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Article

Root Architecture, Growth and Photon Yield of Cucumber Seedlings as Influenced by Daily Light Integral at Different Stages in the Closed Transplant Production System

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Abstract: Optimizing light conditions for vegetable seedling production in a closed transplant production system is critical for plant growth and seedling production. Additionally, energy use efficiency should be considered by growers when managing the light environment. In the present study, cucumber seedlings (*Cucumis sativus* L. cv. Tianjiao No. 5) were grown under six different daily light integrals (DLIs) at 8.64, 11.52, 14.40, 17.28, 23.04, and 28.80 mol m^{-2} d^{-1} created by two levels of photosynthetic photon flux density (PPFD) of 200 and 400 µmol m^{-2} s^{-1} combined with photoperiod of 12, 16 and 20 h d^{-1} provided by white light-emitting diodes (LEDs) in a closed transplant production system for 21 days. Results indicated that quadratic functions were observed between fresh and dry weights of cucumber seedlings and DLI at 6, 11, 16, and 21 days after sowing. Generally, higher DLI resulted in longer root length, bigger root volume and root surface area accompanied with shorter plant height and hypocotyl length; however, no significant differences were observed in root length, root volume, and root surface area as DLI increased from 14.40 to 28.80 mol m^{-2} d^{-1}. Photon yield based on fresh and dry weights decreased with increasing DLI. In conclusion, increased DLI resulted in compact and vigorous morphology but reduced photon yield of cucumber seedlings produced in a closed transplant production system. In terms of plant growth and energy use efficiency, DLI at 14.40–23.04 mol m^{-2} d^{-1} was suggested for cucumber seedling production in the closed production system. Additionally, different control strategies should be applied at different growth stages of cucumber seedlings.

Keywords: light quantity; light-emitting diodes; photoperiod; specific leaf area

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1. Introduction

The seedling stage and its subsequent cultivation stage of horticultural crops are often separated due to differences in plant density, environmental conditions, and control strategies in modern agriculture [1,2]. The demand for vegetable seedlings is gradually increasing as a result of the increasing market requirement of vegetables. For instance, the annual demand for vegetable seedlings in China was more than 680 billion plants in 2018 [3], and the vegetable seedling market in Korea was estimated to be approximately USD 346 million [4,5]. Previous studies have documented that compact seedlings have led to robust mature plants [6,7], higher yield and nutritional qualities [8,9] compared with weak seedlings after transplanting. Therefore, raising high-quality vegetable seedlings is vital for increasing crop yield and farmer income. Cucumber (*Cucumis sativus* L.) is one of the economically main vegetables cultivated worldwide with annual production at 87.8 million tons with China accounting for 80.1% of the world's cucumber production in 2019 [10]. Moreover, the annual demand for cucumber seedlings in China is 47 billion plants [11].

Light plays an important role in regulating plant physiology as both an energy source for photosynthesis and an external signal to activate and regulate plant growth and development [12]. Many studies have investigated the influence of photosynthetic photon flux density (PPFD) or photoperiod on growth and development of vegetable seedlings grown in a closed transplant production system or greenhouse [9,13–15]; however, these two variables cannot independently reflect the plant responses to the light environment. The daily light integral (DLI) represents the total amount of photosynthetic photons received by plant surface during one day, which can be applied to predict yield or adjusted by the management strategies of growers. Many studies have evaluated an increase in DLI, either by extending the photoperiod at the same PPFD [16], or by increasing PPFD at the same photoperiod [17–19]. Suitable DLI created various combinations of PPFD and photoperiod for plant growth were investigated in lettuce seedlings [9], sweetpotato seedlings [2], and tomato seedlings [20]. The linear relationships or quadratic functions were observed between DLI and biomass accumulation [11,16,18], stomatal conductance [19], and nutritional quality [17] of plants grown in a closed production system. However, the relationship between DLI and root architecture of cucumber seedlings is still unclear. In addition, DLI inside the greenhouse can range from very low to high values depending on location, weather pattern, season, and light transmission through the greenhouse. For example, the mean DLI ranges from 5–10 mol m^{-2} d^{-1} across the northern United States in winter and 55–60 mol m^{-2} d^{-1} in the southwestern United States in summer [21,22]. Thus, the impact of a wide range of DLIs created by various combinations of PPFD and photoperiod on seedling quality also requires further study.

High-quality seedlings should be vigorous and compact, with high photosynthetic capacity, short hypocotyl length, thick green leaves and large white roots [9,11]. Numerous studies have focused on leaf morphology [23,24], carbohydrate accumulation [11,20], photosynthesis characters [25] of vegetable seedlings. However, a well-developed root system is vital when transplanting seedlings and for their subsequent growth. The impact of DLI on root architecture of plug seedlings has received limited attention.

Plants grown under a natural light environment have adapted to utilizing a wide spectrum of sunshine by long-term evolution [26,27]. Chen et al. [26] reported that the influence of monochromic light quality on horticultural crops could be demonstrated more objectively and sufficiently when provided a relatively wide spectrum (e.g., white LED). Additionally, previous studies documented that white LED had a similar impact on plant growth associated with higher energy use efficiency and visual assessment compared with red plus blue LED [27,28]. Energy consumption of different light strategies should be considered by commercial growers in crop production. Therefore, DLI strategies provided by white LED in consideration of energy consumption is needed for further investigation in cucumber seedling production.

It appears that studies focusing on the amelioration of DLI from the perspective of plant growth, physiological response, and resource efficiency in vegetable seedlings at different stages under white LEDs are still lacking. This study aimed at determining how different combinations of PPFD and photoperiod affected leaf morphology, root architecture, carbohydrate status and photon yield of cucumber seedlings within a wide range of DLIs (e.g., ranging from 8.6 to 28.8 mol m^{-2} d^{-1}) at different growth periods. The results could be used as a guideline for controlling DLI inside a closed transplant production system or greenhouse to achieve a steady and predictable year-round seedling production.

2. Materials and Methods

2.1. Plant Materials and Growth Conditions

Cucumber seeds (*Cucumis sativus* L. cv. Tianjiao No. 5) (Shuofengyuan Seed Industry Co., Ltd., Qingdao, China) were sown in 72-cell plug trays (53.5 cm × 27.5 cm × 4.0 cm) (Shandong Lige Technology Co., Ltd., Jinan, China) containing a mixture of 60% vermiculite (Shandong Lige Technology Co., Ltd., Jinan, China), 20% peat (The Pindstrup Group, Kongersle, Denmark), and 20% perlite (Shandong Lige Technology Co., Ltd., Jinan, China) in a walk-in plant factory with artificial lighting. The air temperature, CO_2 concentration and relative humidity were 25 ± 1 °C, 400 ± 50 μmol mol^{-1} and 60–70% during growth period, respectively. All cucumber seedlings were sub-irrigated with Hoagland's nutrient solution with pH of 6.0–6.5 and electrical conductivity of 1.8–2.0 mS cm^{-1}. The nutrient solution was comprised of the following components (mg L^{-1}): $Ca(NO_3)_2{\cdot}4H_2O$, 945; KNO_3, 607; $MgSO_4{\cdot}7H_2O$, 493; $NH_4H_2PO_4$, 115; Na_2Fe-EDTA, 30; $MnSO_4{\cdot}H_2O$, 2.13; $CuSO_4{\cdot}5H_2O$, 0.08; $ZnSO_4{\cdot}7H_2O$, 0.22; H_3BO_3, 2.86; $(NH_4)_6Mo_6O_{24}{\cdot}4H_2O$, 0.02, respectively, which were produced by Sinopharm Chemical Reagent Co., Ltd., Shanghai, China. Tap water and 1/2 strength of the standard nutrient solution were applied at 2 days after sowing and at the cotyledon stage, respectively. A full strength of the nutrient solution was used every 2 days after the first true leaf emerged.

2.2. Treatment Design

Cucumber seedlings were grown for 21 days under 6 different daily light integrals of 8.64, 11.52, 14.40, 17.28, 23.04, and 28.80 mol m^{-2} d^{-1} created by two levels of PPFD of 200 and 400 μmol m^{-2} s^{-1} at the plant canopy combined with photoperiods of 12, 16, and 20 h d^{-1} provided by white LEDs (18W, Weifang Hengxin Electric Appliance Co., Ltd., Weifang, China), respectively, in the closed transplant production system (Table 1). Three replicates in each treatment were adopted, and each replicate contained one 72-cell plug tray. The spectral distributions of the LED were measured by a spectrometer (PG100N, United Power Research Technology Corporation, Miaoli, China) at the plant canopy level. The white LEDs applied in our study incorporated a layer of phosphor over a GaN-based blue light emitter, with peak wavelengths of 546 nm and 446 nm, respectively. Fractions of blue (B, 400–499 nm), green (G, 500–599 nm), and red (R, 600–700 nm) lights of PPFD were 28.5%, 49.1%, and 22.4%, respectively (Figure 1).

2.3. Growth Measurements

2.3.1. Chlorophyll Content of Cucumber Seedlings

The second fully-expanded leaf (approximate 0.1 g) of cucumber seedling was cut into small pieces and subsequently extracted in 80% acetone (10 mL) for over 72 h in the dark. Absorbance of the extract at wavelength 663 nm and 645 nm was measured by a spectrophotometer (1810, Shanghai Yoke Instrument Co., Ltd., Shanghai, China). The chlorophyll content was calculated based on the formulas reported by Lichtenthaler and Wellburn [29].

Table 1. Light environment setting with photosynthetic photon flux density (P) and photoperiod (H) for cucumber seedlings grown in the closed transplant production system for 21 days after sowing.

Treatment	Photosynthetic Photon Flux Density (μmol m^{-2} s^{-1})	Photoperiod (h d^{-1})	Daily Light Integral (mol m^{-2} d^{-1})
P200-H12	200	12	8.64
P200-H16		16	11.52
P200-H20		20	14.40
P400-H12	400	12	17.28
P400-H16		16	23.04
P400-H20		20	28.80

Note: Daily light integral (DLI, mol m^{-2} d^{-1}) = Photosynthetic photon flux density (P, μmol m^{-2} s^{-1}) × photoperiod (H, h d^{-1}) × 3600 (s h^{-1}) × 10^{-6}.

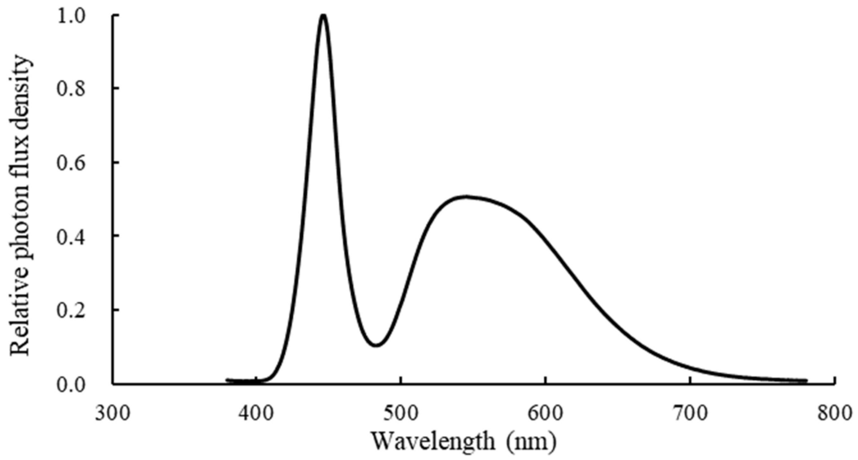

Figure 1. Relative photon flux density of white light emitting-diodes used in the closed transplant production system.

2.3.2. Photosynthetic Characteristic of Cucumber Seedlings

Net photosynthesis rate of cucumber seedling was measured by a portable photosynthesis system (LI-6400XT, LI-COR Inc., Lincoln, NE). Light intensity, leaf temperature and CO_2 concentration were controlled at 200 or 400 µmol m^{-2} s^{-1}, 25 °C, and 400 µmol mol^{-1}, respectively, in the leaf chamber with red and blue LEDs according to Yan et al. [30].

2.3.3. Plant Morphology and Root Architecture of Cucumber Seedlings

Uniform cucumber seedlings were randomly chosen at 6, 11, 16, and 21 days after sowing (DAS), for the following measurements. The plant height and stem diameter were measured from the media surface to the meristem tip and in the middle part between cotyledon and hypocotyl, respectively. Leaf area and root architecture of cucumber seedlings were scanned by a leaf scanner (Yaxin-124, Beijing Yaxin Liyi Technology Co., Ltd., Beijing, China) and a root scanner (V800, Seiko Epson Corp., Nagano, Japan), respectively. Total root length, root surface area, and root volume of cucumber seedlings were analyzed using WinRHIZO software (Version 2016a, Regent Instruments Inc., Quebec, Canada).

2.3.4. Biomass Accumulation and Photon Yield of Cucumber Seedlings

Fresh weight of leave and root of cucumber seedlings was measured by an electronic analytical balance (FA1204B, BioonGroup, Shanghai, China). Subsequently, plants were dried in an oven (GFL-230, Tianjin Labotery Instrument Co., Ltd., Tianjin, China) at 105 °C for 3 h, then, set to 80 °C for 72 h for measuring dry weight. Specific leaf area (SLA) and photon yield (g mol^{-1}) based on fresh and dry weights of cucumber seedlings were calculated according to Dou et al. [17] and Zheng et al. [31]. Where SLA = leaf area/leaf dry weight and photon yield indicated the fresh or dry weight increase per mole of photons delivered during the seedling stage.

2.3.5. Glucose Content of Cucumber Seedlings

Glucose content of cucumber leaves was measured using colorimetric method [32]. The residue obtained after ethanol extraction was resuspended with 0.1 mol L^{-1} sodium acetate buffer (pH 4.8) and boiled for 20 min. The gelatinized starch was digested with amyloglucosidase at 37 °C for 4 h, then the mixture was boiled again to stop the enzymatic reaction. Insoluble materials were removed by centrifugation after cooling and the glucose content in the supernatant was determined.

2.4. Statistical Analysis

Data were analyzed by analysis of variance (ANOVA) to test impacts of different DLIs on all measured parameters of cucumber seedlings using SPSS 18.0 software (IBM, Inc., Chicago, IL, USA) followed by the least significant difference (LSD) test ($p < 0.05$). The regression analysis between biomass accumulation, root morphology, photon yield and DLI was performed using Microsoft Excel 2016 software according to He et al. [2].

3. Results

3.1. Effects of Daily Light Integral on Plant Height and Hypocotyl Length of Cucumber Seedlings Grown in a Closed Transplant System at Different Stages

Generally, plant height and hypocotyl length of cucumber seedlings increased gradually over time, and these two parameters were remarkably affected by DLI (Figure 2A,B). The differences of plant height or hypocotyl length between treatments increased over time. Cucumber seedlings grown with DLI at 8.64 and 17.28 mol m^{-2} d^{-1} led to higher plant height and longer hypocotyl than those grown with DLI at 28.80 mol m^{-2} d^{-1}.

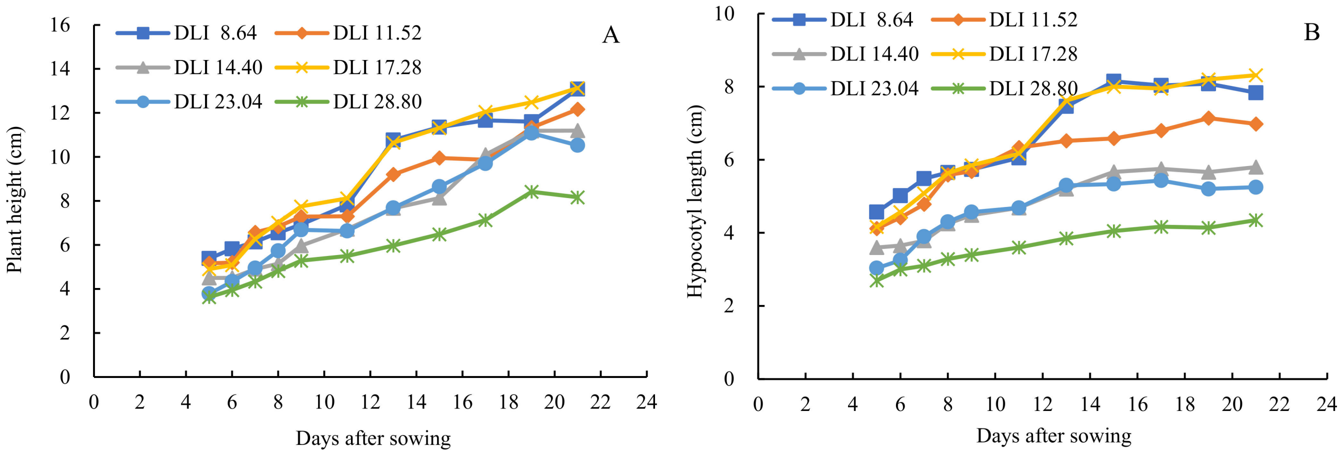

Figure 2. Time course of (**A**) plant height and (**B**) hypocotyl length of cucumber seedlings grown in a closed transplant production system as affected by daily light integral (DLI).

3.2. Impact of Daily Light Integral on Biomass Accumulation of Cucumber Seedlings Grown in the Closed Transplant System at Different Stages

Quadratic relationships were observed between biomass accumulation of cucumber seedlings and DLI, regardless of days after sowing (Figure 3A–D). The differences in biomass accumulation between treatments increased over time. No significant differences were observed in fresh and dry weights of cucumber seedlings grown under DLI at 8.6, 11.5 and 14.4 mol m^{-2} d^{-1} at 6 DAS. However, cucumber seedlings grown under DLI at 14.4 mol m^{-2} d^{-1} exhibited higher-root, fresh and dry weight compared with those grown under the lowest DLI at 11 DAS. Leaf dry weights of cucumber seedlings grown at DLI of 23.04 mol m^{-2} d^{-1} were 89.5%, 126.4%, and 110.6% higher than those grown with DLI at 8.64 mol m^{-2} d^{-1} at 11, 16, and 21 DAS, respectively. Similar results were observed in leaf fresh weight and root fresh weight. Root dry weight increased by 26.5%, 24.2%, and 35.0% as DLI increased from 23.08 to 28.80 mol m^{-2} d^{-1} at 11, 16, and 21 days after sowing, respectively.

3.3. Photon Yield of Cucumber Seedlings Grown under Different Daily Light Integrals in the Closed Transplant System at Different Stages

Photon yield based on fresh and dry weight of cucumber seedlings was influenced by DLI, regardless of days after sowing (Figure 4A,B). Photon yield decreased with increasing DLI in the closed transplant production system. Additionally, remarkable differences were observed in photon yields among treatments at 6 DAS. Photon yield based on fresh weight decreased by 63.4%, 60.4%, 63.0% and 63.9% as DLI increased from 8.64 to 28.80 mol m^{-2} d^{-1} at 6, 11, 16, and 21 DAS, respectively. Moreover, photon yield based on dry weight decreased by more than 30% as DLI increased from 8.64 to 28.80 mol m^{-2} d^{-1} at different stages, respectively.

3.4. Impact of Different Daily Light Integrals on Pigment Content and Net Photosynthetic Rate of Cucumber Seedlings at 21 Days after Sowing

Chlorophyll content of cucumber seedlings was significantly influenced by DLI (Table 2). Generally, chlorophyll a and b content decreased by increasing DLI (increased PPFD or prolonged photoperiod). Chlorophyll a, chlorophyll b, and total chlorophyll of cucumber seedling decreased by 45.9%, 54.1%, and 48.2% as DLI increased from 8.64 to 28.8 mol m^{-2} d^{-1}. Total chlorophyll decreased by 32.7% and 26.5% as photoperiod extended from 12 to 20 h d^{-1} with the same PPFD at 200 and 400 μmol m^{-2} s^{-1}, respectively. The opposite result was observed in chlorophyll a/b, which increased by 19.2% when DLI increased by 233.3% from 8.64 mol m^{-2} d^{-1}; however, no significant differences were observed in chlorophyll a/b as DLI increased from 8.64 to 23.04 mol m^{-2} d^{-1}. The net photosynthetic rate of cucumber leaves increased and then decreased with increasing DLI (Figure 5B). Net photosynthetic rate of cucumber leaves increased by one-fold as DLI increased from 8.64 to 17.28 mol m^{-2} d^{-1}; however, no significant differences were found between cucumber seedling grown under DLI at 17.28 and 23.04 mol m^{-2} d^{-1}.

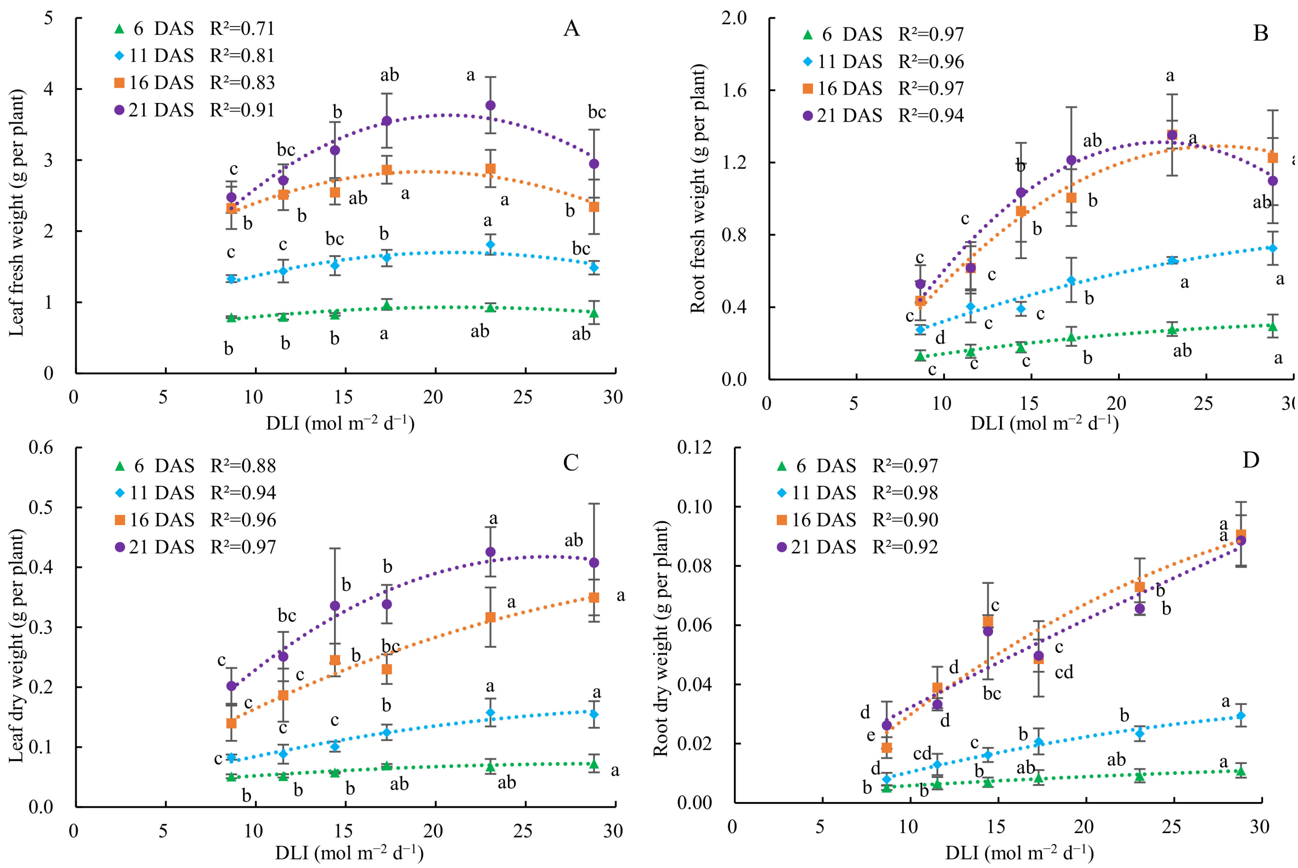

Figure 3. Relationship between daily light integrals (DLI) and (**A**) leaf fresh weight, (**B**) root fresh weight, (**C**) leaf dry weight, and (**D**) root dry weight of cucumber seedlings at 6, 11, 16, and 21 days after sowing (DAS) in a closed transplant production system. Data are presented as mean ± standard deviation. Different letters indicate significant differences at $p < 0.05$.

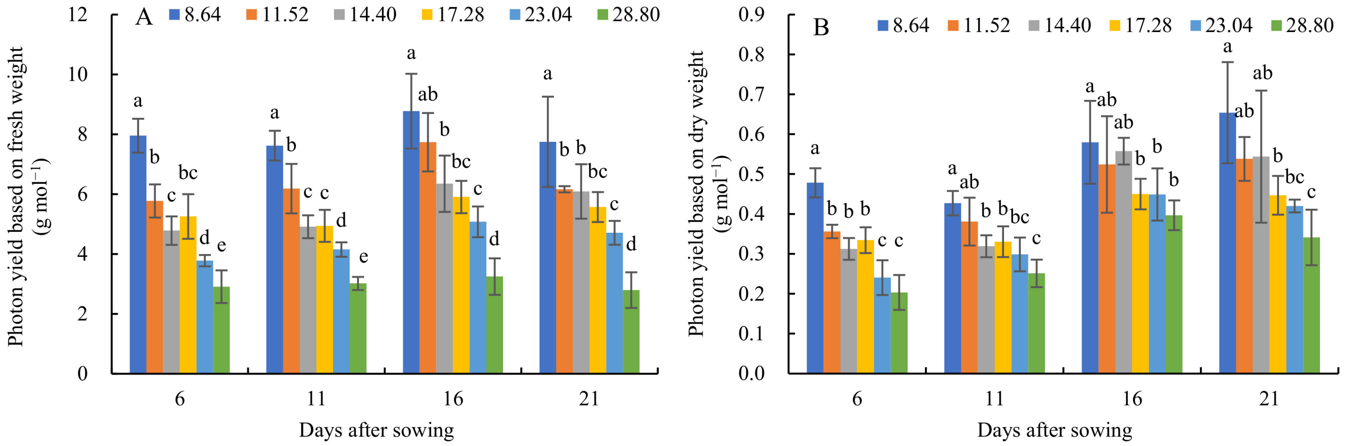

Figure 4. Photon yield based on (**A**) fresh and (**B**) dry weights of cucumber seedlings grown under different daily light integrals (DLIs) at 6, 11, 16, and 21 days after sowing (DAS) in a closed transplant production system. Data are indicated as mean ± standard deviation. Different letters indicate significant differences at $p < 0.05$.

Table 2. Influence of photosynthetic photon flux density (P) and photoperiod (H) with different daily light integrals (DLIs) on pigment content of cucumber seedlings grown for 21 days in a closed transplant production system.

Treatment	Chlorophyll a Content (mg g^{-1})	Chlorophyll b Content (mg g^{-1})	Total Chlorophyll Content (mg g^{-1})	Chlorophyll a/b
P200-H12	1.59 ± 0.22 a	0.61 ± 0.08 a	2.20 ± 0.30 a	2.60 ± 0.12 b
P200-H16	1.38 ± 0.22 a	0.51 ± 0.10 b	1.89 ± 0.31 b	2.70 ± 0.17 b
P200-H20	1.09 ± 0.16 b	0.38 ± 0.05 c	1.48 ± 0.21 c	2.84 ± 0.04 b
P400-H12	1.13 ± 0.15 b	0.41 ± 0.03 c	1.55 ± 0.18 c	2.73 ± 0.22 b
P400-H16	1.08 ± 0.15 b	0.39 ± 0.06 c	1.47 ± 0.21 c	2.80 ± 0.06 b
P400-H20	0.86 ± 0.06 c	0.28 ± 0.02 d	1.14 ± 0.07 d	3.10 ± 0.28 a

Note: Means (± standard deviation) followed by different letters within one column differ significantly ($p < 0.05$) as established by the least significant difference (LSD) test.

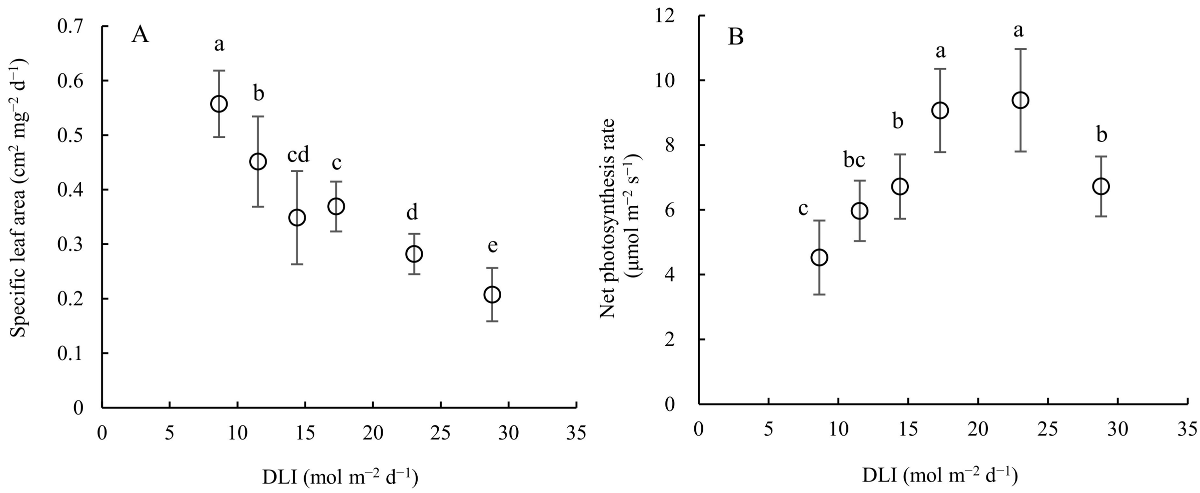

Figure 5. Relationship between daily light integral (DLI) and (**A**) specific leaf area, (**B**) net photosynthesis rate of cucumber seedlings grown for 21 days after sowing (DAS) in the closed transplant production system. Data are presented as mean ± standard deviation. Different letters indicate significant differences at $p < 0.05$.

3.5. Effect of Daily Light Integral on Leaf Morphology, Root Architecture, and Biomass Accumulation of Cucumber Seedlings Grown in a Closed Transplant System

Cucumber seedlings grown at DLI of 8.64 and 17.28 mol m^{-2} d^{-1} (with shorter photoperiod) exhibited higher plant height and hypocotyl length, while those grown at the highest DLI of 28.80 mol m^{-2} d^{-1} had the lowest plant height and shortest hypocotyl length (Table 3). In general, plant height and hypocotyl length decreased with increasing PPFD or extending photoperiod. Plant height and hypocotyl length of cucumber seedlings decreased by 37.5% and 48.9%, respectively, as DLI increased from 8.64 to 28.80 mol m^{-2} d^{-1}. Hypocotyl length of cucumber seedlings decreased by 34.0% and 50.5% as photoperiod extended from 12 to 20 h d^{-1} with the PPFD at 200 and 400 µmol m^{-2} s^{-1}, respectively. SLA of cucumber seedlings decreased with increasing DLI, which decreased by 62.8% as DLI increased from 8.64 to 28.80 mol m^{-2} d^{-1}. SLA of cucumber seedlings decreased by more than 30% as PPFD increased from 200 to 400 µmol m^{-2} s^{-1} with an equal photoperiod (Figure 5A). The stem diameter of cucumber seedlings increased by 26.4% as DLI increased from 8.64 to 23.04 mol m^{-2} d^{-1}. However, a significant decrease was observed in stem diameter as DLI increased from 23.04 to 28.80 mol m^{-2} d^{-1} (Table 3).

Table 3. Leaf morphology and carbohydrate accumulation of cucumber seedlings grown for 21 days after sowing, as impacted by photosynthetic photon flux density (P) and photoperiod (H) with different daily light integrals (DLIs) in a closed transplant production system.

Treatment	Plant Height (cm)	Stem Diameter (cm)	Hypocotyl Length (cm)	Leaf FW (g per Plant)	Root FW (g per Plant)	Leaf DW (g per Plant)	Root DW (g per Plant)
P200-H12	13.08 ± 0.90 a	3.68 ± 0.43 c	7.83 ± 0.68 a	2.48 ± 0.22 c	0.53 ± 0.10 c	0.202 ± 0.030 c	0.026 ± 0.008 d
P200-H16	12.17 ± 1.25 a	3.78 ± 0.25 c	6.73 ± 0.61 b	2.72 ± 0.22 bc	0.62 ± 0.12 c	0.251 ± 0.041 bc	0.033 ± 0.002 d
P200-H20	10.32 ± 1.69 b	4.41 ± 0.30 ab	5.17 ± 0.92 c	3.14 ± 0.39 b	1.04 ± 0.27 b	0.336 ± 0.096 b	0.058 ± 0.016 bc
P400-H12	13.13 ± 1.00 a	4.04 ± 0.25 bc	8.08 ± 0.54 a	3.56 ± 0.38 ab	1.22 ± 0.29 ab	0.339 ± 0.032 b	0.050 ± 0.005 c
P400-H16	10.53 ± 0.74 b	4.65 ± 0.29 a	5.43 ± 0.84 c	3.77 ± 0.40 a	1.35 ± 0.22 a	0.426 ± 0.041 a	0.066 ± 0.002 b
P400-H20	8.17 ± 0.71 c	4.20 ± 0.41 b	4.00 ± 0.71 d	2.95 ± 0.48 bc	1.10 ± 0.24 ab	0.408 ± 0.099 ab	0.089 ± 0.009 a

Note: FW, fresh weight, DW, dry weight. Means (±standard deviation) followed by different letters within one column differ significantly ($p < 0.05$) as established by the least significant difference (LSD) test.

Root architecture of cucumber seedlings was significantly impacted by DLI. In general, higher DLI resulted in longer root length, and bigger root volume and root surface area; however, no significant differences were observed in root length, root volume, and root surface area as DLI increased from 14.40 to 28.80 mol m^{-2} d^{-1} at 21 DAS (Figure 6A–C). Total root length, root volume, and root surface area were higher in cucumber seedlings grown with DLI at 23.04 mol m^{-2} d^{-1}, and they were increased by 102.0%, 172.6% and 135.2% as DLI increased from 8.64 to 23.04 mol m^{-2} d^{-1}. The linear relationships between root fresh weight and root volume or root surface area of cucumber seedlings were observed in the study (Figure 7B,C). Similar trends were also observed between root surface area and root volume (Figure 7A).

Increasing PPFD with shorter photoperiod or prolonging photoperiod with lower PPFD increased the carbohydrate accumulation of cucumber seedlings at 21 DAS in the closed transplant production system (Table 3). Leaf fresh weight, leaf dry weight, root fresh weight, and root dry weight of cucumber seedlings grown with DLI at 23.04 mol m^{-2} d^{-1} increased by 52.2%, 154.7%, 110.9%, and 153.8%, respectively, compared with those grown with DLI at 8.64 mol m^{-2} d^{-1} at 21 DAS.

3.6. Effect of Different Combinations of Photosynthetic Photon Flux Density and Photoperiod on Glucose Content of Cucumber Seedlings at 21 Days after Sowing

Glucose content of cucumber seedlings was significantly influenced by different combinations of PPFD and photoperiod (Figure 8). Generally, longer photoperiod and higher PPFD led to higher glucose content of cucumber seedlings. Glucose content of cucumber seedlings increased by more than 1.5-fold as photoperiod increased from 12 to

20 h d^{-1}, and increased by 53.2%, 65.8%, and 83.6% as PPFD increased from 200 to 400 µmol m^{-2} s^{-1} with photoperiod at 12, 16, and 20 h d^{-1}, respectively.

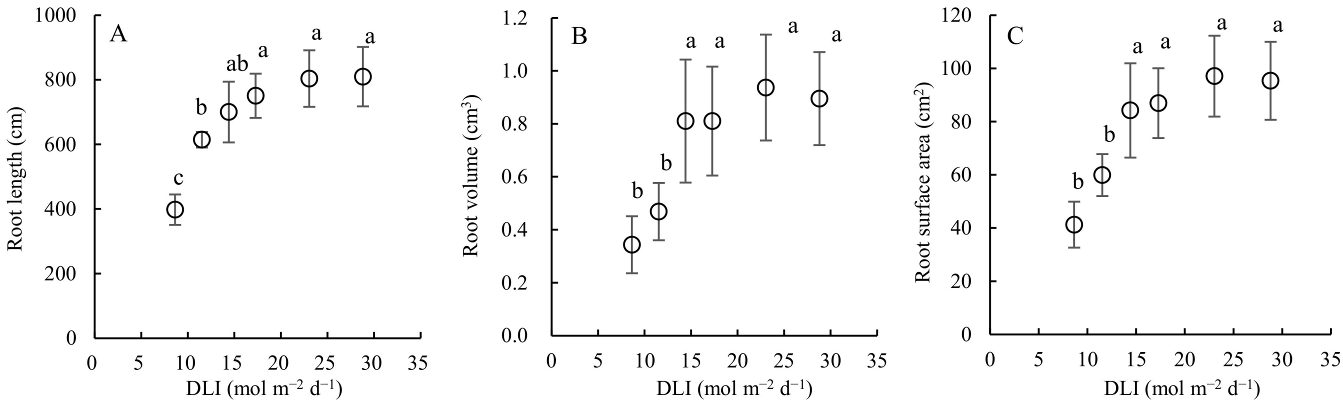

Figure 6. Effect of daily light integrals (DLIs) on (**A**) root length, (**B**) root volume, and (**C**) root surface area of cucumber seedlings at 21 days after sowing in a closed transplant system. Data are presented as mean ± standard deviation. Different letters indicate significant differences at $p < 0.05$.

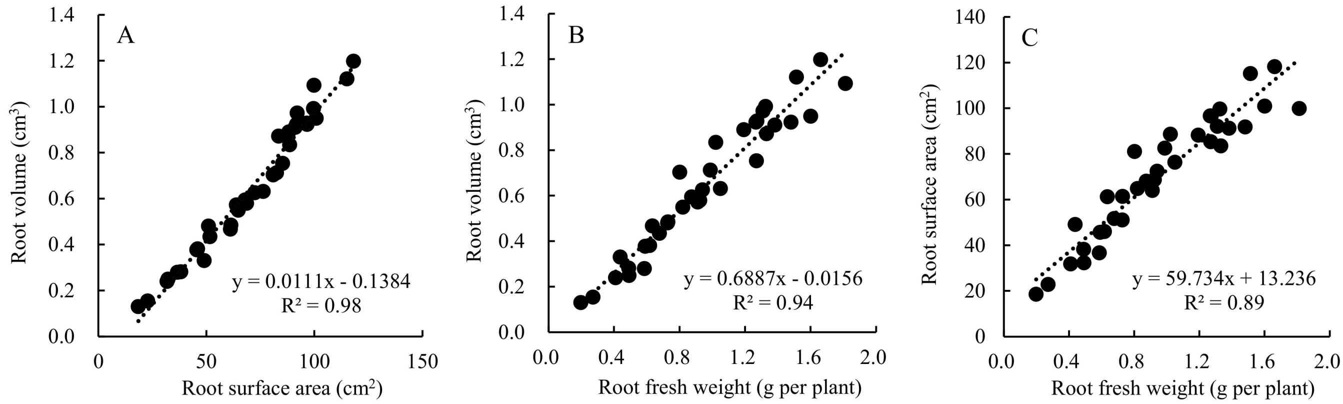

Figure 7. Relationships between (**A**) root surface area and root volume, (**B**) root fresh weight and root volume, and (**C**) root fresh weight and root surface area of cucumber seedlings at 21 days after sowing in a closed transplant system. R^2 represented correlation coefficient; x and y represented the abscissa and ordinate values, respectively.

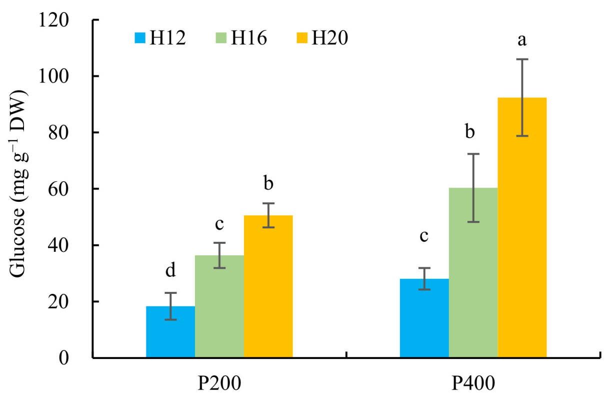

Figure 8. Effect of photosynthetic photon flux density (P) and photoperiod (H) on glucose content of cucumber seedlings at 21 days after sowing (DAS) in a closed transplant production system. Data are presented as mean ± standard deviation. Different letters indicate significant differences at $p < 0.05$.

4. Discussion

4.1. Influence of Daily Light Integral on Leaf Morphology and Root Architecture of Cucumber Seedling

Horticultural plants extend stems and leaves to capture more photosynthetic radiation, and tend to have thin stems and leaves under low PPFD or short photoperiod (low DLI) [9,33]. The decrease in hypocotyl length and plant height is associated with increased stem diameter with increasing DLI, leading to high-quality seedlings (Figure 2A,B and Table 3). Similarly, Zhang et al. [34] indicated that shoot length and hypocotyl length decreased significantly as DLI increased from 1.5 to 2.6 mol m^{-2} d^{-1} at one- or two-leaf stage of cucumber seedlings. The function of gibberellins (GA) in the regulation of hypocotyl elongation of plants was reported by Potter et al. [35], who indicated that increased light intensity reduced endogenous GA content in *Brassica* seedlings, causing inhibition of hypocotyl elongation. SLA is a vital parameter to assess plant growth as it is related to leaf area expansion and dry mass accumulation. A negative correlation was observed between DLI and SLA of cucumber seedlings (Figure 5A), mainly associated with the increased dry weight and decreased leaf area in cucumber seedlings, suggesting that higher DLI led to thicker leaves of plants. Previous studies indicated that increasing PPFD or extending photoperiod resulted in higher SLA in lettuce [19,33], sweet basil [17], and chicory plants [16]. Our results indicated that SLA of cucumber seedlings decreased with increased DLI created by combinations of PPFD and photoperiod.

Most studies focused on the aboveground parts of the crop, and few studies concentrated on the root architecture of cucumber plug seedlings grown under different DLIs. For further understanding of the influences of DLI on the underground part of the cucumber seedling, the root architecture characteristics were measured, which affect its subsequently growth directly after transplanting. The root growth of plants is regulated genetically but is also affected by environmental factors [36]. Our results showed that total root length, root volume, and root surface area increased with increasing DLI (8.64 to 14.40 mol m^{-2} d^{-1}); however, no significant differences were observed as DLI increased from 14.40 to 28.80 mol m^{-2} d^{-1}. Similarly, Park et al. [37] showed that root length of lettuce grown with PPFD at 200 µmol m^{-2} s^{-1} was longer than those grown with PPFD at 100 or 300 µmol m^{-2} s^{-1}. Generally, a relatively higher DLI-promoted root development may be due to the various photosynthetic activity of the plant canopy. We propose that the higher DLI contributes to higher photosynthates and consequently promotes root development of cucumber seedlings. Additionally, the modification of root architecture was observed to be closely related to the root fresh weight. Increased root fresh weight led to increasing root volume and root surface area linearly (Figure 7). Similarly, Chen et al. [38] reported that root volume and root surface area of eggplant seedlings grown under low PPFD (shaded) was reduced significantly compared with those grown under natural solar light. By contrast, no significant differences were observed in maximum root length of *Forsythia suspensa* [39] and *Pterocarpus santalinoides* seedlings [40] as DLI increased from 8 to 18 mol m^{-2} d^{-1} and light intensity increased from approximately 2 to 9 µmol m^{-2} s^{-1}, respectively. These differences may be due to the species, range of DLI, a DLI threshold, or other variables. In general, a longer root length, due to the penetration into the deep substrate layers, allowing roots to absorb water and nutrient elements effectively, was beneficial for plant growth.

4.2. Chlorophyll Content, Photosynthetic Parameter, Biomass Accumulation, and Glucose Content of Cucumber Seedlings Exposed to Varying Daily Light Integrals

Chlorophyll is one class of photosynthetic pigments in higher plants, which are responsible for the light absorption that drives photosynthesis [41]. A decreased trend was observed in the photosynthetic pigment of cucumber seedlings with increasing DLI (Table 2); however, the net photosynthetic rate of cucumber leaves increased and then decreased with increasing DLI (Figure 5B), suggesting that excessive or inadequate light energy resulted in inefficient electron transport within the photosynthesis system. The result may be due to the differences in thickness and mesophyll structure of cucumber leaves. Plants grown under lower DLIs trended to have an increased chlorophyll content to capture more light energy, reflecting a survival strategy of plants adapted to an environment with limited light energy. The higher total chlorophyll content in lower DLIs indicated the crop's' ability to maximize the light-harvesting capacity when plants are exposed to lower light conditions [42]. Similar trends were also observed in sweet basil [17], strawberry runner plants [31], and arugula and cabbage [43]. The net photosynthetic rate of plants was associated with both photosynthetic biochemistry and mesophyll structure of leaves. A higher net photosynthetic rate at higher DLI may be due to higher palisade cells and thicker leaves, and Dou et al. [17] indicated that mesophyll cells of basil leaves under higher DLIs are more compact than those grown under lower DLIs.

A higher biomass of cucumber seedlings was observed at higher DLIs (Figure 3A–D), which was mostly due to better root growth and greater water capacity. Quadratic functions were observed between fresh/dry weight of cucumber seedlings and DLI at different stages; however, no significant differences were found between lower DLIs at early growth stages (Figure 3A–D). Previous studies reported that linear or quadratic functions were often observed between fresh/dry weight of plants and DLI [16,30]. For instance, the linear relationships were found between fresh weight of lettuce [30] as DLI increased from 5.0 to 17.3 mol m^{-2} d^{-1}. Similar trends were also found in basil and rocket as DLI increased from 14.4 to 21.6 mol m^{-2} d^{-1} [16,17]. However, quadratic functions were found by Pennisi et al. [19] in lettuce and basil as DLI increased from 5.8 to 17.3 mol m^{-2} d^{-1}. These differences might arise from the DLIs created by different PPFDs and photoperiods or cultivars. Ji et al. [11] indicated that a maximum level of DLI at 17.3 mol m^{-2} d^{-1} provided by a fluorescent lamp is suggested for cucumber (cv. Yunv) seedling production. However, the possibility that increased DLI led to increased biomass of cucumber seedlings is still not clear. Plant growth and biomass accumulation are dependent on the photosynthetic process, which dynamically responds to the lighting environment. Biomass accumulation of crops in response to light energy often follows an optimum function, and light stress begins to occur when DLI (or PPFD) reaches its maximum. This is due to the fact that excess light energy has a detrimental impact on the photosynthetic apparatus, even resulting in physiological disorders [9,19]. Takahashi and Murata [44] demonstrated that photosystem I could be readily photo-inhibited by high light stress, as well as inhibited the repair of photosystem II. Moreover, a light saturation response occurs when plant growth is limited by other environmental factors, such as temperature and CO_2 concentration [45].

Soluble carbohydrates (e.g., glucose) are vital substrates of metabolism, which help the crop in various developmental and physiological events through regulating the import of carbon to metabolically active sinks [46]. Higher PPFD or longer photoperiod led to higher glucose content of cucumber seedlings (Figure 8). Similarly, a higher PPFD resulted in an increase in glucose content of *Arabidopsis thaliana* [47]. However, the capacity to alter the carbohydrate components may depend on the lighting strategy, plant species, and other environmental variables. For instance, no significant differences were found in glucose content among the four genotypes of cucumber plants under low and high PPFD [48].

4.3. Photon Yield of Cucumber Seedlings Grown in the Closed Transplant Seedling System as Affected by Daily Light Integral

The balance between higher plant biomass and increased electricity requirement at higher DLI should be considered for plant growth in a closed production system, which changes the crop energy use efficiency. The photon yield is used to assess the effectiveness of electric light sources for cultivating crops in a closed production system [49]. Additionally, photon yield may turn out to be a more stable indicator of plant responses to various DLIs. Photon yield of cucumber seedling decreased with increasing DLI from 8.64 to 28.80 mol m^{-2} d^{-1} at different days after sowing (Figure 4A,B). Similarly, Zheng et al. [31] reported that photon yield of hydroponic rooted strawberry runner plants decreased linearly with increasing DLI from 5.2 to 20.7 mol m^{-2} d^{-1}. These results may be due to the fact that plants utilize light energy more effectively at lower PPFD (DLI) to adapt to the light environment, as quantum yield of photosystem II (PSII) was reduced significantly with increasing PPFD [2,50]. Weaver and van Iersel [51] indicated that a larger fraction of the PSII reaction center is closed and a larger proportion of the absorbed light is dissipated as heat to reduce the damage of PSII reaction center at higher PPFD, leading to a decrease in quantum yield. However, photon yield of lettuce and basil grown in a growth chamber increased and then decreased quadratically as DLI increased from 5.8 to 17.3 mol m^{-2} d^{-1}, peaking at 14.4 mol m^{-2} d^{-1} [19], indicating that the relationship between DLI and photon yield of horticultural crops can vary among species, cultivars, and the cultivation periods. For instance, Lu et al. [52] demonstrated that photon yield of green perilla decreased as DLI increased from 5.8 to 17.3 mol m^{-2} d^{-1}; however, no significant differences were found in the photon yield of red perilla as DLI increased from 11.5 to 17.3 mol m^{-2} d^{-1}. Jayalath and van Iersel [50] demonstrated that mizuna had a higher photon yield than lettuce, which was greatest at DLI of 11.5 and 7.2–20.2 mol m^{-2} d^{-1}, respectively. The influence of the higher quantum yield of photosystem II and more chlorophyll in mizuna likely led to a higher electron transport rate and, thus, to a higher photon yield than in lettuce. Generally, cucumber seedlings had higher photon yields based on fresh and dry weights at 16 DAS compared with those grown at 6 and 11 DAS, which was not reported by previous studies. These results indicated that cucumber seedlings can convert incident light into biomass more efficiently at 16 DAS. The photon yield of cucumber seedlings increased as a result of the enhanced effectiveness of the light energy. Consequently, the increased efficiency of the lighting strategies could be applied to achieve increased biomass. The results are essential in commercial production when managing DLI at different stages of vegetable seedlings produced in a closed production system or in a greenhouse with supplementary lightings, due to the fact that the lighting cost accounts for a large portion of total production [53].

5. Conclusions

In a closed transplant production system, the increased DLI, created by different combinations of PPFD and photoperiod provided by white LED, resulted in compact and vigorous morphology but reduced photon yield of cucumber seedlings. Modification of root morphology was also observed to be closely related to the light environment. In consideration of plant growth and energy use efficiency, DLI at 14.40–23.04 mol m^{-2} d^{-1} is suggested for cucumber seedling production in a closed production system. Additionally, different control strategies should be applied at different growth stages of cucumber seedlings due to differences among treatments. Our results provide additional information on the relationship between DLI and root morphology, growth, and photon yield in cucumber seedling production along with a better understanding of how they behave under a wide range of DLI at different stages.

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