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Morphological and physiological acclimation of *Catalpa bungei* plantlets to different light conditions

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Abstract

This study was performed to evaluate the ecophysiological acclimation of *Catalpa bungei* plantlets to different light conditions. We hypothesized that the acclimation of old and newly developed leaves to both increasing and decreasing irradiance should follow different patterns. The growth, photosynthesis, chlorophyll (Chl) content, and Chl fluorescence response were examined over a range of light treatments. The plants were grown under fixed light intensities of 80% (HH), 50% (MM), 30% (LL) of sun light and transferring irradiance of 80% to 50% (HM), 80% to 30% (HL), 30% to 50% (LM) and 30% to 80% (LH). For old leaves, light-saturation point, photosynthetic capacity, dark respiration rate of LH were lower than that of HH, while HL were higher than LL, indicating that light-response parameters were affected by the original growth light environment. Initial fluorescence increased and variable fluorescence decreased in LH and LM after transfer, and the PSII damage was more serious in LH than that in LM, and could not recover within 30 d. It suggested that the photoinhibition damage and recovery time in old leaves was related to the intensity of light after transfer. For the newly emerged leaves with leaf primordia formed under the same light environment, a significant difference was observed in leaf morphology and pigment contents, suggesting that previous light environment exhibited carry-over effect on the acclimation capacity to a new light environment. Our result showed that thinning and pruning intensity should be considered in plantation management, because great changes in light intensity may cause photoinhibition in shade-adapted leaves.

Additional key words: Catalpa bungei; chlorophyll fluorescence; light acclimation; newly developed leaves; photoinhibition.

Introduction

Light is an important and indispensable resource for plants, and either high or low light intensity can modulate plant performance (Valladares and Niinemets 2008). Leaves grown in sun light exhibit often a greater photosynthetic rate, greater thickness, and higher nitrogen content than those raised in a shaded environment. Moreover, sun-grown leaves show well-developed palisade parenchymal layers, while shade-grown leaves usually have only a single layer (Ashton *et al*. 2011, Ivanova 2014, Bündchen *et al*. 2015).

In plantation management, pruning and thinning are critical means of determining the rational distribution and more efficient use of light. However, excessive light may lead to chronic photoinhibition, resulting in extensive

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Abbreviations: AQE – apparent quantum efficiency; Chl – chlorophyll; Car – carotenoids; DAT – days after transfer; DM – dry mass; ETR – apparent electron transport rate; F_o – minimal fluorescence yield of the dark-adapted state; F_o' – minimal fluorescence yield of the light-adapted state; F_m – maximal fluorescence yield of the dark-adapted state; F_s – steady state fluorescence yield; F_v – variable fluorescence; F_v/F_m – maximal quantum yield of PSII photochemistry; HH – high light; LCP – light-compensation point; LL – low light; LSP – light-saturation point; MM – medium light; NPQ – nonphotochemical quenching; P_N – net photosynthetic rate; P_{Nmax} – light-saturated net photosynthetic rate; q_P – photochemical quenching; R_D – respiration rate; SLA – specific leaf area; Yield – quantum yield of PSII.
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damage in nonacclimated plants (Long *et al*. 1994, Szarzynski and Anhuf 2001). Such a photoinhibition is often accompanied by acceleration of nonphotochemical quenching (NPQ) and reductions in capacity of photosynthesis, photochemical efficiency, and quantum yield (Demmig *et al*. 1987). Therefore, the flexibility of the response of shade-grown leaves to modified light environments is pivotal for the growth rate, which ultimately determines plant survival, biomass accumulation, and fitness (Krause *et al*. 2001, Beaudet *et al*. 2007). In order to avoid photoinhibition, shade-adapted or shade-acclimated plants must adjust to a new irradiance in environment. Photoprotection process involves adjusting the photosynthetic pigments, apparatus, and photosynthetic light energy-utilization efficiency of PSII in response to increases in irradiance (Long *et al*. 1994). Different plant species show divergent photoinhibition responses (Naidu and DeLucia 1997, Kitao *et al*. 2000, Einhorn *et al*. 2004).

The morphological and physiological responses of plants to different light intensities (Logan *et al*. 1998, Himrane *et al*. 2004, Gatti *et al*. 2011, Tang *et al*. 2015, Mazzanatti *et al*. 2016) and short- or long-term acclimation after a sudden change in an environment with increased light have been documented in previous studies (Kitao *et al*. 2000, Uemura *et al*. 2000, Naramoto *et al*. 2006, Gatti *et al*. 2011, Lavinsky *et al*. 2014). After thinning or gap formation, acclimation of the existing leaves that initially developed in the shade before the emergence of new leaves seems to be important. Previous leaves acclimate to increasing light by reducing the variable fluorescence (F_v/F_m) ratio and then a slow recovery process begins (Yamashita *et al*. 2000, Guo *et al*. 2006, Naramoto *et al*. 2006, Azevedo and Marenco 2012), leading to an enhancement in the photosynthetic capacity (Azevedo and Marenco 2012). However, in *Minquartia*, no physiological adjustment occurred after transition to increased light conditions and severe photoinhibition and loss of leaves were observed (Azevedo and Marenco 2012). Shortly after exposure, previously shaded mature leaves depend largely on physiological and biochemical acclimation, whereas after some time, newly developed leaves are in functional and structural equilibrium with those developed under the new irradiance (De la Torre and Burkey 1990). In addition, the allocation of resources to new leaf growth is critical for whole-plant acclimation and accumulation of biomass/leaf mass (Yamashita *et al*. 2000). For example, previously shaded leaves dropped and newly developed leaves with a higher photosynthetic rate formed in *Hybanthus prunifolius* after transfer from conditions of low to high irradiance (Kursar and Coley 1999).

Light distribution is more complicated in natural systems, where the light environment of a leaf changes markedly in the process of leaf expansion and canopy development. Leaves in the canopy, where a light gradient occurrs, are likely to encounter different irradiance environments throughout their whole life span (Ishida *et al*. 1999a,b). The acclimation of sun-adapted leaves to shade environments has been also reported in *Fagus sylvatica* plants (Tognetti *et al*. 1998), *Hordeum vulgare* L. Boone (De la Torre and Burkey 1990), and *Fagus* species (Uemura *et al*. 2000). Changes in solar irradiance usually cause variations of photosynthetic properties among canopy leaves. Acclimation of seedlings to varying light intensity was dependent not only on photosynthetic capacity adjustment in previously shaded leaves at the single-leaf level but also on the rapid production of newly sun-adapted leaves on the whole-plant level. Thus, the acclimation of those leaves to changing light environment was critical in both plantations and natural forests, which determines the carbon gain and competition for space from adjacent plants.

Catalpa bungei (*C. bungei*), native to China, is a timber species widely planted in warm-temperature, subtropical regions due to its rapid growth rate and good wood quality (Wu *et al*. 2015). There has been a great deal of research in *C. bungei*, including analyses of fertilization (Qiu *et al*. 2015) and photosynthesis (Wang *et al*. 2013), whereas the acclimation of leaves to different light intensities on *C. bungei* has not been examined. At *C. bungei* plantations, leaves at relatively low positions may encounter conditions of decreasing solar irradiance with canopy closure and increasing irradiance after thinning and pruning. Thus, the question is how these sun- and shade-adapted leaves adjust to opposite changes in their light environment. The issue could have practical consequences in the management of plantations.

This study was performed in order to obtain a better understanding of photoinhibition, both morphological and physiological responses, and to characterize the acclimation of *C. bungei* plantlets to changing light conditions. We addressed the following hypotheses in our research: (*1*) The morphological and physiological acclimation of leaves from C. *bungei* plantlets differed according to light environment. (*2*) The acclimation of old and newly developed leaves (*i.e*., the leaves that already existed and those emerged after the transfer) to both increasing or decreasing irradiance should follow different patterns. (*3*) Original light environment at leaf primordia stage has carry-over effect on potential acclimation capacity in expansion stage of newly developed leaves to new light environments. Shading is widely used in seedling cultivation and production, thus, our results can also provide some scientific reference for cultivation of *C. bungei*. In addition, by analysing leaf properties of *C. bungei* under a range of changing light supplies, our results could also provide a theoretical basis at the leaf level for decision regarding *C. bungei* plantlet cultivation and plantation management (*e.g*., pruning and thinning intensity).

Materials and methods

Plant material: This study was conducted in Xiaolongshan Forestry Science and Technology Research Institute (Tianshui, Gansu Province, China: 105°54′E, 34°28′N, 1,160 m a.s.l.). This area is a temperate zone with a semi-humid monsoon climate, average annual rainfall of 600–800 mm, and an evaporation capacity of 1,290 mm. Stumplings of *C. bungei*, clone 9-1, grafted plantlets were transplanted into pots (35 cm × 35 cm × 30 cm, one stumpling per pot) in early March 2015. Plastic pallets were placed under each pot to prevent water loss and soil erosion. The soil matrix was loess:peat soil (6:4), and the mass of soil in each pot was 15 kg, field capacity was about 31%, bulk density of 1.04 g cm^{-3}, pH 6.86, 2.3 g(total nitrogen) kg^{-1}, 18.14 g(total potassium) kg^{-1}, and 0.8 g(total phosphorus) kg^{-1}.

Experimental design: On 1 June 2015, 70 pots of biennial *C. bungei* grafted seedlings with stem cut processing were transplanted into three fixed light environments; no significant difference between the plantlets was found at the beginning of the experiment. The plantlets were grown under three light regimes: low light, 30% (LL), medium light, 50% (MM), and high light, 80% (HH) consisting of full sun as shown in Table 1. The 30% and 50% shade treatments were reached using black shade nets (resembling square tents) of different types over a rigid frame in the greenhouse, while 80% irradiance was reached without any shading (*i.e.*, the light transmittance of the greenhouse was 80%). The arrangements included 30, 10, and 30 pots in HH, MM, and LL treatments, respectively. After 45 d of shade treatments, 10 plantlets from HH and LL were transferred into different irradiance environments: HL (80–30%), HM (80–50%), LH (30–80%), and LM (30–50%), in order to simulate canopy closure and canopy opening. The black shade cloth was remained at the place for 90 d from the beginning of the experiment. The pots were irrigated as required and fertilized with 2 g of urea fertilizer (nitrogen content of 46%) monthly, to minimize plant heterogeneity in the greenhouse. The pots were placed randomly and the plantlets were moved randomly every 15 d to ensure uniformity of light under each light environment, with ten replicate plants for each treatment (HH, MM, LL, HL, HM, LM, and LH).

Growth conditions: Throughout the experiment, the average air temperature and the relative humidity were 15–34°C and 35–66%, respectively. The leaf-level PAR was measured using an external quantum sensor in an infrared gas analysis (IRGA) system (*LI-6400-40, Li-Cor.,* Lincoln, NE, USA), and it was ensured that the chamber was not covered by other adjacent leaves during the measurement. Diurnal variations of June, July, and August in three control groups (HH, MM, and LL) were measured on sunny, cloudless days, as shown in Table 1 and Fig. 1. Over the experimental period, the values of intercepted PAR were shown in Table 1.

Table 1. Variation of photosynthetically active radiation (PAR) at the leaf level with three different light treatments in three months. Data represent the range and average value (mean ± SD). HH – high light; MM – medium light; LL – low light.

PAR [µmol(photon) m^{-2} s^{-1}]						
	June		July		August	
Light treatment	Range	Average	Range	Average	Range	Average
HH	459–1,322	934 ± 370	136–1,286	679 ± 466	71–1,281	801 ± 462
MM	238–669	457 ± 185	79–679	374 ± 249	41–749	473 ± 275
LL	143–193	247 ± 89	49–409	227 ± 153	18–414	244 ± 149

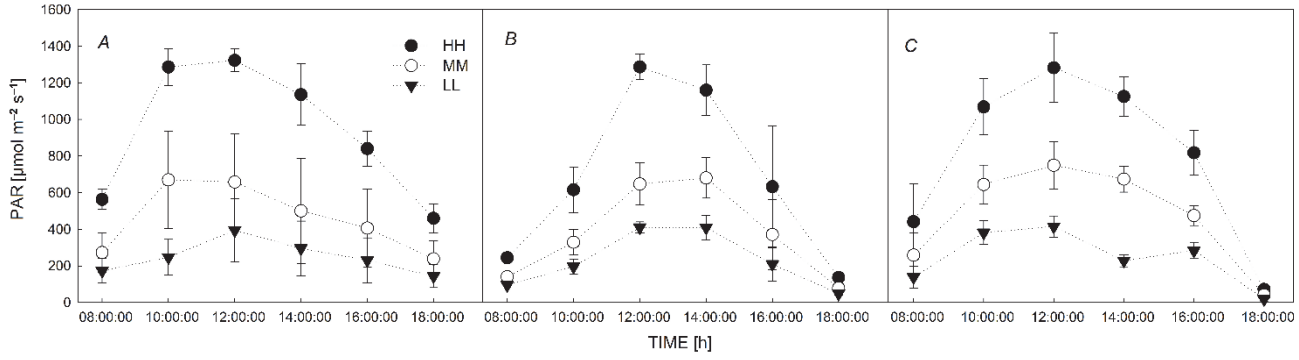

Fig. 1. Diurnal variation of photosynthetically active radiation (PAR), at the leaf level with three different light treatments. *A*, *B*, and *C* represent June, July, and August, respectively. Data show the mean ± SD (n = 25). HH – high light; MM – medium light; LL – low light.

Plant growth determination: Plant height and stem diameter were determined at 15-d intervals from the beginning of the experiment. The stem diameter was measured (about 0.5 cm above the ground) with digital callipers 0.5 cm from the stem cutting point. Various morphological traits (height, stem diameter, biomass, and specific leaf area were recorded at the end of the experiments. In addition, the plants were harvested and oven dried at 75°C for 72 h to calculate root, stem, and leaf biomass. The leaf mass fraction (LMF), stem mass fraction (SMF), and root mass fraction (RMF) were calculated as follows: LMF = (leaf dry mass (DM)/plantlet DM) × 100, RMF = (root DM/plantlet DM) × 100, SML = (stem DM/ plantlet DM) × 100.

To examine possible changes in new leaf production following the changes in the light environment, we examined newly developed mature functional leaf length, width, and area (*LI-3100* leaf area meter, *Li-Cor*, Lincoln, NE, USA) at the end of the experiment. Functional leaves meant here the leaves with a peak of metabolism and physiological activity among three stages during leaf growth, *i.e.*, young leaf, functional leaf, and aged leaf. The specific leaf area (SLA) was estimated as the ratio of leaf area to dry biomass of both existing-old and newly developed leaves. Ten leaves were chosen as replicates for each treatment and leaf samples were oven dried to determine the mass.

Chl fluorescence measurement: To assess the duration and magnitude of photoinhibition in leaves developed under low- and high-light conditions upon exposure to increasing and decreasing light environments, we used a portable fluorometer (*Mini PAM*, *Walz*, Germany). Fully expanded mature leaves of 10 plantlets in each treatment were selected, and the quantum yield of PSII was measured repeatedly for 30 d after the transfer (DAT). Chronic photoinhibition was measured from 09:00–11:00. A leaf clip was applied to the leaf for 20 min for dark acclimation, after which the initial fluorescence (F_o) and maximum fluorescence (F_m) were recorded and F_v/F_m was calculated as $(F_m - F_o)/F_m$. Leaves were light-adapted for about 15 min before measuring the nonphotochemical [$NPQ = (F_m - F_m')/F_m'$] and photochemical quenching [$q_P = (F_m - F_m')/(F_m' - F_o)$] parameters of Chl fluorescence, effective quantum yield of photochemical energy conversion [$Yield = (F_m' - F_s)/F_m'$], and the relative rate of electron transport through PSII (ETR = 0.5 × PAR × Yield). Measurement were obtained over a range of light regimes between 0 and 1,000 μmol(photon) m^{-2} s^{-1}. F_m and F_m' are the maximum fluorescence in the dark- and light-adapted leaf, respectively (PSII centres closed), F_s is steady-state fluorescence at any light level (Maxwell and Johnson 2000).

Light-response curves: The response curves to PPFD were measured at ambient CO_2 concentration (400 ppm) with an infrared gas analysis system [*Li-Cor 6400*-40 with a red-blue light-emitting diode (LED) source, *Li-Cor*, Lincoln, NE, USA]. The curves were measured on fully expanded old leaves, *i.e.*, the round leaves were used for measurement of fluorescence between 09:00 and 13:00 h on a clear, cloudless day. In addition, the relative humidity and air temperature were stable at about 50–60% and 28–35°C, respectively. Each selected leaf was allowed to reach a steady state under PAR of 1,200 μmol(photon) m^{-2} s^{-1} for at least 15–20 min. PPFD was increased from 0, 25, 50, 150, 200, 400, 600, 800; 1,000; 1,200; 1,500; 1,800 to 2,000 μmol m^{-2} s^{-1}. Assimilation was recorded at each step. Five plants and two replicates per plant were used. Photosynthetic capacity was estimated from the light-saturated net photosynthetic rate as determined by fitting P_N/PPFD curves using a nonrectangular hyperbola model (Garcês and Sinha 2009). Light-saturated maximum photosynthesis (P_{Nmax}), respiration (R_D), apparent quantum efficiency (AQE), light-compensation point (LCP), and light-saturation point (LSP) were calculated from light-response curves using *Photosynthesis Assistant* software (*Dundee Scientific Ltd*., Dundee, UK.). Further details can be found in Springer *et al*. (2007).

Pigment contents: Fully expanded leaves (n = 10), *i.e.*, existing-old leaves sampled at 3, 18, and 30 DAT and newly developed mature leaves collected after 30 DAT, were examined for Chl contents (*a*, *b*, and *a+b*) and carotenoids (Car). Pigments were extracted by grinding leaves in 95% ethanol in the dark for 24 h, according to the method of Guo *et al*. (2013) using a spectrophotometer (*722S*, *Leng Guang, Inc.*, Shanghai, China) at the wavelengths of 470, 649, and 665 nm.

Statistical analyses: First, the assumptions of normality (*Shapiro–Wilk*'s test) and homoscedasticity were checked, and then, *F*-test and analysis of variance (*ANOVA*) were used to evaluate the influence of light treatment on both morphological and physiological parameters. Data were analysed using *SPSS* 19.0 software (*SPSS Inc.*, Chicago, IL, USA). Figures were drawn using *SigmaPlot 10.0* software (*Systat Software*, *Inc*., San Jose, CA, USA).

Results

Morphology: The morphological characteristics showed a significant response to the differences in PAR regimes. Height (35%) (Fig. 2*A*), stem diameter (22–52%) (Fig. 2*B*), biomass (29–59%) (Fig. 2*C*), leaf area (41%) (Fig. 2*D*), leaf length (34%) (Fig. 2*G*), and leaf width (31%) (Fig. 2*H*) declined, while SLA (89–161%) (Fig. 2*E*,*F*) increased after MM and LL treatments compared to that of HH treatment, respectively. Significant reductions were found in the stem diameter (11.3–18.7%) and biomass (17–33%) (Fig. 2*B*,*C*) after being transferred

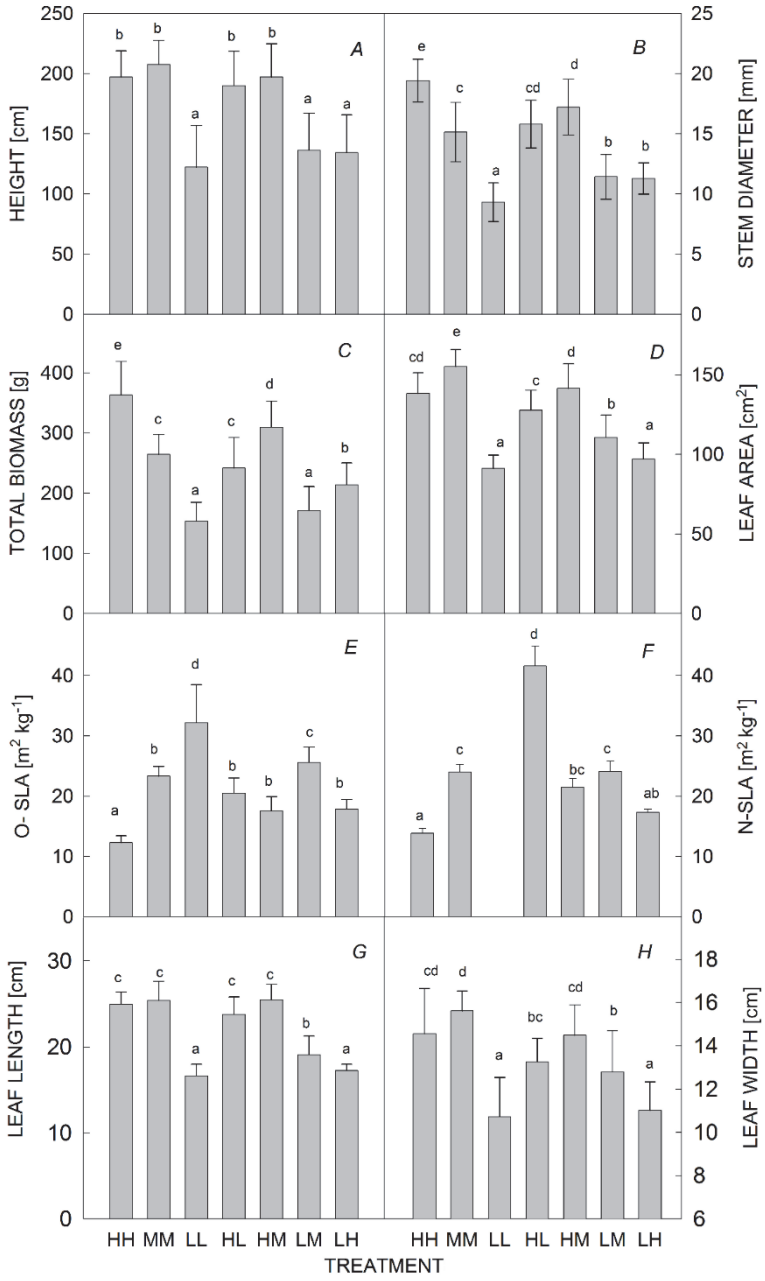

Fig. 2. Plantlet height (*A*), stem diameter (*B*), total biomass (*C*), functional leaf area (*D*), leaf length (*G*), leaf width (*H*) in newly developed leaves after transfer, and specific leaf area of existing-old leaves (O-SLA) (*E*); newly developed leaves (N-SLA) (*F*) in *Catalpa bungei* plants subjected to seven treatments (the LL treatment group had no appropriate newly emerged mature leaves after transfer). Means followed by *the same letter* do not differ significantly from one another (n = 10, P<0.05).

from HH to HL and HM, and the SLA of old leaves (O-SLA) increased by 42–67% (Fig. 2*E*). Significant increases were observed in stem diameter (21.3–22.9%), biomass (39%), leaf length (14.7%), and leaf width (19.1%), while leaf area (21.5%) (Fig. 2*B*,*C*,*D*,*G*,*H*) decreased and O-SLA (20–45%) increased after being transferred from LH and LM, respectively. Plant height showed no significant response after the transfer, whereas the ground diameter was affected by the new light environment. Some significant alterations in biomass allocation were observed (Fig. 3). The RMF was greater in the LL (approximately 76%) than those in the HH and MM treatments, and leaf biomass fraction (LMF) and stem biomass fraction (SMF) were the lowest ones in the LL treatment. When plantlets were transferred to LL, the RMF increased, while LMF and SMF decreased with reducing PAR, the extent of variation was determined by the degree of light intensity variation (Fig. 3).

Chl fluorescence acclimation after transfer: Before the transfer, the F_v/F_m ratio was around 0.8. Sudden exposure of plantlets to MM and HH (50% and 80%) caused a photoinhibitory response that included a substantial reduction of F_v/F_m. With the maximal decrease occurring 2 DAT, the mean minimal values of F_v/F_m were 0.57 and 0.44 in LM and LH leaves, respectively, followed by a

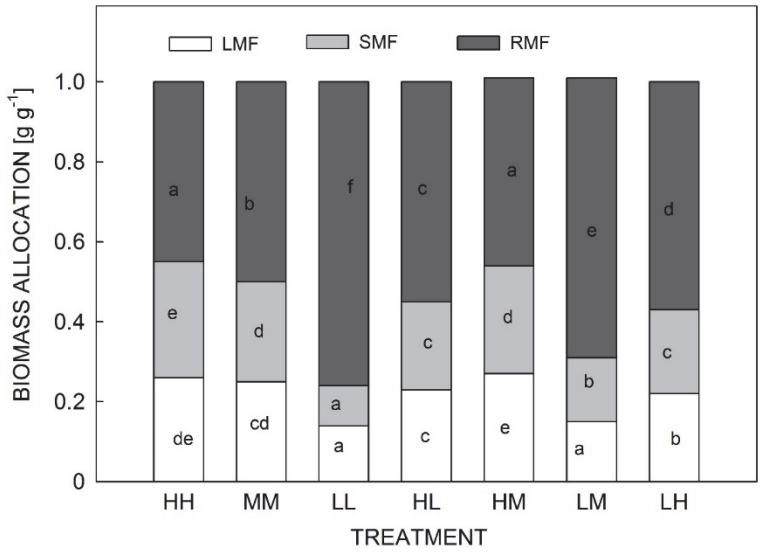

Fig. 3. Biomass allocation traits: RMF – root mass fraction; SMA – stem biomass fraction; LMF – leaf biomass fraction in *Catalpa bungei* plants subjected to seven light treatments. Different *uppercase letters* indicate significant differences between different light treatments (n = 10, P<0.05).

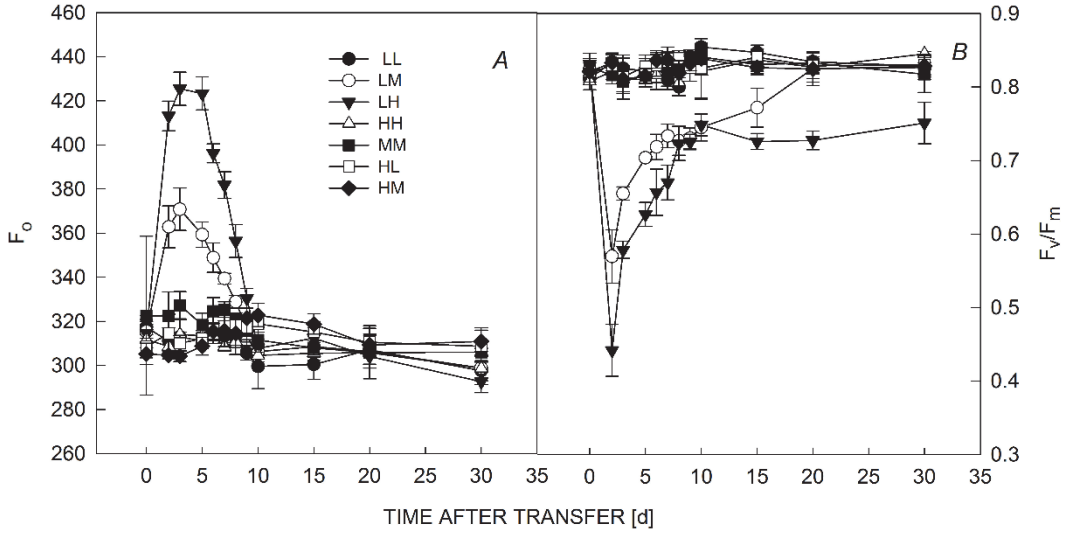

Fig. 4. Time course of the initial fluorescence of PSII (F_o) (*A*) and variable fluorescence (F_v/F_m) (*B*) in existing-old leaves of *Catalpa bungei* seedlings after transfer. Error bars show ± SD.

slow recovery in both LH and LM leaves at 5 DAT (Fig. 4*B*). Moreover, the variation in amplitude depended on the intensity of light environment after transfer. The mean value of F_v/F_m in LH was lower than that of LM, both were significantly lower than others at 20 and 30 DAT for LM and LH, respectively. In addition, high values of F_v/F_m were found in HH, MM, and LL leaves over the entire light acclimation period. In contrast, there was no obvious photoinhibition response in the leaves of HL and HM, with the value of F_v/F_m being slightly below 0.8. By the end of the experiment, there was no significant difference between the treatments, except for the HL group (Fig. 4*B*). F_o increased immediately on sudden exposure to a high light, with the maximum value occurring 3 DAT, followed by a slow recovery in both LH and LM leaves at 5 DAT (Fig. 4*A*). The amplitude of variation was related to the light intensity after transfer. The mean value of F_o in LH was higher than that of LM, and a significant difference was observed after 2–9 DAT. Strikingly, no significant differences were found in other treatments.

Chl fluorescence parameters: Fluorescence parameters showed significant differences between the light treatments (Table 2). No photoinhibition was found as the ratio of F_v/F_m remained high (approximately 0.80), and no significant differences were found between the leaves grown in the same light environment. For old leaves, NPQ of MM was markedly lower than those of the other groups under the fixed light environment. The values of q_P, Yield, and ETR tended to increase with a reduction in light intensity, rising in HL and HM, and decreasing in LH and LM, with a greater magnitude of variation observed in HL and LH than that in HM and LM, respectively. For newly developed leaves, the Chl fluorescence parameters showed

Table 2. Analysis of variance (*ANOVA*) of chlorophyll (Chl) fluorescence parameters in old and newly developed leaves at the end of the experiment. Different *lowercase letters* indicate significant differences between different light treatments ($P<0.05$), ns – no significant difference ($P>0.05$). Data represent the mean ± SD ($n = 6$). F_v/F_m – maximal quantum yield of PSII; NPQ – nonphotochemical quenching; Yield – quantum yield of PSII; q_P – photochemical quenching; ETR – apparent electron transport rate.

	Treatments	F_v/F_m	q_P	NPQ	ETR [μmol(e^{-1}) m^{-2} s^{-1}]	Yield
Old leaves	HH	0.84 ± 0.02^{a}	0.96 ± 0.04^{a}	0.58 ± 0.20^{b}	223.51 ± 10.27^{b}	0.71 ± 0.03^{b}
	MM	0.83 ± 0.03^{a}	0.98 ± 0.03^{a}	0.38 ± 0.10^{a}	233.64 ± 9.72^{c}	0.75 ± 0.03^{c}
	LL	0.82 ± 0.02^{a}	1.08 ± 0.08^{b}	0.60 ± 0.11^{b}	240.78 ± 5.81^{d}	0.77 ± 0.02^{d}
	HL	0.83 ± 0.02^{a}	1.05 ± 0.07^{b}	0.54 ± 0.08^{b}	241.39 ± 5.75^{d}	0.77 ± 0.02^{d}
	HM	0.84 ± 0.01^{a}	1.00 ± 0.03^{a}	0.62 ± 0.11^{b}	232.35 ± 5.79^{c}	0.74 ± 0.02^{c}
	LM	0.83 ± 0.02^{a}	1.05 ± 0.05^{b}	0.80 ± 0.06^{c}	225.26 ± 6.69^{bc}	0.72 ± 0.02^{bc}
	LH	0.73 ± 0.03^{b}	0.96 ± 0.03^{a}	0.59 ± 0.12^{b}	212.83 ± 8.20^{a}	0.68 ± 0.03^{a}
Newly emerged leaves	HH	0.83 ± 0.03^{ns}	0.97 ± 0.06^{a}	0.68 ± 0.13^{b}	222.21 ± 8.01^{a}	0.72 ± 0.03^{a}
	MM	0.83 ± 0.01^{ns}	1.00 ± 0.06^{a}	0.40 ± 0.08^{a}	234.10 ± 11.55^{bc}	0.75 ± 0.02^{bc}
	LL	0.83 ± 0.01^{ns}	1.11 ± 0.10^{b}	0.62 ± 0.09^{b}	239.96 ± 6.18^{c}	0.77 ± 0.02^{de}
	HL	0.84 ± 0.02^{ns}	1.11 ± 0.10^{b}	0.60 ± 0.13^{b}	239.08 ± 10.87^{c}	0.78 ± 0.02^{e}
	HM	0.84 ± 0.01^{ns}	0.95 ± 0.08^{a}	0.45 ± 0.08^{a}	238.72 ± 4.13^{c}	0.76 ± 0.01^{cd}
	LM	0.83 ± 0.01^{ns}	1.00 ± 0.04^{a}	0.44 ± 0.08^{a}	234.61 ± 5.84^{bc}	0.73 ± 0.01^{ab}
	LH	0.83 ± 0.01^{ns}	0.98 ± 0.05^{a}	0.62 ± 0.16^{b}	228.05 ± 7.37^{ab}	0.72 ± 0.04^{a}

no significant differences between treatments under the same irradiance conditions, with the exception of Yield in HM, which was higher than that of LM (Table 1).

Photosynthetic pigments: The concentrations of photosynthetic pigments showed significant differences between various light treatments in both types of leaves. For old leaves, Chl *a*, Chl *b*, Car, and total Chl contents increased, while Chl *a*/*b* decreased with decreasing light intensity in both fixed and changing light environments, with the maximum response observed after 30 DAT (Table 3). For newly emerged leaves, there were no significant differences in pigment contents in high-light (HH and LH) and medium-light environments (MM, HM, and LM) with leaf primordia growing in the same irradiance environ-ment, except Car contents in MM and LM and Chl *a*/*b* in HH and LH. However, significant differences were observed in Chl *a*, Car, Chl (*a*+*b*), and Chl *a*/*b* between LL and HL treatments (Table 2).

Light-response curve parameters: Photosynthetic parameters were significantly different between the light treatments (Fig. 5), except for the AQE values (Fig. 5*C*). With decreasing PAR, LCP, LSP, $P_{Nmax,}$ and R_D tended to decrease in MM and LL (29, 31–45, 35–58, 64%, respectively), HL and HM (12–43%, 19–37%, 34–36%, 21–59%, respectively) than that of HH. LCP, $P_{Nmax,}$ and R_D increased significantly in LH and LM (29–43%, 12–36%, 83–209%, respectively) compared to LL. The extent of the variation depended on the light intensity after the transfer (Fig. 5*A–E*).

Discussion

The morphological and physiological acclimation to different light environments: Irradiance is critical for biomass accumulation and allocation between the leaves, stem, and roots. The biomass is the most direct consequence of plant growth performance (Dawson *et al*. 2012). The plants examined here differed significantly in responses to light conditions, especially in their growth-related parameters (Fig. 2), in a similar way as reported previously in other plant species, such as *Coffea arabica* (Rodríguez-López *et al*. 2014) and *Fagus sylvatica* (Tognetti *et al*. 1998). The morphological response affected the proportion of assimilatory and conductive tissues in leaves (Lambers and Poorter 1992). The SLA increased due to the lower thickness observed in shade-grown plantlets (Fig. 2*E*,*F*), which was an adaptation mechanism to maximize light harvesting under low light conditions (Aranda *et al*. 2007).

Significant differences were observed in carbon accumulation and allocation between light treatments (Fig. 3) as a result of limited photosynthesis (Fig. 5*D*). Many species allocated biomass preferentially to special parts for obtaining the urgently needed resources that limited growth during a seedling stage (Poorter and Nagel 2000). For example, increasing foliage and stem growth occur in order to enhance light interception in low light environment (Minotta and Pinzauti 1996, Tognetti *et al*. 1998). Conversely, larger root biomass allocation and lesser to foliage are reported in young seedlings in the

Table 3. Leaf pigment content for *Catalpa bungei* plantlets in different light treatments after transfer of 3, 15, and 30 days in old leaves and 30 days in newly emerged leaves, respectively. Values represent means ± SD ($n = 6$). Different *lowercase letters* indicate significant differences between different light treatments ($P<0.05$). Chl – chlorophyll; Car – carotenoids; DM – dry mass.

Leaf type	Transfer days	Light treatments	Chl *a* [mg g^{-1}(DM)]	Chl *b* [mg g^{-1}(DM)]	Car [mg g^{-1}(DM)]	Chl (*a*+*b*) [mg g^{-1}(DM)]	Chl *a*/*b*
Old	3	HH	4.53 ± 0.61^{a}	1.81 ± 1.16^{a}	0.94 ± 0.44^{a}	6.35 ± 1.21^{a}	2.37 ± 0.70^{b}
		MM	7.43 ± 1.04^{c}	2.76 ± 0.45^{ab}	1.58 ± 0.15^{bc}	10.19 ± 1.48^{c}	2.70 ± 0.12^{b}
		LL	12.21 ± 0.65^{f}	6.68 ± 1.60^{c}	1.75 ± 0.12^{c}	18.89 ± 2.21^{e}	1.89 ± 0.29^{a}
		HL	7.77 ± 0.71^{c}	3.09 ± 0.33^{b}	1.75 ± 0.15^{c}	10.86 ± 1.04^{c}	2.52 ± 0.05^{b}
		HM	5.87 ± 1.19^{b}	2.21 ± 0.37^{ab}	1.44 ± 0.18^{b}	8.08 ± 1.56^{b}	2.64 ± 0.15^{b}
		LM	10.41 ± 0.60^{e}	5.79 ± 0.90^{c}	1.55 ± 0.07^{bc}	16.20 ± 1.47^{d}	1.82 ± 0.22^{a}
		LH	9.03 ± 0.09^{d}	5.78 ± 0.06^{c}	1.15 ± 0.11^{a}	14.81 ± 0.09^{d}	1.56 ± 0.03^{a}
	15	HH	4.71 ± 0.92^{a}	1.54 ± 0.54^{a}	1.16 ± 0.18^{a}	6.25 ± 1.07^{a}	2.72 ± 0.31^{d}
		MM	8.22 ± 1.34^{c}	3.17 ± 0.67^{bc}	1.66 ± 0.18^{bc}	11.39 ± 2.00^{c}	2.62 ± 0.16^{cd}
		LL	12.48 ± 0.60^{e}	6.99 ± 1.31^{e}	1.81 ± 0.13^{c}	19.47 ± 1.86^{e}	1.83 ± 0.24^{a}
		HL	6.65 ± 1.27^{b}	2.54 ± 0.61^{ab}	1.36 ± 0.36^{ab}	9.19 ± 1.88^{b}	2.65 ± 0.18^{cd}
		HM	5.37 ± 1.12^{a}	2.09 ± 0.53^{a}	1.14 ± 0.32^{a}	7.46 ± 1.58^{a}	2.61 ± 0.30^{cd}
		LM	9.64 ± 0.75^{d}	4.79 ± 1.06^{d}	1.55 ± 0.12^{bc}	14.43 ± 1.77^{d}	2.06 ± 0.26^{ab}
		LH	7.50 ± 0.68^{bc}	3.65 ± 2.03^{c}	1.59 ± 0.61^{bc}	11.14 ± 2.36^{c}	2.26 ± 0.92^{bc}
	30	HH	4.00 ± 0.56^{a}	1.17 ± 0.32^{a}	0.91 ± 0.27^{a}	5.17 ± 0.29^{a}	2.97 ± 0.53^{e}
		MM	8.17 ± 0.48^{d}	4.37 ± 0.74^{d}	1.29 ± 0.08^{bcd}	12.54 ± 1.18^{d}	1.91 ± 0.28^{b}
		LL	10.43 ± 0.14^{g}	7.32 ± 1.19^{f}	1.41 ± 0.26^{d}	17.75 ± 1.20^{f}	1.46 ± 0.21^{a}
		HL	8.67 ± 0.40^{e}	5.41 ± 0.60^{e}	1.13 ± 0.38^{b}	14.08 ± 0.68^{e}	1.62 ± 0.21^{a}
		HM	5.48 ± 0.54^{b}	2.04 ± 0.19^{b}	1.35 ± 0.12^{cd}	7.52 ± 0.69^{b}	2.69 ± 0.19^{d}
		LM	9.24 ± 0.58^{f}	3.99 ± 0.56^{d}	1.63 ± 0.10^{e}	13.23 ± 1.12^{d}	2.34 ± 0.20^{c}
		LH	6.38 ± 0.47^{c}	2.88 ± 0.56^{c}	1.19 ± 0.13^{bc}	9.26 ± 0.96^{c}	2.27 ± 0.33^{c}
Newly emerged	30	HH	3.59 ± 0.61^{a}	1.43 ± 0.39^{a}	0.81 ± 0.19^{ab}	5.02 ± 0.88^{a}	2.67 ± 0.76^{e}
		MM	6.39 ± 0.42^{b}	3.32 ± 0.66^{b}	1.33 ± 0.12^{d}	9.72 ± 0.92^{b}	1.98 ± 0.33^{cd}
		LL	7.64 ± 0.27^{c}	7.28 ± 1.36^{c}	0.67 ± 0.36^{a}	14.93 ± 1.22^{c}	1.09 ± 0.25^{a}
		HL	9.68 ± 0.75^{d}	7.23 ± 1.3^{c}	1.62 ± 0.57^{e}	16.91 ± 1.90^{d}	1.37 ± 0.21^{ab}
		HM	6.46 ± 0.39^{b}	3.45 ± 0.86^{b}	1.26 ± 0.16^{cd}	9.92 ± 1.20^{b}	1.95 ± 0.37^{cd}
		LM	6.47 ± 0.43^{b}	4.00 ± 0.84^{b}	1.06 ± 0.06^{bc}	10.47 ± 1.25^{b}	1.67 ± 0.29^{bc}
		LH	3.62 ± 0.94^{a}	1.91 ± 1.01^{a}	0.93 ± 0.21^{ab}	5.53 ± 1.25^{a}	2.20 ± 0.72^{d}

understorey levels; which allow them to respond rapidly to resource acquisition, such as height growth, with increasing light as a result of canopy opening formation (Poorter and Kitajima 2007). In our study, higher root biomass proportion was observed with decreasing light supply (Fig. 3). One explanation maybe that it was due to the fact that our experimental materials were biennial grafted seedlings, with mature and old roots before the experiments; another explanation might be found in an self-adaptation strategy of *C. bungei*, which needs to be studied further in the future.

The higher NPQ in LM implies that the energy absorbedunder such conditions was higher than photochemical utilization and this might induce photoinhibition (Vasil'ev *et al*. 1998). The NPQ values of LM and LH increased after the transfer, indicating that photoinhibition occurred, moreover, LM was higher than that of LH (Table 2). These results were in accordance with the NPQ mechanism of *Chromera velia* (Mann *et al*. 2014) and *Coffea arabica* (Rodríguez-López *et al*. 2014) plants. Our results showed variation in electron transport in the PSII centre under various shade treatments, and both q_P and Yield increased with decreasing light (Table 2) in agreement with observations in coffee, where declines were observed when transferred from 10 to 100% irradiance (Rodríguez-López *et al*. 2014). In addition, q_P of LH decreased, while that of HL remained unchanged (Table 2), similarly to the observations in previous experiments performed in *Fagus sylvatica* (Tognetti *et al*. 1998), whereas opposite mechanism was observed in *Tetrastigma hemsleyanum* (Dai *et al*. 2009). This indicates that the proportion of open PSII reaction centres was likely to be different in various species with increasing light intensity. The ETR value increased with a reduction in irradiance, in contrast to the response reported in coffee, where ETR decreased with decreasing light intensity over the two measurement time periods of 08:00–10:00 and 14:00–16:00 (Rodríguez-López *et al*. 2014). The ETR of

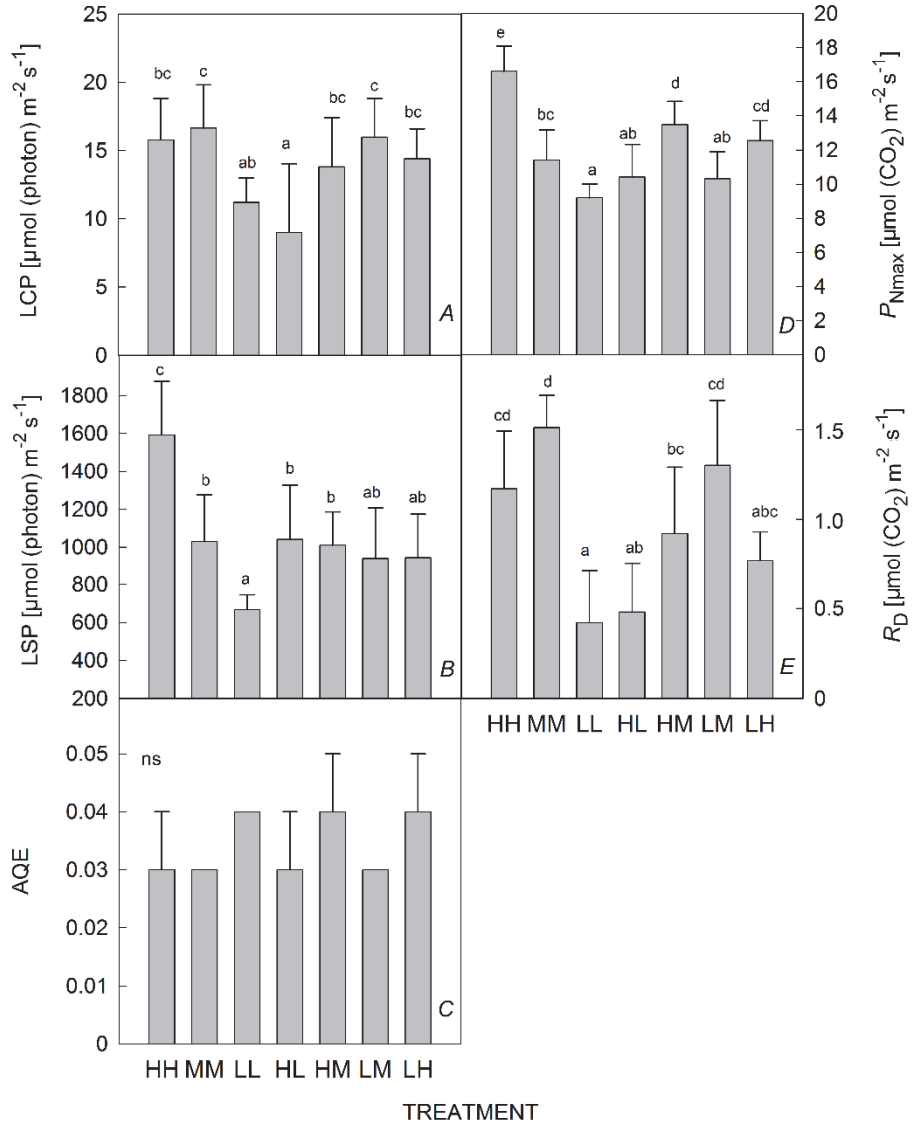

Fig. 5. Photosynthetic variables derived from the net photosynthetic rates and irradiance curves, including light-compensation point (LCP) (*A*); light-saturation point (LSP) (*B*); apparent quantum yield (AQE) (*C*); light-saturated maximum photosynthesis (P_{Nmax}) (*D*); and dark respiration rate (R_D) (*E*) in existing-old mature leaves of *Catalpa bungei* measured at the end of the experiment. Different *lowercase letters* indicate significant differences between different light treatments (n = 5, P<0.05), ns – no significant difference (P>0.05).

LH decreased on exposure to a high-light environment (Table 2). Reductions in ETR might occur due to the reduction of Chl contents in order to decrease excessive light capture (Table 2), which was most likely caused photoinhibition (Flowers *et al*. 2007).

Leaf pigment content is considered to be a common and important reference, where both qualitative and quantitative aspects are required in physiological reactions (Wittmann *et al*. 2001). In our research, for old-existing leaves, all photosynthetic pigment contents increased, whereas Chl *a*/*b* decreased with decreasing PAR, representing an adaptation strategy. The Chl *a*/*b* ratio response was not obvious initially at 18 DAT, but significant changes were observed at 30 DAT (Table 2). Our results were consistent with other studies of many species that showed acclimatory responses of photosynthetic pigments in relation to light intensity (Naramoto *et al*. 2006, Krause *et al*. 2012, Murillo-Amador *et al*. 2013, Rodríguez-López *et al*. 2014). When leaves are exposed to relatively low light intensity, more energy is allocated to increase the density of photosynthetic units in order to enhance absorption and transmission of photons by increasing Chl content; it is contrary when leaves are exposed to relatively high light environments.

The P_{Nmax}, LCP, LSP, and R_D of *C. bungei* plantlets decreased with decreasing light intensity, with the exception of AQE (Fig. 5). The largest P_{Nmax} value was observed in HH and the lowest one in LL individuals, in agreement with the observations of Legner *et al*. (2014). There was no significant difference of light-response curve parameters due to photoinhibition between LH and LL treatments, with the exception of P_{Nmax}, which was in accordance with *Tetrastigma hemsleyanum* Diels et Gilg (Dai *et al*. 2009). The LCP was less affected by the previous irradiance environment, P_{Nmax} of LH was lower than that in HH, although LSP decreased in the HL and HM, HL was still higher than LL, HM was equivalent to MM, the R_D in LM was lower than that of MM (Fig. 5).

This indicates that the ability of using low light was not affected, whereas both LSP, P_{Nmax}, and R_D were influenced by the previous light environment, as observed in coffee (Rodríguez-López *et al*. 2014). There were no significant differences in AQE in the present study (Fig. 5), suggesting that light energy transformation efficiency was unaffected by different light treatments.

The occurrence and recovery from photoinhibition in old leaves: After exposure to the enhanced light intensity, F_o increased sharply with a concurrent reduction of F_v/F_m in the *C. bungei* plantlets, indicating severe damage in the PSII reaction centre, followed by a subsequent recovery; this behaviour implies the reorganization of PSII as the mechanism of photoprotection (Fig. 4). The damage was most likely linked to variations of both electron transport and light-harvesting components in tissues (Schiefthaler *et al*. 1999). The appearance and recovery from photoinhibition in this study were consistent with previous reports (Yamashita *et al*. 2000, Valladares *et al*. 2002, Naramoto *et al*. 2006, Tobita *et al*. 2010, Azevedo and Marenco 2012). The photoprotective mechanisms, including utilization of energy for heat dissipation and electron transport (*e.g*., photorespiration and photosynthesis) are related to the xanthophyll cycle (Demmig-Adams and Adams 2006). In the present study, the mean value of F_v/F_m in LH leaves was lower than that in LM (Fig. 4). The difference in light, neither used in heat dissipation nor in electron transport, played a key role in the degree of photoinhibition, which was similar to that reported in *Fagus crenata* seedlings (Kato *et al*. 2003, Naramoto *et al*. 2006). However, there was no variation in the F_v/F_m ratio when *C. bungei* plantlets were transferred from high to low light (Fig. 4), in agreement with the results reported previously in *Fagus sylvatica* (Tognetti *et al*. 1998).

At the end of the experiment, the F_v/F_m value of LH was still below the others and did not recover within 30 DAT, which indicated that the entire recovery from photoinhibition required more time. However, the F_v/F_m value in LM returned to the normal within 20 DAT, indicating the recovery time was related to the light intensity exposed to (Fig. 4). Moreover, species differed in their recovery time from exposure to a sudden increase in irradiance. For example, the sub-Mediterranean species, *Quercus pyrenaica*, and the temperate species, *Quercus petraea*, showed photoinhibition initially and then fully acclimated photosynthetic features were observed within 46 days after transfer (Rodríguez-Calcerrada *et al*. 2008). *Minquartia* saplings showed 80% recovery, because F_v/F_m was unable to recover to the normal value recorded in control plants and a complete recovery period lasted more than 6 months (Ribeiro *et al*. 2005). In contrast, the transfer of coffee plants from low to high PAR was accompanied with elevated F_v/F_m values, suggesting that coffee plants possess well developed mechanisms for photoprotection against excessive irradiance (Chaves *et al*. 2008, Moraes *et al*. 2010, Pompelli *et al*. 2010). Additionally, this also indicates that the recovery ability of the PSII reaction centre varies among different species.

The carry-over effects of original light environment: At the end of the experiment, all *C. bungei* plantlets produced new leaves, totally adapted to the new irradiance environment. The shade-acclimated leaves remained healthy and vigorous throughout the entire experiment period. Leaf area of *C. bungei* plantlets decreased with a reduction of light (Fig. 2*D*). This result confirmed previous observations in *Tetrastigma hemsleyanum* (Dai *et al*. 2009) and *Posidonia sinuosa* (Gordon *et al*. 1994), where a leaf size was reduced under low-irradiance conditions. The functional leaf area differed between groups under the same light environment after transfer, a larger leaf area was observed in HL than LL, and *vice versa*, smaller in LM and LH compared with MM and HH, respectively. It might be related to the biomass and carbohydrate accumulation under the original light conditions.

Photosynthetic pigment contents differed between plants grown in low and high light environments, with great changes observed in combinations of HL and LH (Table 2), indicating that previous growth light environment impacted pigment contents of newly emerged leaves. The effect was closely related to the magnitude of light modification. Although photoinhibition occurred in old-existing leaves of LH individuals, the F_v/F_m value was around 0.8 in the newly developed leaves. The results showed that there was no carry-over effect on photoinhibition in newly developed leaves in LH treatment. The fluorescence parameters showed no significant difference in leaves with leaf primordium developed under the same light environment, only exception was Yield observed in HM which was different from that of LM. Our results showed that original light environment had lower carry-over effects on Chl fluorescence parameters, suggesting a strong competitiveness of newly emerged leaves. However, the carry-over effect observed on the photosynthesis capacity (*e.g*., parameters of gas exchange and light response) is worthy of studying. On the other hand, Uemura *et al*. (2000) examined the effects of different solar irradiances on leaf characteristics at the leaf primordium and expansion stages; their results showed that effects of current-year irradiance had a greater effect on leaf-area-based daily carbon gain than previous-year irradiance. Our findings further supported that the current irradiance had a greater effect on acclimation potential of newly developed leaves to new light environment than the previous irradiance.

Conclusion: As better performance and no photoinhibition were observed in HH group, we proposed that the *C. bungei* plants, even at the plantlet stage, possess the ability to use fully relatively high light intensity. Thus, *C. bungei* seedlings can be cultivated with only mild shading measures.

For old leaves, the photoinhibition in LH was more serious and longer recovery time was needed than that in LM, which was closely related to difference in the excessive light intensity. For newly emerged leaves, carry-over effect was observed during acclimation to new light environment. Main indicators affected were functional leaf morphology and photosynthetic pigments and the extent of impact depended on the magnitude of light modification.

Our results indicated that plantation management measures, such as thinning and pruning, used to achieve light distribution in the canopy, might lead to photo-inhibition in shade-adapted leaves, leading to a reduction in canopy photosynthesis, and ultimately, yield.

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