

Article

Enhancing the Photon Yield of Hydroponic Lettuce Through Stage-Wise Optimization of the Daily Light Integral in an LED Plant Factory

Ruimei Yang, Hao Yang, Fang Ji and Dongxian He *

Key Laboratory of Agricultural Engineering in Structure and Environment of MOARA, College of Water Resources & Civil Engineering, China Agricultural University, Beijing 100083, China; cauymeir@126.com (R.Y.); yangh1028@163.com (H.Y.); jifang@cau.edu.cn (F.J.)

* Correspondence: hedx@cau.edu.cn; Tel.: +86-10-62737550

Abstract: The widespread application of LED plant factories has been hindered by the high energy consumption and low light use efficiency. Adjustment of the daily light integral (DLI) offers a promising approach to enhance the light use efficiency in hydroponic cultivation within LED plant factories. However, most LED plant factories use a constant DLI during the cultivation process, which often leads to excessive light intensity in the early growth stage and insufficient light intensity in the later stage. To address this issue, this study aimed to improve the photon yield of hydroponic lettuce by optimizing the DLI at different growth stages. A logistic growth model was employed to segment the lettuce growth process, with variable DLI levels applied to each stage. DLIs of 11.5, 14.4, and 18.0 mol m⁻²·d⁻¹ were implemented at the slow growth stage, and the DLIs were adjusted to 14.4, 17.3, and 21.2 mol m⁻²·d⁻¹ at the rapid growth stage. Photoperiods of 16 h·d⁻¹ and 20 h·d⁻¹ were used for the two growth stages, and LED lamps with white and red chips (ratio of red to blue light was 1.5) were used as the light source. The results indicated that the photoperiod had no significant impact on the shoot fresh weight and photon yield under the constant DLI conditions at the slow growth stage (12 days after transplanting). The 14.4 mol m⁻²·d⁻¹ treatment resulted in the highest photon yield due to the significant increases in the light absorption and net photosynthetic rate of the leaves compared to the 11.5 mol m⁻²·d⁻¹ treatment. No significant differences in the specific leaf area (SLA) and leaf light absorption were observed between the 14.4 and 18.0 mol m⁻²·d⁻¹ treatments; however, the photon yield and actual photochemical efficiency (ΦPSII) significantly decreased. Compared with the DLI of 14.4 mol m⁻²·d⁻¹ at the rapid growth stage (24 days after transplanting), the 17.3 mol m⁻²·d⁻¹ treatment with 20 h·d⁻¹ increased the leaf light absorption by 5%, the net photosynthetic rate by 35%, the shoot fresh weight by 25%, and the photon yield by 19%. However, the treatments with DLIs above 17.3 mol m⁻²·d⁻¹ resulted in notable decreases in the photon yield, ΦPSII, and photosynthetic potential. In conclusion, it is recommended to implement a 20 h·d⁻¹ photoperiod coupled with a DLI of 14.4 mol m⁻²·d⁻¹ for the slow growth stage and 17.2 mol m⁻²·d⁻¹ for the rapid growth stage of hydroponic lettuce cultivation in an LED plant factory.



Citation: Yang, R.; Yang, H.; Ji, F.; He, D. Enhancing the Photon Yield of Hydroponic Lettuce Through Stage-Wise Optimization of the Daily Light Integral in an LED Plant Factory.

Agronomy **2024**, *14*, 2949. <https://doi.org/10.3390/agronomy14122949>

Academic Editor: Rosario Muleo

Received: 8 November 2024

Revised: 28 November 2024

Accepted: 9 December 2024

Published: 11 December 2024



Copyright: © 2024 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

Keywords: photon yield; daily light integral; logistic model; growth stages; light interception; photosynthetic potential

1. Introduction

Plant factories with artificial lighting are novel decentralized food production systems that offer precise control of the light, temperature, relative humidity, and CO₂ concentration [1,2]. These systems increase land use efficiency and maximize crop productivity by operating independently of external climates [3,4]. However, the high energy demands, particularly from the lighting, remain a barrier to commercial scalability, with lighting consuming 52% to 80% of the total energy [5]. Therefore, improving the light use efficiency of LEDs has become crucial for reducing operational costs and achieving energy

savings. The photon yield is a key technical metric used to evaluate light use efficiency, representing the fresh weight (in grams) of the available portion that can be produced per mole of photosynthetically active photons. Higher photon yield values indicate more efficient conversion of photon energy into crop biomass, thereby providing a quantifiable measure of the productivity benefits derived from light input. Optimizing the LED lighting environment in LED plant factories is a crucial approach for enhancing both crop yields and photon yields [6].

In optimizing light environments, the daily light integral (DLI) is a fundamental metric that captures the total amount of photosynthetically active radiation (PAR) received by plants in a day. It is determined by multiplying the photosynthetic photon flux density (PPFD) by the photoperiod [7]. As a comprehensive measure of the plant response to light, the DLI has been shown to significantly influence the fresh weight of hydroponic lettuce. Studies demonstrate that increasing the DLI from $5 \text{ mol m}^{-2} \cdot \text{d}^{-1}$ to $17 \text{ mol m}^{-2} \cdot \text{d}^{-1}$ can double lettuce yields [8]. An optimal DLI of $14.4 \text{ mol m}^{-2} \cdot \text{d}^{-1}$ has been identified as the point at which both the yield and resource use efficiency are maximized [9,10]. Due to the varying light requirements of plant species and varieties at different growth stages [11,12], a constant DLI may lead to excessive light use in the early stages and insufficient light supply in the later stages, thereby reducing the light use efficiency. To solve this problem, Jin et al. [13] proposed a dynamic light intensity adjustment method, in which the light intensity was increased by $16 \mu\text{mol m}^{-2} \text{ s}^{-1}$ every three days, ranging from $140 \mu\text{mol m}^{-2} \text{ s}^{-1}$ to $300 \mu\text{mol m}^{-2} \text{ s}^{-1}$. This method significantly improved the dry weight and light use efficiency of hydroponic lettuce, although no significant impact on the shoot fresh weight was observed under the same treatments. Plant responses to light are influenced by the genotype, growth stage, and other environmental factors [14,15]. In C3 plants with the same genotype, the light response varies across different growth stages; in the early growth stages, young leaves respond to light more flexibly than mature leaves [16]. As the plant matures, the rate of photosynthesis may decrease, primarily due to changes in the leaf structure and a decline in Rubisco activity. Therefore, to enhance the photosynthetic efficiency of C3 plants, it is essential to optimize the light conditions based on the specific characteristics of each growth stage, thereby improving the plant's overall light energy use efficiency. Specifically, stage-specific DLI optimization offers substantial promise for enhancing the plant photon yield.

Nonlinear growth models provide an essential framework for understanding the dynamic growth of crops across different stages. They are critical for defining these stages and serve as a scientific basis for optimizing the lighting environment in LED plant factories, ensuring efficient resource use and enhanced crop productivity. For hydroponic lettuce, the growth process is typically divided into three stages: (1) a “slow growth stage” marked by low-slope linear growth, (2) a “rapid growth stage” featuring exponential growth, and (3) a “steady growth stage” reflecting saturated growth. In practice, harvesting is typically carried out during the rapid growth stage, as it offers an optimal yield and resource efficiency [17]. However, the exact timing can vary significantly depending on the lettuce type, market demands, and environmental factors. The logistic, Gompertz, and von Bertalanffy models are commonly used nonlinear growth models for describing plant growth [18–21]. By analyzing the third derivative of the nonlinear growth model, we can identify the start and end points of the rapid growth stage, allowing for more precise determination of the growth stages. This enables the optimization of light environments tailored to specific growth needs [22]. However, while the logistic model offers theoretical markers for defining the growth stages, further validation is required to ensure that these stages align with the actual light requirements of the crop. Establishing the scientific basis of the logistic model in defining the growth stages, and optimizing the DLI based on the light requirements of hydroponic lettuce at different growth stages, is expected to significantly improve its photon yield.

We hypothesized that segmenting the growth stages using growth models and adjusting the DLI based on growth characteristics could effectively enhance the photon yield.

Therefore, three nonlinear growth models were applied to simulate the growth process of hydroponic lettuce, and the best model was selected to determine the key time points for different growth stages. Based on these stages, a varying DLI and photoperiod were applied during the slow and rapid growth stages. The effects of these factors on the light absorption, net photosynthetic rate, and photochemical efficiency were subsequently analyzed. The results provide a scientific basis for optimizing the lighting environment to improve the productivity and photon yield of hydroponic lettuce.

2. Materials and Methods

2.1. Plant Materials and Growth Conditions

Lettuce (*Lactuca sativa* L. cv. Boston Cream, Beijing APEX Agricultural Corporation, Beijing, China) was cultivated in a 20-foot container-type growth chamber at an LED plant factory (China Agricultural University, Beijing, China). Seeds were sown in sponge cubes (23 mm × 23 mm × 23 mm) soaked in deionized water and placed into plastic containers measuring 520 mm × 360 mm × 90 mm. The seeds underwent a 2-day dark germination period with a controlled temperature of 20 ± 1 °C and relative humidity of $75 \pm 10\%$ before sprouting. Once the second true leaf had fully expanded, seedlings were transplanted onto a 192-hole density board (1200 mm × 60 mm) and placed in cultivation troughs of the same size. The seedling stage lasted 21 days. Based on previous research [10,23], albeit with different cultivars in cv. Boston Cream, during the seedling stage, the light conditions were set to a PPFD of $200 \mu\text{mol m}^{-2} \text{s}^{-1}$ with a photoperiod of 16 h d^{-1} . The temperatures were maintained at 22 °C during the photoperiod and 18 °C during the dark period, with the relative humidity controlled at $70\% \pm 5\%$ and $65\% \pm 10\%$, respectively. The CO_2 concentration was maintained at $800 \pm 50 \mu\text{mol mol}^{-1}$ during the photoperiod and without control during the dark period. After the seedling stage, the lettuce was transplanted onto cultivation boards, each holding 28 plants at a cultivation density of 38.9 plants per m^2 . The temperature, humidity conditions, and CO_2 concentration remained consistent with the seedling stage, while the light environment was adjusted according to the treatment parameters for the rest of the cultivation period.

Yamasaki lettuce nutrient solution was applied to provide the flowing components (mg L^{-1}): $\text{Ca}(\text{NO}_3)_2 \cdot 4\text{H}_2\text{O}$, 236; KNO_3 , 404; $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$, 123; $\text{NH}_4\text{H}_2\text{PO}_4$, 57; Fe-DTPA (7%), 28.571; $\text{MnSO}_4 \cdot \text{H}_2\text{O}$, 0.615; $\text{CuSO}_4 \cdot 5\text{H}_2\text{O}$, 0.039; $\text{ZnSO}_4 \cdot 7\text{H}_2\text{O}$, 0.088; H_3BO_3 , 1.127; and $(\text{NH}_4)_6\text{Mo}_7\text{O}_{24} \cdot 4\text{H}_2\text{O}$, 0.013, respectively. The compound used in this study was a commercially available standard product (Shanghai Wintong Ecological Engineering Co., Ltd., Shanghai, China). The nutrient solution was adjusted to electrical conductivity (EC) at 1.0–1.2 ms cm^{-1} and a pH of 6.0–6.5. In the first two days after sowing, the lettuce seedlings were irrigated with tap water once daily. During the cotyledon stage, a half-strength nutrient solution was introduced. After the second true leaf had fully expanded, a full-strength nutrient solution was applied. To maintain stable EC and pH levels, the nutrient solution was refreshed every seven days following transplanting.

2.2. Light Treatments

Hydroponic lettuce cultivation was initially conducted under a DLI of $14.4 \text{ mol m}^{-2} \cdot \text{d}^{-1}$ (with PPFD of $250 \mu\text{mol m}^{-2} \text{s}^{-1}$ and photoperiod of $16 \text{ h} \cdot \text{d}^{-1}$) until no further significant increase in the fresh weight was observed. During this period, the shoot fresh weight and total leaf area were measured every three days to establish a nonlinear growth model. This model identified the key time points for the slow and rapid growth stages, allowing for precise DLI adjustments. Based on these time points, different DLI values were set for the slow and rapid growth stages. Following the conclusion of the slow growth stage experiments, the optimal DLI for early cultivation in the rapid growth stage was selected. The DLIs for the slow growth stage were set to 11.5, 14.4, and $18.0 \text{ mol m}^{-2} \cdot \text{d}^{-1}$, while the DLIs for the rapid growth stage were set to 14.0, 17.3, and $20.2 \text{ mol m}^{-2} \cdot \text{d}^{-1}$, respectively (Table 1). The photoperiods for the two growth stages were set at $16 \text{ h} \cdot \text{d}^{-1}$ and $20 \text{ h} \cdot \text{d}^{-1}$, respectively. Throughout all the treatments and replicates, the ratio of

red to blue light was maintained at 1.5 by using LED lamps (WR-LED5/1-16W, Beijing Lighting Valley Technology Co., Ltd., Beijing, China). The PPFD was adjusted by varying the number of LEDs.

Table 1. Combinations of three DLIs and two photoperiods at two growth stages.

Growth Stage	Treatment	PPFD ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Photoperiod (h d ⁻¹)	DLI (mol m ⁻² d ⁻¹)
The slow growth stage	S11.5-H16	200	16	11.52
	S14.4-H16	250	16	14.40
	S18.0-H16	315	16	18.00
	S11.5-H20	160	20	11.52
	S14.4-H20	200	20	14.40
	S18.0-H20	250	20	18.00
The rapid growth stage	R14.4-H16	250	16	14.40
	R17.3-H16	300	16	17.28
	R20.2-H16	350	16	20.16
	R14.4-H20	200	20	14.40
	R17.3-H20	240	20	17.28
	R20.2-H20	280	20	20.16

2.3. Evaluation of the Logistic Growth Model

Every three days after transplanting, six lettuce plants were sampled to measure the shoot fresh weight. Subsequently, nonlinear growth models, including the logistic, Gompertz, and von Bertalanffy models, were used to fit the shoot fresh weight data, as described by the following expressions:

$$\text{Logistic : } y = \frac{a}{1 + b e^{-kt}} \quad (1)$$

$$\text{Gompertz : } y = a e^{-e^{-k(t-c)}} \quad (2)$$

$$\text{Von Bertalanffy : } y = a \left(1 - e^{-k(t-c)}\right)^3 \quad (3)$$

where y is the shoot fresh weight; t is the days after transplanting; and a , b , c , and k are the parameters of the logistic model.

The first derivative of the fitted growth curve provides insights into the trend of the absolute growth rate (AGR). The second and third derivatives identify the key inflection points along the curve. The point where the second derivative equals zero indicates the maximum growth rate, while the points where the third derivative equals zero define the start and end of the rapid growth stage.

The two parameters of the coefficient of determination (R^2) and mean absolute percentage error (MAPE) were used to evaluate the goodness of fit of the logistic model:

$$R^2 = 1 - \frac{\sum_{i=1}^n (y_i - \hat{y}_i)^2}{\sum_{i=1}^n (y_i - \bar{y})^2} \quad (4)$$

$$\text{MAPE} = \frac{1}{n} \sum_{i=1}^n \left| \frac{y_t - \hat{y}_t}{y_t} \right| \times 100\% \quad (5)$$

where y_i is the measured value, $\hat{y}_i$ is the predicted value, n is the number of measurements, and $\bar{y}$ is the mean value of the measured values.

2.4. Measurement Indexes and Methods

2.4.1. Growth Parameters

The shoot fresh weight was measured using an electronic analytical balance (AX622ZH, OHAUS Instruments (Changzhou) Co., Ltd., Changzhou, China) with a precision of 0.01 g. The leaves were initially dried in an oven at 105 °C for 3 h, after which the temperature was lowered to 80 °C, and drying continued for an additional 72 h. The shoot dry weight was measured using a precision analytical balance (AX224ZH, OHAUS Instruments (Changzhou) Co., Ltd., Changzhou, China) with a precision of 0.0001 g.

Each leaf was scanned using a flatbed scanner (LiDE 110, Canon Co., Ltd., Beijing, China), and the leaf area was calculated using Photoshop 2021. The formulas for calculating the leaf area index (LAI), fraction of intercepted light (F_{int}), and specific leaf area (SLA) are shown below:

$$\text{LAI} = \frac{\text{LA} \times \text{D}}{\text{S}} \quad (6)$$

$$F_{\text{int}} = 1e^{-k \times \text{LAI}} \quad (7)$$

$$\text{SLA} = \frac{\text{LA}}{\text{SDW}} \quad (8)$$

where LA is the total leaf area per plant, m²; D is the planting density, plants/m²; k is the extinction coefficient, set to 0.8; S is the area of the cultivation board, m²; and SDW is the shoot dry weight, g.

2.4.2. Leaf Absorption Rate

The transmittance and reflectance of the lettuce leaves were measured using a spectrophotometer (UV-3150, Shimadzu Corporation, Japan). Fully expanded and mature leaves were selected, with measurements taken from the central area near the main vein. The spectrophotometer scanned wavelengths ranging from 300 to 800 nm with a resolution of 1 nm. The transmittance and reflectance were measured separately, and the absorption rate was calculated using the following formula: $1 - (\text{reflectance} + \text{transmittance})$.

2.4.3. Chlorophyll Fluorescence Parameters

The actual photochemical efficiency (ΦPSII) was measured using a chlorophyll fluorescence imaging system (CF-Imager, Technologica Ltd., Colchester, UK). The intensity of the actinic light was kept consistent with the light intensity in each experimental treatment.

2.4.4. Photosynthesis Traits

The net photosynthetic rates of the lettuce leaf were measured during the photoperiod using a portable gas exchange system (LI-6400XT, LI-COR Biosciences Inc., Nebraska, USA). The parameters for the measurements were set as follows: the light intensity of the LED source was consistent with the treatment, the leaf chamber temperature was maintained at 22 °C, and the CO₂ concentration was set at 800 µmol mol⁻¹.

The light response curve was measured at a CO₂ concentration of 400 µmol mol⁻¹, with the light intensity gradient set at 1800, 1600, 1400, 1200, 1000, 800, 600, 400, 200, 100, 50, 20, and 0 µmol m⁻²vs⁻¹. The data were fitted into the leaf light response mechanism model [24] to determine the maximum net photosynthetic rate (A_{max}).

The CO₂ response curve was measured at a light intensity of 1200 µmol m⁻² s⁻¹, with the CO₂ concentration gradient set at 100, 150, 200, 250, 300, 350, 400, 450, 500, 550, 650, 800, 1000, 1200, 1500, and 1800 µmol mol⁻¹. The resulting data were input into the FvCB model [25] to calculate the maximum carboxylation rate (V_{cmax}) and the maximum electron transport rate (J_{max}).

2.4.5. Photon Yield

The photon yield of the shoot fresh weight was measured to assess the light use efficiency. The photon yield (g mol^{-1}) means the increase in the shoot fresh weight per mole of photons delivered during the cultivation period. It was calculated using the following formula:

$$\text{PY} = \frac{\Delta\text{SFW} \times D}{\text{OTLI}} \quad (9)$$

$$\text{OTLI} = \sum_{i=0}^n \text{TLI}_i = \text{PPFD}_i \times L_i \times d_i \times 3600 / 10^6 \quad (10)$$

where ΔSFW is the increase in the shoot fresh weight from settlement to harvest, g; D is the lettuce plant density per unit area, plants m^{-2} , OTLI is the total number of light quantum per square meter received by the plant during growth, mol m^{-2} ; L_i is the photoperiod at cultivation stage i , h d^{-1} ; and d_i is the days after transplanting, d.

2.5. Statistical Analysis

Six uniformly growing lettuces were selected for each measurement ($n = 6$). The logistic growth model of the shoot fresh weight was fitted using Origin 2021, while data processing, analysis, and graph plotting were performed using Microsoft Excel 2019 and SPSS 25. An ANOVA was performed using the least significant difference (LSD) method, with Duncan's multiple range test applied at a significance level of $\alpha = 0.05$. Identical letters indicate no significant difference, while different letters indicate significant differences. An asterisk (*) represents a significant difference, and NS indicates no significant difference.

3. Results

3.1. Growth Stage Classification Based on Logistic Growth Models

The fitting formulas and effects of the three nonlinear growth models are shown in Table 2. The logistic model exhibited a correlation coefficient of 0.99 and an MAPE below 0.2, indicating superior accuracy. In contrast, the Gompertz and von Bertalanffy models showed correlation coefficients greater than 0.95, but their MAPE values exceeded 0.2, suggesting relatively higher fitting errors. Thus, the logistic model was determined to be the most effective for accurately describing the growth dynamics of hydroponic lettuce.

Table 2. Fitting formula and evaluation results of the nonlinear growth models.

Models	Formula	R ²	MAPE
Logistic	$y = \frac{167.37}{1 + 57.8 \times e^{-0.22t}}$	0.99	0.12
Gompertz	$y = 170.0 \times e^{-e^{(-0.12(t-14.6))}}$	0.96	0.23
Von Bertalanffy	$y = 260.0 \times \left(1 - e^{-0.06(t-0.86)}\right)^3$	0.98	0.26

To further investigate the growth dynamics, the second and third derivatives of the fitted curves were calculated based on the logistic model (Figure 1). The maximum growth rate, identified at the point where the second derivative equals zero, occurred on the 18th day after transplanting, with an AGR of 9 g d^{-1} . The third derivative, which marks the onset and conclusion of the rapid growth stage, indicated that these points occurred on days 12 and 24 after transplanting, with shoot fresh weights of 32 g and 128 g, respectively. Afterward, the lettuce transitioned into a slower growth stage lasting 12 days.

Analysis of the LAI and F_{int} trends revealed that throughout the cultivation period, the LAI of the hydroponic lettuce followed a sigmoid growth curve. During the slow growth stage, the F_{int} increased substantially before reaching a plateau. When the LAI reached 4.7, the F_{int} also peaked, corresponding with the maximum growth rate of the lettuce. Notably, the growth rate increased significantly before the F_{int} reached its maximum, indicating that the increase in the F_{int} was a key factor promoting growth during the slow stage. Once the rapid growth stage commenced, the F_{int} stabilized at its maximum value and its influence

on the growth rate diminished. At this stage, a moderate increase in the DLI could further optimize the light resource utilization. The fitted growth curve accurately reflected the growth dynamics of the hydroponic lettuce, affirming the model's validity in describing the crop's growth characteristics.

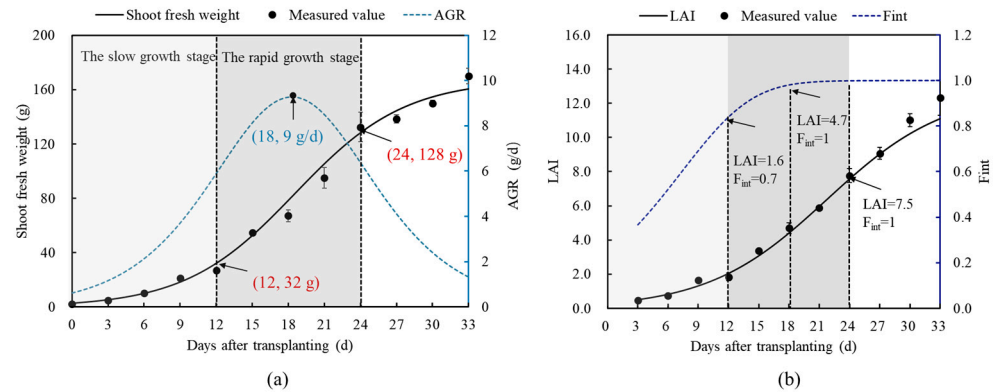


Figure 1. Fitting results of the shoot fresh weight and growth parameters for dividing the growth stage nodes. (a) The dynamic processes the shoot fresh weight and AGR, and (b) the trend of changes in the LAI and F_{int} .

3.2. Effects of DLI and Photoperiod on Growth and Photon Yield of Hydroponic Lettuce in the Slow Growth Stage

The DLI and photoperiod had no significant effect on the total leaf area of the hydroponic lettuce, while the DLI significantly affected the SLA and shoot fresh weight. When the photoperiod was 16 h d⁻¹ and 20 h d⁻¹, increasing the DLI from 11.5 mol m⁻²·d⁻¹ to 14.4 mol m⁻²·d⁻¹ resulted in SLA reductions of 23.6% and 39.3%, respectively. Further increases in the DLI did not lead to significant changes in the SLA (Table 3). Similarly, the DLI had a significant effect on the shoot fresh weight. Under the photoperiod of 16 h d⁻¹, increasing the DLI from 11.5 mol m⁻²·d⁻¹ to 14.4 mol m⁻²·d⁻¹ and then to 18.0 mol m⁻²·d⁻¹ increased the shoot fresh weight by 27% and 12%, respectively. Under the photoperiod of 20 h d⁻¹, the same DLI increases resulted in the shoot fresh weight increasing by 36% and 13%, respectively. Notably, the increase in the shoot fresh weight from 11.5 mol m⁻²·d⁻¹ to 14.4 mol m⁻²·d⁻¹ was particularly pronounced, potentially due to the increased leaf thickness.

Table 3. Effects of the DLI and photoperiod on the leaf morphology, biomass, and photon yield of hydroponic lettuce at the slow growth stage.

Treatment	Leaf Area (cm ²)		SLA (cm ² g ⁻¹)		Shoot Fresh Weight (g)		Photon Yield (g mol ⁻¹)	
S11.5-H16	557 ± 47	ab	470 ± 62	a	28.4 ± 1.1	c	7.5 ± 0.3	ab
S14.4-H16	577 ± 23	ab	359 ± 21	b	35.9 ± 1.2	b	7.7 ± 0.3	a
S18.0-H16	598 ± 44	a	378 ± 48	b	40.2 ± 1.6	a	6.9 ± 0.3	b
S11.5-H20	530 ± 40	b	516 ± 85	a	26.5 ± 0.7	c	7.0 ± 0.2	b
S14.4-H20	524 ± 28	b	313 ± 13	bc	36.1 ± 1.7	b	7.7 ± 0.4	a
S18.0-H20	559 ± 18	ab	268 ± 29	c	40.8 ± 1.2	a	7.0 ± 0.2	b

Identical letters indicate no significant difference, while different letters indicate significant differences.

The DLI significantly affected the photon yield of the hydroponic lettuce, while the photoperiod had no significant effect on the photon yield under the same DLI. As the DLI increased, the photon yield first increased significantly and then decreased. During the slow growth stage, the photon yield peaked at 7.7 g mol⁻¹ when the DLI reached 14.4 mol m⁻²·d⁻¹ under photoperiods of 16 h d⁻¹ and 20 h d⁻¹. However, when the DLI was further increased to 18.0 mol m⁻²·d⁻¹, the photon yield decreased by 11% and 9%, respectively.

Within a certain range, increasing the DLI significantly enhanced the shoot fresh weight of the hydroponic lettuce, which is attributable to the corresponding changes in the leaf absorption rate and net photosynthetic rate. The DLI significantly influenced the leaf light absorption, with extended photoperiods at a constant DLI further enhancing the absorption. At the slow growth stage, increasing the DLI from $11.5 \text{ mol m}^{-2} \cdot \text{d}^{-1}$ to $14.4 \text{ mol m}^{-2} \cdot \text{d}^{-1}$ raised the leaf absorption rate by 4% and 2% under photoperiods of 16 h d^{-1} and 20 h d^{-1} , respectively. Additionally, a higher DLI significantly improved the net photosynthetic rate of the lettuce leaf. When the DLI was raised incrementally from $11.5 \text{ mol m}^{-2} \cdot \text{d}^{-1}$ to $14.4 \text{ mol m}^{-2} \cdot \text{d}^{-1}$, and subsequently to $18.0 \text{ mol m}^{-2} \cdot \text{d}^{-1}$, the net photosynthetic rate rose by 15% and 26% under the photoperiod of 16 h d^{-1} , and by 27% and 23% under the 20 h d^{-1} , respectively. The net photosynthetic rate was significantly higher in the combination of the shorter photoperiod (16 h d^{-1}) with higher light intensity compared to the longer photoperiod (20 h d^{-1}) and lower light intensity under the same DLI.

When the DLI exceeded $14.4 \text{ mol m}^{-2} \cdot \text{d}^{-1}$, the photon yield of the hydroponic lettuce significantly decreased (Figure 2), which was closely associated with changes in the ΦPSII . The ΦPSII reflects the proportion of absorbed light energy in photosystem II (PSII) that is used in photochemical reactions. As the DLI increased from $14.4 \text{ mol m}^{-2} \cdot \text{d}^{-1}$ to $18.0 \text{ mol m}^{-2} \cdot \text{d}^{-1}$, the ΦPSII declined substantially, with lower light intensity treatments exhibiting higher ΦPSII under the same DLI conditions. This reduction in efficiency is likely due to chlorophyll's limited capacity to process surplus light energy through photosynthesis, resulting in increased heat dissipation and energy loss. Sustained exposure to high light levels may also impair the plant's photosynthetic machinery.

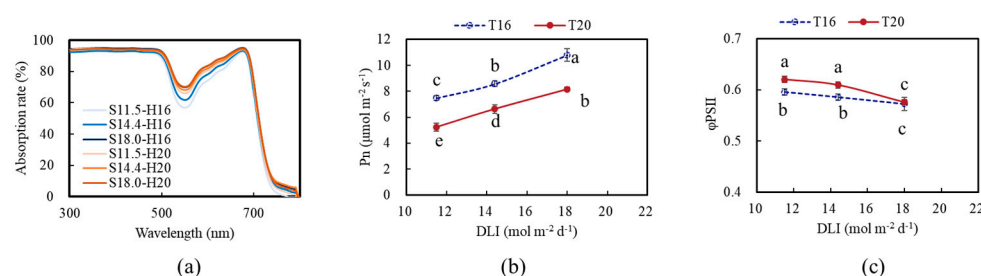


Figure 2. Effects of the DLI and photoperiod on the leaf absorption rate (a), net photosynthetic rate (b), and ΦPSII (c) of hydroponic lettuce at the slow growth stage. Identical letters indicate no significant difference, while different letters indicate significant differences.

In summary, the photon yield of the hydroponic lettuce reached its maximum when the DLI was $14.4 \text{ mol m}^{-2} \cdot \text{d}^{-1}$ at the slow growth stage. Further increases in the DLI did not significantly affect the SLA and resulted in marked declines in both the ΦPSII and photon yield. Consequently, a DLI of $14.4 \text{ mol m}^{-2} \cdot \text{d}^{-1}$ with a photoperiod of either 16 or 20 h d^{-1} is recommended for optimal growth at the slow stage.

3.3. Effects of DLI and Photoperiod on Growth and Photon Yield of Hydroponic Lettuce at the Rapid Growth Stage

During the first 1 to 12 days after transplanting, the lettuce was cultivated under a DLI of $14.4 \text{ mol m}^{-2} \cdot \text{d}^{-1}$, followed by different light treatments during the rapid growth stage. The results showed that although the DLI and photoperiod had no significant effect on the leaf area, the DLI markedly influenced the SLA and shoot fresh weight (Table 4). Increasing the DLI from $14.4 \text{ mol m}^{-2} \cdot \text{d}^{-1}$ to $17.3 \text{ mol m}^{-2} \cdot \text{d}^{-1}$ reduced the SLA by 16% and 19% under photoperiods of 16 h d^{-1} and 20 h d^{-1} , respectively, while the shoot fresh weight increased by 20% and 25%, respectively. However, further increasing the DLI to $20.2 \text{ mol m}^{-2} \cdot \text{d}^{-1}$ did not result in significant differences in the SLA or shoot fresh weight.

Table 4. Effects of the DLI and photoperiod on the leaf morphology and biomass of hydroponic lettuce at the rapid growth stage.

Treatment	Leaf Area (cm ²)		SLA (cm ² g ^{−1})		Shoot Fresh Weight (g)	
R14.4-H16	2122 ± 88	NS	447 ± 44	a	129.7 ± 3.0	b
R17.3-H16	2254 ± 102	NS	376 ± 38	b	155.4 ± 4.6	a
R20.2-H16	2209 ± 199	NS	372 ± 47	b	155.0 ± 5.3	a
R14.4-H20	2071 ± 119	NS	469 ± 36	a	120.4 ± 2.4	c
R17.3-H20	2148 ± 114	NS	382 ± 26	b	155.1 ± 7.7	a
R20.2-H20	2109 ± 90	NS	364 ± 34	b	161.8 ± 2.6	a

Identical letters indicate no significant difference, while different letters indicate significant differences. NS indicates no significant difference.

The DLI had a significant effect on the photon yield of the hydroponic lettuce. The photon yield reached its maximum value of 21.0 g mol^{−1} at the DLI of 17.3 mol m^{−2}·d^{−1} under both photoperiods of 16 and 20 h d^{−1}, representing increases of 11% and 19%, respectively, compared to the DLI of 14.4 mol m^{−2}·d^{−1}. However, when the DLI was further increased to 20.2 mol m^{−2}·d^{−1}, the photon yield significantly decreased (Figure 3).

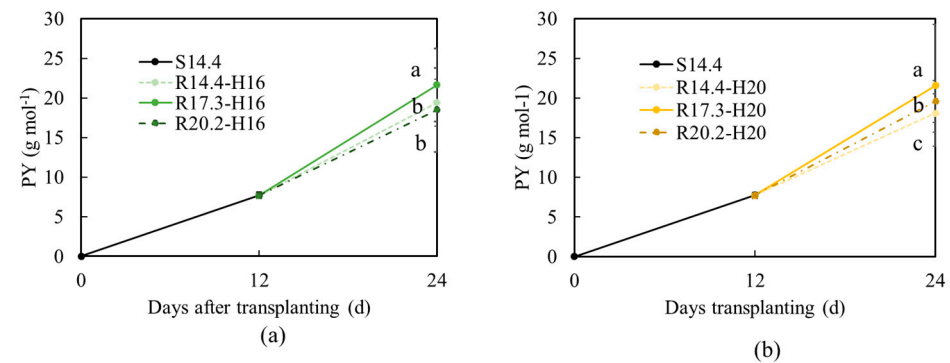


Figure 3. Effects of the DLI and photoperiod on the photon yield of hydroponic lettuce at the rapid growth stage: (a) a photoperiod of 16 h d^{−1}, and (b) a photoperiod of 20 h d^{−1}. Identical letters indicate no significant difference, while different letters indicate significant differences.

When the DLI increased from 14.4 mol m^{−2}·d^{−1} to 17.3 mol m^{−2}·d^{−1}, the net photosynthetic rate rose by 22% and 5% under the photoperiod of 16 h d^{−1}, and by 35% and 7% under the 20 h d^{−1}, with the absorption rate increasing by 4%. Meanwhile, both the V_{max} and J_{max} reached their highest levels at the DLI of 17.3 mol m^{−2}·d^{−1}. However, when the DLI was further increased to 20.2 mol m^{−2}·d^{−1}, no significant increases were observed in the leaf absorption rate, net photosynthetic rate, V_{max} , or J_{max} . This suggests that beyond the DLI threshold of 17.3 mol m^{−2}·d^{−1}, the biomass and photosynthetic potential of lettuce no longer significantly increase.

When the DLI increased from 17.3 mol m^{−2}·d^{−1} to 20.2 mol m^{−2}·d^{−1}, the ΦPSII significantly decreased under both 16 h d^{−1} and 20 h d^{−1}. Additionally, under the same DLI conditions, the treatments with lower light intensity and longer photoperiods exhibited significantly higher ΦPSII compared to those with higher light intensity and shorter photoperiods (Figure 4). This suggests that lower light intensity combined with longer photoperiods is more conducive to maintaining higher ΦPSII .

In conclusion, both the shoot fresh weight and photon yield of the hydroponic lettuce reached their maximum at the DLI of 17.3 mol m^{−2}·d^{−1} at the rapid growth stage. The increase in the photon yield was more pronounced under the photoperiod of 20 h d^{−1}, primarily due to significant improvements in the leaf light absorption and net photosynthetic rate. However, further increases in the DLI significantly reduced the ΦPSII and photosynthetic potential, leading to a marked decline in the photon yield. Therefore, a

DLI of $17.3 \text{ mol m}^{-2} \cdot \text{d}^{-1}$ with a photoperiod of 20 h d^{-1} is recommended for hydroponic lettuce cultivation in this rapid growth stage.

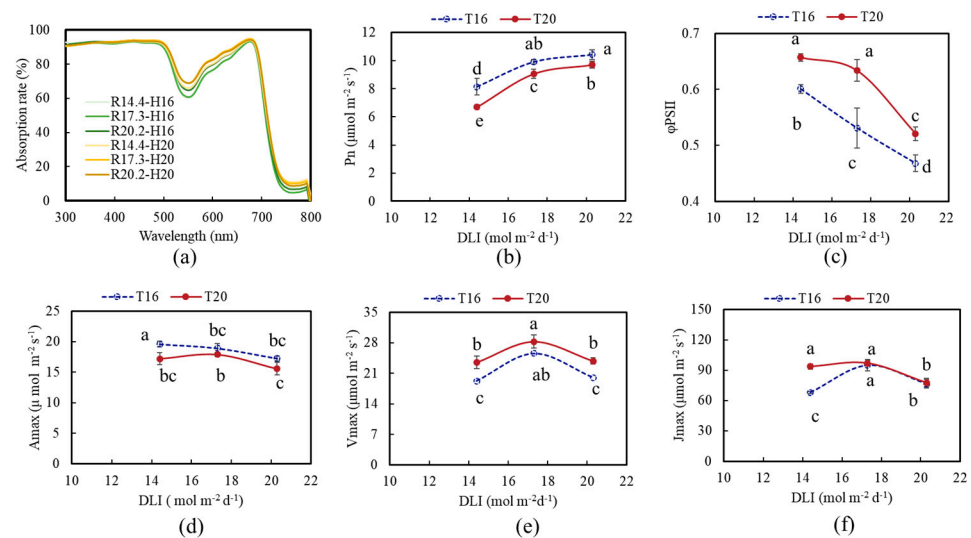


Figure 4. Effects of the DLI and photoperiod on the leaf absorption rate, ΦPSII , net photosynthetic rate, and photosynthetic potential of hydroponic lettuce at the rapid growth stage: (a) the leaf absorption rate, (b) the net photosynthetic rate, (c) the ΦPSII , (d) the maximum net photosynthetic rate, (e) the maximum carboxylation rate, and (f) the maximum electron transport rate. Identical letters indicate no significant difference, while different letters indicate significant differences.

4. Discussion

4.1. Describing the Growth Process Based on the Logistic Model Is Beneficial for Guiding Environmental Control

The growth process of cultivated hydroponic lettuce was quantitatively described using the logistic growth model, offering a scientific basis for defining the growth stages. The model's fitted values are closely aligned with the actual measurements under consistent environmental conditions and crop varieties. For instance, the model predicted the shoot fresh weight of 167 g on the 33rd day after transplanting, while the actual measurement was 170 g, indicating a minimal error. Furthermore, the stage-wise optimization experiments showed that the fitted values for both the slow and rapid growth stages closely matched the actual measurements, further validating the logistic model's accuracy. The logistic model has also been successfully applied to other crops. For instance, when describing the fresh weight variation of three sunflower cultivars sown across three seasons, the logistic model outperformed the Gompertz model in relation to two cultivars [26]. Additionally, the model exhibited high efficiency and accuracy in capturing specific growth stages of pecans, particularly in shell development [27]. For sugarcane, the logistic model has been employed to estimate key growth parameters, such as the maximum growth capacity and growth rate, which are crucial for understanding the growth dynamics and predicting the yield [28]. Unlike previous studies, this research divided the growth stages based on the logistic model and calculated the LAI and F_{int} at different growth nodes. This approach clarified the growth characteristics at various stages and provided valuable guidance for optimizing the light environment.

The logistic model, a well-known nonlinear model, follows an “S”-shaped curve, where parameter a represents the maximum potential yield of the crop, and parameters b and k are associated with the timing of the inflection point and the growth rate, respectively. Further analysis reveals a close correlation between the inflection point of the logistic model and the light interception ratio. At the slow growth stage, the lettuce leaf area is not yet fully expanded, resulting in a lower light interception ratio and limited photosynthetic efficiency, which contributes to a slower growth rate. As the plant transitions into the rapid growth

stage, the leaf area expands rapidly, increasing the light interception to its maximum, which significantly boosts the photosynthetic efficiency and leads to rapid biomass accumulation. However, after the rapid growth stage ends, despite the continued expansion of the leaf area, the light interception gradually reaches saturation. At this stage, the upper leaves intercept most of the light, while the lower leaves are shaded and unable to fully utilize the light, slowing the growth rate.

The amount of intercepted light determines how much energy a crop can capture for photosynthesis, directly affecting its final yield. Jin et al. [13] found that lower light intensity in early growth stages improved the light interception, which increased the dry weight and light use efficiency of hydroponic lettuce. Similarly, Xu et al. [29] increased the canopy light interception by raising the planting density, which boosted the soybean yield. In this study, the DLI was optimized for different growth stages, and future research could further explore the effect of adding far-red light [18] during the early growth stage to further enhance the light interception and improve the photon yield. In this study, a planting density of 38.9 plants per m^2 was used, but varying the density may influence the maximum light interception. Future research could also focus on identifying the best planting density for each growth stage to optimize both the light use efficiency and crop yield.

4.2. The Stage-Wise Optimization of DLI Significantly Enhanced the Photon Yield of Hydroponic Lettuce

Chung et al. [30] proposed calculating the photon yield by dividing “the total fresh weight of the entire plant by the cumulative incident light during the cultivation period” to quantify the efficiency of fresh weight production per mol of photons. In this study, a more practical approach was used by calculating the photon yield based on the fresh weight of the edible portion instead of the whole plant. Since vegetables are usually sold based on their edible parts, this approach gives a more accurate measure of the benefits of optimizing the light environment. It also helps determine the break-even point for the return on investment.

In this study, the DLI was optimized for different growth stages. At the slow growth stage, the DLI was set at $14.4 \text{ mol m}^{-2} \cdot \text{d}^{-1}$, while it was increased to $17.3 \text{ mol m}^{-2} \cdot \text{d}^{-1}$ in the rapid growth stage. This adjustment significantly improved the shoot fresh weight and photon yield of the hydroponic lettuce. Under the photoperiod of 20 h d^{-1} , a 13% increase in light energy led to a 5% increase in the leaf absorption rate and a 35% increase in the net photosynthetic rate. As a result, the shoot fresh weight increased by 25% and the light quantum yield improved by 19% (Figure 5).

The growth of crops depends on the amount of intercepted light and how efficiently it drives photosynthesis [31]. Increasing the DLI from $14.4 \text{ mol m}^{-2} \cdot \text{d}^{-1}$ to $18.0 \text{ mol m}^{-2} \cdot \text{d}^{-1}$ at the slow growth stage increased growth yield but significantly reduced the photon yield of the hydroponic lettuce. At transplanting, the LAI was 0.3 with a light interception ratio of only 0.2. By the end of the slow growth stage, this ratio rose to 0.7. Since over 30% of light energy that hits the cultivation cover is not utilized, raising the light intensity further only adds to the waste. Additionally, the ΦPSII dropped significantly because the leaves could not absorb the extra light, which was lost as heat [32].

During the rapid growth stage, increasing the DLI to $17.3 \text{ mol m}^{-2} \cdot \text{d}^{-1}$ significantly improved the photon yield; of course, this DLI value will be affected by different varieties and environmental changes. At this stage, the light interception ratio exceeded 70%, allowing the plants to effectively absorb most of the light energy. The increased light energy reduced the SLA, meaning the leaves became thicker, which enhanced the light absorption capacity of the leaves. This also significantly boosted the net photosynthetic rate of the leaves, leading to an increase in the shoot fresh weight. However, when the DLI exceeded $17.3 \text{ mol m}^{-2} \cdot \text{d}^{-1}$, the ΦPSII and photosynthetic potential of the hydroponic lettuce began to decline significantly, indicating that further increasing the light intensity would not continue to improve the crop yield.

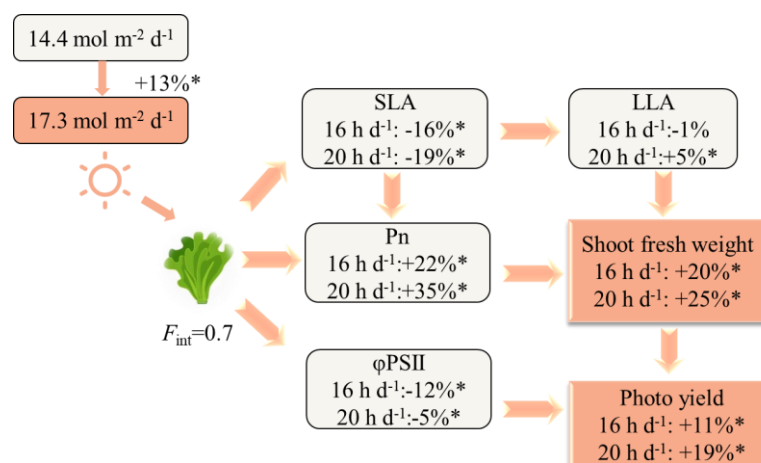


Figure 5. Factors influencing the photon yield of hydroponic lettuce after increasing the DLI at the rapid growth stage. An asterisk (*) represents a significant difference.

The SLA is one of the key factors affecting canopy light absorption. In a certain range, the SLA decreases gradually with the increase of the DLI, indicating that the blade becomes thicker. This aligns with previous studies showing that higher DLI levels increase carbohydrate accumulation, which promotes the enlargement of palisade and spongy cells, leading to thicker leaf tissues [33,34]. The SLA is also closely related to the mesophyll conductance (g_m); the thicker the leaf, the higher the g_m , because thicker leaves have larger intercellular air spaces [35]. Additionally, the increase in leaf thickness reduces the leaf transmittance and increases the reflectance, thereby enhancing the absorption rate of the leaves [36]. The rise in light intensity also enhances the net photosynthetic rate [32]. Within a certain range, the DLI is linearly positively correlated with the shoot fresh weight [10]. For example, under a photoperiod of 14 h d⁻¹, increasing the DLI from 5 mol m⁻²·d⁻¹ to 15 mol m⁻²·d⁻¹ significantly increased the net photosynthetic rate and shoot fresh weight of crepe myrtle lettuce [9]. When the DLI exceeded 17 mol m⁻²·d⁻¹, no significant variation in the SLA was observed, which may be attributed to the elevated leaf temperature in the hydroponic lettuce under high DLI conditions. Thicker leaves contribute to enhanced adaptability under high light conditions. At higher DLIs, the reduced SLA (thicker leaves) lowers the stomatal conductance and limits transpiration, which not only reduces the water loss and improves the water use efficiency (WUE) [37,38] but also mitigates light-induced damage to the photosynthetic system.

The maximum net photosynthetic rate reflects a plant's growth potential under optimal conditions. The maximum carboxylation rate represents Rubisco's highest catalytic activity at a given CO₂ concentration, while the maximum electron transport rate indicates the efficiency of the light reaction center and electron transport chain. Previous studies have demonstrated that an excessively high DLI limits the mesophyll conductance and biochemical reactions, thereby impairing the plant's photosynthetic capacity and potentially damaging its photosynthetic organelles, leading to physiological disorders [32,33]. Prolonged exposure to a high DLI induces short-term heat stress, disrupting the balance between light energy absorption and utilization. This imbalance promotes the accumulation of reactive oxygen species (ROS), which increases the chloroplast and mitochondrial membrane permeability, causing intracellular electrolyte leakage and a significant reduction in the chlorophyll content [39,40]. Consequently, an excessively high DLI reduces the Φ PSII and impairs the photosynthetic mechanism. The recommended DLI range for hydroponic lettuce production is 14–17 mol m⁻²·d⁻¹ [17], consistent with the findings of this study. Fu et al. [41] observed that different light intensities (100, 200, 400, 600, and 800 μ mol m⁻² s⁻¹) had varying effects on the chlorophyll fluorescence parameters and the rapid light response curve of lettuce. The highest light use efficiency occurred at 200 μ mol m⁻² s⁻¹, while the highest yield was achieved at 600 μ mol m⁻² s⁻¹, despite slight

photoinhibition. However, at $800 \mu\text{mol m}^{-2} \text{s}^{-1}$, the light use efficiency dropped significantly, accompanied by reduced antioxidant enzyme activity and severe photoinhibition.

5. Conclusions

In this study, three nonlinear growth models were used to describe the growth process of hydroponic lettuce, with the logistic model providing the best fit. Based on the logistic model, we divided the growth stages of hydroponic lettuce and optimized the light environment. A DLI of $14.4 \text{ mol m}^{-2} \cdot \text{d}^{-1}$ was applied during the slow growth stage (12 days after transplanting), leading to the highest photon yield due to the increased light absorption and net photosynthetic rate of the leaves. During the rapid growth stage (24 days after transplanting), the DLI was increased to $17.28 \text{ mol m}^{-2} \cdot \text{d}^{-1}$ with a photoperiod of $20 \text{ h} \cdot \text{d}^{-1}$. This enhanced the shoot fresh weight and photon yield, mainly due to improved light interception, reduced SLA, higher light absorption, and photosynthetic rate. However, when the DLI exceeded $17.3 \text{ mol m}^{-2} \cdot \text{d}^{-1}$, the photon yield, ΦPSII , and photosynthetic potential significantly declined. This study provides a scientific basis for optimizing lighting environments at different growth stages, leading to improved growth and yield and better light use efficiency in hydroponic lettuce cultivation in LED plant factories.

Author Contributions: Conceptualization, R.Y. and D.H.; methodology, R.Y.; software, R.Y.; validation, R.Y., H.Y. and F.J.; formal analysis, R.Y. and H.Y.; investigation, R.Y.; resources, R.Y.; data curation, R.Y.; writing—original draft preparation, R.Y.; writing—review and editing, R.Y.; visualization, R.Y.; supervision, R.Y.; project administration, F.J.; funding acquisition, D.H. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the Key Research and Development Project of Shandong Province (Grant No. 2022CXGC020708) and the China Agriculture Research System (Grant No. CARS-21).

Data Availability Statement: The original contributions presented in this study are included in the article. Further inquiries can be directed to the corresponding author.

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

References

- SharathKumar, M.; Heuvelink, E.; Marcelis, L.F.M. Vertical Farming: Moving from Genetic to Environmental Modification. *Trends Plant Sci.* **2020**, *25*, 724–727. [\[CrossRef\]](#) [\[PubMed\]](#)
- Van Delden, S.H.; SharathKumar, M.; Butturini, M.; Graamans, L.J.A.; Heuvelink, E.; Kacira, M.; Kaiser, E.; Klammer, R.S.; Klerkx, L.; Kootstra, G.; et al. Current Status and Future Challenges in Implementing and Upscaling Vertical Farming Systems. *Nat. Food* **2021**, *2*, 944–956. [\[CrossRef\]](#) [\[PubMed\]](#)
- Song, R.; Liu, D.; Pan, Y.; Cheng, Y.; Meng, C. Container Farms: Energy Modeling Considering Crop Growth and Energy-Saving Potential in Different Climates. *J. Clean. Prod.* **2023**, *420*, 138353. [\[CrossRef\]](#)
- Zhou, H.; Beynon-Davies, R.; Carslaw, N.; Dodd, I.C.; Ashworth, K. Yield, Resource Use Efficiency or Flavour: Trade-Offs of Varying Blue-to-Red Lighting Ratio in Urban Plant Factories. *Sci. Hortic.* **2022**, *295*, 110802. [\[CrossRef\]](#)
- Balassus, J.; Blank, J.; Babilon, S.; Hegemann, T.; Khanh, T.Q. Energy Efficient Lighting in Plant Factories: Addressing Utilance. *Agronomy* **2021**, *11*, 2570. [\[CrossRef\]](#)
- Thoma, F.; Somborn-Schulz, A.; Schlehuber, D.; Keuter, V.; Deerberg, G. Effects of Light on Secondary Metabolites in Selected Leafy Greens: A Review. *Front. Plant Sci.* **2020**, *11*, 497. [\[CrossRef\]](#)
- Gao, W.; He, D.; Ji, F.; Zhang, S.; Zheng, J. Effects of Daily Light Integral and LED Spectrum on Growth and Nutritional Quality of Hydroponic Spinach. *Agronomy* **2020**, *10*, 1082. [\[CrossRef\]](#)
- Kelly, N.; Choe, D.; Meng, Q.; Runkle, E.S. Promotion of Lettuce Growth under an Increasing Daily Light Integral Depends on the Combination of the Photosynthetic Photon Flux Density and Photoperiod. *Sci. Hortic.* **2020**, *272*, 109565. [\[CrossRef\]](#)
- Yan, Z.; He, D.; Niu, G.; Zhou, Q.; Qu, Y. Growth, Nutritional Quality, and Energy Use Efficiency of Hydroponic Lettuce as Influenced by Daily Light Integrals Exposed to White versus White Plus Red Light-Emitting Diodes. *HortScience* **2019**, *54*, 1737–1744. [\[CrossRef\]](#)
- Zhang, X.; He, D.; Niu, G.; Yan, Z.; Song, J. Effects of Environment Lighting on the Growth, Photosynthesis, and Quality of Hydroponic Lettuce in a Plant Factory. *Int. J. Agric. Biol. Eng.* **2018**, *11*, 33–40. [\[CrossRef\]](#)
- Nozue, H.; Oono, K.; Ichikawa, Y.; Tanimura, S.; Shirai, K.; Sonoike, K.; Nozue, M.; Hayashida, N. Significance of Structural Variation in Thylakoid Membranes in Maintaining Functional Photosystems during Reproductive Growth. *Physiol. Plant.* **2017**, *160*, 111–123. [\[CrossRef\]](#)

12. Chutimanukul, P.; Wanichananan, P.; Janta, S.; Toojinda, T.; Darwell, C.T.; Mosaleeyanon, K. The Influence of Different Light Spectra on Physiological Responses, Antioxidant Capacity and Chemical Compositions in Two Holy Basil Cultivars. *Sci. Rep.* **2022**, *12*, 588. [[CrossRef](#)] [[PubMed](#)]
13. Jin, W.; Ji, Y.; Larsen, D.H.; Huang, Y.; Heuvelink, E.; Marcelis, L.F.M. Gradually Increasing Light Intensity during the Growth Period Increases Dry Weight Production Compared to Constant or Gradually Decreasing Light Intensity in Lettuce. *Sci. Hortic.* **2023**, *311*, 111807. [[CrossRef](#)]
14. Wong, C.E.; Teo, Z.W.N.; Shen, L.; Yu, H. Seeing the Lights for Leafy Greens in Indoor Vertical Farming. *Trends Food Sci. Technol.* **2020**, *106*, 48–63. [[CrossRef](#)]
15. Paradiso, R.; Proietti, S. Light-Quality Manipulation to Control Plant Growth and Photomorphogenesis in Greenhouse Horticulture: The State of the Art and the Opportunities of Modern LED Systems. *J. Plant Growth Regul.* **2022**, *41*, 742–780. [[CrossRef](#)]
16. Yang, R.; Qiu, C.; Zheng, J.; Ji, F.; He, D.; Yang, P. LED Supplementary Strategy Based on Hourly Light Integral for Improving the Yield and Quality of Greenhouse Strawberries. *Int. J. Agric. Biol. Eng.* **2024**, *17*, 96–104. [[CrossRef](#)]
17. Boros, I.F.; Székely, G.; Balázs, L.; Csambalik, L.; Sipos, L. Effects of LED Lighting Environments on Lettuce (*Lactuca sativa* L.) in PFAL Systems—A Review. *Sci. Hortic.* **2023**, *321*, 112351. [[CrossRef](#)]
18. Sari, B.G.; Lúcio, A.D.; Santana, C.S.; Savian, T.V. Describing Tomato Plant Production Using Growth Models. *Sci. Hortic.* **2019**, *246*, 146–154. [[CrossRef](#)]
19. Jiao, X.; Zhang, H.; Zheng, J.; Yin, Y.; Wang, G.; Chen, Y.; Yu, J.; Ge, Y. Comparative Analysis of Nonlinear Growth Curve Models for Arabidopsis Thaliana Rosette Leaves. *Acta Physiol. Plant.* **2018**, *40*, 114. [[CrossRef](#)]
20. Karadavut, U.; Palta, Ç.; Kökten, A.; Bako, A. Comparative Study on Some Non-Linear Growth Models for Describing Leaf Growth of Maize. *Int. J. Agric. Biol.* **2010**, *12*, 227–230.
21. Carini, F.; Cargnelutti Filho, A.; Pezzini, R.V.; Souza, J.M.D.; Chaves, G.G.; Provedi, A. Nonlinear Models for Describing Lettuce Growth in Autumn-Winter. *Cienc. Rural.* **2020**, *50*, e20190534. [[CrossRef](#)]
22. Li, Q.; Gao, H.; Zhang, X.; Ni, J.; Mao, H. Describing Lettuce Growth Using Morphological Features Combined with Nonlinear Models. *Agronomy* **2022**, *12*, 860. [[CrossRef](#)]
23. Yan, Z.; He, D.; Niu, G.; Zhai, H. Evaluation of Growth and Quality of Hydroponic Lettuce at Harvest as Affected by the Light Intensity, Photoperiod and Light Quality at Seedling Stage. *Sci. Hortic.* **2019**, *248*, 138–144. [[CrossRef](#)]
24. Ye, Z.; Suggett, D.J.; Robakowski, P.; Kang, H. A Mechanistic Model for the Photosynthesis–Light Response Based on the Photosynthetic Electron Transport of Photosystem II in C₃ and C₄ Species. *New Phytol.* **2013**, *199*, 110–120. [[CrossRef](#)] [[PubMed](#)]
25. Farquhar, G.D.; Von Caemmerer, S.; Berry, J.A. A Biochemical Model of Photosynthetic CO₂ Assimilation in Leaves of C₃ Species. *Planta* **1980**, *149*, 78–90. [[CrossRef](#)]
26. Mello, A.; Toebe, M.; Marchioro, V.S.; De Souza, R.R.; Paraginski, J.A.; Somavilla, J.C.; Martins, V.; Manfio, G.L.; Junges, D.L.; Da Rocha Borges, M.E. Nonlinear Models in the Description of Sunflower Cultivars Growth Considering Heteroscedasticity. *J. Plant Growth Regul.* **2023**, *42*, 7215–7228. [[CrossRef](#)]
27. Panta, S.; Zhou, B.; Zhu, L.; Maness, N.; Rohla, C.; Costa, L.; Ampatzidis, Y.; Fontainer, C.; Kaur, A.; Zhang, L. Selecting Non-Linear Mixed Effect Model for Growth and Development of Pecan Nut. *Sci. Hortic.* **2023**, *309*, 111614. [[CrossRef](#)]
28. Jane, S.A.; Fernandes, F.A.; Silva, E.M.; Muniz, J.A.; Fernandes, T.J.; Pimentel, G.V. Adjusting the Growth Curve of Sugarcane Varieties Using Nonlinear Models. *Cienc. Rural.* **2020**, *50*, e20190408. [[CrossRef](#)]
29. Xu, C.; Li, R.; Song, W.; Wu, T.; Sun, S.; Han, T.; Wu, C. High Density and Uniform Plant Distribution Improve Soybean Yield by Regulating Population Uniformity and Canopy Light Interception. *Agronomy* **2021**, *11*, 1880. [[CrossRef](#)]
30. Chung, H.-Y.; Chang, M.-Y.; Wu, C.-C.; Fang, W. Quantitative Evaluation of Electric Light Recipes for Red Leaf Lettuce Cultivation in Plant Factories. *HortTechnology* **2018**, *28*, 755–763. [[CrossRef](#)]
31. Palmer, S.; Van Iersel, M.W. Increasing Growth of Lettuce and Mizuna under Sole-Source LED Lighting Using Longer Photoperiods with the Same Daily Light Integral. *Agronomy* **2020**, *10*, 1659. [[CrossRef](#)]
32. Fu, W.; Li, P.; Wu, Y. Effects of Different Light Intensities on Chlorophyll Fluorescence Characteristics and Yield in Lettuce. *Sci. Hortic.* **2012**, *135*, 45–51. [[CrossRef](#)]
33. Poorter, H.; Niinemets, Ü.; Ntagkas, N.; Siebenkäs, A.; Mäenpää, M.; Matsubara, S.; Pons, T. A Meta-analysis of Plant Responses to Light Intensity for 70 Traits Ranging from Molecules to Whole Plant Performance. *New Phytol.* **2019**, *223*, 1073–1105. [[CrossRef](#)] [[PubMed](#)]
34. Carotti, L.; Graamans, L.; Puksic, F.; Butturini, M.; Meinen, E.; Heuvelink, E.; Stanghellini, C. Plant Factories Are Heating Up: Hunting for the Best Combination of Light Intensity, Air Temperature and Root-Zone Temperature in Lettuce Production. *Front. Plant Sci.* **2021**, *11*, 592171. [[CrossRef](#)] [[PubMed](#)]
35. Peguero-Pina, J.J.; Sisó, S.; Flexas, J.; Galmés, J.; García-Nogales, A.; Niinemets, Ü.; Sancho-Knapik, D.; Saz, M.Á.; Gil-Pelegrín, E. Cell-level Anatomical Characteristics Explain High Mesophyll Conductance and Photosynthetic Capacity in Sclerophyllous Mediterranean Oaks. *New Phytol.* **2017**, *214*, 585–596. [[CrossRef](#)]
36. Liang, S.-Z.; Shi, P.; Ma, W.-D.; Xing, Q.-G.; Yu, L.-J. Relational analysis of spectra and red-edge characteristics of plant leaf and leaf biochemical constituent: Relational analysis of spectra and red-edge characteristics of plant leaf and leaf biochemical constituent. *Chin. J. Eco-Agric.* **2010**, *18*, 804–809. [[CrossRef](#)]
37. Clavijo-Herrera, J.; Van Santen, E.; Gómez, C. Growth, Water-Use Efficiency, Stomatal Conductance, and Nitrogen Uptake of Two Lettuce Cultivars Grown under Different Percentages of Blue and Red Light. *Horticulturae* **2018**, *4*, 16. [[CrossRef](#)]

38. Gaofeng, X.; Shicai, S.; Fudou, Z.; Yun, Z.; Hisashi, K.-N.; David, R.C. Relationship Between Allelopathic Effects and Functional Traits of Different Allelopathic Potential Rice Accessions at Different Growth Stages. *Rice Sci.* **2018**, *25*, 32–41. [[CrossRef](#)]
39. Zhao, X.; Sui, X.; Zhao, L.; Gao, X.; Wang, J.; Wen, X.; Li, Y. Morphological and Physiological Response Mechanism of Lettuce (*Lactuca sativa* L.) to Consecutive Heat Stress. *Sci. Hortic.* **2022**, *301*, 111112. [[CrossRef](#)]
40. Zhou, R.; Yu, X.; Li, X.; Mendanha Dos Santos, T.; Rosenqvist, E.; Ottosen, C.-O. Combined High Light and Heat Stress Induced Complex Response in Tomato with Better Leaf Cooling after Heat Priming. *Plant Physiol. Biochem.* **2020**, *151*, 1–9. [[CrossRef](#)]
41. Fu, W.; Li, P.; Wu, Y.; Tang, J. Effects of Different Light Intensities on Anti-Oxidative Enzyme Activity, Quality and Biomass in Lettuce. *Hortic. Sci.* **2012**, *39*, 129–134. [[CrossRef](#)]

Disclaimer/Publisher's Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.