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Nocturnal LED Supplemental Lighting Improves Quality of Tomato Seedlings by Increasing Biomass Accumulation in a Controlled Environment

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Abstract: Tomato (*Solanum lycopersicum* L. cv. Zhongza NO. 9) was used as the experimental material to investigate the effects of nocturnal LED supplemental light with the photosynthetic photon flux density (PPFD) of 100, 200, 300 μmol·m^{-2}·s^{-1}, and the light time of 1, 2 h on the seedling quality in a controlled environment, with seedlings without nocturnal supplemental lighting serving as the control. The results demonstrate that an increase in PPFD at night progressively enhances the plant height and leaf number of tomato seedlings, while stem diameter and leaf area initially increase and subsequently decrease. Although light time and light period-of-time at night did not significantly affect seedling morphology, PPFD and light time notably influenced chlorophyll content and net photosynthetic rate. An optimal lighting energy amount at night augmented photosynthetic capacity. However, excessive PPFD induced photoinhibition in the leaves. Additionally, appropriate nocturnal LED supplemental lighting significantly improved the antioxidant capacity of the seedlings, increased proline content, reduced malondialdehyde content, and bolstered the self-protection mechanisms of the seedlings against nocturnal light stress. Both the PPFD and light time at night promoted biomass accumulation in tomato seedlings. Specifically, when supplemental lighting was applied for 2 h at an intensity of 200 μmol·m^{-2}·s^{-1}, both the fresh and dry weights of the shoot and root significantly increased, and the seedling health index was highest. Therefore, appropriate nocturnal LED supplemental lighting positively impacts the health index and photosynthate accumulation of tomato seedlings, but controlling PPFD is essential to avoid photoinhibition.

Keywords: supplementary lighting; seedling quality; chlorophyll fluorescence; MDA; light stress

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Citation: Song, J.; Zhang, R.; Yang, F.; Wang, J.; Cai, W.; Zhang, Y. Nocturnal LED Supplemental Lighting Improves Quality of Tomato Seedlings by Increasing Biomass Accumulation in a Controlled Environment. *Agronomy* **2024**, *14*, 1888. https://doi.org/10.3390/agronomy14091888

Academic Editor: Małgorzata Szczepanek

Received: 24 July 2024
Revised: 20 August 2024
Accepted: 22 August 2024
Published: 24 August 2024

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1. Introduction

Tomato (*Solanum lycopersicum*) is a horticultural vegetable widely cultivated across the globe, known for its high nutritional value and significant economic benefits. In 2022, the tomato cultivation area in China exceeded 1.33 million hectares, with over two-thirds utilizing nursery transplant methods for production [1]. The current annual demand for tomato seedlings in China surpasses 60 billion plants, accounting for more than 30% of the global demand [1]. High-quality seedlings can effectively enhance tomato yield and quality while reducing the incidence of pests and diseases [2]. Tomato seedling cultivation in China typically occurs in the winter–spring or summer–autumn seasons. During the winter–spring season, low temperatures and limited sunlight or prolonged rain are common, while high temperatures and intense sunlight or typhoons frequently affect the summer–autumn season [3]. These adverse conditions can lead to slow growth or excessive elongation of tomato seedlings, resulting in poor seedling quality [4]. In recent years, technological advancements have popularized factory-based seedling cultivation under the controlled environments. Cultivating tomato seedlings in a controlled environment has becoming an essential strategy to meet market demands, improve seedling conditions, and increase

automation levels in cultivation processes [5,6]. Plant factory with artificial lighting can significantly improve the seedling conditions, enabling high-quality, efficient, and large-scale production. However, due to high energy consumption, substantial investment, and high operational costs, industrial-scale adoption of plant factory with artificial lighting faces limitations [7,8]. For example, during the operation of a plant factory with artificial lighting, electrical energy consumption accounts for over 80% of the total operational costs, with lighting energy consumption comprising 80% of the electrical energy usage [9]. Therefore, reducing energy consumption in a plant factory with artificial lighting and improving light use efficiency in seedling systems has become a current research focus.

Light is a crucial source of energy and a signal for plant growth and development. As a light-loving crop, the light environment directly impacts the quality of tomato seedlings and subsequent yield [10,11]. In controlled environments, enhancing the light conditions for tomato seedlings is essential for improving seedling quality, shortening the seedling period, and reducing energy consumption [12]. Currently, a light-emitting diode (LED) is commonly used as a light source in the seedling production of a plant factory with artificial lighting [13]. As a novel, efficient, energy-saving, and environmentally friendly light source, LEDs offer advantages such as high luminous efficiency, specific light quality, and low heat generation [14], making them the primary artificial supplemental lighting source for tomato seedlings in plant facilities [15]. Research has indicated that appropriate LED supplemental lighting at different growth stages of various vegetable crops can significantly improve cultivation quality [16–18]. For example, increasing the nocturnal LED supplemental lighting intensity is beneficial for the biomass accumulation of tomato seedlings, by enhancing root vitality and improving the seedling health index [19]. LED supplemental lighting can increase leaf area and biomass accumulation in wheat seedlings, while also enhancing antioxidant levels and nutrient accumulation [20]. It can also boost the photosynthetic capacity of cucumber leaves and promote fruit growth [17]. The application of red light with the photosynthetic photon flux density (PPFD) of 20 $\mu mol \cdot m^{-2} \cdot s^{-1}$ to interrupt the night-time period significantly suppresses the increase in plant height, and higher interruption frequency results in more pronounced suppression effects [21]. Conversely, blue light can significantly increase the leaf area of cucumber seedlings and promote stem elongation [22]. During the process of supplemental nocturnal lighting, the use of white and blue light can also improve the quality of greenhouse-grown tomato seedlings [23]. Supplementing far-red or blue light at night with an LED can increase the stem length of leafy vegetables without affecting yield and quality, thereby facilitating mechanical harvesting [24,25].

During the seedling stage of greenhouse tomato cultivation, LED plays a significant role in supplementing lighting, regulating photoperiods, and inducing photomorphogenesis [26,27]. However, there are considerable variations in LED control strategies and methods for supplemental lighting. Currently, the study on the regulation of the light environment for tomato seedlings in a controlled environment primarily focuses on LED light time, PPFD, light quality, and daily light integral (*DLI*) [28–30]. Studies on nocturnal LED supplementation are limited to extending light time [29], night-time light interruption [31], and light quality for supplemental lighting [32]. Consequently, light environment regulation under controlled conditions mainly targets daytime, with strategies including increasing PPFD under low-light conditions [33], extending light time [34], and enhancing *DLI* [35]. Existing research indicates that nocturnal LED supplementation can enhance biomass accumulation in tomato seedlings [19,23] and reduce energy consumption by avoiding peak electricity usage times [36,37]. However, there is limited research on the interactions between nocturnal LED supplemental light time and PPFD, total supplemental light energy, and the timing of supplementation. This study aims to address the high demand for tomato seedlings, poor seedling quality, and high-energy consumption of LED supplemental lighting by investigating the effects of nocturnal LED supplemental light time and PPFD on the quality of tomato seedlings grown in a controlled environment. The

goal is to propose optimal nocturnal LED supplemental lighting parameters to support the cultivation of high-quality tomato seedlings in a controlled environment.

2. Materials and Methods

2.1. Plant Materials

The tomato (*Solanum lycopersicum* L.) variety 'Zhongza 9' (provided by Zhongshu Seed Industry Technology Co., Ltd. Haidian, Beijing, China) was used in this study. The experiment was conducted in a plant factory with artificial lighting at the Key Laboratory of Modern Agricultural Equipment and Technology of Ministry of Education (119.4° E, 32.2° N). After germination hastening, tomato seeds were sown in the standard 72-cell trays. The cultivation substrate was a mixture of perlite, vermiculite, and peat (1V:1V:3V). During seed germination, the temperature was maintained at 28 ± 1 °C, and relative humidity at 75 ± 10%, with no control over CO_2 concentration. After germination, tomato seedlings were exposed to LED plant growth lamps (W-LED5/1-T5-16W, Shengyanggu Technology Co., Ltd., Haidian, Beijing, China) with an R/B (the ratio of red to blue light) of 1.2 and a luminous efficiency of 2.8 μmol·s^{-1}·W^{-1}, and the spectral distribution of the LED was illustrated in Figure 1. During the seedling stage, the photoperiod conditions were set to a temperature of 24 ± 1 °C, relative humidity of 60 ± 10%, and CO_2 concentration of 600 ± 50 μmol·mol^{-1} in the daytime. The dark-period conditions were a temperature of 20 ± 1 °C, and relative humidity of 70 ± 10%, with no control over CO_2 concentration. The tomato seedlings were irrigated with one-third Yamazaki tomato nutrient solution (for tomato). Once the cotyledons had fully expanded, irrigation was performed with two-thirds nutrient solution. When the first true leaf had expanded, the standard-concentration nutrient solution was applied.

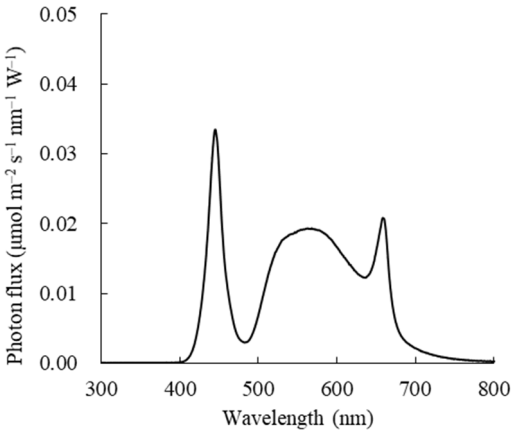


Figure 1. Spectral distribution of LED with red-to-blue ratio (R:B) of 1.2.

2.2. Experimental Design

During the tomato seedling stage, the photoperiod was cyclically controlled by an intelligent timer. During the light period (6:00–18:00), PPFD was maintained at 200 μmol·m^{-2}·s^{-1} for 12 h per day. During the dark period (18:00–6:00), supplemental lighting was provided using LED plant growth lamps controlled by an intelligent timer. The nocturnal LED supplemental lighting experiment included three light intensities: 100 μmol·m^{-2}·s^{-1}, 200 μmol·m^{-2}·s^{-1}, and 300 μmol·m^{-2}·s^{-1}, and two light times: 1 h and 2 h. The specific supplemental light periods are detailed in Table 1. The control group consisted of tomato seedlings without any nocturnal supplemental lighting (CK), resulting in a total of 13 experimental treatments.

Table 1. Experimental design of nocturnal LED supplemental lighting.

Treatment	PPFD ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	Light Time (h)	Light Period-of-Time
CK	0	0	--
P1T1	100	1	23:30–00:30
P1T2		1	21:40–22:10 and 01:50–02:20
P1T3		2	23:00–01:00
P1T4		2	21:20–22:20 and 01:40–02:40
P2T1	200	1	23:30–00:30
P2T2		1	21:40–22:10 and 01:50–02:20
P2T3		2	23:00–01:00
P2T4		2	21:20–22:20 and 01:40–02:40
P3T1	300	1	23:30–00:30
P3T2		1	21:40–22:10 and 01:50–02:20
P3T3		2	23:00–01:00
P3T4		2	21:20–22:20 and 01:40–02:40

2.3. Measurement Indicators and Methods

2.3.1. Measurement of Growth Morphology

When the tomato seedlings reached the four-leaf-one-heart stage, eight seedlings with uniform growth were randomly selected from each treatment for growth and morphological measurements. Plant height, defined as the length from the base of the stem to the top growth point, was measured using a ruler (cm). Stem diameter, defined as the diameter of the stem 1 cm below the cotyledons, was assessed with a slide gauge (mm). The leaf number was recorded as the count of fully developed true leaves, with partially expanded leaves counted as 0.5. Leaf area was determined using an intelligent leaf area measurement system (YMJ-CH, Top Yunnong Technology Co., Ltd., Hangzhou, Zhejiang, China), which scanned all true leaves and recorded the total leaf area per seedling (cm^2). The measurement and calculation methods followed those described by Song et al. [9] and Ma et al. [38].

2.3.2. Measurement of Photosynthetic Capacity

Six leaves from different tomato seedlings in each treatment were randomly selected and taken from the same position on the plants to measure the *chlorophyll a*, *chlorophyll b*, and carotenoid contents using the 80% acetone extraction method [39]. Total chlorophyll content and the *chlorophyll a/b* were then calculated. Additionally, six tomato seedlings from each treatment were randomly selected, and a SPAD chlorophyll meter (SPAD-502, Konica Minolta Investment Ltd., Qiandaitian, Tokyo, Japan) was used to measure the SPAD values of three fully expanded leaves from different positions on the same seedling. The average SPAD value for each seedling was calculated. Furthermore, eight fully expanded leaves from different plants within each treatment were randomly selected to measure net photosynthetic rate, stomatal conductance, intercellular CO_2 concentration, and transpiration rate using a portable photosynthesis system (LI-6400XT, LI-COR Inc., Lincoln, NE, USA). Measurements were taken using a standard red/blue LED light source leaf chamber (6400-02B) with the following settings: PPFD at 250 $\mu mol \cdot m^{-2} \cdot s^{-1}$, CO_2 concentration at 800 $\mu mol \cdot mol^{-1}$, leaf chamber temperature at 24 °C, and airflow rate at 500 $\mu mol \cdot s^{-1}$ [40].

2.3.3. Measurement of Root Activity

Six tomato seedlings in each treatment were randomly selected to assess root activity using the triphenyl tetrazolium chloride (TTC) method. Seedling roots were thoroughly cleaned and air-dried on absorbent paper. Healthy root tips weighing 0.5 g were measured using an electronic balance (ME204E, Mettler Toledo Technology Co., Ltd., Greifensee, Switzerland) and placed in a beaker containing a 0.4% TTC solution and phosphate buffer. The roots were fully immersed and incubated in a dark environment at 37 °C for 2 h. After incubation, 1 $mol \cdot L^{-1}$ sulfuric acid was added to terminate the reaction. The roots were then

blotted dry, ground in a mortar with ethyl acetate and a small amount of quartz sand, and the extract was measured for absorbance at 485 nm using a UV–visible spectrophotometer (UV-2800, Unico Co. Ltd., Songjiang, Shanghai, China). Root activity was calculated using the standard curve and formula [9].

$$\text{Root activity } (\mu g \cdot g^{-1} \cdot h^{-1}) = (C \times M)/(W \times t)$$

where C is the TTF obtained from the standard curve, μg; M is the dilution multiple of extracting solution; W is the weight of root tip, g; and t is the coloration time, h.

2.3.4. Measurement of Chlorophyll Fluorescence Induction Characteristics

Six tomato seedling leaves were subjected to dark adaptation before measurement for at least 30 min using a portable photosynthesis fluorescence meter (Yaxin-1102G, Yaxin Liyi Technology Co. Ltd., Haidian, Beijing, China) with a dark adaptation clip. The actinic PPFD was set to 1500 $\mu mol \cdot m^{-2} \cdot s^{-1}$, and the measurement time was set to 10 s. The chlorophyll fluorescence parameters, including the maximum photochemical efficiency of PSII (F_v/F_m), the probability that an absorbed exciton moves an electron beyond Q_A to the other electron acceptors in the electron transport chain (ψ_o), the quantum yield for electron transport (φE_o), and the performance index based on absorbed light energy (PI_ABS), were calculated from the recorded fast chlorophyll fluorescence induction kinetics (OJIP) curve and JIP-test analysis.

2.3.5. Measurement of Proline

Six leaves from the same position on different tomato plants in each treatment were randomly selected. The seedlings were placed in a temperature-controlled growth chamber and subjected to a low-temperature treatment at 5 °C for 24 h. Fresh leaves were washed, and 0.2 g samples were cut and placed into test tubes. Sulfosalicylic acid solution was added, and the mixture was extracted in a boiling water bath. After cooling, the solution was centrifuged at 3000 $r \cdot min^{-1}$, and the supernatant was collected for further use. A total of 1 mL of the extract was placed into a test tube, to which distilled water, ice-cold acetic acid, and acidic ninhydrin solution were added. The mixture was then heated in a boiling water bath until a red color developed. After cooling, toluene was added, and the mixture was vortexed for 30 s before standing for a short period. The upper layer of toluene containing the red proline solution was transferred to a cuvette. Absorbance was measured at 520 nm using a spectrophotometer, with toluene as the blank. Proline content was calculated based on the standard curve and formula [41].

2.3.6. Measurement of MDA

Six tomato plants were obtained from different experimental treatments, and leaves were collected from the same location on each plant. The seedlings were placed in a temperature-controlled growth chamber and subjected to a low-temperature treatment at 5 °C for 24 h. Fresh leaves were washed, and 0.5 g samples were cut and placed into test tubes with 10% trichloroacetic acid (TCA) and a small amount of quartz sand. The mixture was ground to a homogeneous paste. The homogenate was centrifuged at 4000 $r \cdot min^{-1}$, and the supernatant was collected for further use. One milliliter of the supernatant was transferred to a new test tube, to which thiobarbituric acid (TBA) solution was added. After mixing, the solution was heated in a boiling water bath, then rapidly cooled. The mixture was centrifuged at 10,000 $r \cdot min^{-1}$ for 10 min. The absorbance of the supernatant was measured at wavelengths of 532 nm, 600 nm, and 450 nm using a spectrophotometer. The MDA content was calculated based on the absorbance values [42].

2.3.7. Measurement of Biomass Accumulation

Eight tomato seedlings from each treatment were randomly selected to measure biomass accumulation. The fresh weight of the shoot and root was determined using an analytical balance with a precision of 0.1 mg. The total fresh weight was calculated as

the sum of the shoot fresh weight and root fresh weight. The plants were wrapped in newspaper and placed in an oven at 105 °C for 3 h for initial drying, followed by drying at 60 °C to a constant weight. The total dry weight of the shoot and root was then measured using the same analytical balance. The total dry weight was calculated as the sum of the shoot dry weight and root dry weight [37].

2.3.8. Measurement of Health Index

The quality of tomato seedlings was assessed using the health index, calculated according to the following formula [37]:

$$\text{Health index} = (\text{Stem diameter})/(\text{Plant height}) \times \text{Total dry mass}$$

2.4. Statistical Analysis

Statistical analysis of the experimental data was conducted using Microsoft Excel 2019 and DPS 9.01 software. Analysis of variance (ANOVA) was performed with multiple comparisons using the least significant difference (LSD) method. Graphs and charts were created using GraphPad Prism 6.01.

3. Results

3.1. Growth

Table 2 demonstrates that nocturnal LED supplemental lighting significantly affects the growth morphology of tomato seedlings in the controlled environment. Seedlings exposed to a PPFD of 300 μmol·m^{-2}·s^{-1} exhibited significantly greater plant height compared to those subjected to light intensities of 100 and 200 μmol·m^{-2}·s^{-1}. Except for seedlings receiving a PPFD of 100 μmol·m^{-2}·s^{-1}, there were no significant differences in plant height between tomato seedlings exposed to 2 h and 1 h of supplemental lighting. The stem diameter of seedlings in the P2T3 treatment was the greatest, surpassing the control by 47.2%. This treatment also resulted in significantly greater stem diameter compared to other treatments, although no significant difference was observed between P2T3, P2T2, and P2T4. There was no significant difference in stem diameter between seedlings exposed to light intensities of 100 and 300 μmol·m^{-2}·s^{-1}. The highest number of leaves was observed in seedlings under the P3T3 treatment, but there was no significant difference compared to P2T3 and P3T4 treatments. The trend in leaf area was similar to that of stem diameter, with no significant differences in leaf area among seedlings exposed to 200 μmol·m^{-2}·s^{-1}. Seedlings under P2T3 and P2T4 treatments had significantly greater leaf area compared to those under 100 and 300 μmol·m^{-2}·s^{-1}. In summary, the results indicate that while different supplemental-light periods of time do not significantly affect the growth morphology of tomato seedlings, the intensity of supplemental lighting does have a significant impact. The effects of nocturnal supplemental lighting on plant height, stem diameter, leaf number, and leaf area were predominantly influenced by the PPFD, rather than the light period-of-time.

Table 2. Effect of nocturnal supplemental lighting on growth morphology of tomato seedlings.

Treatment	Plant Height (cm)	Stem Diameter (mm)	Leaf Number (piece)	Leaf Area (cm^2)
CK	6.9 ± 0.8 ^{e}	3.09 ± 0.23 ^{c}	3.5 ± 0.3 ^{d}	51.4 ± 11.2 ^{d}
P1T1	6.1 ± 0.4 ^{e}	3.40 ± 0.53 ^{c}	3.6 ± 0.4 ^{cd}	62.3 ± 10.7 ^{c}
P1T2	6.3 ± 0.3 ^{e}	3.27 ± 0.23 ^{c}	3.9 ± 0.3 ^{c}	66.8 ± 14.2 ^{c}
P1T3	8.2 ± 0.5 ^{d}	3.33 ± 0.17 ^{c}	3.7 ± 0.4 ^{cd}	72.0 ± 8.9 ^{bc}
P1T4	8.6 ± 0.4 ^{c}	3.58 ± 0.28 ^{bc}	3.6 ± 0.3 ^{cd}	86.9 ± 12.8 ^{b}
P2T1	9.3 ± 0.8 ^{bc}	3.69 ± 0.30 ^{b}	4.1 ± 0.2 ^{bc}	119.1 ± 24.6 ^{ab}
P2T2	9.3 ± 0.6 ^{bc}	4.08 ± 0.47 ^{ab}	4.3 ± 0.4 ^{bc}	157.6 ± 36.9 ^{ab}
P2T3	9.6 ± 0.8 ^{b}	4.55 ± 0.62 ^{a}	4.6 ± 0.4 ^{ab}	186.9 ± 73.4 ^{a}
P2T4	9.5 ± 0.7 ^{b}	4.22 ± 0.52 ^{ab}	4.5 ± 0.4 ^{b}	187.6 ± 52.3 ^{a}

Table 2. *Cont.*

Treatment	Plant Height (cm)	Stem Diameter (mm)	Leaf Number (piece)	Leaf Area (cm^2)
P3T1	10.6 ± 1.2^{ab}	3.65 ± 0.47^{bc}	4.2 ± 0.6^{bc}	104.0 ± 40.8^{bc}
P3T2	10.4 ± 0.6^{a}	3.57 ± 0.38^{bc}	4.5 ± 0.4^{b}	110.7 ± 39.5^{b}
P3T3	10.9 ± 0.8^{a}	3.74 ± 0.31^{b}	4.9 ± 0.3^{a}	107.4 ± 22.6^{b}
P3T4	10.6 ± 0.7^{a}	3.69 ± 0.39^{bc}	4.8 ± 0.3^{ab}	101.9 ± 35.7^{b}

Note: The results are expressed by mean ± standard deviation (SD, n = 8), and treatments with different letters are significantly different at $p \leq 0.05$.

3.2. Photosynthetic Capacity

3.2.1. Photosynthetic Pigments

The results of the variance analysis indicate significant differences in total chlorophyll content, *chlorophyll a/b*, and SPAD values of tomato seedling leaves under nocturnal supplemental lighting (Table 3). Specifically, the tomato seedlings in the P2T4 treatment yielded significantly higher total chlorophyll content, compared to other treatments, with increases of 29.1% over the control. However, there were no significant differences between the P2T4 and P2T3 treatments. Under the same PPFD, except for seedlings treated with 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$, there were no significant differences in total chlorophyll content among the other treatments. For light intensities of 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$, seedlings exposed to 2 h of supplemental lighting had a significantly higher *chlorophyll a/b* than those exposed to 1 h. However, there was no significant difference between seedlings under dispersed-1 h and concentrated-2 h supplemental lighting. Similarly, at light intensities of 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$, the SPAD values of seedlings exposed to 2 h of supplemental lighting were significantly higher than those exposed to 1 h. At a PPFD of 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$, there were no significant differences in total chlorophyll content and *chlorophyll a/b* between seedlings subjected to different light times at night.

Table 3. Effects of nocturnal supplemental lighting on photosynthetic pigments of tomato seedlings.

Treatment	Total Chlorophyll Content ($mg \cdot g^{-1}$)	*Chlorophyll a/b*	SPAD Values
CK	2.44 ± 0.16^{c}	2.43 ± 0.13^{d}	35.8 ± 1.6^{f}
P1T1	2.64 ± 0.22^{bc}	2.52 ± 0.16^{cd}	38.5 ± 1.4^{e}
P1T2	2.75 ± 0.18^{b}	2.49 ± 0.17^{cd}	41.6 ± 1.4^{d}
P1T3	2.90 ± 0.31^{b}	2.76 ± 0.23^{bc}	44.3 ± 1.6^{c}
P1T4	2.80 ± 0.26^{b}	2.88 ± 0.21^{ab}	45.3 ± 1.2^{bc}
P2T1	2.71 ± 0.19^{b}	2.76 ± 0.17^{bc}	41.8 ± 1.1^{d}
P2T2	2.84 ± 0.24^{b}	2.83 ± 0.16^{b}	44.9 ± 1.3^{bc}
P2T3	3.03 ± 0.24^{ab}	2.96 ± 0.21^{ab}	48.7 ± 1.7^{a}
P2T4	3.15 ± 0.17^{a}	3.03 ± 0.17^{a}	48.6 ± 1.4^{a}
P3T1	2.85 ± 0.22^{b}	2.75 ± 0.19^{bc}	41.6 ± 1.6^{d}
P3T2	2.88 ± 0.18^{b}	2.59 ± 0.16^{c}	45.8 ± 1.7^{bc}
P3T3	2.89 ± 0.16^{b}	2.56 ± 0.11^{c}	46.2 ± 1.2^{b}
P3T4	2.81 ± 0.16^{b}	2.52 ± 0.09^{cd}	46.5 ± 1.4^{b}

Note: The results are expressed by mean ± SD (n = 6), and treatments with different letters are significantly different at $p \leq 0.05$.

When the supplemental light time was 1 h, SPAD values of tomato leaves increased with higher light intensities. Conversely, at a supplemental lighting of 2 h, SPAD values initially increased with PPFD, but then decreased. For the same light time, there were no significant differences in total chlorophyll content, *chlorophyll a/b*, or SPAD values between different light periods of time. At a supplemental lighting of 1 h, seedlings with dispersed lighting exhibited significantly higher SPAD values compared to those with concentrated

lighting. However, at a supplemental lighting of 2 h, neither dispersed nor concentrated supplemental lighting had a significant impact on the SPAD values of tomato leaves.

3.2.2. Gas Exchange

As shown in Table 4, the tomato seedlings in P2T3 and P2T4 treatments resulted in the highest net photosynthetic rate in tomato leaves, exceeding the control group by more than 59.6%. Under the same PPFD, the net photosynthetic rate of tomato leaves increased with the light time. However, for the same light time, the net photosynthetic rate initially increased with PPFD and then decreased. The highest stomatal conductance was observed in the P1T4 treatment, although it was not significantly different from the P2T3 and P2T4 treatments. At light intensities of 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$, stomatal conductance increased with the light time, but there was no significant difference between seedlings exposed to 1 h of dispersed lighting and those exposed to 2 h of concentrated lighting. Additionally, there were no significant differences in transpiration rate among tomato leaves for the same light time. Similarly, no significant differences were observed between seedlings exposed to 2 h of concentrated lighting and those exposed to 1 h of dispersed lighting. It is noteworthy that, under the same light time, the light period-of-time did not have a significant effect on stomatal conductance, intercellular CO_2 concentration, or transpiration rate in tomato seedlings.

Table 4. Effects of nocturnal supplemental lighting on contents of photosynthetic pigment of tomato seedlings.

Treatment	Net Photosynthetic Rate ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	Stomatal Conductivity ($mol \cdot m^{-2} \cdot s^{-1}$)	Intercellular CO_2 Concentration ($\mu mol \cdot mol^{-1}$)	Transpiration Rate ($mmol \cdot m^{-2} \cdot s^{-1}$)
CK	15.6 ± 0.4^{f}	0.295 ± 0.036^{d}	722 ± 20^{a}	2.12 ± 0.19^{c}
P1T1	18.2 ± 1.2^{e}	0.321 ± 0.042^{cd}	702 ± 16^{ab}	2.39 ± 0.07^{b}
P1T2	18.6 ± 1.3^{e}	0.347 ± 0.038^{c}	693 ± 33^{bc}	2.41 ± 0.14^{b}
P1T3	20.6 ± 0.8^{cd}	0.404 ± 0.043^{bc}	676 ± 19^{bc}	2.62 ± 0.26^{ab}
P1T4	21.8 ± 0.9^{bc}	0.475 ± 0.047^{a}	669 ± 34^{bc}	2.69 ± 0.24^{ab}
P2T1	19.5 ± 0.7^{d}	0.382 ± 0.054^{bc}	688 ± 22^{bc}	2.38 ± 0.16^{b}
P2T2	21.7 ± 1.2^{bc}	0.429 ± 0.059^{b}	672 ± 28^{bc}	2.47 ± 0.19^{b}
P2T3	24.9 ± 1.3^{a}	0.449 ± 0.028^{ab}	657 ± 14^{c}	2.69 ± 0.14^{ab}
P2T4	25.2 ± 1.3^{a}	0.463 ± 0.047^{ab}	641 ± 18^{c}	2.82 ± 0.24^{a}
P3T1	18.8 ± 0.4^{de}	0.336 ± 0.039^{c}	701 ± 36^{b}	2.36 ± 0.22^{b}
P3T2	19.9 ± 0.9^{cd}	0.374 ± 0.052^{bc}	688 ± 34^{bc}	2.48 ± 0.24^{b}
P3T3	22.7 ± 0.9^{b}	0.424 ± 0.022^{b}	672 ± 18^{bc}	2.67 ± 0.18^{ab}
P3T4	21.4 ± 1.3^{c}	0.416 ± 0.037^{b}	669 ± 25^{bc}	2.66 ± 0.23^{ab}

Note: The results are expressed by mean ± SD (n = 8), and treatments with different letters are significantly different at $p \leq 0.05$.

3.3. Resistance Physiology

3.3.1. Root Activity

The effect of nocturnal supplemental lighting on root activity is illustrated in Figure 2. Among the treatments, the tomato seedlings in P2T3 and P2T4 treatments exhibited the highest root activity, surpassing the control group (421.3 $\mu g \cdot g^{-1} \cdot h^{-1}$) by 50.1%. However, there were no significant differences between these two treatments and the P3T3 treatment. Under the same PPFD, root activity of tomato seedlings increased with the light time. Yet, for the same PPFD and light time, there were no significant differences in root activity between seedlings exposed to dispersed lighting and those exposed to concentrated lighting. Additionally, under the same light time and light period-of-time, root activity of tomato seedlings increased with PPFD, although there was a decreasing trend for seedlings exposed to 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$ under dispersed-lighting conditions.

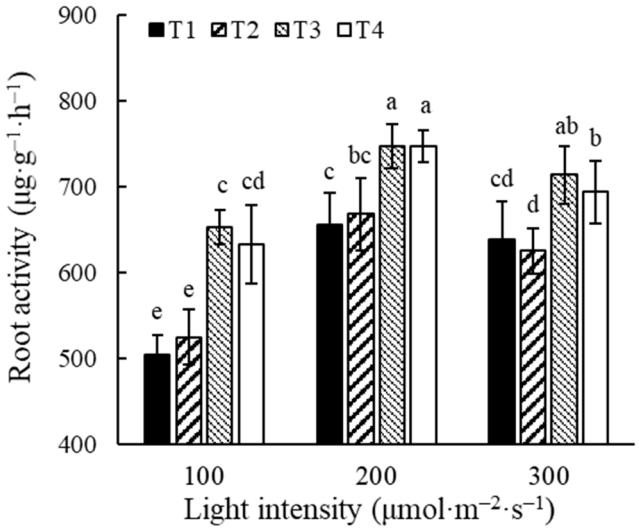


Figure 2. Effect of supplemental lighting at night on root activity of tomato seedlings. Note: the error lines are expressed by standard deviation (SD, n = 8), and treatments with different letters are significantly different at $p \leq 0.05$.

3.3.2. Chlorophyll Fluorescence

Based on the rapid chlorophyll fluorescence induction kinetics (OJIP) curves and JIP-test analysis of tomato seedling leaves, nocturnal LED supplemental lighting did not alter the F_v/F_m in tomato leaves compared to the control group. However, different nocturnal LED treatments significantly affected ψ_o, φE_o, and *PI_ABS* in tomato leaves (Table 5). At light intensities of 200 μmol·m^{-2}·s^{-1} and 300 μmol·m^{-2}·s^{-1}, ψ_o, φE_o, and *PI_ABS* in tomato leaves significantly decreased with longer light exposure. Except for the PPFD of 300 μmol·m^{-2}·s^{-1}, light time did not significantly affect ψ_o, φE_o, and *PI_ABS*. At 1 h of light exposure, there were no significant differences in ψ_o, φE_o, and *PI_ABS* between dispersed- and concentrated-lighting treatments at different light intensities. However, at 2 h of light exposure, ψ_o, φE_o, and *PI_ABS* in tomato leaves gradually decreased with increasing in PPFD.

Table 5. Effects of nocturnal supplemental lighting on chlorophyll fluorescence of tomato seedlings.

Treatment	F_v/F_m	ψ_o	φE_o	*PI_ABS*
CK	0.863 ± 0.023 ^{a}	0.663 ± 0.006 ^{a}	0.567 ± 0.012 ^{b}	4.89 ± 1.12 ^{ab}
P1T1	0.857 ± 0.016 ^{a}	0.653 ± 0.035 ^{ab}	0.580 ± 0.030 ^{ab}	5.83 ± 1.11 ^{a}
P1T2	0.861 ± 0.021 ^{a}	0.656 ± 0.034 ^{ab}	0.583 ± 0.012 ^{a}	5.75 ± 0.35 ^{a}
P1T3	0.860 ± 0.017 ^{a}	0.653 ± 0.021 ^{ab}	0.563 ± 0.006 ^{b}	4.85 ± 0.21 ^{ab}
P1T4	0.864 ± 0.029 ^{a}	0.656 ± 0.019 ^{a}	0.567 ± 0.023 ^{b}	4.69 ± 0.75 ^{b}
P2T1	0.853 ± 0.021 ^{a}	0.660 ± 0.017 ^{a}	0.560 ± 0.026 ^{b}	2.79 ± 1.66 ^{cd}
P2T2	0.853 ± 0.031 ^{a}	0.642 ± 0.019 ^{ab}	0.556 ± 0.019 ^{b}	4.63 ± 0.86 ^{b}
P2T3	0.857 ± 0.032 ^{a}	0.593 ± 0.035 ^{bc}	0.507 ± 0.028 ^{cd}	3.65 ± 1.40 ^{c}
P2T4	0.865 ± 0.024 ^{a}	0.574 ± 0.022 ^{c}	0.469 ± 0.024 ^{d}	2.94 ± 1.12 ^{cd}
P3T1	0.860 ± 0.017 ^{a}	0.660 ± 0.035 ^{ab}	0.563 ± 0.021 ^{b}	4.97 ± 0.16 ^{a}
P3T2	0.862 ± 0.019 ^{a}	0.632 ± 0.034 ^{b}	0.556 ± 0.019 ^{b}	4.33 ± 0.46 ^{bc}
P3T3	0.850 ± 0.026 ^{a}	0.572 ± 0.026 ^{c}	0.520 ± 0.026 ^{c}	3.67 ± 0.79 ^{c}
P3T4	0.857 ± 0.033 ^{a}	0.557 ± 0.024 ^{c}	0.476 ± 0.024 ^{d}	2.68 ± 1.07 ^{d}

Note: The results are expressed by mean ± SD (n = 8), and treatments with different letters are significantly different at $p \leq 0.05$.

3.3.3. Stress Resistance

Figure 3 shows that nocturnal LED supplemental lighting significantly impacts the proline and malondialdehyde (MDA) content in tomato seedlings. At light intensities of 200 μmol·m^{-2}·s^{-1} and 300 μmol·m^{-2}·s^{-1}, the tomato seedlings exposed to 2 h of

supplemental lighting had significantly higher proline content compared to those exposed to 1 h, but no significant differences were observed between dispersed- and concentrated-lighting treatments. Under the same light time and light period-of-time at night, proline content in tomato seedlings initially increased and then decreased with increasing in PPFD. For the same PPFD, there were no significant differences in proline content among treatments with 1 h of supplemental lighting. However, for 2 h of supplemental lighting, MDA content in tomato leaves was significantly higher under dispersed lighting compared to concentrated lighting. PPFD did not significantly affect MDA content in tomato leaves under the same light time and light period-of-time at night.

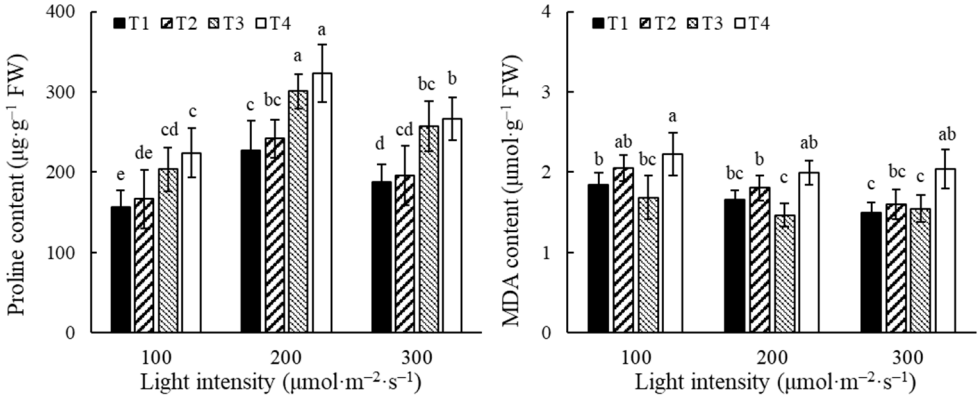


Figure 3. Effect of nocturnal supplemental lighting on proline and MDA content of tomato seedlings. Note: the error lines are expressed by standard deviation (SD, $n = 6$), and treatments with different letters are significantly different at $p \leq 0.05$.

3.4. Biomass Accumulation

Nocturnal LED supplemental lighting significantly affects the biomass accumulation of tomato seedlings (Figure 4). The tomato seedlings in the P2T3 treatment resulted in the highest root fresh weight, shoot dry weight, and root dry weight of the tomato seedlings, although there were no significant differences compared to the P2T4 treatment. At light intensities of 200 μmol·m^{-2}·s^{-1} and 300 μmol·m^{-2}·s^{-1}, tomato seedlings exposed to 2 h of supplemental lighting exhibited significantly higher fresh and dry weights of both aboveground and underground parts, compared to those exposed to 1 h, with no significant differences observed between the P2T4 and P3T3 treatments. Under the same light period-of-time, fresh and dry weights of aboveground and underground parts of tomato seedlings exposed to 1 h of supplemental lighting significantly increased with PPFD. For tomato seedlings exposed to 2 h of supplemental lighting, fresh weights of both parts initially increased and then decreased with higher PPFD, whereas dry weights consistently increased.

At a PPFD of 200 μmol·m^{-2}·s^{-1} with 1 h of supplemental lighting, tomato seedlings under concentrated lighting had significantly higher fresh and dry weights of aboveground and underground parts, compared to those under dispersed lighting. At a PPFD of 300 μmol·m^{-2}·s^{-1} with 1 h of supplemental lighting, concentrated lighting also resulted in significantly higher dry weights of both parts. However, at a PPFD of 100 μmol·m^{-2}·s^{-1}, there were no significant differences in biomass accumulation between dispersed- and concentrated-lighting treatments under the same light time. The impact of nocturnal LED supplemental lighting on the total fresh and dry weights of tomato seedlings is essentially similar to its effect on the fresh and dry weights of the aboveground parts (Figure 5).

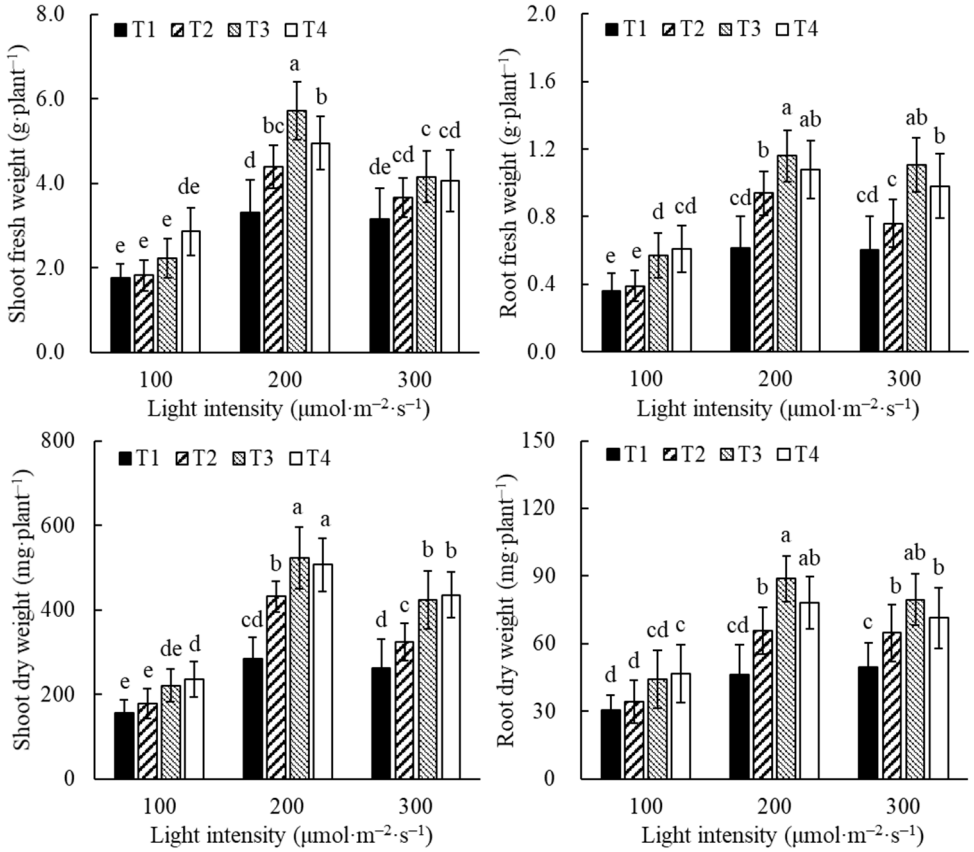


Figure 4. Effect of nocturnal supplemental lighting on biomass distribution of tomato seedlings. Note: treatments with different letters are significantly different at $p \leq 0.05$.

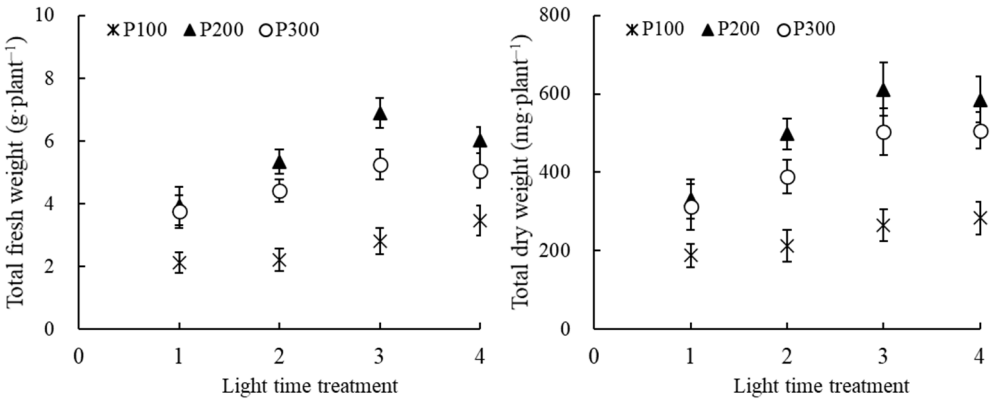


Figure 5. Effect of nocturnal supplemental lighting on total biomass accumulation of tomato seedlings.

3.5. Seedling Quality

As shown in Figure 6, the tomato seedlings in the P2T3 treatment exhibited the highest seedling health index, significantly surpassing other treatments but not significantly different from the P2T4 treatment. At light intensities of 200 μmol·m^{-2}·s^{-1} and 300 μmol·m^{-2}·s^{-1}, the health index of seedlings exposed to 2 h of supplemental lighting was significantly higher than those exposed to 1 h. However, there were no significant differences between seedlings subjected to 2 h of dispersed lighting and those subjected to 1 h of concentrated lighting. Under the same light period-of-time, the health index of tomato seedlings, except for those exposed to 1 h of concentrated lighting, initially increased and then decreased with increasing in PPFD. There were no significant differences in the health index between dispersed- and concentrated-lighting treatments under the same PPFD and light period-of-time.

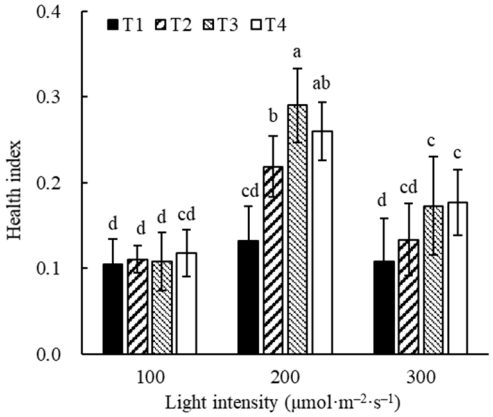


Figure 6. Effect of nocturnal supplemental lighting on health index of tomato seedlings. Note: treatments with different letters are significantly different at $p \leq 0.05$.

4. Discussion

Controlled-environment cultivation is a crucial aspect of efficient tomato production, and plant factories with artificial lighting play a significant role in meeting seedling demands, optimizing the cultivation environment, and enhancing seedling efficiency. However, excessive or insufficient supplementary light time or PPFD can hinder the cultivation of high-quality seedlings [43,44]. The results of this study indicate that nocturnal LED supplemental lighting significantly affects the growth morphology of tomato seedlings. The plant height and leaf number of tomato seedlings increased with the supplementary PPFD, while stem diameter and leaf area initially increased and then decreased, similar to the findings of other studies [45]. This suggests that excessive PPFD at night can cause an accumulation of photosynthetic products in the leaves, thereby limiting their photosynthetic capacity [46]. Extending the supplementary light time at a PPFD of 200 μmol·m^{-2}·s^{-1} increased leaf area and, subsequently, the total captured-light energy, aligning with Knop et al.'s results [47]. Thus, within a certain PPFD, longer supplementary light times are more conducive to cultivating robust tomato seedlings [48]. However, light time and light period-of-time at night had no significant impact on the plant height, stem diameter, leaf number, and leaf area of tomato seedlings, consistent with Xu et al. [49] but differing from Ali et al. [50]. This discrepancy may be due to the relatively short nocturnal supplementary-light period-of-time, which was insufficient to alter the biological rhythm of the seedlings [45].

Increased total chlorophyll content can enhance the photosynthetic capacity of leaves, thereby promoting biomass accumulation [51]. Previous research has shown that chlorophyll and carotenoid content are highly responsive to elevated nocturnal LED supplemental PPFD and time. Specifically, the *chlorophyll b* content increased by 0.68 to 2.23 times, while the *chlorophyll a/b* decreased [52]. This study found that nocturnal LED supplemental lighting significantly increased the chlorophyll content in tomato leaves, especially at an intensity of 200 μmol·m^{-2}·s^{-1}. Different supplementary light period-of-times had no significant effect on total chlorophyll content, but did significantly affect the *chlorophyll a/b*, likely due to the high blue-light content in the LEDs used, which promotes *chlorophyll a* synthesis [53,54]. Both the PPFD and light time of nocturnal LED supplemental lighting significantly impacted the SPAD values of tomato leaves. At a supplementary light time of 1 h, SPAD values increased with PPFD; at 2 h, SPAD values initially increased and then decreased with PPFD. This indicates an optimal total light energy for nocturnal LED supplemental lighting, with excessive light energy potentially causing mechanical damage to the leaves and chlorophyll degradation [55,56]. Research has shown that nocturnal LED supplemental lighting extends the photosynthetic activation time but can increase the net photosynthetic rate of leaves [3]. In this study, increasing the PPFD and light time of nocturnal LED supplemental lighting enhanced the net photosynthetic rate of tomato leaves, with the highest rates observed in the P2T3 and P2T4 treatments, consistent with

other researchers' findings [57]. However, besides net photosynthetic rate, supplementary light period-of-time had no significant impact on stomatal conductance, intercellular CO_2 concentration, and transpiration rate of tomato seedlings, which is not entirely consistent with Liu et al. [58]. This may be due to the shorter and more dispersed supplementary light period-of-time in this experiment.

Tomato seedlings are prone to oxidative stress under unsuitable light conditions, and LED lighting can significantly increase antioxidant enzyme activity [59] to prevent photosystem damage [45]. The root activity of tomato seedlings increased with the PPFD and light period-of-time at night. Analysis of chlorophyll fluorescence characteristics in tomato leaves showed no decrease in F_v/F_m due to nocturnal supplementary lighting. However, in treatments with 2 h supplementary lighting, increasing PPFD significantly reduced ψ_o, φE_o, and *PI_ABS*, similar to Liu et al.'s findings [58,60]. This indicates that nocturnal supplementary lighting induced light stress in tomato leaves, to some extent. Furthermore, the aging of tomato leaves due to prolonged seedling age and excessive accumulation of photosynthetic products may also contribute to light stress [43,45]. Nonetheless, increased nocturnal LED supplemental PPFD and light time also elevated proline content in tomato seedlings, indicating a photoprotective mechanism [61]. Hence, an appropriate nocturnal supplementary lighting environment can enhance the photosynthetic capacity of tomato seedlings. However, excessive total light energy at night may induce light stress, but seedlings can mitigate this by increasing proline content and reducing MDA content, thereby enhancing self-protection.

Biomass accumulation in tomato seedlings results from leaf photosynthesis and accumulation of photosynthetic products. This study found that both the PPFD and light time of nocturnal LED supplemental lighting could promote biomass accumulation in tomato seedlings. For seedlings with 2 h supplementary lighting, shoot fresh weight and shoot dry weight initially increased and then decreased with PPFD, while root fresh weight and root dry weight continuously increased, consistent with Li et al.'s findings [23]. These results indicate a certain total light energy threshold for nocturnal LED supplemental lighting, and that increased nocturnal light energy reduces the water content of tomato plants, promoting photosynthetic product accumulation. Although under the 2 h of supplementary lighting, the total light energy received by tomato seedlings at a supplementary intensity of 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$ was significantly higher than that received at 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$, there was no significant difference in biomass accumulation between these two treatments, both of which were higher than those of the other experimental treatments. This could be due to the fact that increasing supplementary PPFD elevated the net photosynthetic rate, while the prolonged supplementary light time extended the total photosynthesis time [62]. These factors likely influenced carbon metabolism and the absorption and conversion of nutrients in tomato plants [63]. Additionally, excessive nocturnal PPFD can increase photorespiration, limiting the continuous accumulation of photosynthetic products [64]. The seedling health index is a key indicator of tomato seedling quality and growth status. This study found that the analysis results of the seedling health index were consistent with the growth morphology, photosynthetic capacity, and biomass accumulation of tomato leaves under different supplementary lighting treatments. Long-time supplementary lighting at an intensity of 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ was conducive to improving the seedling health index, aligning with previous research [65]. This is mainly because nocturnal LED supplemental lighting enhanced the biomass accumulation of tomato plants, and the red-blue light in LEDs inhibited stem elongation [23,66].

5. Conclusions

This study demonstrates that nocturnal LED supplemental lighting in a controlled environment can significantly enhance the photosynthetic and antioxidant capacities of tomato seedlings, particularly at a supplemental PPFD of 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Unlike the impact of the light period-of-time, the LED light time and PPFD increase the biomass accumulation of the plants, thereby improving the quality of the seedlings. However,

excessive total light energy from nocturnal LED supplementation can lead to a decline in leaf photosynthetic capacity. A comprehensive analysis of growth morphology, photosynthetic ability, biomass accumulation, and seedling health index in a controlled environment suggests optimal nocturnal LED supplemental-lighting parameters for tomato seedlings. This study recommends a PPFD of 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and a light time of 2 h as beneficial for cultivating high-quality tomato seedlings.

Nocturnal LED supplemental lighting results in the accumulation of photosynthetic products in the leaves, affecting their recovery of photosynthetic capacity, while the light quality of LEDs plays a crucial role in regulating this capacity. According to our findings, short-term nocturnal LED supplemental lighting does not disrupt the biological rhythm of tomato seedlings, indicating that research on the light stress and total light energy requirement of tomato seedlings under nocturnal LED conditions remains insufficiently explored. Therefore, future studies should focus more extensively on the light quality and light period-of-time of nocturnal LED supplementation.

Author Contributions: Conceptualization, J.S. and Y.Z.; methodology, J.S. and Y.Z.; validation, J.W.; formal analysis, J.S.; investigation, R.Z. and F.Y.; writing—original draft preparation, J.S. and W.C.; writing—review and editing, J.S. and Y.Z.; visualization, R.Z. and F.Y.; data collection, R.Z. and F.Y.; study design, J.W.; data analysis, J.W. and W.C.; revision, J.S., R.Z., F.Y. and J.W. All authors have read and agreed to the published version of the manuscript.

Funding: This research was Project Funded by the Priority Academic Program Development of Jiangsu Higher Education Institutions (PAPD-2023-87), and Project Funded by the National Local Joint Engineering Research Center for Breeding and Development of New Ginseng Varieties (ZYC202203).

Data Availability Statement: The data presented in this study are available on request from the corresponding author.

Conflicts of Interest: The authors declare no conflicts of interest.

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