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Morphological and Physiological Properties of Greenhouse-Grown Cucumber Seedlings as Influenced by Supplementary Light-Emitting Diodes with Same Daily Light Integral

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Abstract: Insufficient light in autumn–winter may prolong the production periods and reduce the quality of plug seedlings grown in greenhouses. Additionally, there is no optimal protocol for supplementary light strategies when providing the same amount of light for plug seedling production. This study was conducted to determine the influences of combinations of supplementary light intensity and light duration with the same daily light integral (DLI) on the morphological and physiological properties of cucumber seedlings (*Cucumis sativus* L. cv. Tianjiao No. 5) grown in a greenhouse. A supplementary light with the same DLI of 6.0 mol m^{-2} d^{-1} was applied with the light duration set to 6, 8, 10, or 12 h d^{-1} provided by light-emitting diodes (LEDs), and cucumber seedlings grown with sunlight only were set as the control. The results indicated that increasing DLI using supplementary light promoted the growth and development of cucumber seedlings over those grown without supplementary light; however, opposite trends were observed in the superoxide dismutase (SOD) and catalase (CAT) activities. Under equal DLI, increasing the supplementary light duration from 6 to 10 h d^{-1} increased the root surface area (66.8%), shoot dry weight (24.0%), seedling quality index (237.0%), root activity (60.0%), and stem firmness (27.2%) of the cucumber seedlings. The specific leaf area of the cucumber seedlings decreased quadratically with an increase in supplementary light duration, and an opposite trend was exhibited for the stem diameter of the cucumber seedlings. In summary, increased DLI or longer light duration combined with lower light intensity with equal DLI provided by supplementary light in insufficient sunlight seasons improved the quality of the cucumber seedlings through the modification of the root architecture and stem firmness, increasing the mechanical strength of the cucumber seedlings for transplanting.

Keywords: antioxidant enzymes; light quantity; light use efficiency; root activity; stem firmness

1. Introduction

Vegetables are vital components of healthy diets, which are related to lower mortality and morbidity in adult life [1]. In China, the vegetable planting area and the demand for vegetable seedlings were more than 20 million hectares and 680 billion in 2018, respectively [2]. Cucumber (*Cucumis sativus* L.) is one of the most cultivated vegetables worldwide and is economical to produce, with an annual production of 87.8 million tons in 2019, with 80.1% grown in China [3]. However, pronounced differences can be observed in terms of cucumber yield, with the highest and lowest cucumber yields in China being 150,000 kg per hectare and 56,000 kg per hectare, respectively [4]. Previous studies have demonstrated that the quality of vegetable seedlings affects the subsequent growth, yield, and the nutritional quality of mature plants at harvest [5,6]. Therefore, high-quality seedlings are essential to increase crop yield and economic benefits.

Light plays an important role in regulating the architectural development and secondary metabolites of plants [6,7]. Three main variables should be considered regarding the light requirements in horticulture: light intensity, the photoperiod, and light quality. The relatively low light intensity and short photoperiod of sunlight during autumn–winter and early spring results in plants having a longer hypocotyl length [8], lower flavonol content [9], and ultimately culminates in a lower yield [10]; thus, supplementary light is required for greenhouse-grown plants in insufficient sunlight seasons. The daily light integral (DLI, the product of the light intensity and the photoperiod) can be increased through the application of supplementary light, and increasing the DLI in certain situations can shorten growth cycles [6], promote carbohydrate accumulation [11], and increase the crop yield [12,13] and the nutritional quality [14,15] of plants.

Prior studies have indicated that 1% of additional light results in a 0.5% to 1% increase in the amount of harvestable product [5,16]. The dry mass [8], flower truss [13], and fruit weight [17] of greenhouse-grown plants grown with supplementary light increased by more than 23.0%, 12.5%, and 26.5%, respectively, compared to those grown without supplementary light. Supplementary light intensity [18] and duration [19,20] with different DLIs were investigated in greenhouse-grown plants in previous studies. Generally, increasing the light intensity or extending the supplementary light duration (with increasing DLIs) enhanced crop productivity under limited light conditions. Additionally, several combinations of light intensity and photoperiods with the same DLI were conducted in lettuce (*Lactuca sativa*) [21,22], mizuna (*Brassica rapa* var. *japonica*) [23], and strawberry (*Fragaria* × *ananassa*) seedlings [24] in a plant factory with artificial lighting. However, no information about the application of supplemental light with the same DLI is available for greenhouse-grown cucumber seedlings.

Artificial lighting has developed dramatically in the protected cultivation industry in recent decades, allowing it to be applied in fully controlled plant factories or as supplementary light in greenhouses [6,12,25]. Conventional light sources, such as high-pressure sodium (HPS), have a high operating temperature, low electrical efficiency, and limited controllability [1,10]. In contrast, light-emitting diodes (LEDs) provide tremendous potential for horticultural lighting in modern agriculture compared to conventional horticultural light sources due to their long functional life [26], lower heat production [25], spectral configuration flexibility [27], and high photosynthetically active radiation efficiency [28]. HPS lamps have been replaced by LED lamps in controlled agricultural environments, such as in growth chambers and greenhouses, in recent years [29,30]. Red plus blue LEDs were widely examined in various plant experiments due to the absorption spectra of the photosynthetic pigments of higher plants.

Supplementary lights with different red light to blue light ratios (R:B) were investigated in tomato (*Solanum lycopersicum*) seedlings [26], cucumber seedlings [8], peppers (*Capsicum frutescens*) [19], lettuce [31], and basil (*Ocimum basilicum*) [32] in grown in a greenhouse. However, plants have adapted to the broadband spectrum through long-term evolution [33]. Previous studies have shown that horticultural plants grown under white LEDs have higher photosynthetic activity than those grown under monochromatic light [34,35] and that white LEDs lead to higher light energy use efficiency in green leaf lettuce production than red plus blue LEDs [15]. Moreover, the energy consumption of different light strategies should be considered for commercial growers in greenhouse crop production [32]. Therefore, a suitable supplementary lighting strategy provided by white LEDs that considers energy consumption was needed for further investigation in cucumber seedling production.

The aim of this study was to evaluate the impacts of white LEDs as supplementary light with equal DLI on the leaf morphology, pigment content, photosynthetic characteristics, biomass accumulation, root architecture, and antioxidant enzyme activities of cucumber seedlings grown in a greenhouse. The results could be applied as guidelines for a light management strategy wherein supplemental light is administered to cucumber seedlings produced in greenhouses during the autumn–winter period or early spring.

2. Materials and Methods

2.1. Plant Materials and Growth Conditions

Cucumber (*Cucumis sativus* L. cv. Tianjiao No. 5) seeds were sown in a substrate containing a mixture of vermiculite, peat, and perlite (3:1:1, *V*/*V*/*V*) in 72-cell trays (53.5 cm × 27.5 cm × 4.0 cm) in the Venlo-type greenhouse in Qingdao Agricultural University, Qingdao, Shandong Province, China, for 21 days. Gutter height, peak height, and floor area of the greenhouse were 4.5 m, 6.0 m, and 2736 m^2, respectively. Day and night temperatures in the greenhouse were controlled at (25 ± 2) °C and (18 ± 2) °C, respectively, by using a ground source heat pump system. Relative humidity was maintained at 60–70% inside the greenhouse. Hoagland's nutrient solution was applied with an electrical conductivity of 1.8–2.0 mS cm^{-1} and pH of 6.0–6.5 with 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; and $(NH_4)_6Mo_6O_{24}{\cdot}4H_2O$, 0.02. Tap water and 1/2 strength standard nutrient solution were used two days after the sowing and cotyledon stage, respectively. The standard Hoagland's nutrient solution was used after the first true leaf emerged.

2.2. Light Treatments

The average daily light intensity of natural light in the Venlo-type greenhouse was 160 μmol m^{-2} s^{-1} during the experimental period (3–24 December 2020), with an average daily light integral of 5.5 mol m^{-2} d^{-1}. Combined with the suitable daily light integral for the growth of cucumber seedlings based on our previous study [36], they were grown under supplemental DLI at 6.0 mol m^{-2} d^{-1} created by four levels of light intensity at 278, 208, 167, and 139 μmol m^{-2} s^{-1} combined with supplementary light duration at 6, 8, 10, and 12 h d^{-1} provided by white LEDs (Weifang Hengxin Electric Appliance Co., Ltd., China) for 21 days. The supplementary lighting time in the morning and in the afternoon was the same. In addition, cucumber seedlings grown without supplementary light were set as the control (DLI at 5.5 mol m^{-2} d^{-1} from solar radiation only). A randomized complete block designed with three replications and 72 seedlings in each replication was cultivated in this experiment. Each treatment had three plug trays, and each tray was considered as a replication. Spectral distribution of the LED lamps (Figure 1) used in this study as supplementary light was measured by a spectrometer (PG100N, United Power Research Technology Corporation, China) at the plant canopy.

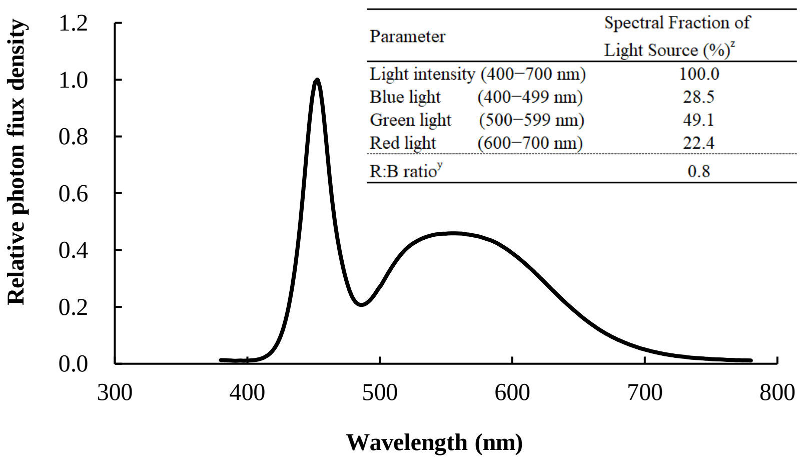

Figure 1. Relative photon flux density of the supplementary light source (white light emitting-diodes) used in the experiment. [z] Data are photon flux-based fractions of blue, green, and red lights. [y] R:B ratio, red light to blue light ratio.

2.3. Growth Measurements

2.3.1. Measurements of Photosynthetic Performance

Net photosynthetic rate, transpiration rate, substomatal CO_2 concentration, and stomatal conductance were measured on the fully expanded leaf by a portable photosynthesis system (LI-6400XT, Li-Cor Inc., Lincoln, NE, USA). Light intensity, leaf temperature, gas flow, and CO_2 concentration in the leaf chamber (6400-02B) were controlled at 400 μmol m^{-2} s^{-1}, 25 °C, 500 μmol s^{-1}, and 400 μmol mol^{-1}, respectively. The soil plant analysis development (SPAD) index of the fully expanded leaf was recorded to quantify relative chlorophyll contents of cucumber seedlings by using a chlorophyll meter (SPAD-502 Plus, Konica Minolta Inc., Tokyo, Japan).

2.3.2. Measurements of Plant Morphology and Growth Parameters

Leaf length and leaf width of maximum leaf blade, shoot, and root fresh weights were measured at 21 days after sowing. The fresh weights of shoots and roots were measured by an electronic analytical balance (FA1204B, BioonGroup, Shanghai, China). Additionally, the fresh roots of cucumber seedlings were washed twice carefully with distilled water, and scanned by a scanning system (V800, Seiko Epson Corp., Nagano, Japan). The data of root surface area and root volume were obtained and analyzed using WinRHIZO software (Version 2016a, Regent Instruments Inc., Quebec, QC, Canada). The shoots and roots were dried in an oven at 105 °C for 3 h, and the oven was subsequently set to 80 °C for 72 h for measuring the dry weights. Seedling quality index and specific leaf area (SLA) of cucumber seedlings were calculated according to Han et al. [37] and Ghorbanzadeh et al. [11], where seedling quality index = (stem diameter/plant height + root dry weight/shoot dry weight) × total dry weight and specific leaf area = leaf area/leaf dry weight.

2.3.3. Measurement of Root Activity

The triphenyl tetrazolium chloride (TTC) method was used to determine the root activity of cucumber seedlings, following Li [38]. The 5 mL TTC (4%) and 5 mL phosphate buffers were added to root samples (0.5 g) in a tube, and then the tube was kept at 37 °C in the dark for 2 h. The reaction was stopped with 2 mL H_2SO_4 (1 mol L^{-1}). Seedling roots were ground and transferred into a tube with ethyl acetate up to 10 mL. The absorbance of the test sample was measured using a spectrophotometer (UV1810, Shanghai Yoke Instrument Co., Ltd., China) at the wavelength of 485 nm.

2.3.4. Stem Firmness and Cellulose Content of Cucumber Seedlings

Stem firmness of cucumber seedlings was measured by a texture analyzer (TMS-Pro, Food Technology Corporation, USA) equipped with a 2 mm diameter probe, which was expressed in Newtons (N). The Updegraff method was used to measure the cellulose of cucumber stems [39].

2.3.5. Measurements of Activities of Antioxidant Enzymes

Leaf samples (0.5 g) were ground in pre-chilled 5 mL of 50 mM phosphate buffer (pH 7.8). The homogenate was centrifuged at 12,000× g for 20 min at 4 °C and the supernatant was applied as enzyme extract. Superoxide dismutase (SOD) activity was measured by determining its ability to inhibit the photochemical reduction in nitroblue tetrazolium (NBT) at a wavelength of 560 nm following the method of Giannopolitis and Ries [40]. Catalase (CAT) activity was assayed based on the oxidation of H_2O_2 and measured as a decline at a wavelength of 240 nm using the above spectrophotometer, as described by Aebi [41].

2.3.6. Supplementary Light Use Efficiency

Supplementary light use efficiency was calculated based on the increase in dry weight, which was reported by Wei et al. [20], where supplementary light use efficiency = ΔBiomass

(Treatment biomass − CK biomass)/(supplementary light duration × leaf area × supplementary light intensity).

2.4. Statistical Analysis

One-way analysis of variance (ANOVA) was conducted using SPSS 19.0 software (IBM, Inc., Chicago, IL, USA) followed by the least significant difference (LSD) test to compare the means between treatments ($p < 0.05$). The results were reported as the mean ± standard deviation values. The regression analysis between treatments and morphological properties of cucumber seedlings was carried out using Microsoft Excel 2016 software.

3. Results and Discussion

3.1. Impacts of Supplementary Light Duration and Light Intensity on Photosynthetic Characteristics of Cucumber Seedlings

The chlorophyll content (SPAD) and photosynthetic characteristics of the cucumber seedlings were significantly influenced by supplementary light (Table 1). The chlorophyll contents of cucumber seedlings increased with the increase in supplementary light duration. However, no pronounced differences were observed as supplementary light duration increased from 8 to 12 h d^{-1} with equal DLI. Increased trends in chlorophyll content were also observed in lettuce [42] and Rudbeckia seedlings [43] grown with a longer photoperiod with equal DLI. This may be due to the fact that longer photoperiod with lower light intensity resulted in shade acclimation responses to capture more light energy. The previous studies also indicated that chlorophyll could be synthesized only in light; thus, extending the photoperiod was beneficial for the synthesis of photosynthetic pigments [44]. In addition, Ni et al. [45] indicated that the shading treatment (15% light intensity, 85% shaded) could promote Passiflora plant (Tainung No. 1) growth in SPAD compared with the non-shaded treatment, suggesting that long-term low-light-intensity treatment increased the relative chlorophyll concentration per leaf area in Passiflora plants. Similar trends were also observed in lettuce [46,47], chicory (Cichorium intybus) [46], cucumber seedlings [4], and strawberry plants [48,49].

Table 1. Photosynthetic characteristics of cucumber seedlings grown in the greenhouse for 21 days after sowing as affected by supplementary light-emitting-diodes with light duration at 0, 6, 8, 10, and 12 h d^{-1} with the same daily light integral.

Supplementary Light Duration ($h \cdot d^{-1}$)	Chlorophyll Content (SPAD)		Net Photosynthetic Rate ($\mu mol \cdot m^{-2} \cdot s^{-1}$)		Transpiration Rate ($mmol \cdot m^{-2} \cdot s^{-1}$)		Substomatal CO_2 Concentration ($\mu mol \cdot mol^{-1}$)		Stomatal Conductance ($mmol \cdot m^{-2} \cdot s^{-1}$)	
0	44.6 ± 2.7	c [z]	3.5 ± 0.4	d	0.39 ± 0.01	c	187 ± 18	c	27.9 ± 0.8	c
6	49.6 ± 5.8	b	6.0 ± 0.6	c	0.68 ± 0.06	b	220 ± 12	b	58.4 ± 1.7	b
8	52.7 ± 1.2	ab	6.8 ± 0.3	b	1.14 ± 0.18	a	267 ± 24	a	97.4 ± 17.6	a
10	53.6 ± 3.0	ab	7.9 ± 0.4	a	1.05 ± 0.14	a	238 ± 13	ab	89.8 ± 12.7	a
12	56.1 ± 0.9	a	6.8 ± 0.4	b	0.76 ± 0.09	b	193 ± 17	bc	58.1 ± 9.1	b

[z] Different letters in the same column indicate significant differences based on the least significant difference (LSD) test at $p < 0.05$.

The net photosynthetic rate of the cucumber seedlings increased as the supplementary light increased from 0 to 10 h d^{-1}, and decreased as the supplementary light increased from 10 to 12 h d^{-1}. Similar trends were found in the transpiration rate, substomatal CO_2 concentration, and stomatal conductance. The net photosynthetic rate, transpiration rate, substomatal CO_2 concentration, and stomatal conductance of cucumber seedlings grown under the supplementary light duration of 10 h d^{-1} increased by 125.7%, 169.2%, 27.3%, and 221.9%, respectively, compared with those grown without supplementary light. These results suggest that prolonging the supplementary light duration with equal DLI within certain ranges promotes the accumulation of photosynthetic pigments and CO_2 exchange rate of plants. However, too long a photoperiod with low light intensity was not suitable for cucumber seedlings under equal DLI. These results demonstrate that it was not useful to provide a high light intensity, as plants cannot utilize the light efficiently to drive photosynthesis [50], which is consistent with the results of a previous study by Weaver and van Iersel [42]. The increased photosynthetic capacity was associated with the increased SPAD and thicker leaves (Figure 2), which may contain more chloroplasts per leaf area, leading to an increase in biomass. Dou et al. [51] reported similar results.

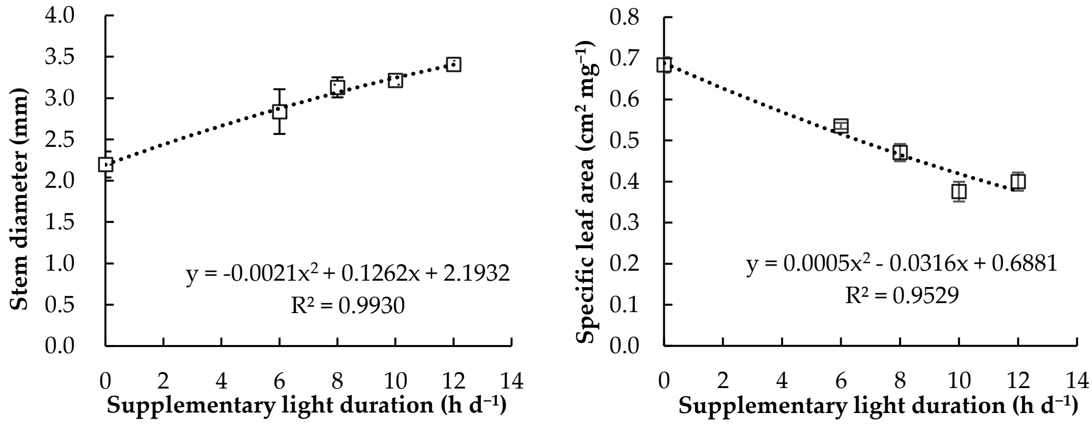

Figure 2. Relationships between supplementary light duration with the same daily light integral and morphological characteristics of cucumber seedlings grown in the greenhouse for 21 days after sowing.

3.2. Influences of Supplementary Light Duration and Light Intensity on Plant Morphology and Growth of Cucumber Seedlings

The supplementary light duration and the light intensity with the same DLI significantly affected the leaf morphology and carbohydrate accumulation of the cucumber seedlings (Table 2). Previous studies suggested that high-quality seedlings should exhibit thick leaves, firm stems, and large white roots [5]. The seedling quality index of cucumber seedlings grown under supplementary light duration with 10 h d^{-1} increased by more than 7-fold compared with those grown without supplementary light. The cucumber seedlings that were exposed to supplementary light resulted in a larger leaf area and higher dry weights of the shoot and root than those grown without supplementary light. The leaf length and leaf width of the cucumber seedlings grown with supplementary light duration at 10 h d^{-1} were 52.5% and 70.4% higher, respectively, than those of the seedlings grown without supplementary light. Cucumber seedlings grown under long supplementary light durations with low light intensity demonstrated an increase in the occurrence of shade avoidance responses, including increased leaf elongation, which increased light interception [15,52]. In general, longer supplementary light duration with the same DLI resulted in higher fresh and dry weights of the cucumber seedlings as the supplementary light duration increased from 6 to 10 h·d^{-1}, and decreased as the supplementary light duration exceeded 10 h d^{-1}, indicating that light drives photochemistry more efficiently at relatively lower light intensity [21,50]. Kelly et al. [22] reported similar results, observing that lettuce grown under a longer photoperiod with a lower light intensity had greater fresh and dry weights than those grown under a shorter photoperiod with a higher light intensity with the same DLI at 10.4 mol·m^{-2}·d^{-1} under a controlled environment. This is likely due to the fact that longer photoperiod with same DLI resulted in higher daily photochemical integral (electron transport rate integrated over a 24 h period) and quantum yield of photosystem II (ΦPSII) [21]. Previous studies suggested that a larger portion of the PSII reaction center closed as the light intensity increased due to the unacceptable additional excitation energy, leading to decreased ΦPSII of sweet potato (*Ipomoea batatas* (L.) Lam.) [6], lettuce [21,40], and golden pothos (*Epipremnum aureum*) [50] with increase in the light intensity. Supplementary light with DLI at 17 mol·m^{-2}·d^{-1} was conducted in greenhouse-grown lettuce by Weaver and van Iersel [40], who concluded that a longer photoperiod with lower light intensity promoted plant growth due to increased photosynthetic light use efficiency. Nevertheless, prolonging the photoperiod (with decreased light intensity) beyond certain ranges was not beneficial for plant growth; this phenomenon was due to the fact that too weak a source of light was inadequate to drive appreciable amounts of photosynthesis (Table 1). Additionally, too long a photoperiod could cause leaf chlorosis and decrease the crop yield [53].

The stem diameter of the cucumber seedlings was positively correlated with supplementary light duration and the SLA of cucumber seedlings exhibited an opposite trend (Figure 1), allowing us to infer that longer light duration with lower light intensity resulted in thick stems and thin leaves with a larger leaf area (Table 2). The SLA of the cucumber seedlings significantly decreased with the administration of supplementary light, which was consistent with previous studies. Previous studies demonstrated that lower DLI led to higher SLA in tomato plants [54], sweet basil [51], and lettuce [11]. However, a decreased trend was observed in the SLA of cucumber seedlings grown with a decreased light intensity (increased light duration) with the same DLI (Figure 2), suggesting that the decreased SLA of cucumber seedlings was due to the impacts of light duration instead of light intensity in plants grown with the same DLI. A previous study indicated that the SLA of basil and chicory presented linear negative responses to an increased photoperiod [55]. Similarly, Elkins and van Iersel [43] observed that the SLA of *Rudbeckia* seedlings decreased linearly from 266 to 197 $cm^2\ g^{-1}$ as the photoperiod increased from 12 to 21 $h\ d^{-1}$ with same DLI at 12 $mol\ m^{-2}\ d^{-1}$. However, no significant differences were observed in the SLA of greenhouse-grown lettuce supplemented with different combinations of light intensity and photoperiod with the same DLI at 17.0 $mol\ m^{-2}\ d^{-1}$ [42]. These differences may be due to the different species, supplementary DLI, or lighting strategies.

The root morphology of the cucumber seedlings was significantly impacted by different combinations of supplementary light intensity and light duration with the same DLI (Figure 3A). The root surface area and root volume increased significantly in cucumber seedlings exposed to supplementary light compared to those grown without supplementary light. The root surface area and root volume increased as the supplementary light duration increased from 6 to 8 $h\ d^{-1}$, but no pronounced differences were found when the supplementary light duration increased from 8 to 12 $h\ d^{-1}$ (Figure 3B,C).

The root quality influenced the growth of the vegetable seedlings directly after transplanting, thus affecting the subsequent yield and nutritional quality of the crops [6,20]. Few studies have been performed on the root growth and physiology of cucumber seedlings grown under different combinations of light intensity and light duration with the same DLI. A previous study suggested that high DLI led to better-developed roots, such as longer root length, thicker root diameter, of Platycodon grandiflorum [56] and Fagus sylvatica seedlings [57] than those exposed to shading conditions and to a higher root fresh weight. The root activity reflected the ability of the roots to absorb nutrients and water or to synthesize certain compounds in the surrounding rhizosphere. The root activity of the cucumber seedlings grown with supplementary light duration at 10 $h\ d^{-1}$ was 1.3-fold higher than those grown with sunlight only (Figure 3D). This may be due to the fact that higher shoot activity contributed partly or fully to higher root activity. Under equal DLI, higher root activity was observed in those cucumber seedlings exposed to supplementary light with a longer photoperiod at 10 $h\ d^{-1}$ and 12 $h\ d^{-1}$ (Figure 3D). Li et al. [58] demonstrated that the average root number of Acacia melanoxylon increased significantly with a prolonged photoperiod, but this trend was not observed in the average root length. A large root absorption area with higher root activity promoted plant growth, which was consistent with other reports [59].

Table 2. Growth and morphological properties of greenhouse-grown cucumber seedlings with supplementary light duration at 0, 6, 8, 10, and 12 h d^{-1} with the same daily light integral provided by light-emitting diodes.

Supplementary Light Duration ($h\ d^{-1}$)	Leaf Length (cm)		Leaf Width (cm)		Shoot Fresh Weight ($g\ plant^{-1}$)		Root Fresh Weight ($g\ plant^{-1}$)		Shoot Dry Weight ($g\ plant^{-1}$)		Root Dry Weight ($g\ plant^{-1}$)		Seedling Quality Index	
0	5.9 ± 0.4	c [z]	5.4 ± 0.5	d	0.96 ± 0.05	c	0.040 ± 0.004	e	0.073 ± 0.008	d	0.002 ± 0.001	d	0.011 ± 0.001	e
6	7.6 ± 0.1	b	7.3 ± 0.6	c	2.97 ± 0.18	b	0.312 ± 0.031	d	0.271 ± 0.016	c	0.018 ± 0.002	c	0.027 ± 0.002	d
8	7.7 ± 0.5	b	8.1 ± 0.3	b	3.22 ± 0.25	b	0.645 ± 0.049	c	0.315 ± 0.004	ab	0.046 ± 0.005	b	0.061 ± 0.004	c
10	9.0 ± 0.1	a	9.2 ± 0.3	a	4.53 ± 0.26	a	1.191 ± 0.131	a	0.336 ± 0.032	a	0.064 ± 0.004	a	0.091 ± 0.005	a
12	8.1 ± 0.4	b	8.0 ± 0.4	b	4.09 ± 0.44	a	0.769 ± 0.037	b	0.298 ± 0.011	b	0.048 ± 0.002	b	0.070 ± 0.002	b

[z] Different letters in the same column indicate significant differences based on the least significant difference (LSD) test at $p < 0.05$.

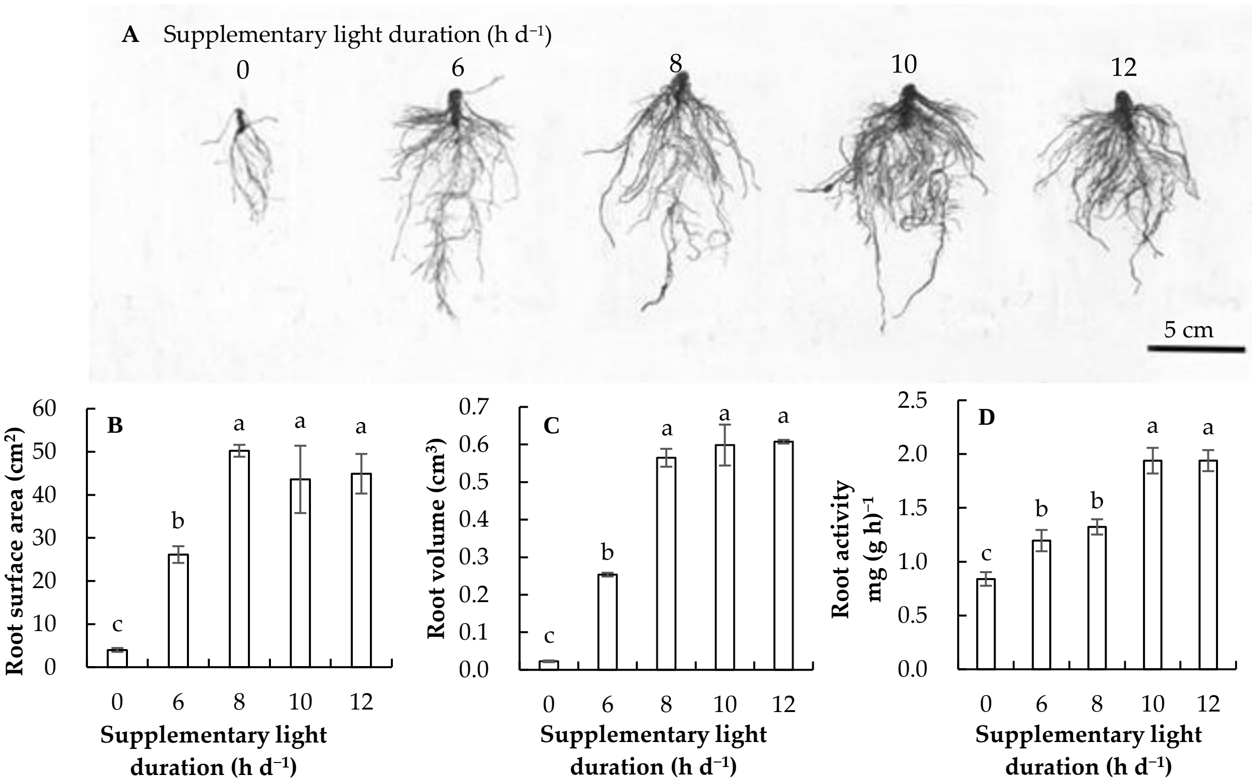

Figure 3. Effects of supplementary light duration with same daily light integral on root morphology and root activity of cucumber seedlings grown in the greenhouse for 21 days after sowing. (**A**) One representative picture was shown for each treatment, (**B**) root surface area, (**C**) root volume, and (**D**) root activity. Means followed by different letters within each parameter are significantly different based on the least significant difference (LSD) test ($p < 0.05$). Error bars show mean ± standard deviation.

3.3. Effects of Supplementary Light Duration and Light Intensity on Stem Firmness and Cellulose Content of Cucumber Seedlings

In general, the stem firmness of the cucumber seedlings increased with the increase in supplementary light duration. The stem firmness of the cucumber seedlings grown with supplementary light increased by more than 30% when compared with cucumber seedlings grown under sunlight only. Generally, positive relationships between cellulose content and stem firmness were observed in the cucumber seedlings; however, no significant differences were found in the cellulose content of the cucumber seedlings grown with supplementary light with the same DLI (Figure 4), as stem firmness could be associated with other chemical compounds, such as pectins, lignin, and hemicelluloses, and these associations also require further study.

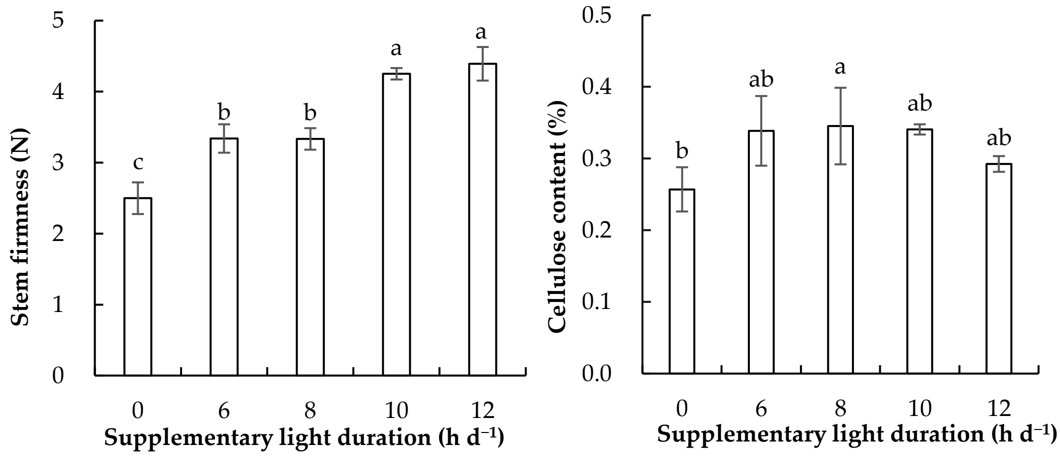

Figure 4. Effects of supplementary light duration with the same daily light integral on stem firmness and cellulose content of cucumber seedlings grown in the greenhouse for 21 days after sowing. Means followed by different letters within each parameter are significantly different based on the least significant difference (LSD) test ($p < 0.05$). Error bars show mean ± standard deviation.

Plant cell walls are constantly remodeled during growth and development and modified in accordance with the environment. Cellulose is the principal component of plant cell walls, which play a critical role in the mechanical strength and morphogenesis of plants [60,61]. Prior studies have demonstrated that soybean (*Glycine max* (L.) Merr.) [60] and maize (*Zea mays* L.) [62] with higher cellulose content in their stems had more lodging resistance than those with lower cellulose content. The cucumber seedlings grown with 8 h d^{-1} supplementary light duration had higher cellulose contents than those grown without supplementary light (Figure 4). No remarkable differences were observed in the cellulose contents of the cucumber seedlings as the supplementary light duration increased from 6 to 12 h d^{-1} with the same DLI.

3.4. Effects of Supplementary Light Duration and Light Intensity on Activities of Antioxidant Enzymes of Cucumber Seedlings

Previous studies suggested that insufficient or excessive light could cause abiotic stresses to grafted watermelon (Citrullus vulgaris) seedlings [20], tomato seedlings [63], and cucumber seedlings [4]. The duration of the supplementary light significantly influenced the activities of the antioxidant enzymes of the cucumber seedlings (Figure 5). The activities of the SOD and CAT were the highest in the cucumber seedlings grown without supplementary light; exposure to supplementary light resulted in decreased activities of the SOD and CAT of the cucumber seedlings compared those grown without supplementary light. The increase in SOD activity in the seedlings that were not treated with supplementary light might be due to the increased production of superoxide radicals, consummating the dismutation of the superoxide radical to hydrogen peroxide [64]. Zhang et al. [65] and Gong et al. [66] reported similar results. However, no pronounced differences were observed in the CAT activity of the cucumber seedlings grown with supplementary light; this may be due to the same DLI provided by the supplementary LEDs. Our results also demonstrated that an undesired light environment (low DLI) resulted in stress resistance in the cucumber seedlings. Zhang et al. [67] indicated that the CAT activities of the cucumber seedlings were reduced by the supplementary light, and it was also related to the light quality, observing that the activity of the CAT of the cucumber seedlings was increased by increasing the blue light proportion as compared to those not treated with supplementary light. Zrig et al. [68] reported similar results, observing that *Thymus vulgaris* L. cultivated in a shady enclosure had a higher SOD and CAT than those cultivated in an open field. Opposite trends were observed the in fresh weight and activities of the antioxidant enzymes in tomato seedlings [69] and peanut (*Arachis hypogaea* L.) seedlings [70], which were consistent with our results. Plants' own reactive oxygen species (ROS) scavenging enzymes, including

SOD and CAT, can adapt to diverse stresses. The accumulation of ROS is detrimental to the photosynthetic systems, and Lu et al. [71] indicated that the lower electron transportation activity between PSII and PSI probably turns the photosynthetic apparatus into a strong ROS source.

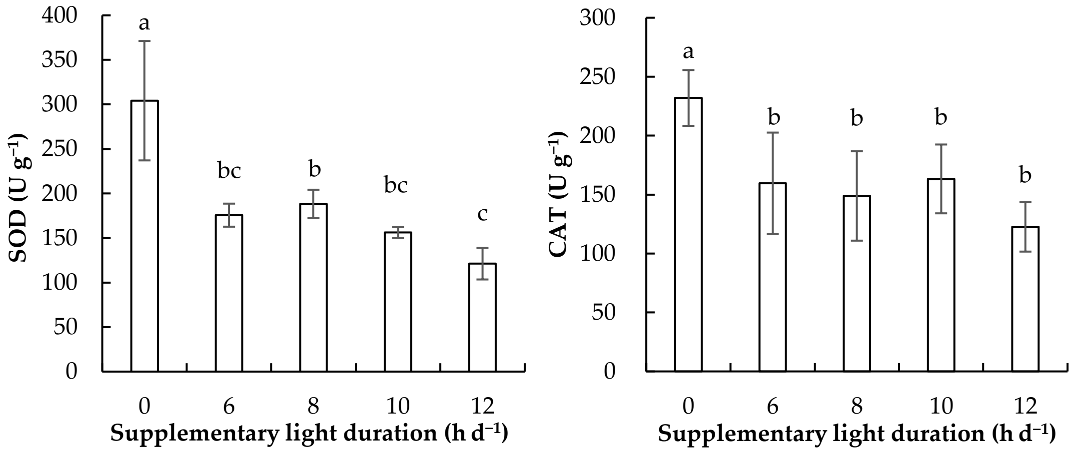

Figure 5. Effects of supplementary light duration with the same daily light integral on the activities of superoxide dismutase (SOD) and catalase (CAT) of cucumber seedlings grown in the greenhouse for 21 days after sowing. Means followed by different letters within each parameter are significantly different based on the least significant difference (LSD) test ($p < 0.05$). Error bars show mean ± standard deviation.

3.5. Supplementary Light Use Efficiency in Cucumber Seedlings Grown in a Greenhouse

The supplementary lighting costs in the greenhouse could be high due to the increased electricity consumption [50]. Thus, effective lighting strategies considering supplementary light use efficiency should be developed [43]. From an energy saving perspective, no pronounced differences were found in supplementary light use efficiency among cucumber seedlings grown with 6, 8, and 10 h d^{-1} of supplementary light (Figure 6), this was due to the fact that similar trends were observed in the leaf area and dry weight as supplementary light duration increased from 6 to 10 h d^{-1} with the same DLI. The decrease in the dry weight and leaf area in the cucumber seedlings grown with supplementary light duration at 12 h d^{-1} led to the decrease in supplementary light use efficiency. Supplementary light duration at 12 h d^{-1} led to the lowest light utilization rate among the supplementary treatments. Wei et al. [20] indicated that 16 h d^{-1} of supplementary light had a lower light use efficiency of the light compared to the 12 h d^{-1} in grafted watermelon seedlings. Additionally, cucumber rootstocks [72], perilla (Perilla frutescens) [14], and strawberry runner plants [49] exposed to higher light intensity or a longer photoperiod with higher DLI had lower light use efficiency.

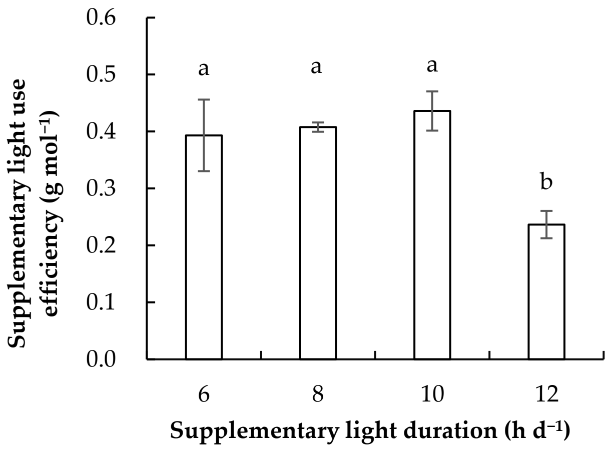

Figure 6. Supplementary light use efficiency of cucumber seedlings grown with light duration at 6, 8, 10, and 12 h d^{-1} with the same daily light integral in the greenhouse for 21 days after sowing. Means followed by different letters within each parameter are significantly different based on the least significant difference (LSD) test ($p < 0.05$). Error bars show mean ± standard deviation.

4. Conclusions

The leaf morphology, photosynthetic characteristics, biomass accumulation, root architecture, and antioxidant enzyme activities of the greenhouse-grown cucumber seedlings were significantly affected by different combinations of light intensity and light duration, with equal DLI provided by supplementary light. In general, increasing DLI with supplementary light promoted the growth and development of the cucumber seedlings grown in seasons where the amount of natural light was insufficient. Additionally, the quality of the cucumber seedlings could be improved by applying relatively longer light durations combined with lower light intensity, which resulted in the modification of the root architecture and an improvement in the stem firmness, increasing the mechanical strength of the cucumber seedlings for transplanting.

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