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Growth and photosynthetic characteristics of sweet potato (*Ipomoea batatas*) leaves grown under natural sunlight with supplemental LED lighting in a tropical greenhouse

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**Abstract**

Leaf growth and photosynthetic characteristics of sweet potato (*Ipomoea batatas* var. Biru Putih) grown under different light quantities were studied in a tropical greenhouse. The stem cuttings of *I. batatas* with adventitious roots were grown hydroponically under (1) only natural sunlight (SL); (2) SL with supplemental LED at a PPFD of 150 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) (SL + L-LED); and (3) SL with supplemental LED at a PPFD of 300 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) (SL + H-LED). One week after emergence, all leaves had similar area and water content. However, leaf fresh weight and dry weight were significantly higher in plants grown under SL + L-LED and SL + H-LED than under SL due to their thicker leaves reflected by the lower specific leaf area. Plants grown under SL had significantly lower concentrations of total chlorophyll (Chl) and total carotenoids (Car) but higher Chl a/b ratio than under SL + L-LED and SL + H-LED. However, all plants had similar Chl/Car ratios. Although midday Fv/Fm ratio was the lowest in leaves grown under SL + H-LED followed by SL + L-LED and SL, predawn Fv/Fm ratios of all leaves were higher than 0.8. Increasing growth irradiance with supplemental LED resulted in higher electron transport rate and photochemical quenching but lower non-photochemical quenching compared to those of plants grown under SL. Measured under their respective growth irradiance in the greenhouse, attached leaves grown under SL + L-LED and SL + H-LED had significantly higher photosynthetic CO2 assimilation rate and stomatal conductance than under SL. However, measuring the detached leaves at 25 °C in the laboratory, there were no significant differences in PS II and Cyt b6f concentrations although light- and CO2-statured photosynthetic O2 evolution rates were slightly higher in leaves grown under SL + H-LED than under SL. Impacts of supplemental LED on leaf growth and photosynthetic characteristics were discussed.

**1. Introduction**

Sweet potato (*Ipomoea batatas* L.) is widely grown in developing countries due to its low production cost and its high adaptability (Lin et al., 2007; Mekonen et al., 2015). Most people grow sweet potato as food and mainly consume their modified root tubers (Yoshimoto et al., 2002). Although the leaves of sweet potato have been neglected, they are consumed as fresh vegetables in tropical areas in Southeast Asia (Nwinya, 1992) because both leaf blades and petioles are rich in protein, dietary fiber, vitamins, antioxidants, essential fatty acids and minerals (Ishida et al., 2000; Johnson and Pace, 2010). Several studies have demonstrated that sweet potato leaves inhibit mutagenicity, diabetes, leukemia and viruses and the growth of colon and stomach cancer cells (Yoshimoto et al., 2002; Kurata et al., 2007; Ludvik et al., 2008).

Due to limited land in Singapore, local farming currently accounts for only 10 per cent of the leafy vegetables consumed. The maintenance of food security, especially the supply of vegetable is an increasing challenge for Singapore where natural resources are limited. Furthermore, the disconnect between supply and demand is the result of the global food supply chains being disrupted in unprecedented ways due to the COVID-19 pandemic. Back to March 2019, the Environment

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**Abbreviations:** A, Photosynthetic CO2 assimilation rate; Car, carotenoids; Chl, Chlorophyll; Ci, Internal CO2 concentration; Cyt b6f, Cytochrome b6f complex; DW, Dry weight; ETR, Electron transport rate; FW, Fresh weight; gs, Stomatal conductance; LED, Light emitting diode; NPQ, Non-photochemical quenching; Pmax, Photosynthetic capacity; Pn, Net photosynthetic O2 evolution rate; PPFD, Photosynthetic photon flux density; qP, Photochemical quenching; RuBP, ribulose-15-bisphosphate; Rubisco, ribulose 1.5-bisphosphate carboxylase/oxygenase; SL, natural sunlight; SL + L-LED, natural sunlight with supplemental LED lighting at a PPFD of 150 \( \mu \text{mol m}^{-2} \text{s}^{-1} \); SL + H-LED, natural sunlight with supplemental LED lighting at a PPFD of 300 \( \mu \text{mol m}^{-2} \text{s}^{-1} \); SLA, specific leaf area; Tr, Transpiration

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and Water Resources Minister, Singapore announced the ambitious “30 by 30” goal to produce 30 per cent of Singapore’s nutritional needs locally by 2030 (Ai-Lien, 2019). Sweet potato leaves are considered an indigenous and tropical leafy vegetable, which could play an important role in alleviating the shortage of leafy vegetables as they grow quickly in the tropics under warm temperature and humid conditions (An et al., 2003). They have much higher annual yield than that of other green vegetables and could be harvested several times a year. Sweet potato plants are mainly grown over a broad range of environment. In Singapore sweet potato leaves are commonly cultured in outdoor soil farms. It was reported that high light intensity enhanced growth of sweet potato plants and thus, shade conditions should be avoided (Oswald et al., 1994). The sweet potato plant is also considered to be a drought tolerant crop (Ghuman and Lal, 1983). However, drought is a major environmental constraint for sweet potato production in the tropical area as its growth and development are significantly influenced by soil moisture (Yooyongwecha et al., 2013).

Soilless cultures such as hydroponics and aeroponics are increasingly adopted as major technological components in the modern greenhouses to replace community gardens and traditional outdoor soil farms in Singapore (He, 2015). Today, in Singapore, all kinds of leafy vegetables are grown all year round in the greenhouse using soilless culture systems with adequate water and nutrient supplies, which is not affected by drought conditions. Apart from water, light intensity critically affects plant growth. In the past two decades, Singapore has been frequently experiencing increasingly unpredictable cloudy and hazy weather (Nobre et al., 2016), resulting in lowered light intensity which reduced crop productivity (Jones, 2006). We have previously reported that in Singapore, when lettuce (He et al., 2011) and Brassica albohbabra (Chinese broccoli) plants (He et al., 2019b) were grown under low light during the haze episodes in the greenhouse, lower photosynthetic rate, stomatal conductance and productivity were measured. To circumvent the problem of insufficient sunlight, in another study with lettuce plants, light emitting diode (LED) lighting was supplemented to low sunlight intensity in the greenhouse (Choong et al., 2018). In the study with B. albohbabra (Chinese broccoli), we have found that plants grown under shade with supplemental LED lighting improved photosynthetic CO₂ assimilation, stomatal conductance and productivity (He et al., 2019). As mentioned earlier, sweet potato leaves are tropical leafy vegetables and have fast growth rates in the tropics under warm and humid conditions (An et al., 2003). The nutrient-rich leaf blade and petiole make it as one of the suitable vegetable crops to achieve the Singapore’s goal to produce 30 per cent of nutritional needs locally by 2030. However, little is known about its photosynthetic characteristics when grown under different light intensities using soilless culture such as hydroponics. We hypothesize that plant growth should increase with increasing of growth irradiance, with leaf traits adjustment that enhance light capture and carbon fixation in the tropical greenhouse. Therefore, this study aimed to investigate the effects of two different supplementary LED lightings with photosynthetic photon flux density (PPFD) of 150 and 300 μmol m⁻² s⁻¹ respectively on the leaf growth of sweet potato leaves, I. batatas (var. Biru Putih) in the tropical greenhouse. Impacts of supplementary LED quantity on photosynthetic light use efficiency measured by chlorophyll fluorescence, the functions of PSI II and Cyt b₆f, and photosynthetic gas exchanges were also studied.

### 2. Materials and methods

#### 2.1. Plant materials and experimental design

Sweet potato leaves, I. batatas (var. Biru Putih), were purchased from one of the local farms (KOK FAH Technology Farm Pte Ltd). Apical stems were cut into 15 cm pieces. Roots were induced from cuttings grown hydroponically under modified half strength Netherlands Standard Composition nutrient solution (details are given below) for 1 week. After root induction, the stem cuttings with adventitious roots were grown hydroponically in greenhouse under three different quantities of lights: (1) only natural sunlight (SL) with average maximum PPFD of 800 μmol m⁻² s⁻¹; (2) SL with supplemental LED lighting at a PPFD of 150 μmol m⁻² s⁻¹ (SL + L-LED); and (3) SL with supplemental LED lighting at a PPFD of 300 μmol m⁻² s⁻¹ (SL + H-LED). The photosynthetic assimilation of supplemental LED lighting (Dissis LED Lighting Technology, Singapore) was 12-h (from 0700 h to 1900 h) provided by a combination of red- (633 nm and 656 nm) and blue-LED (463.5 nm) lightnings 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). All treatments were supplied with modified full strength Netherlands Standard Composition nutrient solution (Douglass, 1985) with 2.0 ± 0.2 μS cm⁻¹ conductivity and pH 6.0 ± 0.2. The modified full strength Netherlands Standard Composition solution had the following composition: N, 191.89 ppm; P, 33.29 ppm; K, 309.00 ppm; Ca, 210.29 ppm; Mg, 60.04 ppm; S, 125.45 ppm; Fe, 9.36 ppm; B, 0.105 ppm; Mn, 0.238 ppm; Zn, 0.014 ppm; Cu, 0.015 ppm; Mo, 0.408 ppm; Na, 3.860 ppm. The fluctuating ambient temperatures of 24–43 °C and relative humidity of 26–96 % were recorded using DataHog2 (Skye Instruments Ltd, UK).

**2.2. Measurements of leaf fresh weight (FW) and dry weight (DW), leaf area, specific leaf area (SLA) and leaf water content**

The just-emerged leaves of I. batatas plants were labeled 27 days after transplanting and they were harvested one week after emergence from 0730 h to 0800 h. The cut leaves were kept in sealed plastic bags with sheets of damp paper towel and brought back to lab. The FW of leaf (blade only) was first recorded before measuring their areas using a leaf area meter (WinDIAS3 Image Analysis system). All leaves were then wrapped individually in pre-weighed aluminium foil, dried at 80 °C for at least four days, before re-weighing them to obtain DW. Specific leaf area (SLA) was determined as L₅/L₀, where L₅ = leaf area (cm²) and L₀ = leaf DW(g) (Hunt et al., 2002). Leaf water content (LWC) was determined as (L₅W – L₀)/L₅W where L₅W = leaf FW (g).

**2.3. Measurements of Chl and carotenoids (Car) pigments**

For each measurement, two leaf discs (1 cm in diameter) were cut from the youngest fully expanded leaves 15 days after transplanting and soaked in 2.5 ml of N,N-dimethylformamide (N,N-DMF, Sigma Chemical Co.) 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. Chl a, Chl b and Car concentrations were calculated as described by Wellburn (1994).

**2.4. Measurements of predawn and midday F₆/F₅ ratio**

The maximum photochemical efficiency of PS II was estimated in dark-adapted samples by the F₆/F₅ ratio. Predawn and midday F₆/F₅ ratios were measured from the attached youngest fully expanded leaves in the greenhouse before photoperiod and during mid-photoperiod on sunny days after transplanting for 34 days using the Plant Efficiency Analyser (Hansatech Instruments, UK) according to He et al. (2001).
2.5. Measurements of electron transport rate (ETR), photochemical quenching (qP) and non-photochemical quenching (NPQ)

After 30 days of transplanting, the youngest fully expanded leaves were harvested between 0900 h–1000 h and ETR, qP and NPQ were determined at 25 °C in the laboratory. Prior to measurements, the leaves were pre-darkened for 15 min. By using the IMAGING PAM MAXI (Walz, Effeltrich, Germany), images of fluorescence emission were digitized within the camera and transferred via ethernet interface (GigEVision) to the PC for storage and analysis. Measurements and calculations of ETR, qP and NPQ were described previously (He et al., 2017b).

2.6. Measurements of light response curves of net photosynthetic O₂ evolution rate (Pₐ), PS II concentration and Cyt b₆f concentration

These parameters were measured according to He and Chow (2003), and Zhu et al. (2017). O₂ evolution from leaf discs was measured in a gas-phase oxygen electrode (Hansatech, King’s Lynn, UK) chamber maintained at 25 °C. Each leaf disc was 3.4 cm² in area, punched from the similar part of the youngest fully expanded I. batatas leaves grown under different light conditions. The sample chamber contained 1% CO₂ supplied by fabric matting moistened with 1 M NaHCO₃/Na₂CO₃ (pH 9). 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 net rate of O₂ evolution 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 drift in the signal before and after repetitive-flash illumination was subtracted algebraically from the net rate of O₂ evolution during flash illumination to obtain the gross rate of flash-induced O₂ 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 O₂ 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 O₂ molecule (Chow et al., 1991). Second, after repetitive-flash illumination, a light response curve of Pₐ was measured under continuous white light. The leaf disc was illuminated at 15 different light intensities, starting from the lowest PPFD of 0–1870 μmol m⁻² s⁻¹. The leaf disc was illuminated at each PPFD over several minutes until steady-state of photosynthetic O₂ evolution rate was obtained. The saturating, continuous irradiance (1870 μmol m⁻² s⁻¹) was used to determine the photosynthetic capacity (Pₘₐₓ). The post-illumination drift was subtracted algebraically from the steady-state net O₂ evolution rate at PPFD of 1870 μmol m⁻² s⁻¹ to yield the gross O₂ evolution rate, Pₚₘₐₓ. For calibration of the oxygen signals, 1 ml of air at 25 °C (taken to contain 8.584 μmol O₂) was injected into the gas-phase O₂ electrode chamber.

Calculation of the Cyt b₆f concentration: After measurements of p and Pₚₘₐₓ, the Cyt b₆f concentration (f) was calculated from the equation, Pₚₘₐₓ = 1/[(0.022/p)+(0.004/p)], all parameters being on a leaf area basis. The Cyt b₆f concentration, calculated from the two activity measurements, represents the functional Cyt b₆f concentration in leaves (Zhu et al., 2017)

2.7. Measurements of photosynthetic CO₂ assimilation rate (A), stomatal conductance (gₛ), internal CO₂ concentration (Cᵢ) and transpiration (Tᵣ)

A, gₛ, Cᵢ and Tᵣ were measured from the youngest fully expanded attached leaves under growth irradiances in the greenhouse using the LI-COR Portable Photosynthetic System (LI-6400, Bioscience, USA) from 1030 h to 1230 h. During the measurement, the average ambient CO₂ concentration in the greenhouse was 383 ± 6 μmol mol⁻¹, the relative humidity was 40 ± 10 % and the temperature was 39 ± 4 °C. The measurement was performed twice on both the 44th and 45th days after transplanting. The results presented were the means of data collected in these two days.

2.8. Statistical analysis

One-way analysis of variance (ANOVA) was used to test for significant differences of variances crossed with the three different treatments. LSD multiple comparison tests were used to discriminate between means of the different treatments, where means with p < 0.05 has significant differences (IBM, SPSS Version 25).

3. Results

3.1. Leaf growth, leaf productivity and leaf water content

It was observed that all leaves were fully expanded after one week emergence regardless of growth irradiances. Fig. 1 shows an average leaf area and a SLA of fully-expanded leaves developed under different growth irradiances. Although the average leaf area of sweet potato leaves grown under SL + H-LED (56 cm²) was slightly larger than those grown under SL + L-LED (50 cm²) and SL (51 cm²), statistically, there were no significant differences in their values (Fig. 1A). However, sweet potato leaves grown under SL had significantly higher SLA compared to those grown under SL + L-LED and SL + H-LED (Fig. 1B). For leaf FW and leaf DW, they were significantly higher in sweet potato plants grown under SL + L-LED and SL + H-LED than under only natural SL (Fig. 2A and B). However, all leaves had similar water content (Fig. 2C).
3.2. Photosynthetic pigments

Sweet potato leaves grown under SL + H-LED had the highest concentrations of Chl a, Chl b, total Chl and total Car followed by those grown under SL + L-LED. For plants grown under SL, their leaves had the lowest Chl a, Chl b, total Chl and total Car concentrations (Fig. 3A–D). However, Chl a/b ratio of sweet potato leaves grown under SL was significantly higher than those grown under SL + L-LED and SL + H-LED (Fig. 3E). There were no significant differences in Chl/Car ratios among the leaves grown under different light conditions (Fig. 3F).

3.3. Photosynthetic light utilization efficiency measured by Fv/Fm ratio, ETR, qP and NPQ

Fig. 4 shows the predawn and midday Fv/Fm ratios measured from the attached leaves on the same sunny day in the greenhouse. The measurements were repeated once on another sunny day and similar
results were obtained. All leaves had their predawn $F_v/F_m$ ratios greater than 0.8 although leaves grown under SL had $F_v/F_m$ ratio significantly higher than those grown under SL + L-LED and SL + H-LED (Fig. 4A). Leaves grown under SL + H-LED had significantly lower midday $F_v/F_m$ ratio (0.689) than those grown under SL (0.750) and SL + L-LED (0.744) (Fig. 4B).

The youngest fully expanded leaves were also harvested to measure the light response curves of ETR, $q_P$ and NPQ, starting from the lowest PPFD of $0–1501 \mu\text{mol m}^{-2}\text{s}^{-1}$. The measurements were repeated once on a different day and similar results were obtained. The readings of ETR increased as PPFDs increased from $0–1501 \mu\text{mol m}^{-2}\text{s}^{-1}$ for all leaves (Fig. 5A). All leaves had similar values of ETR when they were measured under PPFDs $< 111 \mu\text{mol m}^{-2}\text{s}^{-1}$. However, leaves grown under SL had significantly lower ETR compared to those grown under SL + L-LED and SL + H-LED when they were measured under PPFDs from 146 to 1501 $\mu\text{mol m}^{-2}\text{s}^{-1}$. Measured under the two highest PPFDs of 1076 and 1501 $\mu\text{mol m}^{-2}\text{s}^{-1}$, leaves grown under SL + H-LED had the highest ETR, followed by those grown under SL + L-LED and the leaves grown under SL had the lowest ETR under these two PPFDs (Fig. 5A). The values of $q_P$ decreased with increasing PPFDs from $0–1501 \mu\text{mol m}^{-2}\text{s}^{-1}$ for all leaves (Fig. 5B). All leaves had similar decrease rates of $q_P$ when they were measured under PPFDs from 0 to 56 $\mu\text{mol m}^{-2}\text{s}^{-1}$. However, decreases in $q_P$ were significantly faster in leaves grown under SL than under SL + L-LED and SL + H-LED when measured under PPFDs above 81 $\mu\text{mol m}^{-2}\text{s}^{-1}$ except for the higher PPFD of 1501 $\mu\text{mol m}^{-2}\text{s}^{-1}$, under which all leaves had similar lowest level of $q_P$ (Fig. 5B). Similar to the changes of ETR, NPQ of all leaves increased with increasing PPFDs from $0–1501 \mu\text{mol m}^{-2}\text{s}^{-1}$ (Fig. 5C). When measured under PPFDs $< 146 \mu\text{mol m}^{-2}\text{s}^{-1}$, all leaves had similar levels of NPQ. Leaves grown under SL + H-LED had significantly lower NPQ compared to those grown under SL + L-LED and SL under PPFDs from 146 to 611 $\mu\text{mol m}^{-2}\text{s}^{-1}$. However, under the two highest PPFDs of 1076 and 1501 $\mu\text{mol m}^{-2}\text{s}^{-1}$, NPQ values were similarly higher in leaves grown under SL + L-LED and SL + H-LED than under SL (Fig. 5C).

3.4. Light response curves of $P_N$, PS II and Cyt $b_{6f}$ concentrations of detached leaves measured in the laboratory

Fig. 6 shows light response curves $P_N$, PS II and Cyt $b_{6f}$ concentrations measured from the same detached leaves in the laboratory at 25°C. $P_N$ increased with increasing PPFDs similarly in all leaves from 0 to 602 $\mu\text{mol m}^{-2}\text{s}^{-1}$, and started to saturate between 602–808 $\mu\text{mol m}^{-2}\text{s}^{-1}$ (Fig. 6A), after which, slow increases of $P_N$ were still observed from 808 to 1435 $\mu\text{mol m}^{-2}\text{s}^{-1}$ in leaves grown under SL + H-LED. Thus, the light response curve of $P_N$ measured from leaves grown under SL + H-LED was above those grown under SL + L-LED and SL. Measured under the two highest PPFDs of 1435 and 1870 $\mu\text{mol m}^{-2}\text{s}^{-1}$, leaves grown under SL + H-LED had significantly higher $P_N$ than those grown under SL + L-LED while leaves grown under SL + H-LED and SL had similar $P_N$ (Fig. 6A). However, there were no significantly differences in
and SL (Fig. 7C). However, all leaves had similar grown under SL + H-LED compared to those grown under SL + L-LED measured under their respective growth irradiance with similar but potato leaves grown under a PPFD of 300 μmol m\(^{-2}\) s\(^{-1}\) at a PPFD of 150 μmol m\(^{-2}\) s\(^{-1}\) are not secured due to the fact that its productivity is influenced by variation in sunlight availability and intensity. To the best of our knowledge, this was the first project to grow sweet potato leaves in the tropical greenhouse using hydroponic systems under supplemental LED lighting to prevailing natural sunlight. Light is the most crucial factor for plant growth and development as well as the efficiency of the photosynthesis (Vialet-Chabrand et al., 2017; Gombers, 2020). Plants can adjust their morphological and physiological traits such as leaf size, SLA, leaf mass and Chl content when they are subjected to changing light conditions (Liu et al., 2016; He et al., 2017a). This study was carried out in the tropical greenhouse from the middle of February to early April 2020, when the weather was warm and sunny. The average highest ambient temperature was about 34–36 °C under full sunlight and maximum PPFD in an open field on sunny days outside the greenhouse ranged from 1400 to 1600 μmol m\(^{-2}\) s\(^{-1}\) for at least 4 h from 1100 h to 1500 h. However, the average maximum PPFD inside the greenhouse was round 700–800 μmol m\(^{-2}\) s\(^{-1}\), which was 50 % of full sunlight but the average ambient temperature could be as high as 38–40 °C with the highest of 43 °C during midday for at least 4 h. It was a surprise to observe that inside the hot greenhouse, the leaves of all sweet potato plants grew very fast and were very healthy, especially those grown under SL supplemented with constant PPFDs of either 150 (SL + L-LED) or 300 μmol m\(^{-2}\) s\(^{-1}\) (SL + H-LED), for a 12 h photo-period. These observations were supported by the results shown in Figs. 1 and 2. Although there was no significant difference in leaf area of the youngest fully expanded leaves grown under different light conditions one week after emergence (Fig. 1A), leaf FW and DW were significantly higher in leaves grown under SL + L-LED and SL + H-LED than under SL alone (Fig. 2A and B). All leaves had similar water content (Fig. 2C) and thus, higher leaf FW and DW resulted from the greater thickness of those grown under supplemental LED lighting, which was supported by the lower SLA (Fig. 1B). Low SLA is associated with greater leaf thickness as SLA is measured as the ratio of leaf area to leaf dry mass (Hunt et al. 2002). It was previously reported by our studies that both light quantity and quality affected SLA of leafy vegetables within the species (Choong et al., 2018; He et al., 2019).

Grown under low-light conditions, plants usually develop leaves with higher SLA compared to those grown under high-light conditions (He et al., 2017a; Vialet-Chabrand et al., 2017; Zhang et al., 2019). According to Poorter et al. (2018), light-capture-related traits such as SLA and Chl content are strongly related to light, and therefore vary mostly within species. The higher SLA of sweet potato leaves grown under low-light conditions such as only SL (Fig. 1B) could be interpreted as a mechanism to optimize light harvesting. However, under high-light conditions such as SL + H-LED conditions, lower SLA (Fig. 1B) could help plants to increase the efficiency of light capture (Evans and Poorter, 2001; Liu et al., 2016). In the study with soybean, Fan et al. (2018) and Feng et al. (2019) reported that Chl a, Chl b, total Chl and Car contents increased with the increase in light intensity, which were directly associated with leaf thickness. The results of this study with potato leaves grown under SL + L-LED and SL + H-LED conditions having higher Chl a, Chl b, total Chl and Car concentrations on a per area basis (Fig. 3A–D) are consistent with those previous results (Fan et al., 2018; Feng et al., 2019). However, Anderson et al. (1988) demonstrated that it was not the Chl concentration per leaf area but the ratio of Chl a/b showed a close correlation to the growth irradiance. In this study, when growth irradiance was increased by supplementing LED lighting to SL, Chl a/b ratio of sweet potato leaves decreased (Fig. 3E). Increasing light intensity decreased Chl a/b ratio was also reported in soybean (Feng et al., 2019). These results are not in accordance with the usually increased Chl a/b ratio of plants grown under high-irradiance compared to those grown under low-irradiance (Evans and Poorter, 2001). Zivcak et al. (2014) 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. In this study, the supplemental LED-lighting was provided by a combination of red- and blue-LED lighting in the ratio of 9:1. The

![Fig. 6. Light response curves of photosynthetic O₂ evolution (A), PS II concentration (B) and Cyt b6f concentration (C) measured from the youngest fully expanded leaves of I. batatas grown under different light conditions. Means with different letters are statistically different (P < 0.05; n = 3) as determined by LSD multiple comparison test. SL, Sunlight; SL + L-LED, SL with supplemental LED at a PPFD of 150 μmol m\(^{-2}\) s\(^{-1}\); SL + H-LED, SL with supplemental LED at a PPFD of 300 μmol m\(^{-2}\) s\(^{-1}\).](image)

### 3.5. A, gₛ, Cₒ, Tₒ of attached leaves measured in the greenhouse

Fig. 7A and B show the results of A and gₛ of sweet potato leaves measured under their respective growth irradiance with similar but much higher values obtained from leaves grown under SL + L-LED and SL + H-LED than under SL. The Ci was significantly lower in leaves grown under SL + H-LED compared to those grown under SL + L-LED and SL (Fig. 7C). However, all leaves had similar Tₒ (Fig. 7D).

### 4. Discussion

Although sweet potato leaves have been consumed in Singapore as a high nutritional leafy vegetable, they are mainly cultivated in outdoor soil farms. The supply of sweet potato leaves to the vegetable markets is not secured due to the fact that its productivity is influenced by...
The midday Fv/Fm ratio remained higher for leaves of plants grown to the highest PPFD about 1150 μmol m$^{-2}$ s$^{-1}$. Generally, Car concentration was higher for sun-acclimated leaves compared to that of shade-grown leaves (Demmig-Adams and Adam, 1996; Lichtenhaler, 2007). Carotenoids play important roles in photosynthesis (Pogson et al., 2005) and protect plants from the harmful effects of excess exposure to light by maintaining proper Chl/Car ratio (or Car/Chl ratio) for optimal photosynthesis and photoprotection (Hashimoto et al., 2016). All sweet potato leaves had similar Chl/Car ratios as those grown under higher growth irradiance increased the concentrations of both total Chl and total Car concentrations (Fig. 3C and D). In the study with barley leaves (Hordeum vulgare L.), Zivcak et al. (2014) also reported that no significant changes were observed in the Chl/Car ratio between sun and shade leaves.

Biosynthesis of Chl increases with increasing light intensity (Björkmann, 1981). However, under adverse environmental conditions such as high temperature, high light inhibits Chl formation due to photoinhibition (He et al., 1996). In this study, all leaves had predawn Fv/Fm ratio > 0.8 (Fig. 4A), indicating that no chronic photoinhibition occurred in any plants. However, dynamic photoinhibition occurred in most native orchid species in Singapore midday caused dynamic photoinhibition but no sustained chronic photoinhibition (He et al., 2017a; Tay et al., 2019).

Chls are essential molecules that catch light energy to drive photosynthetic electron transfer (Fromme et al., 2003). Sweet potato leaves grown under high-irradiance had thicker leaves and higher Chl concentrations are associated with higher ETR compared to those grown under low-irradiance (Fig. 5A). When measurements were carried out from 801 to the highest 1501 μmol m$^{-2}$ s$^{-1}$, which were within the maximum ranges of PPFD under which all leaves were developed, the ETR readings were 80–98 % and 55–75 % respectively higher in SL + H-LED and SL + L-LED leaves than that in leaves grown under SL (Fig. 5A). Not only ETR but also qP was modified by the light conditions, with slower declines in qP in leaves grown under SL + L-LED and SL + H-LED compared to that in leaves grown under SL except for the measurements at the higher PPFD of 1501 μmol m$^{-2}$ s$^{-1}$ (Fig. 5B). The values of qP were significantly higher for the leaves grown under high-irradiance such as SL + L-LED and SL + H-LED than those under lower irradiance of SL inside the greenhouse, indicating that high-irradiance improve photosynthetic light use efficiency (Feng et al., 2019). It was reported that high growth irradiance increased ETR and qP while decreased the NPQ (Zivcak et al., 2014; Feng, 2019). These were also observed in this study with sweet potato leaves grown under SL + H-LED had low NPQ when measurements were made from 146 to 611 μmol m$^{-2}$ s$^{-1}$ compared to those grown under SL. However, decreased NPQ was not observed in leaves grown under SL + L-LED (Fig. 5C).

High growth irradiance enhances ETR and qP that could increase photosynthetic rate by improving the energy transport from PSII to PSI in tobacco leaves (Yamori et al., 2010) and soybean leaves (Yang et al., 2018). It was also reported earlier that pea leaves grown under high-light had higher concentrations of PS II and Cyt b6f and thus a higher capacity for electron transport and photosynthetic oxygen evolution compared to those grown under low-light (Leong and Anderson, 1984; Chow and Anderson, 1987). Similar results were also reported in spinach (Chow and Hope, 1987), Alocasia macrorrhiza (Chow et al., 1988) and Hordeum vulgare (De la Torre and Burkey, 1990). However, in this study, sweet potato leaves grown under SL + L-LED and SL + H-LED increased ETR and qP while the concentrations of PS II (Fig. 6B) and Cyt
Cyt b₆f (Fig. 6C) remained unchanged compared to those grown under SL. Higher ETR and qP observed in this study may be due to the tuning of the amount of active PSII reaction centres and regulating the electron transfer by the Cyt b₆f complex (Tikkkanen et al., 2012) rather than the modified concentrations. As all leaves in this study were developed under the maximum PPFs about 700–800 μmol m⁻² s⁻¹ where P_N started to saturate (Fig. 6A), they may have produced maximum amount of PS II and Cyt b₆f complex. On the other hand, P_N was measured at the temperature (25 °C) lower than the maximum growth temperature of sweet potato leaves, which may also be another factor affecting the values of P_N (to be discussed in the next section). In our future study, corrections among ETR, qP, PS II, Cyt b₆f and P_N in sweet potato leaves should be carried out under different light intensity and different leaf temperatures.

Many studies have shown that PS II and Cyt b₆f may be the site of the rate-limiting step in the electron transport (Heber et al., 1988; Eichelmann et al., 2000). The concentration of Cyt b₆f is the main rate-limited factor that determines light and CO₂-saturated photosynthetic capacity (Tikkkanen et al., 2012; Zhu et al., 2017). In this study, there was a slightly higher P_N measured from leaves grown under SL + H-LED at the highest PPF of 1870 μmol m⁻² s⁻¹ compared to that of leaves grown under SL (Fig. 6A), which could be due to the similar concentrations of Cyt b₆f (Fig. 6B) among all leaves. Although all detached leaves had similar P_N measured at 25 °C in the laboratory under saturated CO₂ (Fig. 6A), there were significant differences in A, gₛ, and C₅ measured from attached leaves under their respective growth irradiance in the greenhouse (Fig. 7). Generally, leaves developed under high-irradiance are thicker than those grown under low-irradiance and thus enhance light use efficiency for carbon fixation (Terashima et al., 2006). In their paper, Terashima et al. (2006) confirmed that there were sufficient mesophyll surfaces in the thicker sun leaves for CO₂ dissolution and transport to the chloroplasts. Thicker sun leaves of C₅ plants could maintain the CO₂ concentration in the chloroplast as high as possible for ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) (Terashima et al., 2006). Furthermore, thicker leaves accumulated more photosynthetic enzymes on a leaf area basis and thus contributed to greater CO₂ fixation capacity of high-light grown leaves (Evans and Poorter, 2001). The results of this study support those earlier studies as photosynthetic CO₂ assimilation rate, A was 31 and 40 % higher in SL + L-LED and SL + H-LED, respectively than that of SL (Fig. 7A). Generally, plants grown at higher temperatures have a higher optimal temperature of photosynthetic rate (Yamasaki et al., 2002). In many species, the optimal temperature of photosynthetic rate increases with increasing growth temperature (Hikosaka et al., 2006). These earlier studies explain why the values of A (Fig. 7A) measured from the attached leaves in the greenhouse with their leaf temperatures as high as 38–43 °C under ambient CO₂ were higher than those of P_N (Fig. 6A) measured from detached leaves at 25 °C in the presence of a saturating CO₂ concentration in the laboratory. It has been reported that gₛ is sensitive to temperature, humidity and light (Bunce, 2001; Lawson, 2009). Generally, high temperature promotes stomatal opening to facilitate leaf cooling. In this study, there were small variations in leaf temperature and humidity among sweet potato leaves as they were grown in the same area of the same greenhouse. However, the values of gₛ were significantly higher in sweet potato leaves grown under SL + L-LED and SL + H-LED than that of leaves grown under SL (Fig. 7B). Different light conditions could be the main factors resulting in different gₛ. Optimal combinations of blue- and red-LED used in this study could enhance gₛ, which have been previously reported in cucumber (Hernández and Kubota, 2016) and lettuce (Wang et al., 2016; Choong et al., 2018). It is well known that stomata are responsible for balancing photosynthetic CO₂ uptake with water loss through transpiration. Although it was unable to measure the root biomass in this study, all sweet potato plants had well developed big root systems to ensure water and nutrient uptake (Poorter et al., 2012).

Thus, all leaves had similar transpiration rate (Fig. 7D) although leaves grown under SL had significantly lower gₛ compared to those grown under SL supplemented with LED lighting. In certain species, the greater A by plants grown under high-irradiance means that they have lower C₅ than those grown under low-irradiance (Hanba et al., 2002; Yamori et al., 2010; Huang et al., 2014). For instance, Huang et al. (2014) reported that sun-grown tobacco leaves had greater A, leading to lower C₅. In this study, sweet potato leaves grown under the highest irradiance (SL + H-LED) also had the highest A which was as high as 38.1 μmol CO₂ m⁻² s⁻¹ (Fig. 7A) and the lowest C₅ of 236.8 μmol CO₂ mol⁻¹ compared to those grown under low-irradiance (Fig. 7C). Lower C₅ could result in higher ribulose-1,5-bisphosphate (RuBP) oxygenation rate in sun-grown-leaves than in shade-grown-leaves and thus upregulate photorespiratory pathway. However, lower C₅ of sun-grown leaves also increased RuBP regeneration resulting from higher electron transport capacity and thus RuBP oxygenation and regeneration were balanced (Foyer et al., 2012; Huang et al., 2014). In this study, sweet potato leaves grown under high-irradiance also had higher electron transport capacity (Fig. 5A). Instead of suppressing A, enhancement of photorespiratory pathway through enhanced RuBP regeneration potentially improved the A in Arabidopsis thaliana (Timm et al., 2012) and tobacco leaves (Huang et al., 2014). Sweet potato leaves grown in the tropical greenhouse under high-irradiance may also have higher photorepression which enhanced photosynthetic CO₂ assimilation and at the same time prevented them from suffering sustained chronic photoinhibition supported by their predawn Fₘ/Fₗ ratios of greater than 0.8 (Fig. 3A). Changes in the light dependence of photosynthesis may be ascribed to changes in not only CO₂ concentration in the chloroplasts but also the activity and amount of photosynthetic components especially the activation and the amount of Rubisco (Simkin et al., 2015, 2019). Compared to sweet potato leaves grown under low-irradiance such as SL only, leaves grown under high-irradiance such as SL + H-LED probably have increased synthesis of Rubisco. Supplemental LED lighting to SL increased total leaf soluble protein and Rubisco protein of Cos lettuce (Lactuca sativa L.) grown in the same greenhouse (unpublished data). In this study, samples have been collected for the analysis of total leaf soluble protein and Rubisco protein. Unfortunately, we were unable to determine these parameters as we had to close our laboratory due to the COVID-19 pandemic. The effects of light on Rubisco protein would be studied in near future. We also hypothesize that supplementing LED to natural SL enhances not only leaf growth and photosynthetic characteristics of sweet potato leaves in a tropical greenhouse but also their nutritional quality, which also merits our further study.

5. Conclusion

The results of this study show that supplemental LED lighting to natural SL increased leaf fresh and dry weights of hydroponically grown sweet potato (I. batatas var. Biru Putih) in the hot tropical greenhouse. The enhancement of leaf biomass was due to the increased thickness of high-irradiance grown leaves, which improved electron transport capacity and photosynthetic CO₂ assimilation rate of attached leaves under their growth temperature and irradiances. Corrections among ETR, qP, PS II, Cyt b₆f, P_N and Rubisco protein in sweet potato leaves under different light intensities and different leaf temperatures merit our further study.

Author contributions

JH initiated and funded the expenses for the project, planned and carried out some parts of the experiments and wrote most part of the manuscript. LQ planned, carried out most experiments, analyzed the data and wrote some part of the manuscript.
CRediT authorship contribution statement

Jie He: Conceptualization, Methodology, Investigation, Writing - original draft, Writing - review & editing, Lin Qin: Formal analysis, Investigation, Methodology, Project administration, Writing - review & editing.

Declaration of Competing Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Appendix A. Supplementary data

Supplementary material related to this article can be found in the online version, at https://doi.org/10.1016/j.jplhp.2020.153239.

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