

## CHANGES IN LIGHT INTENSITY AFFECT LEAF GAS EXCHANGE, CHLOROPHYLL FLUORESCENCE, AND NON-STRUCTURAL CARBOHYDRATES OF MA BAMBOO (*DENDROCALAMUS LATIFLORUS* MUNRO)

FAN, L.<sup>1</sup> – TARIN, M. W. K.<sup>2</sup> – HU, W.<sup>1</sup> – HAN, Y.<sup>1</sup> – RONG, J.<sup>1</sup> – CHEN, L.<sup>1</sup> – HE, T.<sup>1</sup> – ZHENG, Y.<sup>1\*</sup>

<sup>1</sup>College of Forestry, Fujian Agriculture and Forestry University, Fuzhou, Fujian 350002, PR China

<sup>2</sup>College of Arts & College of Landscape Architecture, Fujian Agriculture and Forestry University, Fuzhou, Fujian 350002, PR China

\*Corresponding author

e-mail: zys1960@163.com; phone: +86-50-397-265

(Received 17<sup>th</sup> Sep 2021; accepted 22<sup>nd</sup> Dec 2021)

**Abstract.** Many physiological traits are thought to play an important role in the low-light adaptation of plants. Therefore, we tested light intensity regulation of chlorophyll pigments, gas exchange, chlorophyll fluorescence, and non-structural carbohydrates in Ma bamboo (*Dendrocalamus latiflorus* Munro) leaves under five varying light intensities; such as L0 (100%), L1 (40%), L2 (30%), L3 (20%), and L4 (10%). We found that Ma bamboo grown under low light conditions synthesized more chlorophyll [total chlorophyll (Chls) and carotenoids (Car)], whereas net photosynthetic rate ( $P_n$ ) under 10-40% light treatments was lower than that of those established under full sunlight. The decrease in light intensities increased PSII actual photochemical efficiency ( $\Phi_{PSII}$ ), electron transport rate (ETR), and PSII photochemistry ( $F_v/F_m$ ), while low radiation led to a reduction in photochemical quenching coefficient (qP) and an increase in non-photochemical quenching coefficient (NPQ) of the leaves. Low light intensity was more conducive to accumulating non-structural carbohydrates with higher soluble sugar and starch. These parameters analyzed by principal component analysis (PCA) could be considered critical physiological traits to evaluate Ma bamboo's adaptation to low light. Our findings implied that Ma bamboo had better adaptive strategies in low light conditions, which had substantial implications for the management and cultivation of Ma bamboo's plantation.

**Keywords:** low-light conditions, bamboo seedlings, shade tolerant, photosynthetic efficiency, photosynthetic products

**Abbreviations:** Chls - total chlorophylls, Car - carotenoid, Chl a/b - chlorophyll a/b, Car/Chls - carotenoid/total chlorophylls,  $P_n$  - net photosynthetic rate,  $g_s$  - stomatal conductance,  $C_i$  - intercellular CO<sub>2</sub> concentration,  $T_r$  - transpiration rate,  $\Phi_{PSII}$  - PSII actual photochemical efficiency, ETR - apparent photosynthetic electron transport rate,  $F_v/F_m$  - PSII photochemistry, qP - photochemical quenching coefficient, NPQ - non-photochemical quenching coefficient, SS/starch - soluble sugar/starch, and NSCs - non-structural carbohydrates

### Introduction

Light is an essential abiotic factor affecting plant growth and productivity. Light is absorbed by photosynthetic pigments and converted into biochemical energy (ATP and NADP), which are used for carbon dioxide (CO<sub>2</sub>) fixation to produce carbohydrates or plant biomass (Matsudo et al., 2012; Minagawa, 2013). Average plant growth requires optimal light irradiance, however excessive or low irradiance might impact plant photosynthesis, which is critical for plant productivity and severely restricts plant growth (Ma et al., 2015). In forests, plants growing in the understory are subjected to some degree of shade during their life span due to varying

light gradients from plant canopies (Valladares and  lo Niinemets, 2008; Lu et al., 2018). As a result, plants progressively evolve various traits to adapt to low-light conditions during their life cycle, especially in the early stages, such as morphological and physiological plasticity, biochemistry, and metabolic regulation (Nicotra et al., 2010; Liu et al., 2020).

Plants grown under low-light conditions can strengthen their adaptation by changing their photosynthetic traits. Generally, plants increase their light-use efficiency by prioritizing light capture over photosynthetic capacity to adapt to low light conditions (Var, 2017; Tang et al., 2020). In addition, plants grown under low-light conditions are known to optimize their light absorption efficiency by increasing pigment production (Lichtenthaler et al., 2007a; Tang et al., 2015; Shafiq et al., 2020). Chlorophyll fluorescence focuses on photosynthesis regulation and plant response to the environment due to its sensitivity, convenience, and non-destructive characteristics (Dai et al., 2009; Tang et al., 2015). In a light-induced environment, plants tend to improve photosystem II (PSII) efficiency, which protects the photosynthetic machinery from irreversible damage caused by excessive light energy (Cai and Xu, 2002). As a result, in the current research, we attempt to gain insight into the ability of Ma bamboo (*Dendrocalamus latiflorus* Munro) grown under varying light conditions, to confirm the significance of their photosynthetic attributes.

Furthermore, as a source of plant energy storage, leaf non-structural carbohydrates (NSCs) (including soluble sugars and starch), can be mobilized to support growth or other plant physiological functions and can be used to resist external adverse environments (Poorter and Kitajima, 2007; Richardson et al., 2015; Hartmann and Trumbore, 2016). The NSCs storage can enhance the ability of plants to adapt to low light (Sala et al., 2012). Some studies have shown that plants have higher NSC contents under low light conditions by reducing their growth rate and increasing their chances of survival during periods of carbon budget imbalance (Meyer et al., 2006; Jing et al., 2009; Athar et al., 2016; Lin et al., 2018). Starch and soluble sugar can also help plants to resist external interference, such as temperature stress (Jain et al., 2007; Lu et al., 2014; Yang et al., 2020), water deficit (Meier et al., 1990; O'Brien et al., 2014), salt stress (Boriboonkaset et al., 2013), etc., and play an important role in the recovery after interference. Consequently, we attempt to explore the response mechanism of non-structural carbohydrates to different light intensities, especially low light.

Ma bamboo is a wide-distribution clump bamboo species in China. The south area of the Yangtze River in China is the main production area of Ma bamboo shoots, with abundant resources to meet the needs of bamboo growth. However, in the early stage of bamboo shoots, the main production area has continuous rainfall and Ma bamboo has a large leaf area, which would exacerbate the lack of sunlight in the forest understory. Ma bamboo bushes, composed of different quantities of individual bamboo, have different light gap sizes from the canopy. In contrast, the mosaic of diffuse light and direct light from the gaps may affect early shoot development to promote understory renewal. However, its physiological aspects, such as the potential photosynthetic or carbohydrate storage to widely varying light conditions, are unknown.

Therefore, we hypothesized whether Ma bamboo has good adaptability to low-light conditions or varying light intensities will influence their photosynthetic activity and NSCs storage. To test this hypothesis, we used various light intensities; from full sunlight (100%) to a minimum (10%) to determine whether Ma bamboo would reach its growth potential in light levels approximately equivalent to the forest-edge gradient.

The objectives of this study were: (i) to examine the variation of leaf photosynthetic characteristics in Ma bamboo, (ii) to examine responses in NSCs to different levels of light intensities in Ma bamboo. The study will provide valuable insights into optimum light conditions for the growth of Ma bamboo.

## Materials and methods

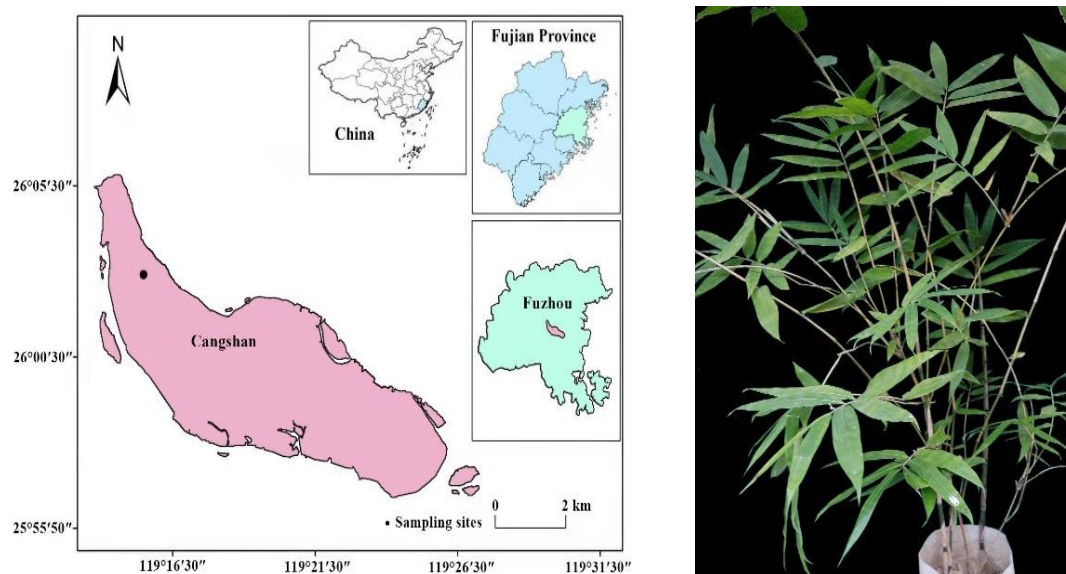
### *Study site*

The present study was conducted out at Fujian Agriculture and Forestry University, Fujian Province, China. Geographically it is situated 26°05'29.88" North at latitude, 119°14'47.37" East at longitude (Fig. 1). Climatically the study area falls in the subtropical oceanic monsoon regions of south China, where the climate is warm and humid. The mean annual sunshine is 1700-1980 h with the mean annual frost-free period of 326 days and the mean annual precipitation of 900-2100 mm. The mean annual temperature is 16-20 °C with minimum and maximum temperatures of 1.2 °C in January or February and 42.3 °C in July or August, respectively.

### *Description of plant material and soil*

Three-year-old Ma bamboo seedlings were selected as materials, which were purchased from Yunnan Zhenzhu Agricultural Technology Co., Ltd. The mean height of seedlings was 105.5 cm, the mean ground diameter was 4.66 mm, and the crown width (north-south × east-west) was 71.1 cm × 69.5 cm. The seedlings were transplanted in non-woven bags in October 2018, with a size of 35 cm × 33 cm × 30 cm (upper diameter × lower diameter × height) (Fig. 1).

Potted substrate soil was yellow soil and peat soil (volume ratio 3:1). The mean weight of one potted substrate was 15.48 kg with a pH value of 5.77 and organic carbon content of 13.67 g·kg<sup>-1</sup>. The total nitrogen, total phosphorus, and total potassium content were 0.35, 0.50, and 50.01 g·kg<sup>-1</sup>, respectively.



**Figure 1.** Geographical location of Fujian Agriculture and Forestry University (left) and Ma bamboo seedlings (right)

### **Experimental design and growing conditions**

After transplanting, Ma bamboo seedlings were grown in the greenhouse of the Forestry College of Fujian Agriculture and Forestry University. The shading treatment was carried out on April 10, 2019. The experiment included five light intensity treatments: 100% (L0 as control), 40% (L1), 30% (L2), 20% (L3), and 10% (L4) of natural light. All the pots were arranged in a completely randomized design with four replicates for each treatment.

A black plastic shade net was used to build a shade chamber (height = 3 m, width = 1.2 m, length = 3 m), and different light intensities were managed by covering plastic shade nets with different needles and layers. Each shade chamber was oriented east-west to allow full exposure of light.

The light intensity gradients were chosen based on the daily variable spectrum of light intensity under natural management conditions of the Ma bamboo forest, forest gap, and forest edge. The Taiwan Hipoint handheld spectrometer (HP350) measured the light intensity under different shaded chambers (*Table 1*). The shaded chambers were separated by 1.2 m to avoid mutual interference between treatments. Six months after the experiment, gas exchange attributes were measured and the leaf tissues were sampled for analyzing photosynthetic pigments and leaf non-structural carbohydrate contents. During the experiment, the field water holding capacity was maintained at more than 60%. Inorganic fertilizers (N: P: K-15: 15: 15) of 10 gram was applied to all treatments at one time. The maximum temperature in the shaded chamber was controlled (below 35 °C), and the relative air humidity was kept above 85%. Furthermore, carbendazim was sprayed every 15 days for disinfection, and weeds were artificially eradicated.

**Table 1.** Light intensity of different shading treatments

Treatments	Light transmittance (%)	Illuminance (lx)	PPFD ( $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ )
L0	100	10343.67 $\pm$ 233.59a	185.66 $\pm$ 4.37a
L1	40	4062.00 $\pm$ 154.02b	73.252 $\pm$ 2.97b
L2	30	3116.67 $\pm$ 240.25c	55.96 $\pm$ 4.35c
L3	20	2066.00 $\pm$ 172.39cd	49.44 $\pm$ 4.27cd
L4	10	1054.00 $\pm$ 101.25d	39.25 $\pm$ 2.04d

L0, L1, L2, L3, and L4 refer to 100%, 40%, 30%, 20%, and 10% of natural light, respectively. Different letters indicate significant differences ( $P < 0.05$ ) of means and  $\pm$  denotes the standard errors of the means (SE) (n = 4)

### **Determination of chlorophyll pigments**

The chlorophyll pigment contents were estimated using the same samples used to monitor gas exchange attributes. After collection of leaf samples, these were washed with distilled water, dried on filter paper, cut along midribs, and mixed to weigh 0.1 g. After that, the chlorophyll pigments were directly extracted from 25 ml mixed solution (acetone: absolute ethanol: distilled water = 4.5: 4.5: 1) for 48-72 h in darkness until their color changed completely to white (Gao, 2006). The absorbance of the extracted solution was measured at 645 nm, 663 nm, and 470 nm, respectively. Later the chlorophyll concentrations [chlorophyll a (Chl a), chlorophyll b (Chl b), total

chlorophylls (Chls), and carotenoid (Car)] were calculated using the equations of Lichtenthaler (1987). Besides, the ratio of Chl a and Chl b (Chl a/b) and the ratio of Car and Chls (Car/Chls) were also calculated.

### ***Determination of leaf gas exchange attributes***

The upper-middle and healthy leaves were selected from each replicate (five readings) to monitor the gas exchange attributes which include net photosynthetic rate ( $P_n$ ), stomatal conductance ( $g_s$ ), intercellular CO<sub>2</sub> concentration ( $C_i$ ), and transpiration rate ( $T_r$ ). All the measurements were recorded between 08:30-11:30 am. A standard leaf chamber (2 cm × 3 cm) with red/blue light sources and the portable photosynthesis instrument (LI-6400 XT, LI-COR Biosciences, Lincoln, NE, USA) were used to test photosynthetic characteristics at a saturated light intensity of 1600  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  photosynthetic photon flux density (PPFD), with a measurement period of 120-180 s. The CO<sub>2</sub> was supplied by an external CO<sub>2</sub> small steel bottle, and the concentration was adjusted to 400  $\text{mmol}\cdot\text{mol}^{-1}$ . Prior to the measurements, the testing leaves were illuminated under a light intensity of 1600  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  (PPFD) for 20-30 min.

### ***Determination of chlorophyll fluorescence***

The upper-middle and healthy leaves from each replicate were chosen for measuring chlorophyll fluorescence using the OS5p portable chlorophyll fluorescence instrument (OPTI-sciences, USA). After dark-adaptation of samples for 30 min, the maximum quantum efficiency of PSII photochemistry ( $F_v/F_m$ ) was measured after 5-7 min of ambient light. In addition, other fluorescent parameters were determined under ambient light, including PSII actual photochemical efficiency ( $\Phi_{\text{PSII}}$ ), apparent photosynthetic electron transport rate ( $ETR$ ), photochemical quenching coefficient ( $qP$ ), non-photochemical quenching coefficient ( $NPQ$ ).

### ***Determination of the non-structural carbohydrate contents***

From each replicate, the fresh leaves were cut into pieces and mixed to weigh 0.1 g. The soluble sugar and starch concentrations were estimated using the chemical kits (Suzhou Keming Biotechnology Co., Ltd.) based on anthrone colorimetry method at an absorbance of 620 nm by UV spectrophotometer (TU-1901, Beijing, China) and the ratio was also calculated. The non-structural carbohydrate contents (NSCs) were calculated as the sum of the soluble sugar and starch contents.

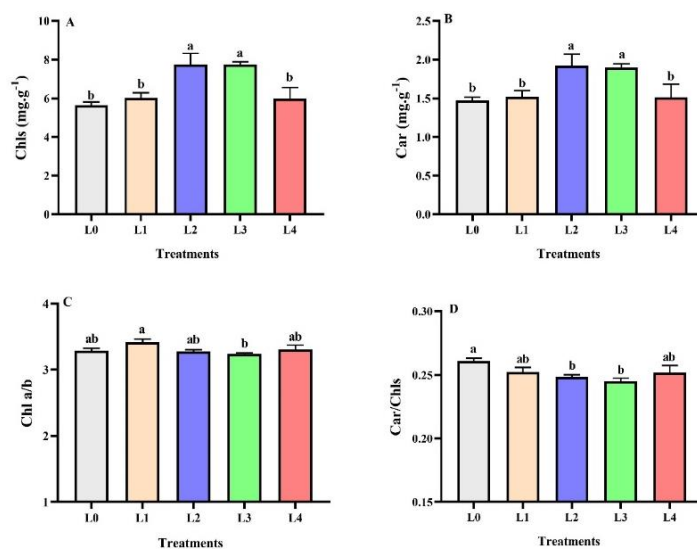
### ***Statistical analysis***

The statistical analysis was done using SPSS program (version 20.0, IBM Corp., Armonk, NY, USA). The analysis of variance (ANOVA) was applied to all the results. However, if there were significant differences between various treatments, the means were differentiated ( $\alpha = 0.05$ ) using the Tukey HSD (honestly significant difference). Besides, principal component analysis (PCA) was performed using correlation matrix data for comprehensive analysis of the test data under varying light intensities and reflecting the relationship between different parameters. The data was presented as means  $\pm$  standard errors (SE). Prism v. 8.0.1 (GraphPad, San Diego, CA, USA), Origin 9.5 (OriginLab OriginPro, 2019), and Microsoft Excel-2016 were used for graphical illustrations and tables, respectively.

## Results

### *Changes in the concentrations of photosynthetic pigments under different light intensities*

We found that the plants established under L2 and L3 treatments (30% and 20% light intensities, respectively), their leaves' Chls increased significantly ( $P < 0.05$ ) compared to L0 (Fig. 2A). Similarly, the leaf's Car contents also increased significantly ( $P < 0.05$ ) under L2 and L3 treatments compared to all other treatment combinations (Fig. 2B). Compared to L0, no significant differences were noticed for Chl a/b concentrations under low light treatments (Fig. 2C). However, Car/Chls decreased significantly ( $P < 0.05$ ) to 4.75% and 6.10% under L2 and L3 treatments, respectively compared to L0 (Fig. 2D).



**Figure 2.** Changes in photosynthetic pigments of Ma bamboo under different light treatments. (A) Chls - total chlorophylls, (B) Car - carotenoid, (C) Chl a/b - chlorophyll a/b, and (D) Car/Chls - carotenoid/total chlorophylls, respectively. L0, L1, L2, L3, and L4 refer to 100%, 40%, 30%, 20%, and 10% of natural light, respectively. Values are the means  $\pm$  SE of four replicates per treatment. Different lowercase letters above the bars represent significant differences ( $P < 0.05$ ) between treatments

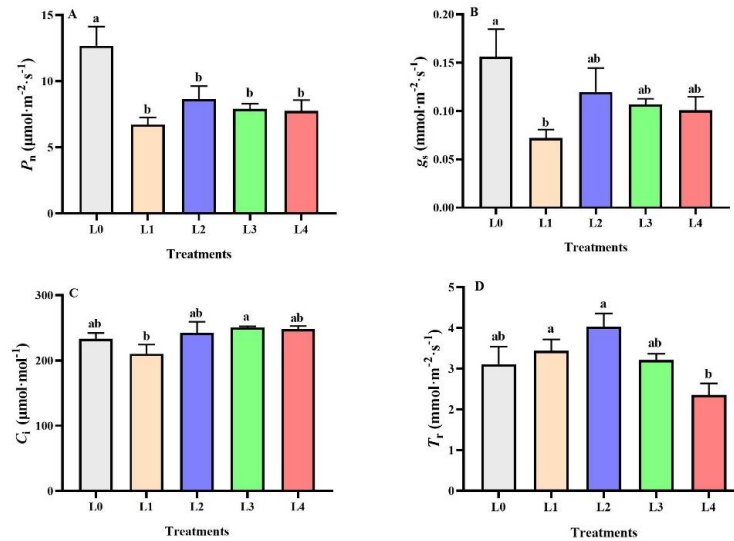
### *Changes in gas exchange attributes under different light intensities*

Compared to L0,  $P_n$  decreased significantly ( $P < 0.05$ ) as the light intensity was reduced (Fig. 3A). Similarly,  $g_s$  showed parallel changes with  $P_n$  under light treatments (Fig. 3B). Compared to other shade treatments, the values of  $P_n$  ( $8.65 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) and  $g_s$  ( $0.12 \text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) were higher under L2 treatment (Fig. 3A and B). Additionally, no significant differences were observed for  $C_i$  under low light treatments compared to L0 (Fig. 3C). Compared to L0,  $T_r$  increased significantly ( $P < 0.05$ ) up to 29.76% under L2 treatment (Fig. 3D).

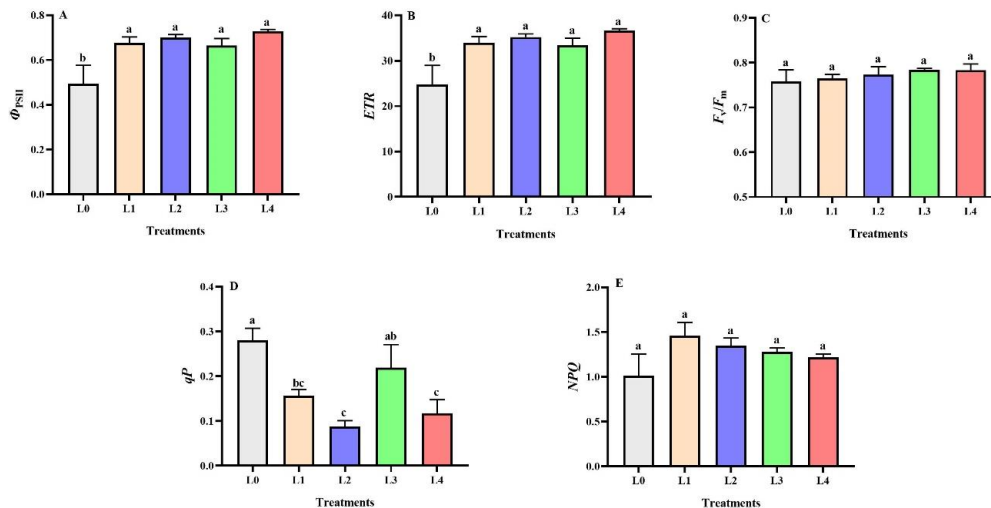
### *Changes in chlorophyll fluorescence parameters under different light intensities*

Compared to L0,  $\Phi_{\text{PSII}}$  and  $ETR$  increased significantly ( $P < 0.05$ ) under all light treatment combinations as shown in Figures 4A and B. In comparison to L0, seedlings established under L4 treatment significantly ( $P < 0.05$ ) improved their  $\Phi_{\text{PSII}}$  by 47.67%

and  $ETR$  by 47.78%.  $F_v/F_m$  increased as the light intensity decreased, while no significant impact of varying light intensities was noticed for the values (Fig. 4C). The values of  $NPQ$  were higher than that of  $qP$ , which decreased significantly ( $P < 0.05$ ) in shading treatments compared to L0 (Fig. 4D and E).



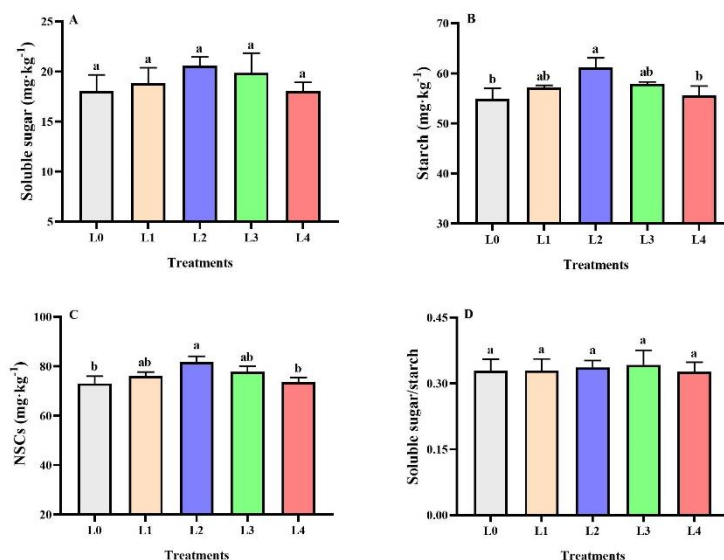
**Figure 3.** Changes in gas exchange attributes of Ma bamboo under different light treatments. (A)  $P_n$  - net photosynthetic rate, (B)  $g_s$  - stomatal conductance, (C)  $C_i$  - intercellular  $\text{CO}_2$  concentration, and (D)  $T_r$  - transpiration rate. L0 refers to full light as the control level. L1, L2, L3, and L4 refer to 40%, 30%, 20%, and 10% of natural light, respectively. Values are the means  $\pm$  SE of four replicates per treatment. Different lowercase letters above the bars represent significant differences ( $P < 0.05$ ) between treatments



**Figure 4.** Changes in chlorophyll fluorescence of Ma bamboo under different light treatments. (A)  $\Phi_{PSII}$  - PS II actual photochemical efficiency, (B)  $ETR$  - apparent photosynthetic electron transport rate, (C)  $F_v/F_m$  - PSII photochemistry, (D)  $qP$  - photochemical quenching coefficient, and (E)  $NPQ$  - non-photochemical quenching coefficient. L0 refers to full light as the control level. L1, L2, L3, and L4 refer to 40%, 30%, 20%, and 10% of natural light, respectively. Values are the means  $\pm$  SE of four replicates per treatment. Different lowercase letters above the bars represent significant differences ( $P < 0.05$ ) between treatments

### Changes in light intensity affect non-structural carbohydrate contents

Compared to L0, a certain degree of reduction in light intensity increased the leaves soluble sugar up to 13.78% under L2 treatment, while a minimum reduction of 0.07% was found under L4 treatment (Fig. 5A). Overall, the seedlings established under various shading treatments exhibited greater starch and NSCs over L0 treatment. Compared to L0, L2 treatment resulted in significant ( $P < 0.05$ ) increases in starch by 11.30% and NSCs by 11.91% (Fig. 5B and C). The soluble sugar/starch did not show any differences under various light treatments (Fig. 5D).



**Figure 5.** Changes in leaf non-structural carbohydrates of Ma bamboo under different light treatments. (A) soluble sugar, (B) starch, (C) NSCs - non-structural carbohydrates, and (D) soluble sugar/starch. L0 refers to full light as the control level. L1, L2, L3, and L4 refer to 40%, 30%, 20%, and 10% of natural light, respectively. Values are the means  $\pm$  SE of four replicates per treatment. Different lowercase letters above the bars represent significant differences ( $P < 0.05$ ) between treatments

### Principle component analysis (PCA) on all parameters under different light intensities

The results of the PCA revealed that the first two components accounted for 78.22% of the total variation, and the first and second PCA accounted for 52.08% and 26.14% of the total variability, respectively as depicted in Figure 6. The photosynthetic pigments (Chls and Car) grouped with non-structural carbohydrate parameters (soluble sugar, starch, and NSCs) presented with PC1 were favored under L2 and L3 treatments. The gas exchange ( $P_n$  and  $g_s$ ) and chlorophyll fluorescence ( $qP$ ) parameters had significant positive correlations with PC2 under L0 treatment.

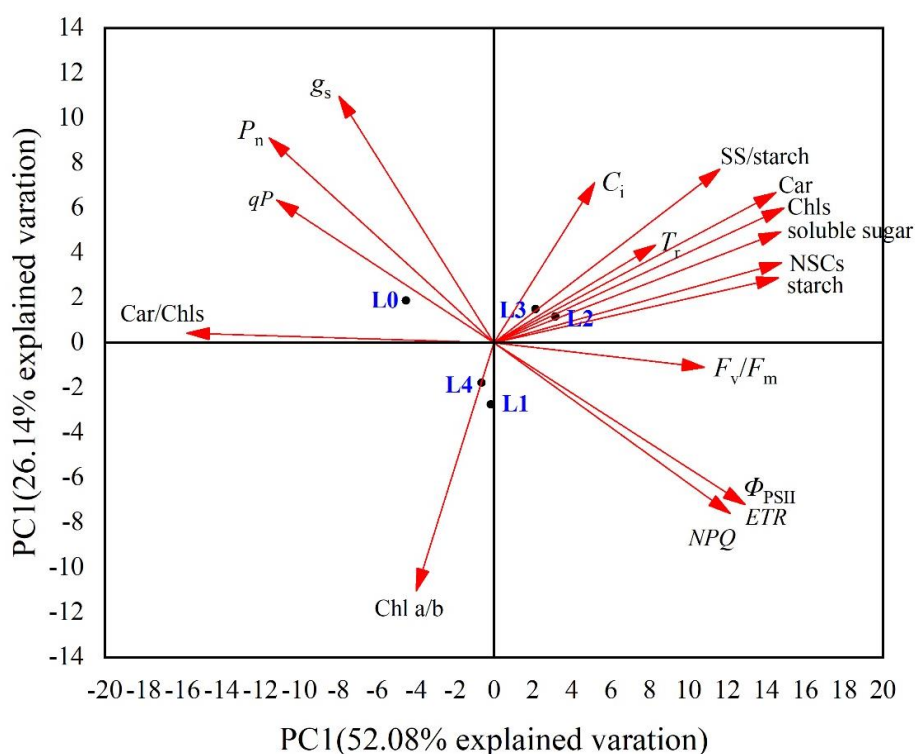
## Discussion

### Changes in light intensity affect the contents of photosynthetic pigments

Plants' absorption of light energy and the mechanism of photosynthesis are regulated by photosynthetic pigments, and their quality and ratio are essential measures of how well



plants respond to their environment (Jin et al., 2016; Wu et al., 2020). The leaves acclimated to low light require more chlorophyll synthesis to improve the photosynthetic efficiency (Sharma and Sharma, 2001). We found that when the seedlings were exposed to low light intensity, leaf Chls and Car increased, which was conducive to improving light utilization and enhancing the light-harvesting capacity of leaves in a low light environment, which has been confirmed by the previous research (Stewart et al., 2015). Under 20-30% light, the growth of Ma bamboo exhibited lower Chl a/b and higher Chls, indicating that the seedlings tend to enhance the absorption of blue-violet light and effectively capture more available light energy (Bell et al., 2000; Wittmann et al., 2001). In comparison, the seedlings grown in full light with a strong reduction in Chls and Car and a higher Car/Chls might dissipate excess light energy by Car to protect the photosynthetic mechanism from severe light damage (Yao et al., 2017).



**Figure 6.** Biplot of principal component analysis of the first two principal components of all parameters and light intensities. Chls - total chlorophylls, Car - carotenoid, Chl a/b - chlorophyll a/b, Car/Chls - carotenoid/total chlorophylls,  $P_n$  - net photosynthetic rate,  $g_s$  - stomatal conductance,  $C_i$  - intercellular  $CO_2$  concentration,  $T_r$  - transpiration rate,  $\Phi_{PSII}$  - PS II actual photochemical efficiency, ETR - apparent photosynthetic electron transport rate,  $F_v/F_m$  - PSII photochemistry,  $qP$  - photochemical quenching coefficient, NPQ - non-photochemical quenching coefficient, SS/Starch - soluble sugar/starch, and NSCs - non-structural carbohydrates. L0 refers to full light as the control level. L1, L2, L3, and L4 refer to 40%, 30%, 20%, and 10% of natural light, respectively

### Changes in light intensity affect the characteristics of gas exchange attributes

Leaf photosynthetic characteristics exhibit remarkable plasticity in response to variations in the light intensities (Katahata et al., 2007). A reduction in light intensity

due to shading has detrimental impacts on leaf gas exchange parameters (Lakshmanakumar et al., 2015). In our research, shading significantly reduced the PPFD value of the canopy of Ma bamboo seedlings. Plants at high irradiance increase  $P_n$  to fix large amounts of carbon for photosynthesis (Tang et al., 2015; Var, 2017). Similarly, our findings are in the line with previous research where the plants exposed to full light intensities exhibited significantly greater  $P_n$  over shaded plants (Shafiq et al., 2020). Therefore, we reported that L2 was advantageous to other shade treatments in terms of increasing  $P_n$  to enhance the carbon sequestration ability of Ma bamboo. At saturating PPFD, the decrease in  $g_s$  was attributed to the decrease in  $P_n$ , indicating that low  $g_s$  led to weakening leaf photosynthetic biochemical pathways and the accumulation of photosynthetic products (Lichtenthaler et al., 2007a, b). However, low  $g_s$  can reduce or prevent transpiration and related water loss compared to full light (Tarin et al., 2020). Compared with L0, the maximum  $T_r$  value under L2 treatment showed a higher water transport capacity and was able to maintain a better leaf water state during the day to avoid the restriction of noon stomata (Zhang et al., 2013). These traits enhanced the ability of Ma bamboo seedlings to tolerate under low light conditions.

### ***Changes in light intensity affect chlorophyll fluorescence***

$\Phi_{PSII}$  is an indicator that reflects the actual photosynthetic efficiency of plants and the relative rate of electron transfer, whereas  $ETR$  determines the efficiency of external photosynthetic electron transfer in plant leaves under actual light intensity (Szabó et al., 2014; Wang et al., 2021). Under 10-40% light, the differences in  $\Phi_{PSII}$  and  $ETR$  of Ma bamboo showed parallel changes, which were significantly ( $P < 0.05$ ) higher than that of full light. The weak light can improve the photochemical efficiency of Ma bamboo, speed up the electron transmission efficiency, and enhance the ability to adapt to low light conditions. On the contrary, under 100% light,  $\Phi_{PSII}$  and  $ETR$  decreased, where there was obvious light suppression. The increase of  $F_v/F_m$  with the decrease of light intensities is an obvious feature of plants adapting to low-light environments (Hussain et al., 2019). Our research confirmed that Ma bamboo showed strong resistance to negative under 10-20% light intensity with the increased  $F_v/F_m$ . In a non-stress environment, plants can maintain a stable range of  $F_v/F_m$  (0.75-0.85) (Rascher et al., 2010). The normal values of  $F_v/F_m$  in our study suggested that Ma bamboo performed well in low light.  $qP$  indicates the strength of the electron transfer activity of plant PSII (Wang, 2014).  $NPQ$  indicates the ability of plants to convert excess light energy into heat dissipation (Müller et al., 2001). At a low light-induced period, plants are not able to utilize the absorbed energy, whereas under these conditions an increase in non-radiative dissipation can be observed as non-photochemical quenching of  $NPQ$  (Busch et al., 2008). In the current research, the proportion used for photochemical reactions decreased, while the proportion of conversion into heat dissipation increased, which was considered a protective mechanism formed by the adaptation of Ma bamboo to low light.

### ***Changes in light intensity affect the accumulation of NSCs***

Generally, plants cannot maximize growth under low light conditions, but transfer a large number of photosynthetic products for storage, so that plants can tolerate periods of low light close to or below the entire plant's light compensation point (Montgomery and Chazdon, 2002). In the previous research, Ma bamboo had good light energy

utilization under 20-30% light intensity (Table A1), which demonstrated strong resistance to shade. Many studies have shown that shade-tolerant tree species can accumulate higher carbohydrate content under low light conditions (Myers and Kitajima, 2007; Poorter and Kitajima, 2007; Liu et al., 2020). Our research showed that soluble sugar, starch, and NSCs contents of the seedlings grown under L2 treatment were all higher than those under L0 treatment, indicating that 30% light was more conducive to the conversion and accumulation of non-structural carbon. However, as the degree of light intensities decreased, the contents of soluble sugar, starch, and NSCs all decreased, indicating that moderate shading can promote the accumulation of photosynthetic products in the leaves of seedlings. The carbon assimilation of Ma bamboo leaves was reduced under L1 treatment, which may result in sugar consumption with the increased respiration rate to maintain growth.

In our research, the reduction in the accumulation of carbohydrates in leaves was possibly related to photosynthetic capacity. Ma bamboo had higher light-harvesting chlorophylls under low light, which allows plants to capture light energy under low light, which is conducive to plant carbon accumulation (Cave et al., 1981; Meyer et al., 2006). In addition, the photosynthetic rate is sensitive to the demand for carbon assimilation (Chantuma et al., 2009). Since the light intensities reduced, Ma bamboo tended to increase the distribution of photosynthetic products and carbohydrates accumulation in leaves which negatively regulated the photosynthetic rate (Evans and Poorter, 2001; Moreau et al., 2012). However, Ma bamboo seedlings maintained high  $P_n$  in full light, more likely allocated more carbon to meet the needs of other metabolisms (Wu et al., 2019) and therefore NSCs decreased. The ratio of soluble sugar and starch in leaves reflects the distribution of NSCs (Xie et al., 2018). We noticed that Ma bamboo exposed to 20-30% light had higher soluble sugar/starch with higher NSCs, indicating that the seedlings had a strong ability to produce soluble sugar converted from starch to promote the metabolic activities for new bamboo growth consumption, which has already been confirmed in the previous research (Xie et al., 2018; Liu et al., 2020).

### ***Evaluation of all parameters under different light intensities by PCA***

PCA can fully explain the interrelationships between test indicators (Lu et al., 2021). The PCA analyzed with strong correlations may be screened out and can be used to assess plant adaptation to varying light intensities (El-Hendawy et al., 2017). The photosynthetic pigments were grouped with non-structural carbohydrates, which exhibited strong correlations with PC1, indicating that Ma bamboo can strengthen their tolerance to low light conditions by accumulating more chlorophylls and NSCs. Ma bamboo under 20-30% light can alleviate the low light stress by these mechanisms. The negative correlations between  $P_n$  and  $g_s$ , with photosynthetic pigments and non-structural carbohydrates, revealed that Ma bamboo was accumulating more photosynthetic products as a consequence of a higher photosynthetic rate. As a result, all photosynthetic parameters and carbohydrates could be considered as key physiological traits to evaluate the low light tolerance of Ma bamboo.

### **Conclusion**

Differences in light intensity affected leaf photosynthetic characteristics and non-structural carbohydrates of Ma bamboo. We found that Ma bamboo grown in low light conditions increased light utilization efficiency by preferentially synthesizing more

chlorophyll (Chls and Car) to tolerate low light at the expense of photosynthesis capacity. The decrease in light intensities increased  $\Phi_{PSII}$ ,  $ETR$ , and  $F_v/F_m$ , which was conducive to enhancing shade-tolerance ability. However, low radiation can improve the heat dissipation capacity of Ma bamboo and weaken the phenomenon of light inhibition. The increase of NSCs was the adaptive strategies of shade-tolerant Ma bamboo to poor light environments. As a result, Ma bamboo may undergo physiological plasticity changes in response to low light. These results have implications for the management of Ma bamboo: (i) moderate shading may provide sufficient light to the growth of young seedlings; (ii) the number or structure of bamboo clumps can be adjusted by artificial pruning, to create a higher understory lighting environment for shoot regeneration and a further increase in productivity.

**Acknowledgments.** This work was supported by the “National Key R&D Program of China” (2018YFD0600100); program for scientific and technological innovation teams for universities of Fujian province (No.2018[49]).

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

## REFERENCES

- [1] Athar, H., Ambreen, S., Javed, M., Hina, M., Ashraf, M. (2016): Influence of sub-lethal crude oil concentration on growth, water relations and photosynthetic capacity of maize (*Zea mays*, L.) plants. – *Environmental Science and Pollution Research* 23: 1-12. DOI: 10.1007/s11356-016-6976-7.
- [2] Bell, G. E., Danneberger, T. K., McMahon, M. J. (2000): Spectral irradiance available for turfgrass growth in sun and shade. – *Crop Science* 40: 189-195. DOI: 10.2135/cropsci2000.401189x.
- [3] Boriboonkaset, T., Theerawitaya, C., Yamada, N., Pichakum, A., Supaibulwatana, K., Cha-um, S., Takabe, T., Kirdmanee, C. (2013): Regulation of some carbohydrate metabolism-related genes, starch and soluble sugar contents, photosynthetic activities and yield attributes of two contrasting rice genotypes subjected to salt stress. – *Protoplasma* 250: 1157-1167. DOI: 10.1007/s00709-013-0496-9.
- [4] Busch, F., Hüner, N. P. A., Ensminger, I. (2008): Increased air temperature during simulated autumn conditions impairs photosynthetic electron transport between photosystem II and photosystem. – *Plant Physiology* 147: 402-414. DOI: 10.1104/pp.108.117598.
- [5] Cai, S., Xu, D. (2002): Light intensity-dependent reversible down-regulation and irreversible damage of PSII in soybean leaves. – *Plant Science* 163: 847-853. DOI: 10.1016/S0168-9452(02)00234-0.
- [6] Cave, G., Tolley, L. C., Strain, B. R. (1981): Effect of carbon dioxide enrichment on chlorophyll content, starch content and starch grain structure in *Trifolium subterraneum* leaves. – *Physiologia Plantarum* 51: 171-174. DOI: 10.1111/j.1399-3054.1981.tb02694.x.
- [7] Chantuma, P., Lacoïnte, A., Kasemsap, P., Thanisawanyangkura, S., Gohet, E., Clement, A., Guilliot, A., Ameglio, T., Thaler, P. (2009): Carbohydrate storage in wood and bark of rubber trees submitted to different level of C demand induced by latex tapping. – *Tree Physiology* 29: 1021-1031. DOI: 10.1093/treephys/tpp043.
- [8] Dai, Y., Shen, Z., Liu, Y., Wang, L., Hannaway, D., Lu, H. (2009): Effects of shade treatments on the photosynthetic capacity, chlorophyll fluorescence, and chlorophyll

- content of *Tetrastigma hemsleyanum* Diels et Gilg. – *Environmental & Experimental Botany* 65: 177-182. DOI: 10.1016/j.envexpbot.2008.12.008.
- [9] El-Hendawy, S. E., Hassan, W. M., Al-Suhaibani, N. A., Refay, Y., Abdella, K. A. (2017): Comparative performance of multivariable agro-physiological parameters for detecting salt tolerance of wheat cultivars under simulated saline field growing conditions. – *Frontiers in Plant Science* 08: 435. DOI: 10.3389/fpls.2017.00435.
- [10] Evans, J. R., Poorter, H. (2001): Photosynthetic acclimation of plants to growth irradiance: the relative importance of specific leaf area and nitrogen partitioning in maximizing carbon gain. – *Plant, Cell & Environment* 24: 755-767. DOI: 10.1046/j.1365-3040.2001.00724.x.
- [11] Gao, J. (2006): *Experimental Guide of Plant Physiology*. – Higher Education Press, Beijing.
- [12] Hartmann, H., Trumbore, S. (2016): Understanding the roles of nonstructural carbohydrates in forest trees from what we can measure to what we want to know. – *The New Phytologist* 211: 386-403. DOI: 10.1111/nph.13955.
- [13] Hussain, S., Iqbal, N., Brestic, M., Raza, M. A., Pang, T., Langham, D. R., Safdar, M. E., Ahmed, S., Wen, B., Gao, Y. (2019): Changes in morphology, chlorophyll fluorescence performance and Rubisco activity of soybean in response to foliar application of ionic titanium under normal light and shade environment. – *Science of The Total Environment* 658: 626-637. DOI: 10.1016/j.scitotenv.2018.12.182.
- [14] Jain, M., Prasad, P. V. V., Boote, K. J., Hartwell, A. L., Chourey, P. S. (2007): Effects of season-long high temperature growth conditions on sugar-to-starch metabolism in developing microspores of grain sorghum (*Sorghum bicolor* L. Moench). – *Planta* 227: 67-79. DOI: 10.1007/s00425-007-0595-y.
- [15] Jin, H., Li, M., Duan, S., Fu, M., Dong, X., Liu, B., Feng, D., Wang, J., Wang, H. (2016): Optimization of light-harvesting pigment improves photosynthetic efficiency. – *Plant Physiology* 172: 1720-1731. DOI: 10.1104/pp.16.00698.
- [16] Jing, Y., Li, G., Gu, B., Yang, D., Xiao, L., Liu, R., Peng, C. (2009): Leaf gas exchange, chlorophyll fluorescence and growth responses of *Melaleuca alternifolia* seedlings to flooding and subsequent recovery. – *Photosynthetica* 47: 595-601. DOI: 10.1007/s11099-009-0085-5.
- [17] Katahata, S. I., Naramoto, M., Kakubari, Y., Mukai, Y. (2007): Photosynthetic capacity and nitrogen partitioning in foliage of the evergreen shrub *Daphniphyllum humile* along a natural light gradient. – *Tree Physiology* 27: 199-208. DOI: 10.1093/treephys/27.2.199.
- [18] Lakshmanakumar, P., Bana, O., Guru, S. (2015): Morphological and physiological characteristics of wheat (*Triticum aestivum* L.) under different light condition. – *International Research Journal of Natural and Applied Sciences* 2: 84-105.
- [19] Lichtenthaler, H. K. (1987): Chlorophylls and carotenoids: pigments of photosynthetic biomembranes. – *Methods in Enzymology* 148: 350-382.
- [20] Lichtenthaler, H. K., Ač, A., Marek, M. V., Kalina, J., Urban, O. (2007a). Differences in pigment composition, photosynthetic rates and chlorophyll fluorescence images of sun and shade leaves of four tree species. – *Plant Physiology and Biochemistry* 45: 577-588. DOI: 10.1016/j.plaphy.2007.04.006.
- [21] Lichtenthaler, H. K., Fatbardha, B., Gabriele, L. (2007b). Chlorophyll fluorescence imaging of photosynthetic activity in sun and shade leaves of trees. – *Photosynthesis Research* 93: 235-244. DOI: 10.1007/s11120-007-9174-0.
- [22] Lin, W., Guo, X., Pan, X., Li, Z. (2018): Chlorophyll composition, chlorophyll fluorescence, and grain yield change in ESL mutant rice. – *International Journal of Molecular Sciences* 19: 2945. DOI: 10.3390/ijms19102945.
- [23] Liu, Q., Huang, Z., Wang, Z., Chen, Y., Tigabu, M. (2020): Responses of leaf morphology, NSCs contents and C:N:P stoichiometry of *Cunninghamia lanceolata* and *Schima superba* to shading. – *BMC Plant Biology* 20: 354. DOI: 10.1186/s12870-020-02556-4.

- [24] Lu, D., Cai, X., Yan, F., Sun, X., Wang, X., Lu, W. (2014): Effects of high temperature after pollination on physicochemical properties of waxy maize flour during grain development. – *Journal of the Science of Food and Agriculture* 94: 1416-1421. DOI: 10.1002/jsfa.6433.
- [25] Lu, D., Wang, G. G., Yan, Q., Gao, T., Zhu, J. (2018): Effects of gap size and within-gap position on seedling growth and biomass allocation: is the gap partitioning hypothesis applicable to the temperate secondary forest ecosystems in Northeast China? – *Forest Ecology and Management* 429: 351-362. DOI: 10.1016/j.foreco.2018.07.031.
- [26] Lu, Y., Zeng, F. J., Li, X. Y., Zhang, B. (2021): Physiological changes of three woody plants exposed to progressive salt stress. – *Photosynthetica* 59: 171-184. DOI: 10.32615/ps.2021.007.
- [27] Ma, X., Song, L., Yu, W., Hu, Y., Liu, Y., Wu, J., Ying, Y. (2015): Growth, physiological, and biochemical responses of *Camptotheca acuminata* seedlings to different light environments. – *Frontiers in Plant Science* 6: 1-12. DOI: 10.3389/fpls.2015.00321.
- [28] Matsudo, M. C., Bezerra, R. P., Sato, S., Converti, A., de Carvalho, J. C. M. (2012): Photosynthetic efficiency and rate of CO<sub>2</sub> assimilation by *Arthrospira* (*Spirulina*) *platensis* continuously cultivated in a tubular photobioreactor. – *Biotechnology Journal* 7: 1412-1417. DOI: 10.1002/biot.201200177.
- [29] Meier, S., Grand, L. F., Schoeneberger, M. M., Reinert, R. A., Bruck, R. I. (1990): Growth, ectomycorrhizae and nonstructural carbohydrates of loblolly pine seedlings exposed to ozone and soil water deficit. – *Environmental Pollution* 64: 11-27. DOI: 10.1016/0269-7491(90)90092-Q.
- [30] Meyer, S., Cerovic, Z. G., Goulas, Y., Montpied, P., Demotes-Mainard, S., Bidel, I. P. R., Moya, I., Dreyer, E. (2006): Relationships between optically assessed polyphenols and chlorophyll contents, and leaf mass per area ratio in woody plants: a signature of the carbon-nitrogen balance within leaves? *Plant, Cell and Environment* 29: 1338-1348. – DOI: 10.1111/j.1365-3040.2006.01514.x.
- [31] Minagawa, J. (2013): Dynamic reorganization of photosynthetic supercomplexes during environmental acclimation of photosynthesis. – *Frontiers in Plant Science* 4. DOI: 10.3389/fpls.2013.00513.
- [32] Montgomery, R., Chazdon, R. (2002): Light gradient partitioning by tropical tree seedlings in the absence of canopy gaps. – *Oecologia* 131: 165-174. DOI: 10.1007/s00442-002-0872-1.
- [33] Moreau, D., Allard, V., Gaju, O., Le Gouis, J., Foulkes, M. J., Martre, P. (2012): Acclimation of leaf nitrogen to vertical light gradient at anthesis in wheat is a whole-plant process that scales with the size of the canopy. – *Plant Physiology* 160: 1479-1490. DOI: 10.1104/pp.112.199935.
- [34] Müller, P., Li, X., Niyogi, K. (2001): Non-photochemical quenching. A response to excess light energy. – *Plant Physiology* 125: 1558-1566. DOI: 10.1104/pp.125.4.1558.
- [35] Myers, J. A., Kitajima, K. (2007): Carbohydrate storage enhances seedling shade and stress tolerance in a neotropical forest. – *Journal of Ecology* 95: 383-395. DOI: 10.1111/j.1365-2745.2006.01207.x.
- [36] Nicotra, A. B., Atkin, O. K., Bonser, S. P., Davidson, A. M., Finnegan, E. J., Mathesius, U., Poot, P., Purugganan, M. D., Richards, C. L., Valladares, F., van Kleunen, M. (2010): Plant phenotypic plasticity in a changing climate. – *Trends in Plant Science* 15: 684-692. DOI: 10.1016/j.tplants.2010.09.008.
- [37] O'Brien, M. J., Leuzinger, S., Philipson, C. D., Tay, J., Hector, A. (2014): Drought survival of tropical tree seedlings enhanced by non-structural carbohydrate levels. – *Nature Climate Change* 4: 710-714. DOI: 10.1038/nclimate2281.
- [38] Poorter, L., Kitajima, K. (2007): Carbohydrate storage and light requirements of tropical moist and dry forest tree species. – *Ecology* 88: 1000-1011. DOI: 10.1890/06-0984.

- [39] Rascher, U., Liebig, M., Lüttge, U. (2010): Evaluation of instant light-response curves of chlorophyll fluorescence parameters obtained with a portable chlorophyll fluorometer on site in the field. – *Plant Cell & Environment* 23: 1397-1405. DOI: 10.1046/j.1365-3040.2000.00650.x.
- [40] Richardson, A. D., Carbone, M. S., Huggett, B. A., Furze, M. E., Czimczik, C. I., Walker, J. C., Xu, X., Schaberg, P. G., Murakami, P. (2015): Distribution and mixing of old and new nonstructural carbon in two temperate trees. – *New Phytologist* 206: 590-597. DOI: 10.1111/nph.13273.
- [41] Sala, A., Woodruff, D. R., Meinzer, F. C. (2012): Carbon dynamics in trees: feast or famine? – *Tree Physiology* 32: 764-775. DOI: 10.1093/treephys/tpr143.
- [42] Shafiq, I., Hussain, S., Hassan, B., Shoaib, M., Mumtaz, M., Wang, B. (2020): Effect of simultaneous shade and drought stress on morphology, leaf gas exchange, and yield parameters of different soybean cultivars. – *Photosynthetica* 58: 1200-1209. DOI: 10.32615/ps.2020.067.
- [43] Sharma, O. C., Sharma, S. D. (2001): Genetic divergence in seedling trees of Persian walnut (*Juglans regia* L.) for various metric nut and kernel characters in Himachal Pradesh. – *Scientia Horticulturae* 88: 163-171. DOI: 10.1016/S0304-4238(00)00204-1.
- [44] Stewart, J. J., Adams, W. W., Cohu, C. M., Polutchko, S. K., Lombardi, E. M., Demmig-Adams, B. (2015): Differences in light-harvesting, acclimation to growth-light environment, and leaf structural development between Swedish and Italian ecotypes of *Arabidopsis thaliana*. – *Planta* 242: 1277-1290. DOI: 10.1007/s00425-015-2368-3.
- [45] Szabó, M., Wangpraseurt, D., Tamburic, B., Larkum, A. W. D., Schreiber, U., Suggett, D. J., Kühl, M., Ralph, P. J. (2014): Effective light absorption and absolute electron transport rates in the coral *Pocillopora damicornis*. – *Plant Physiology and Biochemistry* 83: 159-167. DOI: 10.1016/j.plaphy.2014.07.015.
- [46] Tang, H., Hu, Y. Y., Yu, W. W., Song, L. L., Wu, J. S. (2015): Growth, photosynthetic and physiological responses of *Torreya grandis* seedlings to varied light environments. – *Trees* 29: 1011-1022. DOI: 10.1007/s00468-015-1180-9.
- [47] Tang, X., Liu, G., Jiang, J., Lei, C., Liu, X. (2020): Effects of growth irradiance on photosynthesis and photorespiration of *Phoebe bournei* leaves. – *Functional Plant Biology* 47: 1053. DOI: 10.1071/FP20062.
- [48] Tarin, M. W. K., Fan, L., Shen, L., Lai, J., Li, J., Deng, Z., Chen, L., He, T., Rong, J., Zheng, Y. (2020): Rice straw biochar impact on physiological and biochemical attributes of *Fokienia hodginsii* in acidic soil. – *Scandinavian Journal of Forest Research* 35: 59-68. DOI: 10.1080/02827581.2020.1731591.
- [49] Valladares, F., ülo Niinemets (2008): Shade tolerance, a key plant feature of complex nature and consequences. – *Annual Review of Ecology Evolution & Systematics* 39: 237-257.
- [50] Var, L. (2017): Interaction effects of light intensity and nitrogen concentration on growth, photosynthetic characteristics and quality of lettuce *Lactuca*. – *Scientia Horticulturae* 214: 51-57. DOI: 10.1016/j.scienta.2016.11.020.
- [51] Wang, L. F. (2014): Physiological and molecular responses to drought stress in rubber tree (*Hevea brasiliensis* Muell. Arg.). – *Plant Physiology and Biochemistry* 83: 243-249. DOI: 10.1016/j.plaphy.2014.08.012.
- [52] Wang, Y., Wang, J., Zhang, H., Guo, D., He, G., Sun, G. (2021): An intermediate concentration of atmospheric nitrogen dioxide enhances PSII activity and inhibits PSI activity in expanded leaves of tobacco seedlings. – *Ecotoxicology and Environmental Safety* 209: 111844. DOI: 10.1016/j.ecoenv.2020.111844.
- [53] Wittmann, C., Aschan, G., Pfanz, H. (2001): Leaf and twig photosynthesis of young beech (*Fagus sylvatica*) and aspen (*Populus tremula*) trees grown under different light regime. – *Basic and Applied Ecology* 2: 145-154. DOI: 10.1078/1439-1791-00047.
- [54] Wu, Y., Zhao, B., Li, Q., Kong, F., Du, L., Zhou, F., Shi, H., Ke, Y., Liu, Q., Feng, D., Yuan, J. (2019): Non-structural carbohydrates in maize with different nitrogen tolerance

- are affected by nitrogen addition. – PLOS ONE 14: e0225753. DOI: 10.1371/journal.pone.0225753.
- [55] Wu, G. X., Ma, L., Sayre, R. T., Lee, C. H. (2020): Identification of the optimal light harvesting antenna size for high-light stress mitigation in plants. – *Frontiers in Plant Science* 11. DOI: 10.3389/fpls.2020.00505.
- [56] Xie, H., Yu, M., Cheng, X. (2018): Leaf non-structural carbohydrate allocation and C:N:P stoichiometry in response to light acclimation in seedlings of two subtropical shade-tolerant tree species. – *Plant Physiology and Biochemistry* 124: 146-154. DOI: 10.1016/j.plaphy.2018.01.013.
- [57] Yang, H., Wang, T., Yu, X., Yang, Y., Wang, C., Yang, Q., Wang, X. (2020): Enhanced sugar accumulation and regulated plant hormone signalling genes contribute to cold tolerance in hypoploid *Saccharum spontaneum*. – *BMC Genomics* 21: 507. DOI: 10.1186/s12864-020-06917-z.
- [58] Yao, X., Zhou, H., Zhu, Q., Li, C., Zhang, H., Wu, J. J., Xie, F. (2017): Photosynthetic response of Soybean leaf to wide light-fluctuation in Maize-soybean intercropping system. – *Frontiers in Plant Science* 8: 1695. DOI: 10.3389/fpls.2017.01695.
- [59] Zhang, Y., Meinzer, F. C., Qi, J., Goldstein, G., Cao, K. (2013): Midday stomatal conductance is more related to stem rather than leaf water status in subtropical deciduous and evergreen broadleaf trees. – *Plant, Cell & Environment* 36: 149-158. DOI: 10.1111/j.1365-3040.2012.02563.x.

## APPENDIX

**Table A1.** Various light response parameters of Ma bamboo under shading treatments

Treatments	$\alpha$ ( $\mu\text{mol}\cdot\mu\text{mol}^{-1}$ )	<i>LSP</i> ( $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ )	<i>LCP</i> ( $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ )	$R_d$ ( $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ )
L0	0.052	1532.245	23.195	0.999
L1	0.043	2113.669	11.573	0.453
L2	0.061	2647.497	11.129	0.616
L3	0.072	2466.379	10.698	0.713
L4	0.084	1054.247	6.695	0.537

$\alpha$  - initial quantum efficiency, *LSP* - light saturation point, *LCP* - light compensation point, and  $R_d$  - dark respiration rate respectively. L0 refers to full light as the control level. L1, L2, L3, and L4 refer to 40%, 30%, 20%, and 10% of natural light, respectively