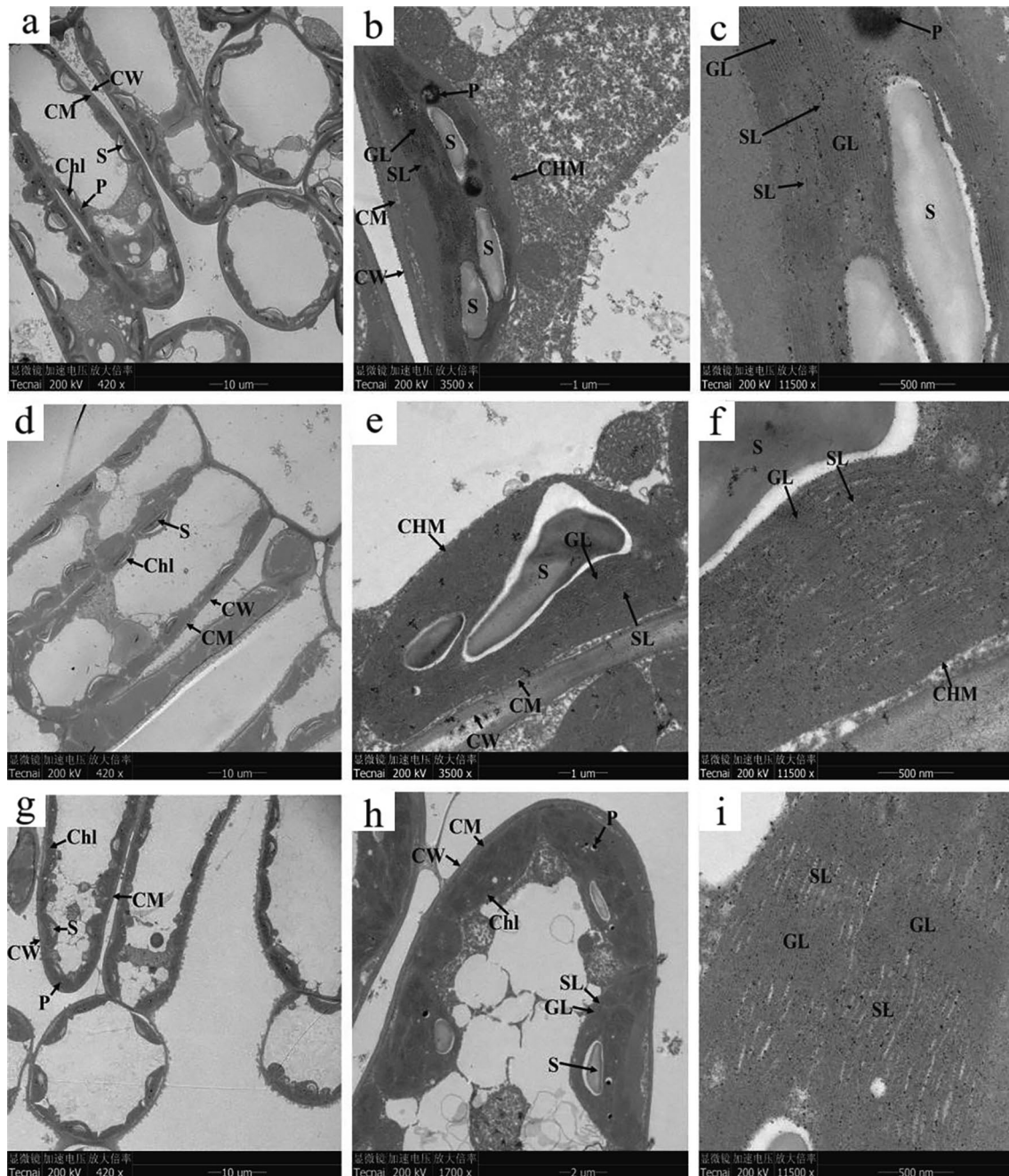
plasts; CHM Chloroplast membrane; GL Grana lamella; SL Stroma lamella; S Starch grains; P Osmiophilic globule

#### Catalase activity

Overall, CAT activity gradually increased with treatment time under different light intensities. There were no significant difference in CAT activity among the different treatments on the 20th d. On the 40th and 60th d, CAT activity in L2 leaves was significantly higher than in L1 leaves and slightly higher than that in L3 leaves (Fig. 5c).

#### Peroxidase activity

With a decrease in light intensity, POD activity gradually increased. Compared with the shading treatments, POD activity in L1 leaves was at a low level and in L2 leaves, it was always at a moderate level. In particular, POD activity in L3 leaves was significantly higher than that in the other treated leaves (Fig. 5d).



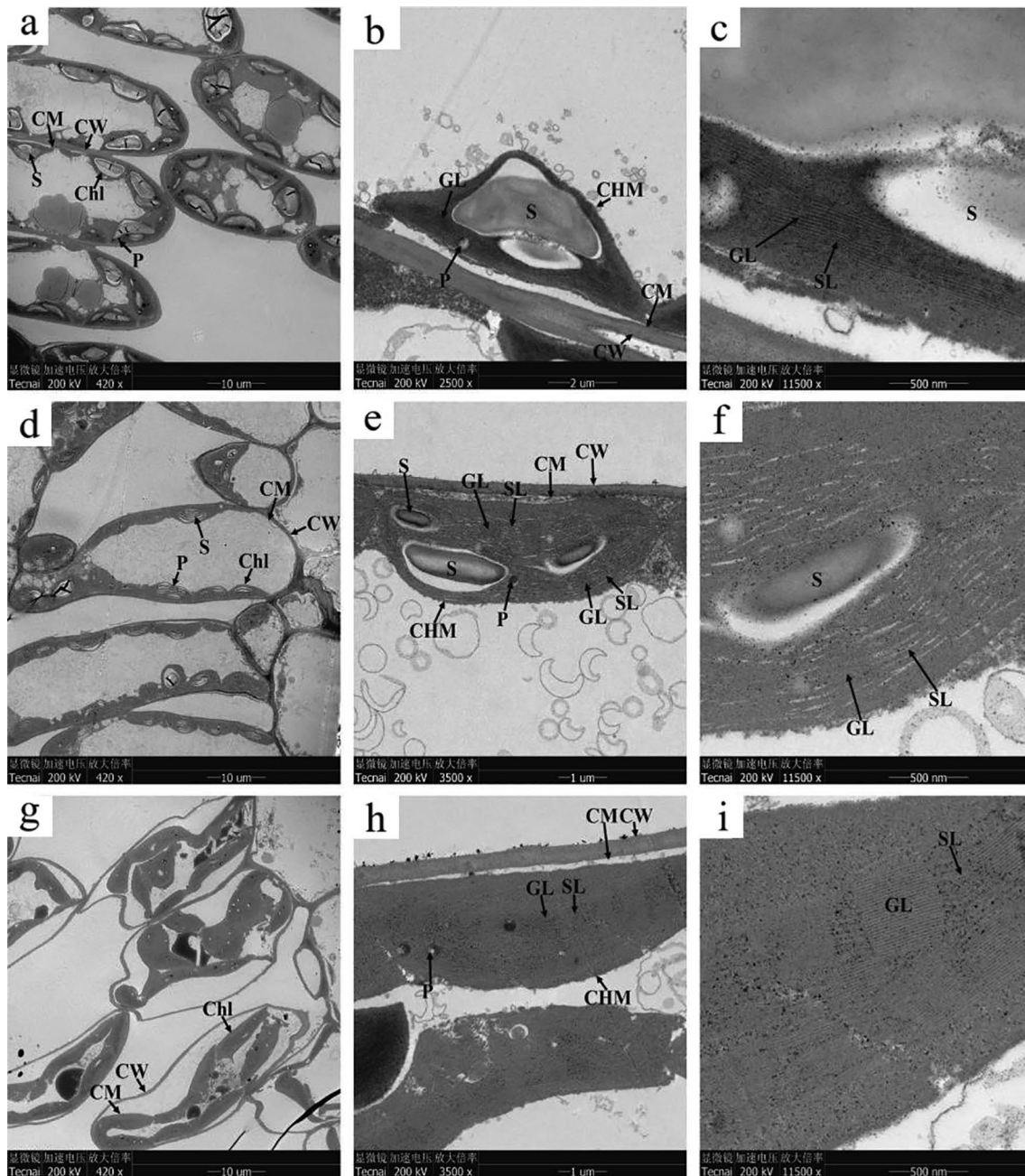
**Fig. 3** Ultrastructure of mesophyll cells in the leaves of *T. sinense* saplings on the 40th d of shading treatment (abbreviations: see Fig. 2)

#### *Soluble sugar content*

In general, SS levels under the three light intensities were significantly different during the experiment. The SS content in L1 leaves was always highest compared with shaded leaves, with SS levels in L3 leaves significantly lowest; but remained at a moderate level in L2 leaves (Fig. 5e).

#### *Soluble protein content*

During the experiment, SP levels in L1 and L2 leaves were significantly higher than those in L3 leaves. Compared to shaded leaves, SP in L1 leaves was always at a high level, except for being lower than in L2 leaves in the early stages (Fig. 5f).



**Fig. 4** Ultrastructure of mesophyll cells in the leaves of *T. sinense* saplings on the 60th d (Abbreviations: see Fig. 2)

#### Free proline content

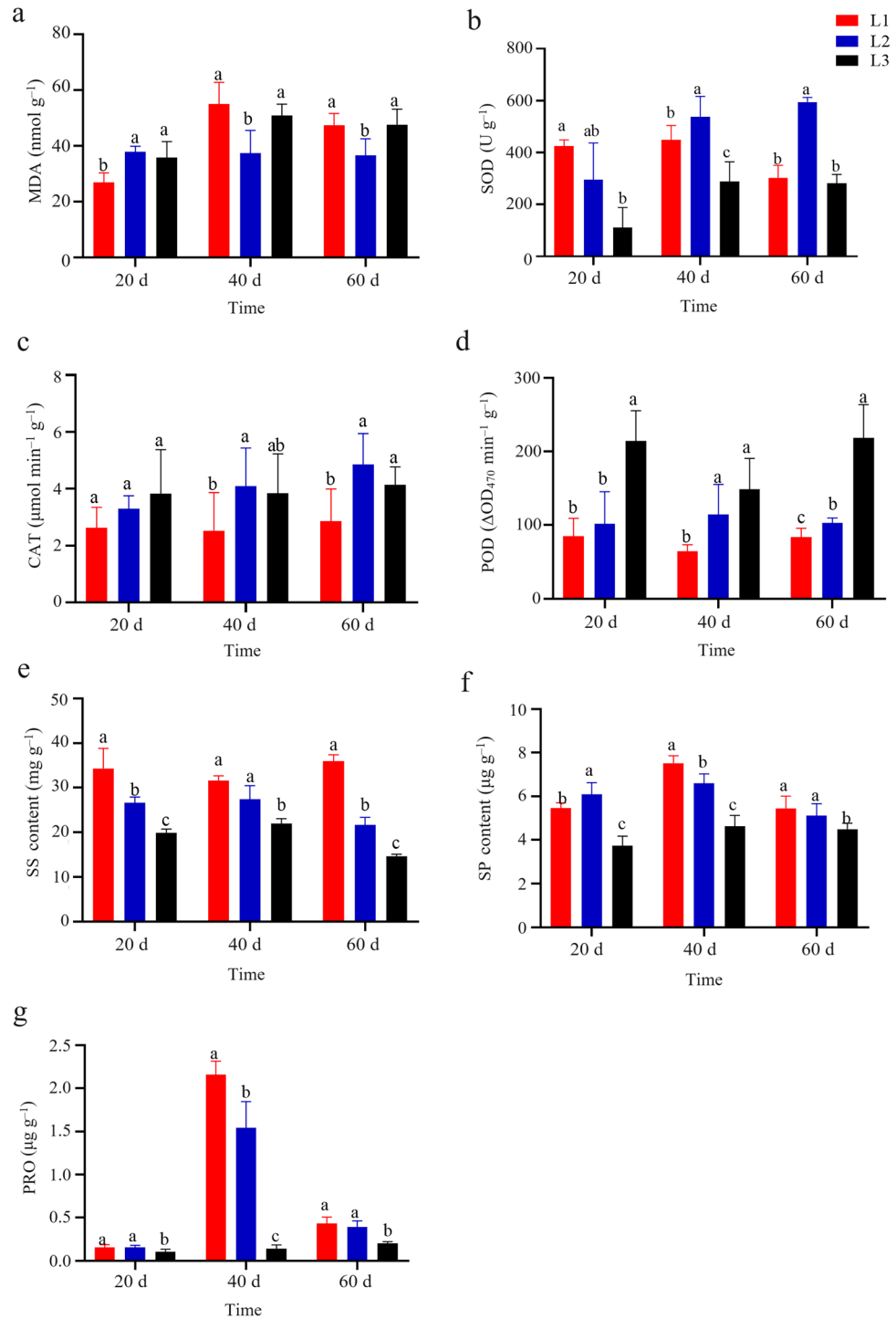
With the increase in treatment time, the PRO content initially increased and then decreased in L1 and L2 leaves. Throughout the experiment, PRO levels in L3 leaves were significantly lower than in L1 and L2 leaves (Fig. 5g).

#### Effects of different light intensities on photosynthetic characteristics of *T. sinense* saplings

##### Chlorophyll content

Shading generally significantly increased  $C_a$ ,  $C_b$ ,  $C_T$ , and  $C_{a/b}$  and they remained at high levels in L3 leaves (Fig. 6).

**Fig. 5** Activities of (a) MDA, (b) SOD, (c) CAT, (d) POD, the contents of (e) SS, (f) SP and (g) PRO in leaves under different light intensities on the 20th, 40th and 60th d; red bars, L1 (100% NS); blue bars, L2 (50% NS); black bars, L3 (10% NS). 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  $\pm$  SE



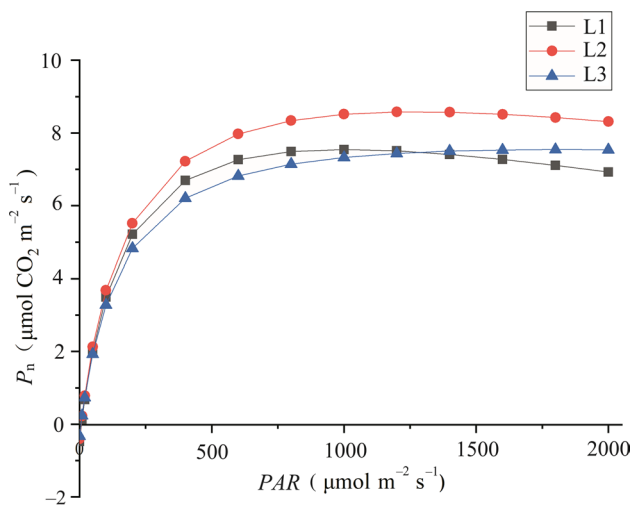
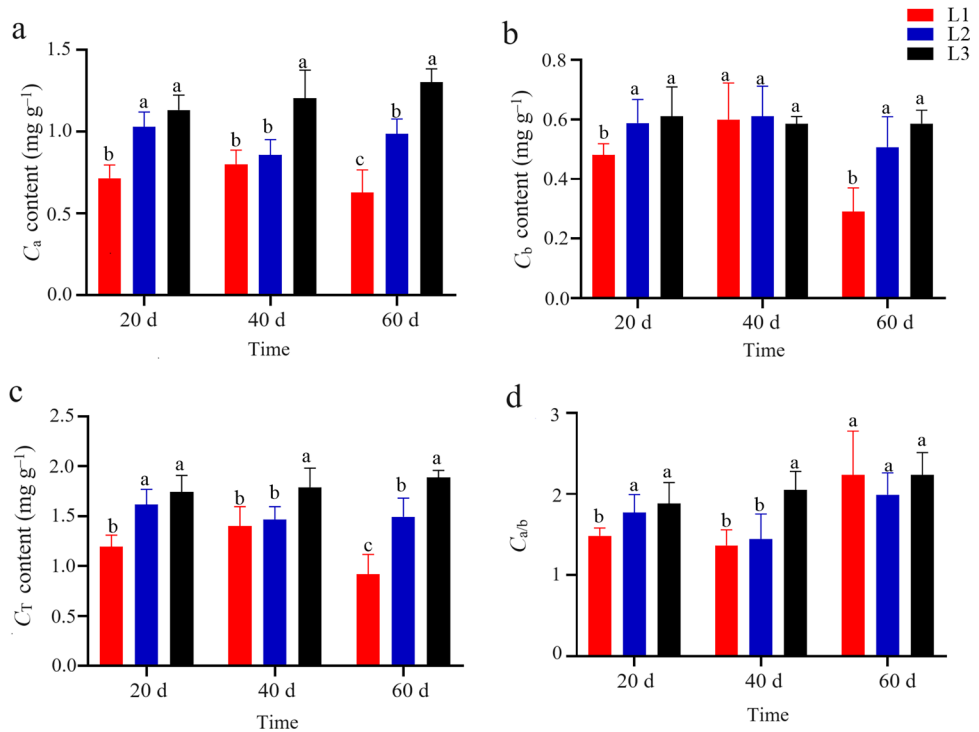
With an increase of treatment time,  $C_b$  of sapling leaves in L2 and L3 treatments remained basically unchanged compared with L1 leaves (Fig. 6b). Although  $C_a$  and  $C_{a/b}$  levels in L2 leaves decreased slightly, they rebounded on the 60th d (Fig. 6b, d). However, on the 60th d of shading, the contents of  $C_a$ ,  $C_b$  (particularly), and  $C_T$  in 100% light intensity decreased significantly but the  $C_{a/b}$  ratios increased significantly (Fig. 6).

#### Light response curve

The net photosynthetic rate ( $P_n$ ) gradually increased with increasing photosynthetically active radiation (PAR). When PAR ranged from 0 to 500  $\mu\text{mol}\cdot\text{m}^{-2}\text{ s}^{-1}$ ,  $P_n$  increased rapidly with increasing light intensity. When  $\text{PAR} > 500 \mu\text{mol}\cdot\text{m}^{-2}\text{ s}^{-1}$ , the rise of  $P_n$  slowed and stabilized; when PAR reached 1000  $\mu\text{mol}\cdot\text{m}^{-2}\text{ s}^{-1}$ ,  $P_n$  in L1 leaves



**Fig. 6** Contents of (a)  $C_a$ , (b)  $C_b$ , (c)  $C_T$  and (d)  $C_{a/b}$  ratios in leaves under different light intensities on the 20th, 40th and 60th d. (Abbreviations: see Fig. 5)



**Fig. 7**  $P_n$ – $PAR$  of *T. sinense* sapling leaves under different light intensities on the 60th d; black curve, L1 (100% NS); red curve, L2 (50% NS); blue curve, L3 (10% NS); the same below

reached a maximum and then decreased with the increase in  $PAR$ . When  $PAR$  reached  $1700 \mu\text{mol m}^{-2} \text{s}^{-1}$ ,  $P_n$  in L2 leaves reached a maximum and decreased slightly thereafter. When  $PAR$  reached  $1800 \mu\text{mol m}^{-2} \text{s}^{-1}$ ,  $P_n$  reached its maximum in L3 leaves and gradually stabilized. Overall, the  $P_n$  in L2 leaves was greater than in L1 and L3 leaves (Fig. 7).

The  $AQY$  and  $P_{nmax}$  initially increased and then decreased with lower light intensity (Table 2). There was no significant difference in  $AQY$  among different light intensities.  $P_{nmax}$  in L2 leaves was significantly higher than in other leaves.  $LSP$  increased gradually with the decrease of light intensity, and  $LSP$  in L2 and L3 leaves was significantly higher than in L1 leaves. The changes of  $LCP$  and  $R_d$  were opposite to that of  $LSP$ .

*Light response process of  $C_p$ ,  $G_s$ ,  $T_p$ ,  $WUE$  and  $LUE$*

The effects of different light intensities on  $C_i$ ,  $G_s$ ,  $T_p$ ,  $WUE$  and  $LUE$  in each treatment were similar. With an

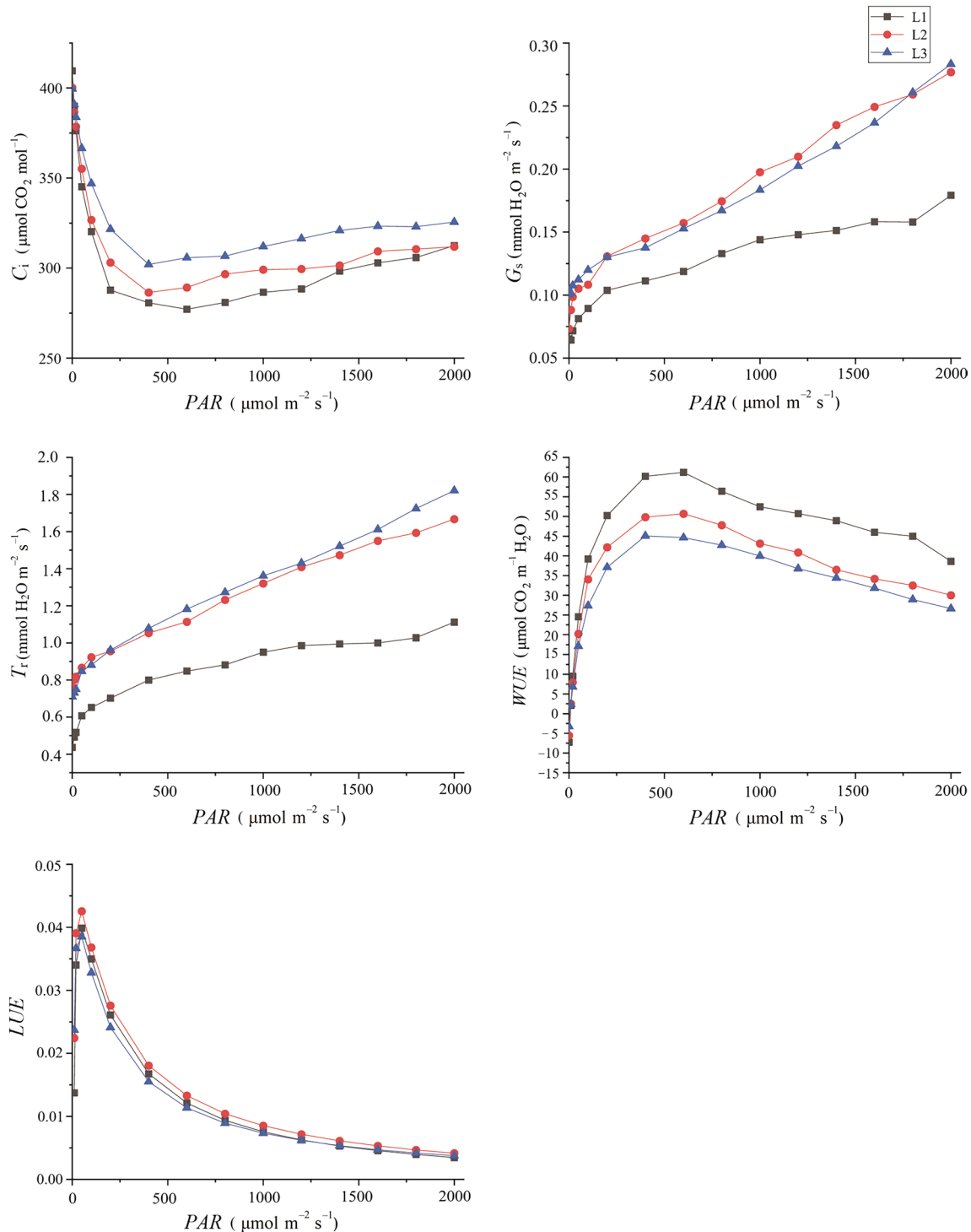
**Table 2** Photosynthesis rate-light response parameters of *T. sinense* saplings under different light intensities

Treatment	$AQY$ (mmol $\text{CO}_2/\text{mol photons}$ )	$P_{nmax}$ ( $\mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ )	$LSP$ ( $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ )	$LCP$ ( $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ )	$R_d$ ( $\mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ )
L1	$0.066 \pm 0.002^a$	$7.72 \pm 0.35^b$	$1016.86 \pm 76.70^b$	$7.37 \pm 0.07^a$	$0.49 \pm 0.01^a$
L2	$0.068 \pm 0.01^a$	$8.87 \pm 0.40^a$	$1732.82 \pm 151.59^a$	$5.59 \pm 0.61^b$	$0.36 \pm 0.04^b$
L3	$0.061 \pm 0.002^a$	$7.80 \pm 0.25^b$	$1876.06 \pm 209.88^a$	$5.39 \pm 0.32^b$	$0.34 \pm 0.02^b$

$AQY$ ,  $P_{nmax}$ ,  $LSP$ ,  $LCP$  and  $R_d$  in leaves of *T. sinense* saplings on the 60th d. Data were subjected to a one-way ANOVA test; Lowercase letters represent significant differences in light intensities at the 0.05 level. Data are mean  $\pm$  standard deviation

increase in  $PAR$ ,  $C_i$  first rapidly decreased and then gradually increased in the order of  $L3 > L2 > L1$ ;  $G_s$  increased gradually in the order of  $L2 > L3 > L1$ ;  $T_r$  also increased

gradually in the order of  $L3 > L2 > L1$ ;  $WUE$  first increased and then decreased in the order of  $L1 > L2 > L3$ ;  $LUE$  gradually decreased in the order  $L2 > L1 > L3$  (Fig. 8).



**Fig. 8**  $C_i$ ,  $G_s$ ,  $T_r$ ,  $WUE$  and  $LUE$  of *T. sinense* sapling leaves under different light intensities on the 60th d (abbreviations:  $C_i$  intercellular carbon dioxide concentration;  $G_s$  stomatal conductance;  $T_r$  transpiration rate;  $WUE$  water use efficiency;  $LUE$  light energy use efficiency)

## Discussion

### Effects of light intensity on morphological indexes of *T. sinense* saplings

Light is a critical factor that affects plant growth and survival (Park et al. 2012; Wang et al. 2016; Pan et al. 2020). Different plants have different light intensity requirements. Light intensity that is too strong or too weak affects growth and survival of plants (Pan et al. 2016; Chai et al. 2018). Morphological features are more sensitive to light intensity and show adaptive changes when subjected to light stress. Adjustment of height, basal diameter, biomass allocation and leaf morphology are strategies for plants to cope with light intensity (Poorter et al. 2006; Tang et al. 2022). In general, strong light can inhibit the elongation of the plant stem but can promote root growth and increase root/shoot ratios (Walter et al. 2006; Poorter et al. 2012; Fu et al. 2017; Formisano et al. 2022). However, on the 60th d of the shading treatments, there was no significant difference in the variation in height and root/shoot ratios of *T. sinense* saplings among the different light intensities, which may be related to their slow growth and the short treatment time. As environmentally sensitive organs, leaves are highly variable and plastic (Poorter et al. 2006). Our results indicate shading was beneficial for increasing the *SLA* of *T. sinense* saplings to capture more light energy (Aleric et al. 2005; Larbi et al. 2015; Zhou et al. 2017; Hitz et al. 2019). Additionally, the saplings showed the response of decreasing *LA* and  $\Delta D$  to weak light, while decreasing their *LA*, *SLA* and increasing  $\Delta D$  after being stressed by strong light. The growth of *T. sinense* saplings was best in medium light where the leaves could effectively capture light energy and synthesize more organic matter in response to the optimal light intensity. Thus, adjusting basal diameter, leaf morphology, and leaf number are main morphological strategies to cope with variations in light intensity.

### Effect of light intensities on leaf ultrastructure of *T. sinense* saplings

Light intensity affects photosynthesis and the structure of photosynthetic organs (Ivanova et al. 2008; Yamazaki et al. 2013). Chloroplasts are sites where plants undergo photosynthesis, which is closely related to their photosynthetic performance (Liang et al. 2011; Ren et al. 2016b; Chen et al. 2018). The core reaction of photosynthesis occurs in thylakoids; therefore, the structure and number of thylakoid membranes are key determinants of photosynthetic activity (Allen et al. 2001). In our study, *T. sinense* saplings in strong light showed large starch grains, which may be attributed to the rapid transformation into starch after the synthesis of organic matter by photosynthesis and temporary storage

in chloroplasts. In addition, the low levels of  $G_s$  and  $T_r$  of leaves in the strong light condition indicated the hindrance of assimilated product transportation, resulting in the accumulation of starch in the chloroplasts and the formation of large grains (Liu et al. 2008; Wu et al. 2014). However, the strong light also caused a large number of osmiophilic globules in cells, indicating that the formation of synthetic thylakoid lamella was reduced, and leaf senescence occurred (Huang et al. 2007).

Mild shading was beneficial for improving the photosynthetic efficiency of saplings, but was hindered by excessive shading. Under mild shading (50% NS), the number of chloroplast grana was large, the lamella stack thick, and the lamellae of grana and stroma closely arranged and filled the entire chloroplast. This promoted more photosynthetic enzymes and light-compensating pigments to adhere to the lamella, which is conducive to absorbing more light energy, promoting the transmission of light energy to the thylakoid and improving photosynthetic efficiency. These results are consistent with those reported for *Ipomoea tricolor* Cav. (Hikosaka 1996) and *Phalaenopsis amabilis* Blume (Lin et al. 2004). However, under excessive shading (10% NS), there were a small amount of starch grains but many osmiophilic globules in cells, which might be attributed to weak light destroying photosynthetic components, disrupting metabolic processes, and reducing the efficiency of light energy utilization, resulting in the reduction of assimilates (Han et al. 2015). From examining chloroplast ultrastructure, there was no indication that saplings responded positively to strong or weak light stress, and these light stresses damaged the structure of chloroplasts, which was not conducive to the photosynthesis.

### Effects of light intensities on MDA, antioxidant enzymes and osmoregulation substances

The removal and production of reactive oxygen in plants are in a dynamic balance but this is destroyed when plants are under stress, and reactive oxygen species such as superoxide anions and hydrogen peroxide accumulate in cells, causing membrane lipid peroxidation (Koca et al. 2006; Yi et al. 2020; He et al. 2021). In the early stage of the experiment, high levels of SOD and CAT activities effectively removed reactive oxygen from the cells under strong light conditions (Becana et al. 2000; Del Rio et al. 2005), reducing the adverse effects of strong light. This was also confirmed by low MDA levels on the 20th d of treatment (Yamauchi et al. 2008; Bao et al. 2020; Zhang et al. 2021, 2022). Plants can adapt to changing light conditions by increasing osmoregulatory substance contents (Ozturk et al. 2021; Wang et al. 2021). Compared to the shading treatment, higher SP, SS and PRO levels were consistently observed under 100% light intensity throughout the experimental period, indicating that

*T. sinense* saplings reduced the adverse effects of intense light by producing more osmoregulation substances (Li et al. 2002). Unfortunately, the effective removal of reactive oxygen did not occur because of the low activity of antioxidant enzymes and the damaged chloroplast structure, resulting in poor sapling growth with leaf yellowing and senescence under strong light. This was also confirmed by high MDA levels on the 40th and 60th d, and long-term exposure to this unfavorable environment might result in saplings death. However, the saplings in 50% light intensity showed the opposite trend. With the increase of treatment time, low MDA places the saplings under the least environmental pressure, possibly related to moderate levels of antioxidant enzymes to remove reactive oxygen and medium levels of osmoregulation substances to maintain osmotic pressure which enabled saplings to better adapt to changing light conditions. Therefore, a good physiological state of saplings under appropriate light intensity results in optimal growth.

Compared to the other light intensities, SS, SP and PRO levels in leaves under 10% light intensity were significantly lower, which suggests that photosynthesis may have been blocked by low light. Interestingly, throughout the experiment, POD activity in 10% light intensity was significantly high, which may be related to its dual roles. It can remove the hydroxyl radicals produced by cells and participate in the production of reactive oxygen and the degradation of chlorophyll at the early stage of leaf aging and after strengthening adversity stress, leading to cell membrane lipid peroxidation (Khodadady et al. 2014; Zhang et al. 2019a). Therefore, only when sufficient antioxidant enzymes and appropriate activity of osmoregulation substances interact will *T. sinense* saplings actively respond to changing light environment.

### Effects of light intensity on photosynthetic characteristics of *T. sinense* saplings

Light is an indispensable energy source for photosynthesis and a major factor in photosynthesis (Sukhova et al. 2018; Babla et al. 2020; Wang et al. 2021). Excessive or insufficient light is not conducive to photosynthesis (Guo et al. 2006; Naramoto et al. 2006). Chlorophyll is closely involved in photosynthesis and plays an important role in the absorption, transmission, and transformation of light (Baig et al. 2005; Croft et al. 2017). In this study, shading significantly increased the chlorophyll content of sapling leaves, indicating that they could synthesize sufficient chlorophyll to capture more light energy to cope with a weak light environment (Lichtenthaler et al. 2007; Yamazaki et al. 2013; Zhang et al. 2019b). However, excessively poor light conditions would cause the destruction of chloroplast structures, and the quantity reduction of chloroplasts and grana, resulting in poor growth status of saplings. Although  $C_a$  and  $C_{a/b}$  decreased slightly on the 60th d of shading, the

$C_b$  of leaves under 50% light remained basically unchanged compared with 100% light intensity, indicating the strongest regulatory ability in the 50% light condition. However, on the 60th d of treatment, chlorophyll contents under 100% light decreased significantly, but the  $C_{a/b}$  ratio increased significantly, suggesting that the saplings reduced photoinhibition by decreasing the absorption of light energy. The decrease in photosynthetic pigment content might be due to intense light seriously impairing the photosynthetic system which was not conducive to photosynthesis.

A light response curve may be used to study the photosynthetic capacity of plants (Fan et al. 2021). Both *LSP* and *LCP* reflect the ability of plants to utilize strong and weak light, and low values indicate that plants maximize the use of low-light quantum flux under limited light conditions to maximize photosynthesis, enabling the accumulation of plants as much organic matter as possible under low-light conditions (Kaelke et al. 2001; Zhu et al. 2014). In this study, shading significantly decreased the *LCP* and the  $R_d$  (dark respiration rate) of leaves, indicating that *T. sinense* saplings were able to use weak light to accumulate organic matter (Gyimah et al. 2007; Dias et al. 2018). However, shading significantly increased the *LSP*, indicating that *T. sinense* saplings failed to quickly reach  $P_{nmax}$  under shade conditions. The low *LSP* in strong light would lead to photoinhibition.

$P_n$  is an important indicator of plant photosynthetic ability. It is influenced by  $C_i$ ,  $G_s$ , and  $T_r$ .  $G_s$  reflects the ability to exchange  $CO_2$  and water, and it directly impacts photosynthesis and transpiration (Favaretto et al. 2011). In our results, compared with 50% light intensity, lower  $P_n$  and  $G_s$  but higher  $C_i$  and  $T_r$  were observed for saplings in 10% light intensity, indicating that the decrease in the photosynthetic rate under 10% light intensity was caused by non-stomatal factors such as the change in enzyme carboxylation efficiency and chloroplast structure (Farquhar et al. 1982; Wang et al. 2012).  $P_n$ ,  $G_s$ ,  $C_i$  and  $T_r$  in L1 leaves were lower than for L2 leaves, indicating that stomatal limitation occurred under intense light conditions. This resulted in a lower photosynthetic rate, which hindered the transportation of water, photosynthetic products, and mineral nutrients (Ding et al. 2013; Lv et al. 2013). The  $G_s$  of L2 leaves were greater than in L1 and L3 leaves, indicating that too strong or too weak light limited stomatal opening, increasing the resistance of  $CO_2$  and water vapor in and out of stomata. Which was not conducive to photosynthesis (Zhou et al. 2010; Lv et al. 2013).

### Conclusion

Different light intensities significantly affected the eco-physiological characteristics of *T. sinense* saplings. The saplings responded most favorably at intermediate light

levels by optimizing eco-physiological characteristics compared to high and low light intensities. The saplings under intermediate light were capability to stable chlorophyll contents, synthesize enough osmotic regulatory substances and maintain high activity of antioxidant enzyme. This ensured complete chloroplast structure and strong photosynthetic capacity. Therefore, eco-physiological synergies in the saplings improve adaptability to the light environment. In order to promote sapling establishment and population recovery of *T. sinense* during in situ conservation, 50% natural light should be created. Which include but not limit to artificially sow seeds in the forest edge or gap, and provide appropriate shade protection for seedlings and saplings in the open.

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