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ORIGINAL ARTICLE

# Quantity of supplementary LED lightings regulates photosynthetic apparatus, improves photosynthetic capacity and enhances productivity of Cos lettuce grown in a tropical greenhouse

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## Abstract

Although cooling their rootzone allows year-round (temperate) vegetable production in Singapore's warm climate, these crops have frequently experienced increasingly unpredictable cloudy and hazy weather. Supplementary lighting with light-emitting diodes (LEDs) could be used to reduce the impacts of low light intensity. This study investigated the responses of temperate Cos lettuce (*Lactuca sativa* L.) to different quantities (photosynthetic photon flux density, PPFD of 0, 150, 300 µmol $m^{-2}$ $s^{-1}$) of supplementary LED lightings in the tropical greenhouse. Increasing light intensity significantly increased total leaf area, shoot and root fresh weight (FW) and dry weight (DW), total chlorophyll (Chl) and carotenoids (Car) contents, light-saturated photosynthetic $CO_2$ assimilation rate ($A_{sat}$) and transpiration rate ($T_r$)**.** There were no significant differences in $F_v/F_m$ ratio, total reduced nitrogen, specific leaf area (SLA) and PSII concentration among the three light treatments. However, there was an increasing trend with increasing light intensity for Chl *a*/*b* ratio, net photosynthetic $O_2$ evolution rate ($P_N$), cytochrome $b_6f$ (Cyt $b_6f$), leaf total soluble protein and Rubisco concentrations. This study provides the basic understanding of photosynthetic apparatus and capacity of temperate crops grown under different supplementary LED lightings in the tropical greenhouse.

**Keywords** Cos lettuce · LED lighting · Photosynthetic capacities · Plant growth · Tropical greenhouse

## Abbreviations

| | |
|---|---|
| $A_{sat}$ | Light-saturated photosynthetic $CO_2$ assimilation rate |
| Car | Carotenoids |
| Chl | Chlorophyll |
| $C_i$ | Internal $CO_2$ concentration |
| Cyt $b_6f$ | Cytochrome $b_6f$ complex |
| DW | Dry weight |
| ETR | Electron transport rate |
| FW | Fresh weight |
| LED | Light-emitting diode |
| $P_{max}$ | Photosynthetic capacity |
| $P_N$ | Net photosynthetic $O_2$ evolution rate |
| PPFD | Photosynthetic photon flux density |
| PS I | Photosystem I |
| PS II | Photosystem II |
| RuBP | Ribulose 1,5-bisphosphate |
| Rubisco | Ribulose 1.5-bisphosphate carboxylase/oxygenase |
| SL + 0 PPFD | Only natural sunlight |
| SL + 150 PPFD | Natural sunlight and supplementary LED light with PPFD of 150 µmol $m^{-2}$ $s^{-1}$ |
| SL + 300 PPFD | Natural sunlight and supplementary LED light with PPFD of 300 µmol $m^{-2}$ $s^{-1}$ |
| SLA | Specific leaf area |
| $T_r$ | Transpiration rate |

## Introduction

Temperate vegetable crop, such as lettuce (*Lactuca sativa* L.), has been successfully grown in the tropical greenhouse in Singapore with aeroponic systems by exposing only their roots to cool temperature between 15 and 25 °C while shoots were maintained at fluctuating hot ambient temperatures of 25–40 °C (He and Lee 1998a, b; He et al. 2001; He and Lee 2004). Apart from temperature, light is another factor that

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affects the growth and development of lettuce plants (Fu et al. 2012; Galieni et al. 2016; Zhou et al. 2019). In Singapore, low natural sunlight conditions are often encountered after a few clear sunny days, followed by days of cloudy weather (He et al. 1996). Since 1982, Singapore has also been frequently experiencing increasingly unpredictable environmental conditions of hazy weather (Nobre et al. 2016), which is believed to be one of the main causes of global dimming. During the hazy period in 2013, the average midday maximum PPFD was around 220 μmol $m^{-2}$ $s^{-1}$ (prevailing sunlight) inside our greenhouse (He et al. 2019b). Low light intensity reduced the productivity of crop plants in Southeast Asia (Jones 2006) including Singapore (He et al. 2011a, 2015, 2019b). Light intensity is the most critical environmental factor for photosynthetic rate, many other crop physiological processes and biochemistry (Kouřil et al. 2013; Feng et al. 2019).

Low light intensity can negatively impact the photosynthetic apparatus and capacity and, thus leading to reduced crop yield (Kouřil et al. 2013; Jin et al. 2016; Fu et al. 2017). We have previously reported that in Singapore, when butter head lettuce plants were grown under low PPFD during the haze periods in the greenhouse, low shoot productivity with large amount of bolting, reduced photosynthetic rate and stomatal conductance were measured (He et al. 2011a). In the study with lettuce (*L. sativa*, var. Youmaicai) by Fu et al. (2017) on the effects of varying combination of light intensity and nitrogen (N) supply, it was found that high light intensity increased biomass production, and net photosynthetic rate under all N levels. These results indicated that increasing light intensity had positive effects on growth and photosynthetic rate regardless of N supply.

Photosynthesis is carried out in the thylakoid membrane, which is important for photosynthetic apparatus. Two photosystems (PS II and PS I, respectively) and their light-harvesting complexes (pigment-protein complexes) reside in the thylakoids. PS II and PS I are electronically connected by an intermediate membrane supercomplex, Cyt $b_6f$, the core of the photosynthetic apparatus (Nelson and Yocum 2006; Yamori et al. 2010). The Cyt $b_6f$ is the major rate-limiting step in linear electron flow from PS II to PS I under light and $CO_2$-saturation conditions (Zhu et al. 2017). It has been reported that leaves grown under low light had lower Cyt $b_6f$ compared to those grown under high light (Chow and Anderson 1987; Chow et al. 1988). Apart from the activities and contents of light capturing components and electron transport chain, the amount and activity of important enzyme involved in $CO_2$ fixation such as ribulose 1.5-bisphosphate carboxylase/oxygenase (Rubisco) determined the capability of photosynthesis in plants under different light conditions (Pons 2012; Parry et al. 2013; He et al. 2017). In a study to investigate the effect of light intensity on $CO_2$ assimilation rate in tobacco leaves (*Nicotiana tabacum*), Yamori et al. (2010) reported an increase in Cyt $b_6f$ and Rubisco contents in plants exposed to increasing light intensity. There is a close correction between the photosynthetic electron transport capacity and the Cyt $b_6f$ (Yamori et al. 2010).

Light-emitting diodes (LEDs) with combinations of different wavelengths are now used not only for commercial production of horticultural crops but also in studying physiological responses of plants to light (He et al. 2019a). Our previous study showed that quality of LED lighting affected the productivity of different vegetable crops grown indoors (He et al. 2017, 2019a) and in the greenhouse (Choong et al 2018). Our recent studies have also showed that photosynthetic light-use efficiency and photosynthetic machinery such as PS II and Cyt $b_6f$ concentrations and photosynthetic gas exchange rate were affected by the quality of LED lighting (He et al. 2019a). However, there is very little study carried out to investigate the responses of plants to different quantities of supplementary LED lightings to natural sunlight. In this study, Cos lettuce (*L. sativa* L. cv. CL—2741) were grown aeroponically in a tropical greenhouse with their roots misted with full strength nutrient solution at a constant temperature of 25 °C while the aerial parts were subjected to fluctuating ambient temperature. All plants were exposed to 100% prevailing sunlight supplemented with two levels of LED lighting with photosynthetic photon flux density (PPFD) of 150 and 300 μmol $m^{-2}$ $s^{-1}$, respectively. The main objectives were to investigate the effects of quantity of supplementary LED lighting to natural sunlight on leaf growth and shoot and root productivity of temperate lettuce grown in the tropical greenhouse. Impacts of supplementary LED quantity on photosynthetic apparatus and capability measured by the photosynthetic pigments, functions of PSII, Cyt $b_6f$, photosynthetic gas exchange and Rubisco were studied.

## Materials and methods

### Plant materials and experimental design

After germination, seedlings of Cos lettuce (*Lactuca. sativa* L. cv. CL—2741) were inserted into polyurethane cubes and soaked in water. These seedlings were left to acclimatize to ambient tropical greenhouse conditions for 7 days before being transplanted into the aeroponic system. The shoots of plants were exposed to three different quantity of lights, (1) only natural sunlight with average maximum PPFD of 500 μmol $m^{-2}$ $s^{-1}$ from 1200 to 1500 h on sunny days (termed as SL + 0 PPFD) (2) natural sunlight and supplementary LED light with PPFD of 150 μmol $m^{-2}$ $s^{-1}$ (termed as SL + 150 PPFD) from 0700 to 1900 h and (3) natural sunlight and supplementary LED light with PPFD of 300 μmol $m^{-2}$ $s^{-1}$ (termed as SL + 300 PPFD) from 0700 to 1900 h. The photoperiod of supplemental LED lighting

(Dissis LED Lighting Technology, Singapore) was 12-h (from 0700 to 1900 h) provided as a combination of red- (633 nm and 656 nm) and blue-LED (463.5 nm) lightings in the ratio of 9:1. All the light intensities were measured by holding PAR quantum sensor with a reading unit (SKP 215 and 200, Skye Instruments Ltd, Llandrindod Wells, UK) beside leaf until reading stabilizes. The roots were misted with modified full strength Netherlands Standard Composition (Douglas 1985) nutrient solution (EC 2.2 mS $cm^{-1}$, pH 6) for 30 s between 5 min intervals and root zone temperatures were kept at 25 ± 3 °C for the entire period of plant growth. The fluctuating ambient temperatures of 23–38 °C and relative humidity of 30–96% were recorded using DataHog2 (Skye Instruments Ltd, UK). In this study, the Cos *lettuce* was cultivated twice from mid-May to mid-June 2018 and mid-September to mid-October 2018, respectively. All measurements were carried out twice with similar results, which are presented from only one experiment.

### Measurements of leaf number, fresh weight (FW) and dry weight (DW) of shoot and root, total leaf area and specific leaf area (SLA)

After 28 days of transplanting, between 0900 and 1000 h, six plants from each treatment were harvested. Total leaf number and shoot and root FW were recorded. Total leaf area was measured using a leaf area meter (WinDIAS3 Image Analysis system, Delta T-Devices Ltd., England). Plant tissues were wrapped individually in aluminium foil, dry for 4 days at 80 °C before reweighing to record DW. SLA was calculated by dividing leaf area over dry mass (Hunt et al. 2002).

### Measurements of Chl and Car contents

Fresh leaves of 0.05 g were harvested 21 days after transplanting and then soaked in 5 ml of N,N-dimethylformamide in darkness for 48 h at 4 °C. The absorption of pigments was measured using a spectrophotometer (UV-2550 Shimadzu, Japan) at 647 nm, 664 nm, and 480 nm, respectively. Pigment contents were calculated as described by Wellburn (1994).

### Measurements of midday Chl fluorescence $F_v/F_m$ ratio

The maximum photochemical efficiency of PS II was estimated in dark-adapted leaves by the $F_v/F_m$ ratio. After 21 days of transplanting, midday $F_v/F_m$ ratio was measured during mid-photoperiod (1230–1330 h) using the Plant Efficiency Analyser (Hansatech Instruments, UK) according to He et al. (2011b).

### Measurements of light response curves of net photosynthetic $O_2$ evolution rate ($P_N$), PS II and Cyt $b_6f$ concentrations

These parameters were measured according to He and Chow (2003) and Zhu et al. (2017). $O_2$ evolution from leaf discs, which were harvested 21 days after transplanting, was measured in a gas-phase oxygen electrode (Hansatech, King's Lynn, UK) chamber maintained at 25 °C. Each leaf disc was 3.4 $cm^2$ in area, punched from the similar part of the youngest fully expanded Cos lettuce leaves grown under different light conditions. The sample chamber contained 1% $CO_2$ supplied by fabric matting moistened with 1 M $NaHCO_3$/$Na_2CO_3$ (pH 9). To avoid ionic effects of the bicarbonate, the leaf disc was protected by placing a perforated stainless-steel disc on the top of fabric matting. Two illumination regimes were used: (1) repetitive flash illumination with saturating, single-turnover flashes or (2) continuous white light from light-emitting diodes. First, repetitive flash illumination of the leaf sample with saturating, single-turnover xenon flashes (at 10 Hz) was performed to obtain a $P_N$ on a leaf area basis. Following an initial dark equilibration for 10 min, the repetitive flash illumination was applied for 4 min, followed by 4 min darkness. This was followed by a second cycle of flashes and darkness. The average dark drift in the signal before and after repetitive flash illumination was subtracted algebraically from the net rate of $O_2$ evolution during flash illumination to obtain the gross rate of flash-induced $O_2$ evolution. A small heating artefact signal due to flash illumination was obtained by substituting a green paper disc for a leaf disc, and was corrected for. The limitation of linear electron transport by PS I was minimized by the use of background far-red light. The ratio of the gross rate of $O_2$ evolution to the flash frequency was used to derive the PS II concentration on a leaf area basis ($p$), assuming that after four flashes, each active PS II evolves one $O_2$ molecule (Chow et al. 1991). Second, after repetitive flash illumination, a light response curve of $P_N$ was measured under continuous white light. The leaf disc was illuminated at 15 different light intensities, starting from the lowest PPFD of 0 to 1800 µmol $m^{-2}$ $s^{-1}$. The leaf disc was illuminated at each PPFD over several minutes until steady-state of photosynthetic $O_2$ evolution rate was obtained. The light response curve was obtained by plotting $P_N$ against respective PPFD. The saturating, continuous PPFD of 1800 µmol $m^{-2}$ $s^{-1}$ was used to determine the photosynthetic capacity ($P_{max}$). The post-illumination drift was subtracted algebraically from the steady-state net $O_2$ evolution rate at PPFD of 1800 µmol $m^{-2}$ $s^{-1}$ to yield the gross $O_2$ evolution rate, $P_{max}$. For calibration of the oxygen signals, 1 mL of air at 25 °C (taken to contain 8.584 µmol $O_2$) was injected into the gas-phase $O_2$ electrode chamber. After measurements of $p$ and $P_{max}$, the Cyt $b_6f$ concentration ($f$) was calculated from

the equation, $P_{max} = 1/[(0.022/f) + (0.004/p)]$, all parameters being on a leaf area basis. The Cyt $b_6f$ concentration, calculated from the two activity measurements, represents the functional Cyt $b_6f$ concentration in leaves (Zhu et al. 2017).

### Measurements of light-saturated photosynthetic $CO_2$ assimilation rate ($A_{sat}$), internal $CO_2$ concentration ($C_i$) and transpiration ($T_r$)

After 24 days of transplanting, readings were taken between 0900 and 1100 h using an open infrared gas analysis system with a 6 $cm^2$ chamber, LI-COR, (LI-COR Portable Photosynthetic System, LI-6400, Biosciences, US) with LED light source, which supplied 1000 µmol•$m^{-2}$•$s^{-1}$ of PPFD. Wavelength of light source was between 420–510 nm and 610–730 nm. Average ambient $CO_2$ concentration was 410 ± 10 µmol•$mol^{-1}$ and relative humidity was around 70%. When $A_{sat}$, $C_i$ and $T_r$ were stable, the measurements were recorded. Four readings were made from four different plants for each treatment.

### Measurement of total reduced N concentration

Dried shoot tissues (0.05 g) were digested with a Kjeldahl tablet and 5 ml of concentrated sulphuric acid for 60 min at 350 °C and the mixture was allowed to cool before total reduced N was determined by a Kjeltec 2300 analyzer (Foss Tecator AB, Höganäs, Sweden) through titration. The concentration of total reduced N *w*as calculated as a unit of mg $g^{-1}$ FW.

### Determination of leaf total soluble protein and Rubisco protein by SDS-PAGE

Leaf total soluble proteins were extracted and determined according to He et al. (2017). Protein extract of fresh leaves was diluted (1:1 ratio) with solubilizing solution (20% glycerol, 0.02% bromophenolblue, 5% SDS, 0.125 M Tris and 10% β-mercaptoethanol) and boiled for 5 min, before loading onto a precast gradient gel (PROTEAN TGX precast gel, any KD, BIO-RAD, USA). Electrophoresis was performed under constant voltage. The gel was then stained in coomassie brilliant blue (0.2% coomassie brilliant blue in 10% acetic acid, 50% methanol) and destained with 7% acetic acid and 25% ethanol. Fluor Chem 8800 gel imaging system was used to analyse the resultant bands under visible light.

### Statistical analysis

Levene's test was carried out to ensure that the variances across samples in groups of different light intensities are equal. One-way analysis of variances (ANOVA) and Tukey's multiple comparison tests were carried out to discriminate between the means of the different groups, where $p < 0.05$ indicates that the means are significantly different. The statistical analysis was performed using SPSS statistics software.

## Results

### Leaf growth, shoot and root productivity

Total leaf number and total leaf area of Cos lettuce grown under sunlight with additional 150 PPFD and 300 PPFD were significantly higher than those grown only under natural light (SL + 0 PPFD), with plants grown under SL + 300 PPFD being the highest (Fig. 1a, b). The results showed that

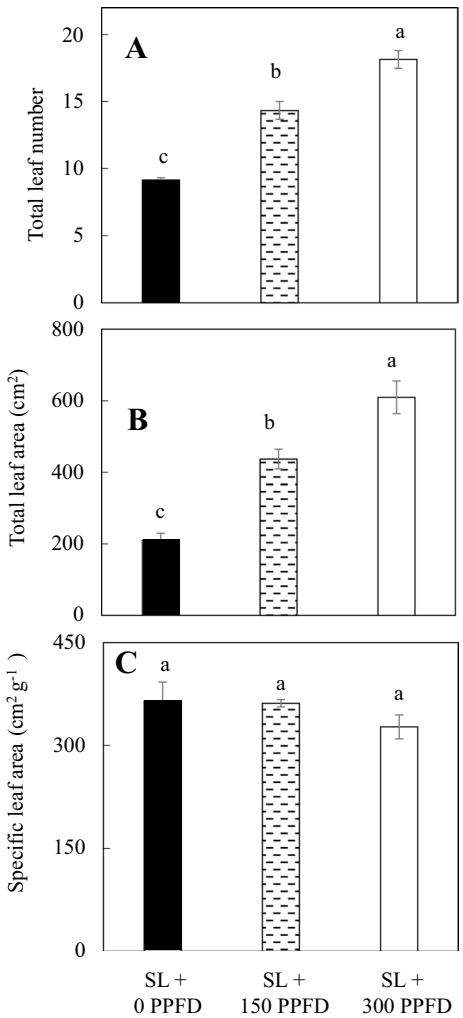


**Fig. 1** Total leaf number (**a**), total leaf area (**b**) and SLA (**c**) of Cos lettuce grown under different light intensities for 28 days. Standard errors are represented by vertical bars. Means with different letters are statistically different ($p < 0.05$; $n = 6$) as determined by Tukey's multiple comparison test

the total leaf number increased by 56% and 98%, respectively, under SL + 150 PPFD and SL + 300 PPFD (Fig. 1a) as opposed to those grown under SL + 0 PPFD. For the total leaf area, the increments were even greater, which increased by 108% and 190%, respectively, in plants grown under SL + 150 PPFD and SL + 300 PPFD, than under SL + 0 PPFD (Fig. 1b). There was no significant difference in the SLA of plants grown under different light intensities (Fig. 1c).

Shoot FW (Fig. 2a) and root FW (Fig. 2b) significantly increased with increasing light intensity. Compared to those under SL + 0 PPFD, shoot FW and root FW increased by 247% and 282%, respectively, in Cos lettuce grown under SL + 300 PPFD. The increases were 103% and 131%, respectively, for shoot FW and root FW in Cos lettuce grown under SL + 150 PPFD (Fig. 2a, b). Shoot/root ratio FW (Fig. 2c) of plants grown under SL + 0 PPFD was significantly higher compared to those grown under additional 150 PPFD and 300 PPFD of LED lightings. Shoot DW, root DW, and shoot/root ratio DW showed similar responses as those of FW to different light conditions (data not shown).

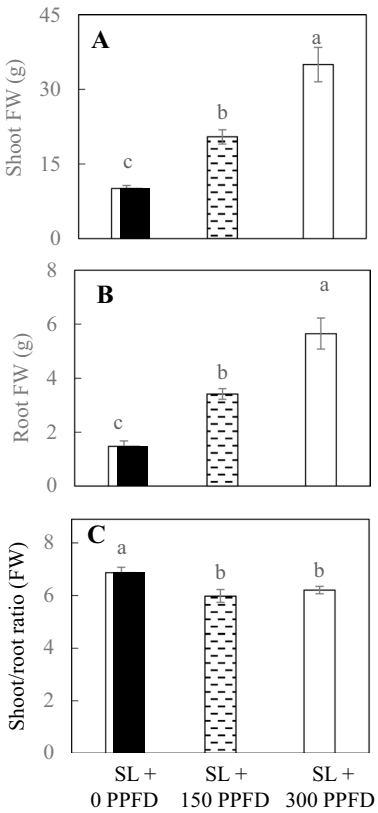


**Fig. 2** Shoot FW (**a**), root FW (**b**), and shoot/root ratio FW (**c**) of Cos lettuce grown under different light intensities for 28 days. Standard errors are represented by vertical bars. Means with different letters are statistically different from ($p < 0.05$; $n = 6$) as determined by Tukey's multiple comparison test

## Photosynthetic pigments

Cos lettuce grown under SL + 0 PPFD had a significantly lower total Chl (Fig. 3a) and total Car contents (Fig. 3c) compared to those grown under SL + 150 PPFD and SL + 300 PPFD. Total Chl and total Car contents of plants grown under SL + 0 PPFD were about 11–12% and 12–17%, respectively, lower than those of plants growth under SL + 150 PPFD and SL + 300 PPFD. There were no significant differences in total Chl and Car contents between Cos lettuce grown under SL + 150 PPFD and SL + 300 PPFD. Plants grown under SL + 300 PPFD had significantly higher Chl a/b ratio compared to plants grown under SL + 0 PPFD, which had a similar Chl a/b ratio as that of plants grown under SL + 150 PPFD (Fig. 3B). Chl/Car ratio decreased significantly with increasing light intensity (Fig. 3d).

## $A_{sat}$, $C_i$, $T_r$ and water use efficiency (WUE)

$A_{sat}$ increased significantly with increasing light intensity with the highest reading obtained from SL + 300 PPFD plants and the lowest value found in plants grown under SL + 0 PPFD (Fig. 4a). The $A_{sat}$ values of Cos lettuce grown under SL + 150 PPFD and SL + 300 PPFD were 2.09- and 5.68-fold of those grown under SL + 0 PPFD. However, the value of $C_i$ for plants grown under SL + 300 PPFD was significantly lower than that of the other two light conditions, which showed no significant statistical difference (Fig. 4b). The Cos lettuce grown under SL + 150 PPFD and SL + 300 PPFD had significantly higher $T_r$ values than that of plants grown under SL + 0 PPFD (Fig. 4c). WUE calculated as $A_{sat}/T_r$ was significantly higher in plants grown under SL + 300 PPFD than those grown under SL + 150 PPFD and SL + 0 PPFD (Fig. 4d). The values of WUE were 248% and 21%, respectively, greater in Cos lettuce grown under SL + 300 PFD and SL + 150 PPFD than that of plants grown under SL + 0 PPFD.

## $F_v/F_m$ ratio, light response curves of $P_N$, PS II and Cyt $b_6f$ concentrations

There was no significant difference in the $F_v/F_m$ ratio of plants among the different light treatments (Fig. 5a). Cos lettuce grown under SL + 300 PPFD had a significantly higher $P_N$ compared to those grown under SL + 0 PPFD and SL + 150 PPFD when measurements were made at PPFD ≥ 600 µmol $m^{-2}$ $s^{-1}$ (Fig. 5b). For instance, Cos lettuce Grown under SL + 300 PPFD increased its $P_N$ by 55% and 168%, respectively, compared to those grown under SL + 150 PPFD and SL + 0 PPFD. It seemed that the PS II concentration for plants grown under SL + 300 PPFD was greater than those of plants grown under the other two light conditions. However, statistically, there were no significant

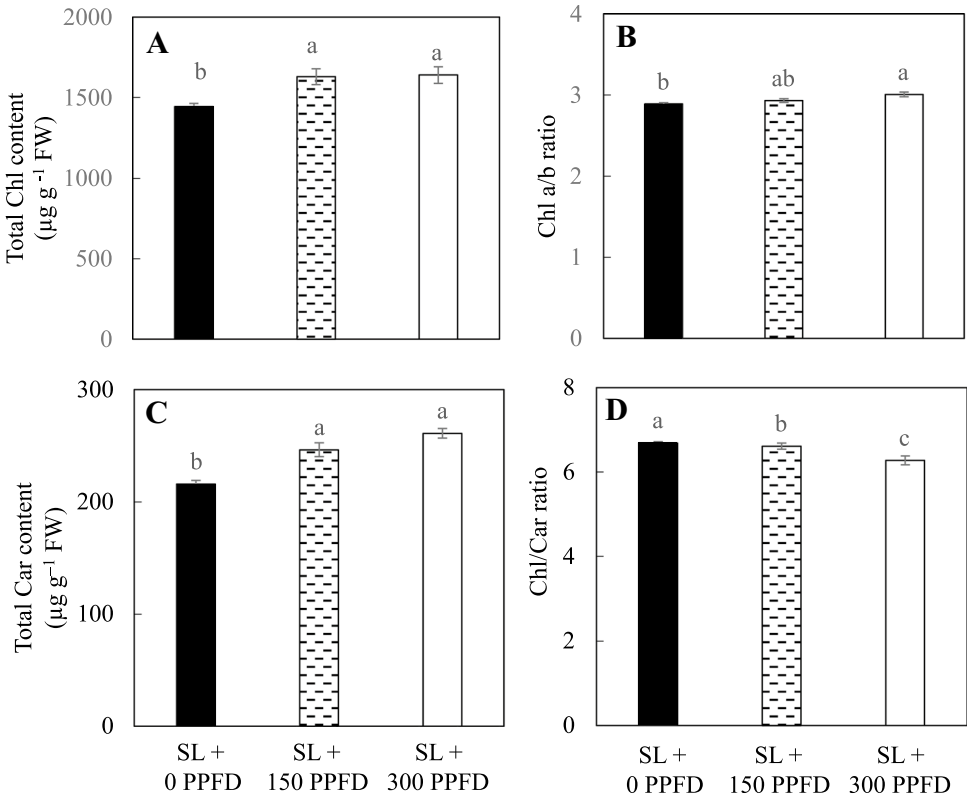


**Fig. 3** Total Chl content (**a**), Chl a/b ratio (**b**), total Car content (**c**) and Chl/Car ratio of Cos lettuce grown under different light intensities for 21 days. Standard errors are represented by vertical bars. Means with different letters are statistically different ($p < 0.05$; $n = 5$) as determined by Tukey's multiple comparison test

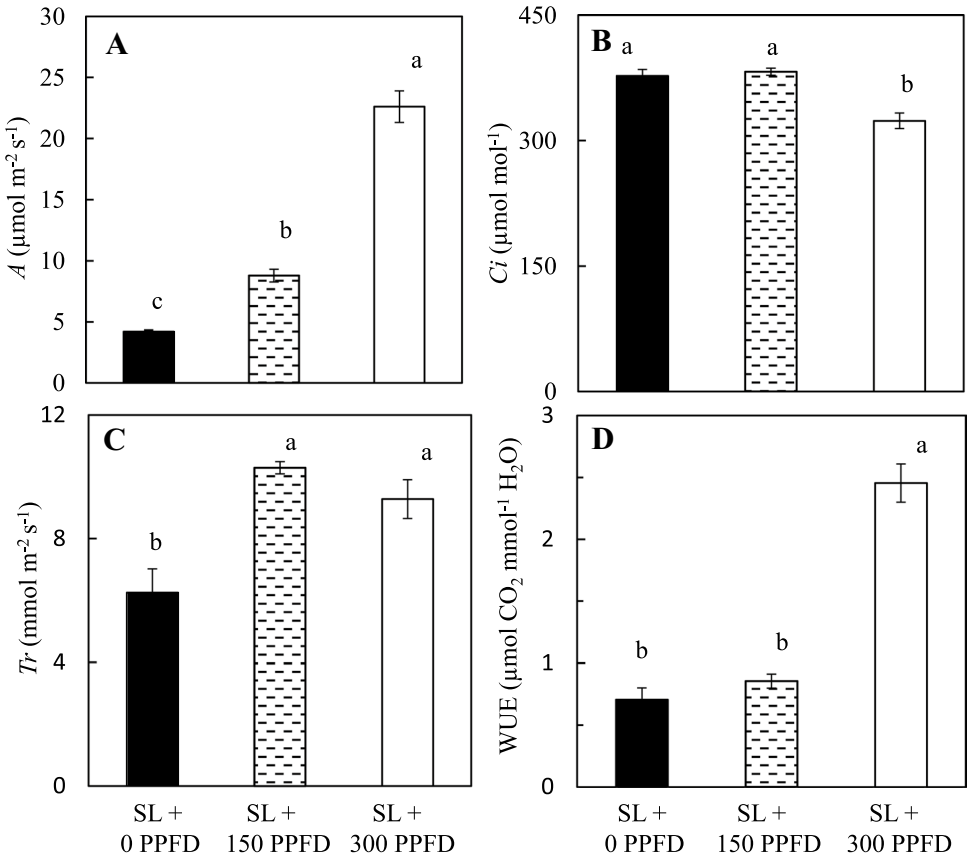


**Fig. 4** $A_{sat}$ (**a**), $C_i$ (**b**), $T_r$ (**c**), and WUE (**d**) of Cos lettuce grown under different light intensities for 24 days. Standard errors are represented by vertical bars. Means with different letters are statistically different ($p < 0.05$; $n = 4$) as determined by Tukey's multiple comparison test

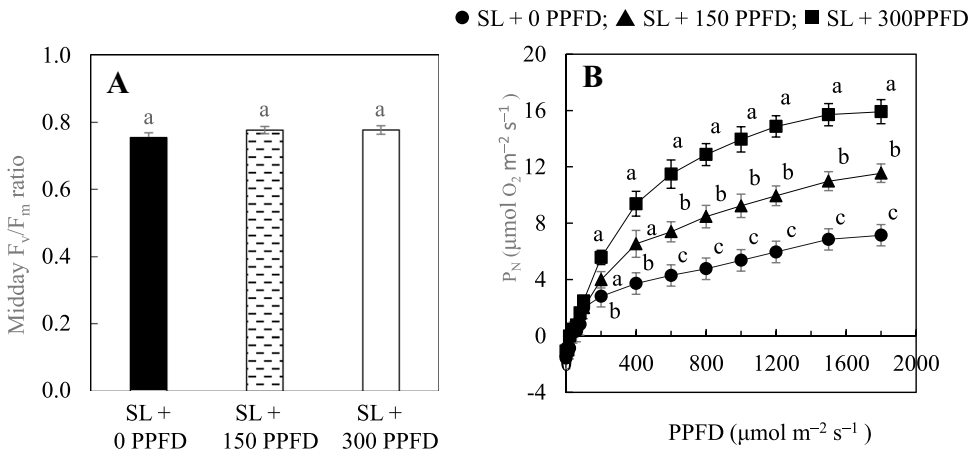


**Fig. 5** Midday $F_v/F_m$ ratio (**a**) and light response curves of $P_N$ (**b**) of Cos lettuce grown under different light intensities for 21 days. Standard errors are represented by vertical bars. Means with different letters are statistically different ($p < 0.05$; $n = 6$ and $n = 4$ for midday $F_v/F_m$ and $P_N$, respectively) as determined by Tukey's multiple comparison test

differences in PS II concentrations among all three treatments (Fig. 6a). Cyt $b_6f$ concentration showed a general increase with increasing light intensity (Fig. 6b). Cyt $b_6f$ concentration for plants grown under SL + 300 PPFD was significantly greater (86% greater) than those of plants grown under SL + 0 PPFD. However, Cyt $b_6f$ concentration for plants grown under SL + 150 PPFD did not significantly differ from that of plants grown under SL + 300 PPFD (Fig. 6B).

### Total reduced N, leaf total soluble protein and Rubisco concentrations

Shoot total reduced N concentrations were not significantly different among all three light treatments (Fig. 7a). Leaf total soluble protein (Fig. 7b) and Rubisco protein (Fig. 7c) concentrations showed a general increasing trend with increasing light intensity. Leaf total soluble protein and Rubisco protein concentrations of Cos lettuce grown under SL + 300 PPFD were significantly different from higher than that of plants grown under SL + 0 PPFD. Cos lettuce grown under SL + 300 PPFD had an increase in leaf total soluble protein and Rubisco protein concentrations by 35% and 138%, respectively. However, there were no significant differences in leaf total soluble protein and Rubisco protein between SL + 300 PPFD and SL + 150 PPFD conditions, and between the conditions of SL + 150 PPFD and SL + 0 PPFD.

## Discussion

### Supplementary LED lightings significantly increase total leaf number, total leaf area and biomass accumulation but not SLA

Light intensity influences multiple aspects of plant functioning including leaf development and growth, biomass accumulation and photosynthetic capacity (Long et al. 2006; Jin et al. 2016; Feng et al. 2019). In this study, total leaf number, total leaf area, shoot and root FW and shoot and root DW increased significantly with increasing light intensity (Figs. 1, 2). These results correspond with the studies which have shown that higher light intensities drive greater photosynthetic capacity (Figs. 4a, 5b) leading to higher biomass production (Jin et al. 2016; Simkin et al. 2019). In the present study, both total leaf number (Fig. 1a) and total leaf area (Fig. 1b) increased with increasing growth light level. The increases in total leaf area were greater than in total leaf number, indicating that increased total leaf resulted from both more leaves and individual bigger leaves. Greater

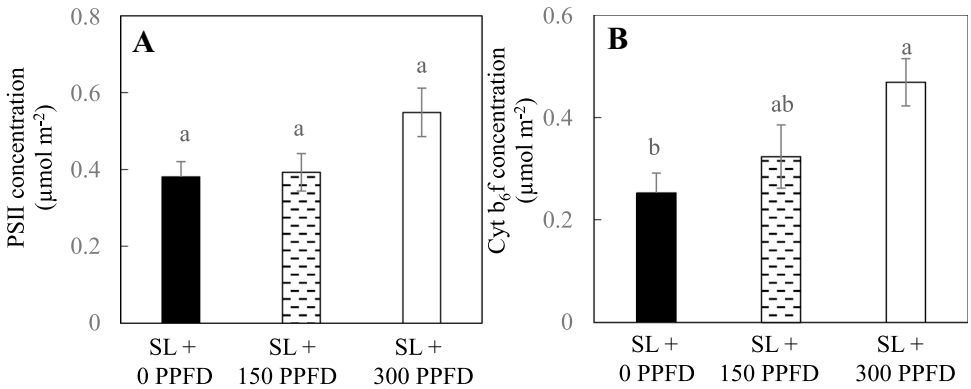


**Fig. 6** PS II (**a**) and Cyt $b_6f$ concentrations (**b**) of Cos lettuce grown under different light intensities for 21 days. Standard errors are represented by vertical bars. Means with different letters are statistically different ($p < 0.05$; $n = 4$) as determined by Tukey's multiple comparison test

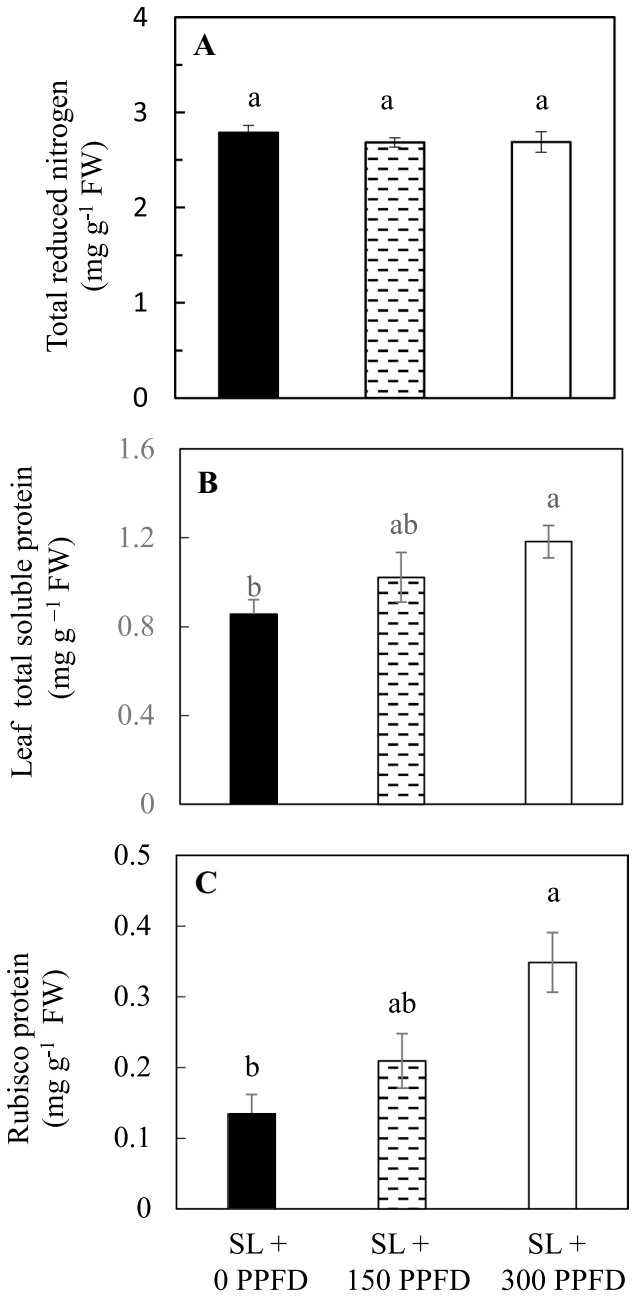


**Fig. 7** Shoot total reduced nitrogen (**a**), leaf soluble protein (**b**), and Rubisco protein (**c**) concentrations of Cos lettuce grown under different light intensities for 24 days. Standard errors are represented by vertical bars. Means with different letters are statistically different ($p < 0.05$; $n = 4$) as determined by Tukey's multiple comparison test

biomass accumulation for plants exposed to increasing light intensity could be supported by greater total number of leaves (Fig. 1a) and the individual larger area (Fig. 1b) for light interception and photosynthesis (Weraduwage et al. 2015). Light harvesting can also be directly influenced by leaf thickness. In this study, leaf thickness as SLA is measured as the ratio of leaf area to leaf dry mass (Hunt et al. 2002). In general, plants acclimated to low light have higher SLA than to high light (Zheng and Labeke 2018; He and Qin 2020). In the study with Chrysanthemum, Zheng and Labeke (2018) reported that low light intensity caused a decrease in leaf thickness, which is an acclimation common to plants grown under low PPFD to optimize light penetration into leaf for light absorption. We have previously reported that both light quantity and quality affected SLA of leafy vegetables within the species (Choong et al. 2018; He et al. 2019a; He and Qin 2020). However, there were no significant differences in SLA of Cos lettuce grown under different light conditions (Fig. 1c). Increased shoot biomass accumulation is associated with stem and leaf masses. The partition of biomass to different plant organs depends on the environment experienced by the plant (Poorter and Nagel 2000; He et al. 2009). Since all plants had similar SLA and water content (data not shown), the greater percentage increase in shoot FW (Fig. 2a) by 247%, compared to those percentage increase in total leaf area (190%) (Fig. 1b) in Cos lettuce growth under SL + 300 PPFD, indicates that shoot biomass accumulation was more sensitive to supplementary lighting. Thus, enhanced growth in Cos lettuce grown under supplementary lighting could also be partly due to the greater amount of photosynthetic products partitioned into the stem. In this study, Cos lettuce grown under supplementary LED lightings has much thicker stems compared those grown under natural sunlight alone. Root growth responds rapidly to increase in light intensity due to the accumulation of carbon, which ultimately results in the decrease of shoot/root ratio (Walter and Nagel 2006). In this study, shoot/root ratio FW was also significantly lower in plants exposed to additional LED lighting compared to those only exposed to natural sunlight (Fig. 2c).

It has been shown that many plant traits are better related to daily light integral (DLI, mol $m^{-2}$ $day^{-1}$), than to instantaneous PPFD levels at any given time (Poorter and Van der Werf 1998). Inside the greenhouse, there are fluctuations in PPFD at a given spot on clear days. Although solar DLI was not measured in the greenhouse, plants grown under SL + 150 PPFD and SL + 300 PPFD for 12 h had a constant additional DLI of 6.48 and 12.96 mol $m^{-2}$ $day^{-1}$, respectively. In their meta-analyses, Poorter et al. (2019) determined how 70 traits related to plant anatomy, morphology, chemistry, physiology, growth and reproduction were affected by DLI. They found that many traits increased with DLI in a saturating fashion. In the study with purple leaf lettuce (*L. sativa* L. cv. Ziwei), Zhang et al. (2018) reported that leaf FW and DW increased linearly as DLI increased. In this study, when supplementary DLI increased by double, leaf growth and shoot and root biomass of Cos lettuce grown in a tropical greenhouse with root zone temperatures kept at 25 °C showed significant increases (Figs. 1, 2). However, there were no significant increases in leaf thickness

(decreased SLA) with increasing DLI (Fig. 1c). Although low SLA could help plants to increase the efficiency of light capture (Evans and Poorter 2001; Liu et al. 2016), leaf thickness is not the only factor driving increase in biomass accumulation with increasing DLI (Poorter et al. 2019). Other factors such as photosynthetic pigments, photosynthetic capacity and photosynthetic apparatus on a per-area basis could have played crucial roles in biomass accumulation.

## Photosynthetic pigments

Yamori et al. (2010) reported that tobacco leaves grown under lower light intensities increased Chl content and decreased Chl *a*/*b* ratio to enhance light acquisition. However, others found that low light availability caused a reduction in total Chl content on a per-area basis (Fan et al. 2018; Feng et al. 2019). Similarly, in this study, Cos lettuce grown under SL + 0 PPFD had a significantly lower total Chl content compared to those of plants grown under SL + 150 PPFD and SL + 300 PPFD (Fig. 3a). Our recent study with tropical sweet potato (*Ipomoea batatas)* leaves grown under natural sunlight with supplemental LED lightings in the same greenhouse also had higher total Chl content on a per-area basis compared to those grown under natural sunlight alone (He and Qin 2020). It was found that total Chl content of soybean increased with the increase in light intensity, which were directly associated with the greater leaf thickness (Fan et al. 2018; Feng et al. 2019). However, in this study, no significant differences in SLA were observed among Cos lettuce grown under different light conditions (Fig. 1c).

Dou et al. (2018) reported that sweet basil (*Ocimum basilicum*) grown indoors under high DLIs provided by LED lighting had lower total Chl content per leaf FW, higher Chl *a*/*b* ratios and larger and thicker leaves compared with those under lower DLIs. Grown under lower DLIs, the increased total Chl content per leaf FW demonstrated the plants' ability to maximize the light-harvesting capacity under lower PPFD (Dai et al. 2009). In contrast to Chl content per leaf FW, on a per-area basis, sweet basil leaves under lower DLIs had a significantly lower total Chl content due to the thinner leaves compared to those grown under higher DLIs (Dou et al. 2018). Similar results were reported in 'Ararat' basil (Polyakova et al. 2015) and *Glycyrrhiza uralensis* (Hou et al. 2010) grown under different DLIs. In this study, although the total Chl contents on a per leaf FW basis of Cos lettuce grown under additional DLIs of 6.48 and 12.96 mol $m^{-2}$ $day^{-1}$ were similar, they were significantly higher compared to those grown under natural sunlight without supplementary DLI (Fig. 3a). This study was carried out in the tropical greenhouse from the middle of September to early December 2018. During this period, there were frequent cloudy and rainy days with the average maximum PPFD inside the greenhouse was around 500 µmol $m^{-2}$ $s^{-1}$ only from 1200 to 1500 h on non-rainy days, which was 30–35% of full sunlight. It seems that with additional DLI of 6.48 mol $m^{-2}$ $day^{-1}$, Cos lettuce grown in the tropical greenhouse had maximized the leaf N allocated to Chl synthesis and thus there was no further increase in total Chl content when DLI increased by double. Anderson et al. (1988) demonstrated that it was not the Chl content per leaf area but the Chl *a*/*b* ratio showed a close correlation to light intensity. However, Chl *a*/*b* ratio of Cos lettuce grown under SL + 0 PPFD was significantly lower than those exposed to SL + 300 PPFD, while Chl *a*/*b* ratio of plants grown under SL + 150 PPFD was not significantly different to the other two light conditions (Fig. 3b). Kouřil et al. (2013) reported that there was a decreasing trend in Chl a/b ratio with decreasing light intensity in *Arabidopsis thaliana*. The decrease in Chl a/b ratio in *Arabidopis thaliana* (Kouřil et al. 2013) and in Cos lettuce (Fig. 3b) exposed to low light intensity indicates an increase in proportion of antenna pigments to increase chances of light capture thus increasing light-use efficiency (Fu et al. 2012). This is also a shade acclimation. In tobacco leaves, Yamori et al. (2010) also reported that plants grown under lower light intensity decreased Chl *a*/*b* ratio to enhance light acquisition. However, decreasing light intensity increased Chl *a*/*b* ratio was reported in soybean (Feng et al. 2019) and in sweet potato leaves (He and Qin 2020). These controversial results suggested that effects of light intensity on Chl *a*/*b* ratio is not a universal phenomenon and the dependence of Chl *a*/*b* ratio on light intensity is strongly correlated to plant species (Zivcak et al. 2014) and to other growth condition such as shoot and root temperature differential in this study.

Carotenoids play important roles in protecting plants from photodamage by maintaining proper Chl/Car ratio (Hashimoto et al. 2016). Plants acclimated to high light generally have higher Car content compared to that of low light acclimated plants (Lichtenthaler 2007), which was supported by this study (Fig. 3c). A lower Chl/Car ratio resulting from a greater increase in Car (Fig. 3c) than in Chl (Fig. 3a) was observed. However, in the study with sweet potato plant grown under different light conditions, all leaves had similar Chl/Car ratios (He and Qin 2020). Similarly, other studies also showed no significant changes in the Chl/Car ratio between sun and shade leaves (Zivcak et al. 2014). All these suggest that the synthesis of photosynthetic pigments, Chl *a*/*b* ratio and Chl/Car ratio in response to light environment vary according to species and growth light intensity.

## Supplementary LED lightings improve photosynthetic capacity through an increase in both Cyt $b_6f$ and Rubisco contents

It has well known that thicker leaves accumulated more photosynthetic enzymes on a per-area basis and thus contributed to greater $CO_2$ fixation capacity of high-light-grown leaves

(Evans and Poorter 2001; Terashima et al. 2006). The results of sweet potato plants grown under hot ambient conditions also support those earlier studies (He and Qin 2020). In this study, $A_{sat}$ of Cos lettuce grown under SL + 150 PPFD and SL + 300 PPFD were, respectively, 2.09- and 5.68-fold of those plants grown under SL + 0 PPFD (Fig. 4a) even if all leaves had similar thickness. It has been reported that plants acclimated to high light had higher $A$ and thus lower $C_i$ than those grown under low light (Yamori et al. 2010; Huang et al. 2014). Leaves of sun-grown tobacco had greater $A$, leading to lower $C_i$ (Huang et al. 2014). Cos lettuce grown under SL + 300 PPFD with the highest $A_{sat}$ (Fig. 4a) also had lower $C_i$ compared to other plants (Fig. 4b). Lower $C_i$ could result in higher ribulose 1,5-bisphosphate (RuBP) oxygenation rate in leaves grown under high light than under low light and thus stimulates photorespiratory pathway. On the other hand, lower $C_i$ of leaves grown under high light also increased RuBP regeneration and thus RuBP oxygenation and regeneration were balanced (Huang et al. 2014). In the present study, Cos lettuce grown under low light condition may result in lower ATP availability, in turn, RuBP regeneration, thus limiting the rate of $CO_2$ fixation. Reduction in total Chl content in leaves grown under low light (Fig. 3a) and similar midday $F_v/F_m$ ratios ranged from 0.76 to 0.77 observed in all leaves (Fig. 5a) suggest that there was no obvious decrease in maximal efficiency of PS II photochemistry occurred in any leaves grown under different light intensities. Cos lettuce leaves grown under the highest PPFD or DIL were not suffered from excess light energy which could be safely dissipated by heat if any. This was supported by its higher total Car content (Fig. 3c) and lower Chl/Car ration (Fig. 3d). Indirectly, leaves of Cos lettuce grown under low light may not generate sufficient ATP for RuBP regeneration as well as the biosynthesis of Chl and other components of photosynthetic apparatus.

Stomata are responsible for balancing photosynthetic $CO_2$ uptake with water loss through transpiration. Generally, high light coupled with high temperature promotes stomatal opening to facilitate leaf cooling (Lawson 2009). The values of $T_r$ (Fig. 4c) were significantly higher in Cos lettuce grown under SL + 150 PPFD and SL + 300 PPFL than under SL + 0 PPFD. Cos lettuce grown under SL + 300 PPFD and SL + 150 PPFD developed much bigger root systems to ensure water and nutrient uptake compared to those grown under SL + 0 PPFD (Fig. 2b). WUE defined the ratio of $A_{sat}/_{Tr}$ and is important for estimating plant productivity and water status (Cui et al. 2018; Yu and Gao 2020). The greatest value of WUE (Fig. 4d), total leaf number (Fig. 1a), total leaf area (Fig. 1b) and biomass accumulation (Fig. 2) in Cos lettuce grown under SL + 300 PPFD followed by SL + 150 PPFD compared to those grown under natural sunlight only, implying that supplementary LED lightings increase both productivity and WUE.

Supplementary LED lightings improve photosynthetic capacity is further supported by the light response curves of $P_N$ measured from detached leaves of Cos lettuce in the laboratory at 25 °C under saturated $CO_2$ concentration (Fig. 5a). Cos lettuce grown under SL + 300 PPFD had a significantly higher $P_N$ compared to those grown under SL + 150 PPFD, the lowest values of $P_N$ were observed in leaves grown under SL + 0 PPFD (Fig. 5b), when measured at PPFD ≥ 600 μmol $m^{-2}$ $s^{-1}$. Plants grown at higher light intensities enhanced the capacity of light utilization, could also be through the increases of PS II and Cyt $b_6f$ concentrations as these two components of photosynthetic apparatus may be the sites of the rate-limiting step in the electron transport chain (Eichelmann et al. 2000). In this study, PS II and Cyt $b_6f$ concentrations were obtained from the same detached leaves which used for the measurements of light response curves $P_N$ in the laboratory at 25 °C. In the study with sweet potato plants grown in the same greenhouse, supplementary LED lightings influenced neither PS II nor Cyt $b_6f$ concentrations (He and Qin 2020). Although all Cos lettuce leaves also had similar PS II concentrations, Cyt $b_6f$ concentration of leaves grown under SL + 300 PPFD was 50% and 92%, respectively, higher than those grown under SL + 150 PPFD and SL + 0 PPFD (Fig. 6b). These results indicate that the lower concentration of Cyt $b_6f$ is the main rate-limited factor that determines light- and $CO_2$-saturated photosynthetic capacity of Cos lettuce grown under lower light intensity (Eichelmann et al. 2000; Zhu et al. 2017). The Cyt $b_6f$ is also considered to be a key rate-limiting step for RuBP regeneration as it is important in generating a transmembrane electrochemical difference which acts as the driving force of ATP synthase (Yamori et al. 2011).

RuBP regeneration rate is also determined by the Calvin cycle enzymes (Yamori et al. 2011). Generally, thicker leaves of plants grown under high light intensity accumulate more photosynthetic enzymes such as Rubisco on a leaf area basis and thus contributed to greater $CO_2$ fixation capacity (Evans and Poorter 2001). Cos lettuce leaves grown under SL + 300 PPFD and SL + 150 PPFD had 61% and 254%, respectively, higher Rubisco content (Fig. 7c) than those grown under SL + 0 PPFD (Fig. 1c). However, the differences in leaf total soluble protein were not as great as Rubisco protein among the plants grown under different light intensities (Fig. 7b). Light intensity affected not only leaf N content but also N partitioning among the photosynthetic apparatus (Yamori et al. 2010). Plants acclimated to low light intensity generally enhances N allocation to the Chl (Hikosaka and Terashima 1996; Makino et al. 1997). This was not observed in this study although all leaves had similar level of total reduced N (Fig. 7a), indicating that temperate Cos lettuce plant was unable to acclimate to low light environments. However, Cos lettuce plant grown under high light enhanced the capacity of light utilization, through

increases in both Cyt $b_6f$ and Rubisco contents (Hikosaka and Terashima 1996; Makino et al. 1997). In the previous study with sweet potato plants (He and Qin 2020), natural SL inside the greenhouse was much higher (average maximum PPFD ~ 800 µmol $m^{-2}$ $s^{-1}$) than that of this study (average PPFD ~ 500 µmol $m^{-2}$ $s^{-1}$). Furthermore, Cos lettuce plants were exposed to many cloudy and rainy days in the present study. Further research is needed to explore how the levels of total Chl, Cyt $b_6f$ and Rubisco protein are regulated when LED lightings are supplemented to fluctuating natural sunlight inside the tropical greenhouse and what strategies may be employed to increase their contents and thus the final yield.

## Conclusion

Temperate Cos lettuce was able to acclimate to high PPFD under supplementary LED lights in a tropical greenhouse. Supplementary LED lightings promote both leaf initiation and expansion with greater increase of leaf expansion, instead of leaf thickness of Cos lettuce. Fast leaf expansion with increased photosynthetic pigments, higher Cyt $b_6f$ and Rubisco protein contents on a per-area basis improve photosynthetic capacity and thus enhance productivity.

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### Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflicts of interest.

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