horticulturae

MDPI

Article

Response of Common Ice Plant (*Mesembryanthemum crystallinum* L.) to Photoperiod/Daily Light Integral in Vertical Hydroponic Production

Jiaqi Xia and Neil Mattson *

School of Integrative Plant Science, Cornell University, Ithaca, NY 14850, USA; jx338@cornell.edu
* Correspondence: nsm47@cornell.edu; Tel.: +1-607-255-0621

Abstract: Common ice plant (*Mesembryanthemum crystallinum* L.) is a novel edible plant with a succulent and savory flavor emerging as new crop for greenhouse and plant factory growers. Currently very limited information is available on the response of ice plant to photoperiod and to daily light integral (DLI). The objective of this study was to determine the impact of photoperiod/DLI on the growth of ice plant for indoor vertical production. Four-week old seedlings of ice plant were transplanted into vertical hydroponic systems and given five photoperiod/DLI treatments: 8/6.3, 12/9.5, 16/12.7, 20/15.8, and 24/19.0 h/mol·m^{-2}·d^{-1}. Sequential destructive harvests to determine plant growth occurred 14, 21, and 28 days after lighting treatments began. Plants performed better with increasing photoperiod/DLI from 8 h/6.3 mol·m^{-2}·d^{-1} to 20 h/15.8 mol·m^{-2}·d^{-1}. By day 28, shoot fresh weight increased from 160 g to 639 g as the photoperiod/DLI increased from 8 h/6.3 mol·m^{-2}·d^{-1} to 20 h/15.8 mol·m^{-2}·d^{-1}. The continuous lighting treatment, 24 h/19 mol·m^{-2}·d^{-1}, showed a negative effect on the plant fresh weight (FW) and dry weight (DW). Light treatment did not have obvious effects on shoot:root ratio and macronutrient uptake except that potassium (K) uptake decreased slightly with increased photoperiod/DLI. Plants receiving higher photoperiod/DLI showed the same number of leaves (indicating the same development stage) but had smaller, thicker, and darker green leaves compared to lower photoperiod/DLI treatments. Leaf water content was not affected by light treatment up to 20 h/15.8 mol·m^{-2}·d^{-1} but decreased at 24 h/19 mol·m^{-2}·d^{-1}. Further research is needed to separate the physiological response of increasing/continuous photoperiod from the response of increasing DLI.

Keywords: artificial lighting; vertical farming; plant factory; hydroponics; cultural management; controlled environment agriculture (CEA)

Citation: Xia, J.; Mattson, N. Response of Common Ice Plant (*Mesembryanthemum crystallinum* L.) to Photoperiod/Daily Light Integral in Vertical Hydroponic Production. *Horticulturae* **2022**, *8*, 653. https://doi.org/10.3390/horticulturae8070653

Academic Editor: Julė Jankauskienė

Received: 16 June 2022
Accepted: 12 July 2022
Published: 19 July 2022

1. Introduction

Common ice plant (*Mesembryanthemum crystallinum* L.) is a succulent edible plant emerging as a new ingredient for salad. Ice plant is reported to have a high nutritional value for humans due to its abundant content of antioxidants such as phenolic compounds [1]. Ice plant is used as food, as medical treatment, and in therapeutic cosmetics [2]. As hydroponics and controlled environment technologies become more widely used for the cultivation of fresh and high-quality vegetables, greenhouse growers are looking to expand the crops they produce, and some have added ice plant into their production lists.

Controlled environment agriculture (CEA) refers to an intensive approach for controlling plant growth and development by capitalizing on advanced horticultural techniques and innovations in technology [3]. Greenhouses and plant factories are two typical forms of CEA [4]. Plant factories, also known as indoor farming and vertical farming, incorporate hydroponics and light-emitting diode (LED) technologies. In such systems, crops are grown vertically on well-engineered shelves, and there is precise control of environmental parameters including: temperature, light, nutrients, and atmosphere (relative humidity

and CO_2) [5–7]. The first commercial plant factory appeared in Japan in 1983 [7]. Over the past decade, plant factories have developed rapidly across the world, especially with accelerating urbanization. Plant factories provide "local production for local consumption" that minimizes food mileage and maximizes food freshness as well as job opportunities for people who live in the city and enjoy working with plants [7]. In North America, there were more than 30 plant factories and more than 100 shipping container farms (a smaller version of a plant factory) as of 2017 [8]. Indoor production has several benefits. In addition to optimizing crop performance, plant factories can deal with global issues including fresh water shortage, limited arable land, extreme weather, pesticide overuse, and carbon emission during food transportation [7,9]. Furthermore, with the development of new technologies such as artificial intelligence (AI), big data, cloud computing, and especially 5G and Internet of Things (IoT), indoor farming has stepped into a new generation that is known as smart farming [10]. Resources can be allocated in a more efficient way, and agricultural production is moving towards highly automatic, intelligent, and efficient modes where people, plants, data, and clouds are all connected [10]. However, the costs of LED lights (both upfront costs and operating costs) still remain high with correspondingly large carbon footprints [7,9]. High energy costs/carbon footprint make indoor farming only feasible for limited types of crops, such as perishable, nutrient-dense, high-yielding crops. Candidates may include microgreens and medical herbs such as saffron, mushrooms, and medical marijuana. Ice plant, with its high economic value, may become a top choice for indoor farming growers.

LEDs are the only primary source of lights in plant factories [11]. They provide a controlled light quantity (can be measured as daily light integral (DLI)) and light quality (light spectrum). Growers can customize the lighting for each specific crop, as each crop has peculiar/distinct requirement for different light wavelengths and total light amount [12]. Plentiful research has been conducted on lighting in greenhouses and vertical farms, especially for common leafy greens and herb crops such as lettuce and basil [13,14]. For example, Stutte et al. [15] demonstrated that LED lights can be used to increase the production of bioprotective compounds in red leaf lettuce. UV-B radiation doses were selected by Dou et al. [16] for increasing the phenolic compounds in basil without yield reduction. Far-red LEDs were shown by Runkle et al. [17] to regulate seedling growth and flowering.

DLI, the amount of photosynthetically active radiation (PAR) received each day, is a critical measure of light quantity and is determined by both instantaneous light intensity (i.e., photosynthetic photon flux density [PPFD]) and duration of lighting (i.e., photoperiod). Plants typically have an increased rate of photosynthesis with increased PPFD and reach a maximum rate of photosynthesis at certain PPFD due to a limited number of chloroplasts, carbon dioxide (CO_2), or temperature [18]. While there are diminishing marginal returns to increasing PPFD (i.e., adding an additional photon results in smaller increase in photosynthesis), increasing photoperiod is another way to increase DLI and gross photosynthesis [19,20]. Palmer and van Iersel [21] treated lettuce and mizuna with different combinations of PPFD and photoperiod that provided the same DLI, and plants performed better when the radiation was provided over longer period, indicating more efficient photosynthesis under lower PPFD. Elkins and van Iersel [22] also demonstrated that the efficiency of photosynthesis was decreased with increased PPFD. In other words, when plants received a higher PPFD, the fraction of absorbed light used for photosynthesis was actually lower.

Currently, research is lacking on ice plant in response to light quantity and quality. Kim et al. [23] evaluated the performance of ice plant under fluorescent lamps, monochromatic red LEDs, and blue LEDs at 120 and 150 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PPFD with a photoperiod of 14 h (resulting in 6.05 and 7.56 $mol \cdot m^{-2} \cdot d^{-1}$ DLI) and found higher growth of ice plant under higher PPFD and red LEDs and higher antioxidant accumulation under blue LEDs. However, the DLI in their study was relatively low (compared to 12–30 $mol \cdot m^{-2} \cdot d^{-1}$ used for common greenhouse crops). No information is available on the yield response of ice plant to increasing photoperiod/DLI in a plant factory system. The objective of this project

was to determine the response (yield and morphology) of ice plant to a broad range of photoperiod/DLI to inform production practices in plant factories.

2. Materials and Methods

2.1. Plant Material

Seeds of ice plant (Baker Creek Heirloom Seeds, Mansfield, MO) were started in 2.5 cm rockwool cubes that were pre-soaked with 21 N–2.2 P–16 K Jack's All Purpose Fertilizer (JR Peters Inc., Allentown, PA, USA) at a concentration of 150 mg·L^{-1} N and placed in trays. The trays were kept in a controlled indoor environment with 21 °C (70 °F) day and night temperature. Lighting fixtures with "Vegmax" spectrum (Sananbio U.S., Albuquerque, NM) were used at 200 µmol·m^{-2}·s^{-1} for a photoperiod of 20 h per day resulting in a DLI of 14.4 mol·m^{-2}·d^{-1}. Germination generally occurred 2 to 3 days after sowing, and seedlings were thinned to one per rockwool cube 3 weeks after sowing. The entire germination stage took 4 weeks. The seedlings had 4–6 leaves at this stage, and they were then selected for uniformity and transplanted to the experimental setting.

2.2. Experimental Setting

A vertical hydroponic system made by Sananbio U.S. (Albuquerque, NM, USA), The Radix module, was used for this experiment. The system is a hybrid of nutrient film technique (NFT) and deep water culture (DWC) with gravity-driven water circulation (Figure 1). The system has five layers, which were used for five experimental treatments. The distance between layers (i.e., light-to-bed height) is 30 cm. Lighting fixtures with Sananbio "Vegmax" spectrum were connected to timers set to supply photoperiods of 8, 12, 16, 20, and 24 h, respectively at each layer. Each layer provided the same PPFD as described below (light fixtures allowed adjustment of photoperiod but not PPFD). The entire system was covered by black and white poly film with the white side facing inside and black side facing outside (Figure 2). The white side reflected light back to the internal space, which increased lighting uniformity and DLI. A fan was assembled at the side of each layer to facilitate horizontal air flow (HAF). The system was located in an office-type room with controlled temperature of 21 °C.

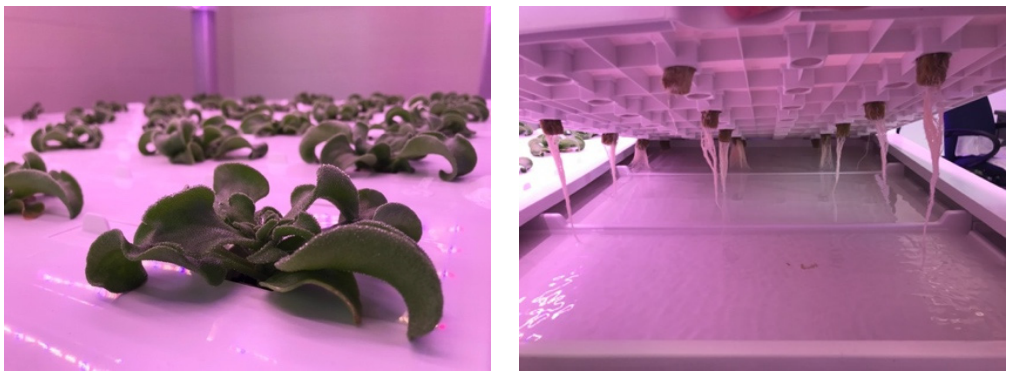

Figure 1. The Radix module (Sananbio U.S., Albuquerque, NM, USA), a vertical hydroponic system with a hybrid of nutrient film technique and deep water culture, demonstrating ice plant shoots (**left**) and roots (**right**) 10 days after transplanting.

The circulating hydroponic nutrient solution was made by combining equal parts (0.75 g·L^{-1} each) of 5 N–5.2 P–21.6 K Jack's Professional Water-Soluble Fertilizer (J. R. Peter's Inc., Allentown, PA) and 15.5 N–0 P–0 K YaraLiva Calcinit (Yara International, Oslo, Norway) [24]. This nutrient recipe provided 150 mg·L^{-1} nitrogen (N), 39 mg·L^{-1} phosphorus (P), 162 mg·L^{-1} potassium (K), 139 mg·L^{-1} calcium (Ca), 47 mg·L^{-1} magnesium (Mg), 62 mg·L^{-1} sulfur (S), 2.3 mg·L^{-1} iron (Fe), 0.38 mg·L^{-1} manganese (Mn), 0.11 mg·L^{-1} zinc (Zn), 0.38 mg·L^{-1} boron (B), 0.113 mg·L^{-1} copper (Cu), and 0.075 mg·L^{-1} molybdenum (Mo). Following the results of previous research, 0.05 M sodium chloride was

added to the nutrient solution to facilitate the optimum growth of ice plants [25]. The pH of the nutrient solution was adjusted every day to a range of 5.6–6.0, using 1 M potassium hydroxide (KOH) and 1 M sulfuric acid (H_2SO_4). New nutrient solution was added to the reservoir every few days to maintain water levels. NaCl was added to maintain electrical conductivity (EC) in a range of 7.8–8.5 mS/cm.

Figure 2. The vertical hydroponic system covered with black and white poly film.

Plants were transplanted into the system at a density of 27.8 plants/m^2. There were 30 (5 × 6) plants in each layer, of which 12 (3 × 4) plants at the center were used for the experiment and the 18 plants at the outer edges were treated as border plants because lighting was less uniform at the border. Five lighting treatments were assigned, from top to bottom, to the five layers of the vertical hydroponic system: 8, 12, 16, 20, and 24 h photoperiods. The PPFD was 220 ± 5.2 (mean ± std dev.) $\mu mol \cdot m^{-2} \cdot s^{-1}$ for the central 12 plants. Using 220 $\mu mol \cdot m^{-2} \cdot s^{-1}$ as a basis for calculation, the calculated DLI, from top to bottom layer, respectively, was 6.34, 9.50, 12.67, 15.84, and 19.01 $mol \cdot m^{-2} \cdot d^{-1}$. The experimental design did not allow for separating the effects of the DLI from the photoperiod (i.e., the vertical growing system did not have dimmable lights).

2.3. Measurements

Three plants from each treatment (a total of fifteen plants) were harvested at day 14, day 21, and day 28 after transplanting (Figure 3). At each harvest, measurements were taken for: fresh weight (FW) and dry weight (DW, following 72 h in an oven at 70 °C) of plant, shoot, leaf, and root; number of leaves on main stem; leaf surface area (LSA) with an LI-3100 LSA meter (LI-COR Inc., Lincoln, Nebraska); and tissue analysis (only plants harvested at day 28 after transplanting with plants from the same treatment pooled together) at the Cornell Nutrient Analysis Lab (Ithaca, NY, USA). The experiment was replicated over time for a total of three times [25].

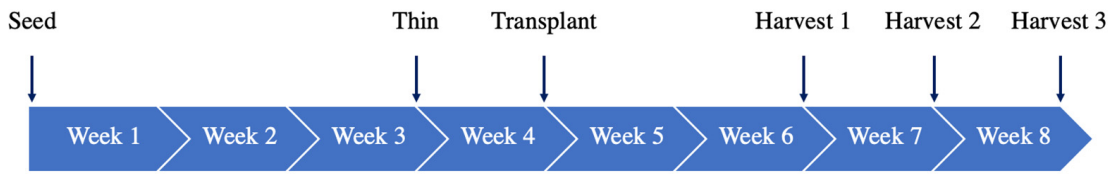

Figure 3. Timeline for each of the three crop cycles in the experiment.

2.4. Experimental Design and Statistical Analysis

The experiment was based on a randomized complete block design (RCBD). The experiment was replicated three times, and these replications were treated as different blocks. Within each block, the experimental unit was one plant randomly harvested at a specified layer. There were nine experimental units for each of the five lighting treatments per block. Three experimental units from each lighting treatment were destructively harvested at three time points (day 14, 21, 28 after transplanting). The data were analyzed using JMP software (SAS Institute, Cary, NC, USA). Analysis of variance (ANOVA) and Tukey's honest significance difference (HSD) test were used to determine differences in measured responses based on lighting treatment. Linear and quadratic regression were conducted to model plant growth over time for each lighting treatment.

3. Results

3.1. Fresh Weight

Ice plant exhibited greater shoot, root, and total FW with increased photoperiod/DLI up to 20 h/15.8 mol·m^{-2}·d^{-1}. This pattern started to appear in the first week of measurement (14 days) and became greater over time (Table 1). The 24 h/19.0 mol·m^{-2}·d^{-1} treatment had similar results as the 16 h/12.7 mol·m^{-2}·d^{-1} treatment and ranked second among all treatments in terms of shoot, root, and total FW. From the timeline perspective, all treatments showed significant ($p < 0.001$) linear growth in terms of shoot, root, and total FW (Table 1 and Figure 4). All treatments also exhibited a significant ($p < 0.05$) quadratic growth pattern (i.e., growth rates increased between the second and third harvest).

Table 1. Mean plant fresh weight, shoot fresh weight, and root fresh weight of ice plant in response to photoperiod/daily light integral (DLI) treatment over time (plants harvested 14, 21, or 28 days after treatment). Data represent means (± SE) of 3 experimental units times 3 replications over time.

Photoperiod (Hours of Light per Day, h)/ DLI (mol·m^{-2}·d^{-1})	14 Days	21 Days	28 Days	Significance across Time
	Plant Fresh Weight (g)			
8/6.34	25.4 ± 4.1 ^{C}	73.5 ± 11.3 ^{D}	167.1 ± 11.3 ^{D}	L*** Q *
12/9.50	50.7 ± 3.2 ^{B}	149.6 ± 8.3 ^{C}	314.8 ± 15.3 ^{C}	L *** Q *
16/12.67	66.2 ± 5.5 ^{AB}	200.3 ± 11.3 ^{B}	521.1 ± 22.2 ^{B}	L *** Q ***
20/15.84	75.0 ± 4.3 ^{A}	272.6 ± 11.9 ^{A}	683.6 ± 20.4 ^{A}	L *** Q ***
24/19.01	51.7 ± 5.8 ^{B}	184.9 ± 15.8 ^{BC}	477.1 ± 23.1 ^{B}	L *** Q **
	Shoot Fresh Weight (g)			
8/6.34	23.7 ± 3.6 ^{C}	69.1 ± 10.3 ^{D}	159.8 ± 10.6 ^{D}	L *** Q *
12/9.50	46.5 ± 3.0 ^{B}	139.8 ± 7.8 ^{C}	298.3 ± 15.5 ^{C}	L *** Q *
16/12.67	60.0 ± 5.1 ^{AB}	186.0 ± 10.3 ^{B}	486.7 ± 20.1 ^{B}	L *** Q ***
20/15.84	67.5 ± 3.9 ^{A}	253.6 ± 10.9 ^{A}	638.6 ± 19.9 ^{A}	L *** Q ***
24/19.01	45.9 ± 5.2 ^{B}	168.6 ± 14.6 ^{BC}	449.2 ± 21.8 ^{B}	L *** Q **
	Root Fresh Weight (g)			
8/6.34	1.8 ± 0.5 ^{C}	4.5 ± 1.2 ^{C}	7.2 ± 1.7 ^{D}	L *** Q ^{NS}
12/9.50	4.2 ± 0.3 ^{B}	9.8 ± 0.7 ^{B}	16.6 ± 1.7 ^{CD}	L *** Q ^{NS}
16/12.67	6.2 ± 0.4 ^{AB}	14.4 ± 1.2 ^{AB}	34.5 ± 5.2 ^{AB}	L *** Q ^{NS}
20/15.84	7.5 ± 0.5 ^{A}	19.0 ± 1.4 ^{A}	44.9 ± 3.5 ^{A}	L *** Q ^{NS}
24/19.01	5.7 ± 0.6 ^{AB}	16.3 ± 1.3 ^{A}	27.9 ± 2.6 ^{BC}	L *** Q ^{NS}

Letters represent mean separation comparison across light treatments within the same harvest day using Tukey's HSD (alpha = 0.05). Significance of linear (L) or quadratic (Q) regression of a given treatment over treatment time: NS, *, **, *** denotes nonsignificant or significant at $p \leq 0.05$, 0.01, or 0.001, respectively.

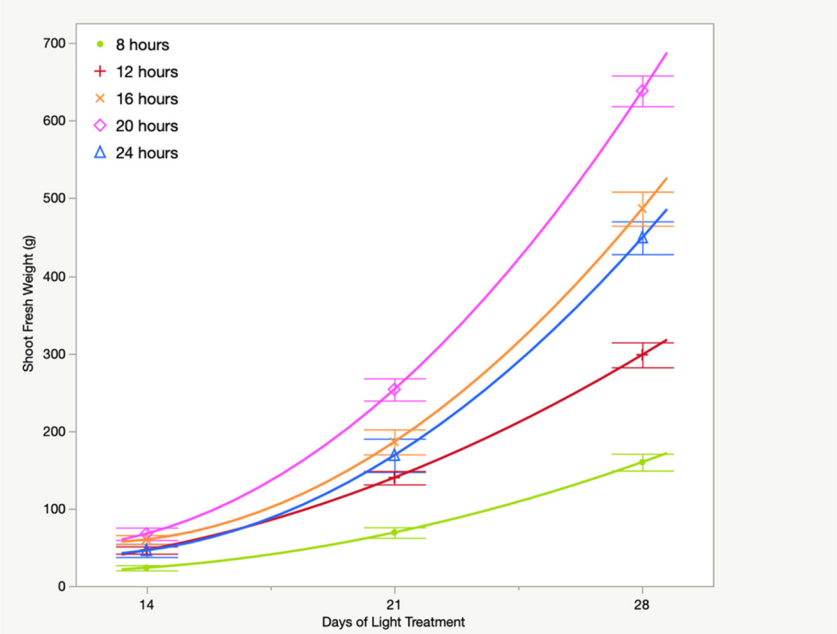

Figure 4. Mean shoot fresh weight (FW) of ice plant in response to photoperiod/daily light integral (DLI) treatment over time (plants harvested 14, 21, or 28 days after treatment). Data are means (± SE) of 3 experimental units times 3 replications over time. The green dot, red plus, orange x, pink diamond, and blue triangle represent 8/6.34, 12/9.50, 16/12.67, 20/15.84, and 24/19.01 h/mol·m^{-2}·d^{-1} treatments, respectively.

3.2. Dry Weight

Shoot, root, and total DW generally followed the same pattern as FW, although, in the last week of measurement (28 days), the 24 h/19.0 mol·m^{-2}·d^{-1} treatment was not statistically different from the 20 h/15.8 mol·m^{-2}·d^{-1} treatment in terms of total DW (Table 2). From the timeline perspective, all treatments exhibited significant ($p < 0.001$) linear growth over time in terms of shoot, root, and total DW. The 16 h/12.7 mol·m^{-2}·d^{-1}, 20 h/15.8 mol·m^{-2}·d^{-1}, and 24 h/19.0 mol·m^{-2}·d^{-1} treatments showed a significant ($p < 0.01$) quadratic growth pattern in terms of shoot, root, and total DW, with the exception of 16 h/12.7 mol·m^{-2}·d^{-1} and 24 h/19.0 mol·m^{-2}·d^{-1} treatments, which showed a linear growth pattern for root DW.

Table 2. Mean plant dry weight, shoot dry weight, root dry weight, and shoot:root ratio of ice plant in response to photoperiod/daily light integral (DLI) treatment over time (plants harvested 14, 21, or 28 days after treatment). Data represent means (± SE) of 3 experimental units times 3 replications over time.

Photoperiod (Hours of Lighting per Day, h)/ DLI (mol·m^{-2}·d^{-1})	14 Days	21 Days	28 Days	Significance across Time
	Plant Dry Weight (g)			
8/6.34	0.650 ± 0.129 ^{C}	1.726 ± 0.179 ^{D}	3.411 ± 0.303 ^{D}	L *** Q ^{NS}
12/9.50	1.372 ± 0.076 ^{B}	3.451 ± 0.161 ^{C}	6.318 ± 0.269 ^{C}	L *** Q ^{NS}
16/12.67	1.998 ± 0.121 ^{A}	4.811 ± 0.313 ^{B}	11.198 ± 0.399 ^{B}	L *** Q **
20/15.84	2.417 ± 0.114 ^{A}	6.827 ± 0.256 ^{A}	15.733 ± 0.731 ^{A}	L *** Q **
24/19.01	1.947 ± 0.160 ^{A}	5.478 ± 0.283 ^{B}	13.976 ± 0.818 ^{A}	L *** Q **
	Shoot Dry Weight (g)			
8 /6.34	0.599 ± 0.116 ^{C}	1.574 ± 0.152 ^{D}	3.148 ± 0.252 ^{D}	L *** Q ^{NS}
12/9.50	0.238 ± 0.069 ^{B}	3.136 ± 0.146 ^{C}	5.724 ± 0.272 ^{C}	L *** Q ^{NS}
16/12.67	1.776 ± 0.112 ^{A}	4.319 ± 0.276 ^{B}	10.027 ± 0.375 ^{B}	L *** Q ***
20/15.84	2.119 ± 0.101 ^{A}	6.149 ± 0.239 ^{A}	13.954 ± 0.961 ^{A}	L *** Q **
24/19.01	1.799 ± 0.156 ^{A}	4.881 ± 0.263 ^{B}	12.866 ± 0.740 ^{B}	L *** Q ***

Table 2. *Cont.*

Photoperiod (Hours of Lighting per Day, h)/ DLI (mol·m^{-2}·d^{-1})	14 Days	21 Days	28 Days	Significance across Time
	Root Dry Weight (g)			
8/6.34	0.051 ± 0.014 ^{D}	0.151 ± 0.032 ^{D}	0.263 ± 0.071 ^{C}	L *** Q ^{NS}
12/9.50	0.134 ± 0.009 ^{C}	0.316 ± 0.018 ^{C}	0.593 ± 0.067 ^{C}	L *** Q ^{NS}
16/12.67	0.222 ± 0.013 ^{B}	0.492 ± 0.042 ^{B}	1.171 ± 0.146 ^{B}	L *** Q ^{NS}
20/15.84	0.298 ± 0.019 ^{A}	0.678 ± 0.037 ^{A}	1.779 ± 0.106 ^{A}	L *** Q **
24/19.01	0.148 ± 0.017 ^{C}	0.597 ± 0.042 ^{AB}	1.110 ± 0.090 ^{B}	L *** Q ^{NS}
	Shoot:Root Ratio			
8/6.34	12.187 ± 1.178 ^{AB}	10.798 ± 0.771 ^{A}	12.255 ± 0.388 ^{A}	L ^{NS} Q ^{NS}
12/9.50	9.193 ± 0.479 ^{BC}	10.286 ± 0.366 ^{A}	10.224 ± 0.757 ^{AB}	L ^{NS} Q ^{NS}
16/12.67	8.042 ± 0.582 ^{C}	9.197 ± 0.407 ^{A}	10.661 ± 1.163 ^{AB}	L ^{NS} Q ^{NS}
20/15.84	7.084 ± 0.440 ^{C}	9.433 ± 0.479 ^{A}	8.183 ± 0.532 ^{B}	L ^{NS} Q *
24/19.01	13.077 ± 1.249 ^{A}	9.023 ± 1.140 ^{A}	11.740 ± 0.471 ^{A}	L ^{NS} Q *

Letters represent mean separation comparison across light treatments within the same harvest day using Tukey's HSD (alpha = 0.05). Significance of linear (L) or quadratic (Q) regression of a given treatment over treatment time: ^{NS}, *, **, *** denotes nonsignificant or significant at $p \leq 0.05$, 0.01, or 0.001, respectively.

3.3. Shoot:Root Ratio

There was not a consistent pattern over time, but in the first week the intermediate treatments had a lower shoot:root ratio (i.e., distributed less biomass to shoots than to roots) than the 8 h/6.3 mol·m^{-2}·d^{-1} or 24 h/19.0 mol·m^{-2}·d^{-1} treatments. In addition, during the last week of harvest (28 days), the 20 h/15.8 mol·m^{-2}·d^{-1} treatment had lower shoot:root ratio than other treatments (Table 2). The other treatments had similar shoot:root ratios.

3.4. Leaf Number on the Main Stem, Leaf Fresh Weight, Leaf Dry Weight, Specific Leaf Area

All treatments had similar number of leaves on the main stem suggesting that lighting treatment did not affect plant development rate (i.e., leaf unfolding rate) (Table 3). The weight of leaves generally followed the same pattern as shoot and total FW/DW (Table 3). With increased photoperiod/DLI up to 20 h/15.8 mol·m^{-2}·d^{-1}, the leaves had similar water content (%), and therefore, the differences in DW corresponded to the differences in FW (i.e., DW and FW had the same pattern) (Table 4). However, the 24 h/19.0 mol·m^{-2}·d^{-1} treatment had lower leaf water content. As a result, although it acquired similar leaf DW as the 20 h/15.8 mol·m^{-2}·d^{-1} treatment, its leaf FW was about 30% less than that of the 20 h/15.8 mol·m^{-2}·d^{-1} treatment. Additionally, increased photoperiod/DLI caused thicker leaves (i.e., less specific leaf area) (Table 4). Plants treated with greater photoperiod/DLI visually had darker green color and curlier leaves (Figure 5).

Figure 5. Images of ice plants harvested after 21 days of light treatment. Columns from left to right show 8, 12, 16, 20, and 24 h treatments.

Table 3. Mean leaf number on the main stem, leaf fresh weight, and leaf dry weight of ice plant in response to photoperiod/daily light integral (DLI) treatment over time (plants harvested 14, 21, or 28 days after treatment). Data represent means (± SE) of 3 experimental units times 3 replications over time.

Photoperiod (Hours of Lighting per Day, h)/ DLI (mol·m^{-2}·d^{-1})	14 Days	21 Days	28 Days	Significance across Time
	Leaf Number on the Main Stem			
8/6.34	11.6 ± 0.4 ^{A}	15.3 ± 0.3 ^{AB}	16.8 ± 0.3 ^{A}	L *** Q ^{NS}
12/9.50	12.4 ± 0.3 ^{A}	15.3 ± 0.1 ^{AB}	17.2 ± 0.1 ^{A}	L *** Q ^{NS}
16/12.67	12.2 ± 0.4 ^{A}	15.3 ± 0.1 ^{AB}	17.1 ± 0.2 ^{A}	L *** Q ^{NS}
20/15.84	12.9 ± 0.4 ^{A}	15.6 ± 0.2 ^{A}	16.9 ± 0.2 ^{A}	L *** Q ^{NS}
24/19.01	12.7 ± 0.2 ^{A}	14.6 ± 0.2 ^{B}	16.2 ± 0.3 ^{A}	L *** Q ^{NS}
	Leaf Fresh Weight (g)			
8/6.34	23.2 ± 3.4 ^{C}	66.2 ± 9.6 ^{C}	145.6 ± 9.4 ^{D}	L *** Q *
12/9.50	45.1 ± 2.8 ^{B}	129.2 ± 7.1 ^{B}	256.4 ± 13.2 ^{C}	L *** Q ^{NS}
16/12.67	57.7 ± 4.9 ^{AB}	169.7 ± 9.0 ^{B}	395.9 ± 18.3 ^{B}	L *** Q **
20/15.84	64.7 ± 3.6 ^{A}	224.3 ± 9.6 ^{A}	507.1 ± 14.5 ^{A}	L *** Q ***
24/19.01	44.1 ± 5.0 ^{B}	151.5 ± 12.9 ^{B}	351.6 ± 18.6 ^{B}	L *** Q *
	Leaf Dry Weight (g)			
8/6.34	0.568 ± 0.105 ^{C}	1.479 ± 0.136 ^{D}	2.730 ± 0.215 ^{D}	L *** Q ^{NS}
12/9.50	1.168 ± 0.062 ^{B}	2.770 ± 0.124 ^{C}	4.501 ± 0.219 ^{C}	L *** Q ^{NS}
16/12.67	1.654 ± 0.103 ^{A}	3.711 ± 0.226 ^{B}	7.183 ± 0.343 ^{B}	L *** Q ^{NS}
20/15.84	1.967 ± 0.093 ^{A}	5.014 ± 0.184 ^{A}	9.582 ± 0.537 ^{A}	L *** Q ^{NS}
24/19.01	1.678 ± 0.148 ^{A}	4.113 ± 0.220 ^{B}	9.069 ± 0.539 ^{A}	L *** Q *

Letters represent mean separation comparison across light treatments within the same harvest day using Tukey's HSD (alpha = 0.05). Significance of linear (L) or quadratic (Q) regression of a given treatment over treatment time: ^{NS}, *, **, *** denotes nonsignificant or significant at $p \leq 0.05$, 0.01, or 0.001, respectively.

Table 4. Mean leaf water content and specific leaf area of ice plant in response to photoperiod/daily light integral (DLI) treatment over time (plants harvested 14, 21, or 28 days after treatment). Data represent means (± SE) of 3 experimental units times 3 replications over time.

Photoperiod (Hours of Lighting per Day, h)/ DLI (mol·m^{-2}·d^{-1})	14 Days	21 Days	28 Days	Significanceacross Time
	Leaf Water Content (%)			
8/6.34	97.5 ± 0.1 ^{A}	97.7 ± 0.1 ^{A}	98.2 ± 0.1 ^{A}	L *** Q ^{NS}
12/9.50	97.4 ± 0.1 ^{A}	97.8 ± 0.1 ^{A}	98.2 ± 0.1 ^{A}	L *** Q ^{NS}
16/12.67	97.1 ± 0.1 ^{AB}	97.8 ± 0.1 ^{A}	98.2 ± 0.1 ^{A}	L *** Q ^{NS}
20/15.84	97.0 ± 0.1 ^{B}	97.7 ± 0.1 ^{A}	98.1 ± 0.1 ^{A}	L *** Q ^{NS}
24/19.01	96.0 ± 0.2 ^{C}	97.0 ± 0.3 ^{B}	97.4 ± 0.2 ^{B}	L ** Q ^{NS}
	Specific Leaf Area (cm^{2}·g^{-1})			
8/6.34	280.9 ± 5.7 ^{A}	293.9 ± 5.9 ^{A}	365.1 ± 6.9 ^{A}	L *** Q **
12/9.50	250.1 ± 3.3 ^{B}	293.0 ± 5.2 ^{A}	360.0 ± 8.9 ^{A}	L *** Q ^{NS}
16/12.67	196.0 ± 3.9 ^{C}	238.1 ± 7.5 ^{B}	305.5 ± 13.5 ^{B}	L *** Q ^{NS}
20/15.84	171.9 ± 6.5 ^{D}	209.8 ± 7.3 ^{B}	247.3 ± 15.4 ^{C}	L *** Q ^{NS}
24/19.01	112.1 ± 5.8 ^{E}	154.6 ± 15.0 ^{C}	172.8 ± 7.3 ^{D}	L *** Q ^{NS}

Letters represent mean separation comparison across light treatments within the same harvest day using Tukey's HSD (alpha = 0.05). Significance of linear (L) or quadratic (Q) regression of a given treatment over treatment time: NS, *, **, *** denotes nonsignificant or significant at $p \leq 0.05$, 0.01, or 0.001, respectively.

3.5. Nutrient Analysis

Regarding primary macronutrients, the five treatments had similar concentrations of N and P in their shoot tissues (Table 5). K concentration decreased with increased photoperiod/DLI. Regarding secondary macronutrients, the five treatments generally had similar concentrations of Ca, Mg, and S. The 8 h/6.3 mol·m^{-2}·d^{-1} treatment had relatively lower Ca and higher Mg than other treatments.

Table 5. Mean nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), and sulfur (S) concentration of ice plant shoot tissue in response to photoperiod/daily light integral (DLI) treatment. Data represents 1 pooled sample of the 3 experimental units at the end of each crop cycle with 3 replications over time.

Photoperiod (Hours of Lighting per Day, h)/ DLI (mol·m^{-2}·d^{-1})	**Nitrogen (mg·kg^{-1})**	**Phosphorus (mg·kg^{-1})**	**Potassium (mg·kg^{-1})**
8/6.34	57,955 ± 716 ^{A}	9146 ± 536 ^{A}	37,708 ± 204 ^{A}
12/9.50	53,085 ± 1939 ^{A}	8981 ± 403 ^{A}	35,859 ± 1188 ^{AB}
16/12.67	51,372 ± 636 ^{A}	9484 ± 572 ^{A}	32,240 ± 1924 ^{ABC}
20/15.84	51,932 ± 2522 ^{A}	10,364 ± 234 ^{A}	29,304 ± 1672 ^{BC}
24/19.01	47,658 ± 4131 ^{A}	11,114 ± 1141 ^{A}	29,805 ± 1261 ^{C}
Photoperiod (hours of lighting per day, h)/ DLI (mol·m^{-2}·d^{-1})	Calcium (mg·kg^{-1})	Magnesium (mg·kg^{-1})	Sulfur (mg·kg^{-1})
8/6.34	7228 ± 457 ^{B}	5682 ± 156 ^{A}	3989 ± 236 ^{A}
12/9.50	8104 ± 425 ^{AB}	4731 ± 214 ^{B}	3599 ± 158 ^{A}
16/12.67	10,017 ± 1148 ^{AB}	4553 ± 36 ^{B}	3815 ± 63 ^{A}
20/15.84	10,455 ± 769 ^{AB}	4319 ± 119 ^{B}	3738 ± 203 ^{A}
24/19.01	10,877 ± 838 ^{A}	4216 ± 252 ^{B}	4370 ± 243 ^{A}

Letters represent mean separation comparison across light treatments within the same harvest day using Tukey's HSD (alpha = 0.05).

4. Discussion

Overall, ice plants raised in the indoor vertical hydroponic system performed better as photoperiod/DLI increased from 8 h/6.3 mol·m^{-2}·d^{-1} to 20 h/15.8 mol·m^{-2}·d^{-1}. The results corresponded with Kim et al. [23] with higher PPFD correlating with higher growth for ice plant. However, Kim et al. [23] only had two PPFD treatments: 120 and 150 µmol·m^{-2}·s^{-1}, and their corresponding DLI and range of DLI treatments were low. With a photoperiod of 14 h, the corresponding DLI from Kim et al. [23] were 6.05 and 7.56 mol·m^{-2}·d^{-1}, respectively, which were similar to the lowest light treatment (8 h/6.3 mol·m^{-2}·d^{-1}) of the current study. Additionally, the highest shoot FW reported by Kim et al. [23] (52.03 g from plants treated with monochromatic red LEDs at 150 µmol·m^{-2}·s^{-1} PPFD for 28 days) was lower than that of the plants of the same age (the 8 h/6.3 mol·m^{-2}·d^{-1} treatment at day 21) in the current study. In the current study, 0.05 M NaCl was added to the nutrient solution based on previous work showing that a low concentration of NaCl had stimulating effect on the growth of ice plant [2,25–27].

In the current research, further increase in photoperiod/DLI from 20 h/15.8 mol·m^{-2}·d^{-1} to 24 h/19.0 mol·m^{-2}·d^{-1} had a negative effect on the growth of ice plant. In other words, an upper threshold of lighting benefits occurred at a photoperiod/DLI of 20 h/15.8 mol·m^{-2}·d^{-1}. This response may be due to either a negative response of continuous lighting (24 h photoperiod) or due to stress from too high DLI. Photoperiod can affect plants through complicated pathways involving detection of light signals, entrainment of circadian rhythms, production of mobile signals, etc. and induce various plant responses such as flowering and tuberization [28]. While no available data can be found on ice plant, other leafy greens such as lettuce generally showed better performance (or no negative effect) with increased photoperiod up to 24 h [20,29]. Other plants have been shown to respond negatively to 24 h continuous lighting [30]. For example, tomatoes and peppers showed negative responses to 24 h continuous lighting, which was associated with an accumulation of sugar and starch in the leaves (i.e., a limitation in exporting the photosynthate out of the leaves) [31]. Eggplants had leaf chlorosis under continuous lighting [32]. Although ice plant is not reported to be photoperiod sensitive, previous studies have not used a 24 h continuous photoperiod treatment.

The current experimental design does not allow separating the effects of continuous lighting from the effects of DLI. Therefore, the negative response to 24 h/19.0 mol·m^{-2}·d^{-1}

could also be due to excess light. Too much light can create reactive oxygen species (ROS) and cause damage to the reaction center of photosystem II, D1-polypeptide (i.e., photooxidative damage) [33,34]. Xu and Shen [35] described photoinhibition as a light-induced decrease in photosynthetic efficiency when light energy received by plants is more than the amount they need for photosynthesis. Additionally, stomatal closure and the resulting decrease in gas exchange might explain the poorer performance of the 24 h/19.0 mol·m^{-2}·d^{-1} treatment [36]. Since this research did not separate photoperiod treatments from DLI treatments, experiments separating these two variables remain to be performed. However, since ice plant grows under full sun conditions in nature, continuous lighting is more likely to be the issue. Palmer and van Iersel [21] treated lettuce and mizuna with different combinations of PPFD and photoperiod providing the same DLI. A similar experiment could be conducted on ice plant. Additionally, research can be conducted with different PPFD and same photoperiod resulting in different DLI.

In this research, plants receiving higher photoperiod/DLI developed smaller, thicker, and darker green leaves (Tables 3 and 4). This is a typical morphological response to high light. Sun leaves are thicker and have less leaf surface area, which reduces water loss through transpiration, whereas shade leaves are thinner and have more leaf surface area in order to intercept more light in shaded areas [37,38]. Additionally, leaves of ice plant were curlier (less flat) when receiving more light (Figure 5). Although further research needs to be conducted, ice plant may also use the smaller/thicker/curlier leaf strategy to reduce the surface area exposed to direct light and therefore reduce the total amount of incident light energy and mitigate photoinhibition.

The uptake of macronutrients in this research were generally not affected by light treatments; however, K uptake decreased at high photoperiod/DLI (Table 5). Walters and Currey [39] observed that K concentration in sweet basil decreased with increasing DLI, but Gent [40] observed the opposite trend for lettuce. Mansfield and Jones [41] and Nu-may and Bonner [42] found abscisic acid (ABA) treatment reduced K concentrations in guard cells and in leaf tissues as a whole. ABA plays a critical role in stomatal closure [43,44]. Ice plant switches from C3 metabolism to crassulacean acid metabolism (CAM) when exposed to high salinity as a strategy to prevent water loss [45], and this is induced by ABA [46]. Higher ABA concentrations and stomatal closure might also explain the negative effect of continuous lighting/high DLI (the 24 h/19.0 mol·m^{-2}·d^{-1} treatment); this requires further experimental studies.

5. Conclusions

Overall, ice plant in vertical growth towers exhibited better plant performance as photoperiod/DLI increased from 8 h/6.3 mol·m^{-2}·d^{-1} to 20 h/15.8 mol·m^{-2}·d^{-1}. The continuous lighting treatment, 24 h/19.0 mol·m^{-2}·d^{-1}, had a negative effect on the growth of ice plant. This study presents a much broader DLI response than previous research with ice plant and is also the first to determine ice plant response to continuous lighting. This study informs greenhouse and plant factory production practices of ice plant as an edible leafy green. Based on this research, optimum plant performance was achieved at a photoperiod DLI treatment of 20 h/15.8 mol·m^{-2}·d^{-1}. Further research remains to be conducted on separating photoperiod from DLI to determine if the negative effect of 24 h photoperiod is due to continuous lighting or an excessively high DLI. Specially, an experiment could target same DLI but with different combinations of PPFD and photoperiod. Another experiment could control photoperiod but vary PPFD and the resulting DLI. Further research should also be conducted on light–NaCl interaction and the nutritional response of ice plant to various cultural practices (e.g., how light spectrum, PPFD, and salt addition affect nutritional composition of ice plant).

Author Contributions: Conceptualization, J.X. and N.M.; methodology, J.X. and N.M.; software, J.X.; formal analysis, J.X.; investigation, J.X.; resources, N.M.; data curation, J.X.; writing—original draft preparation, J.X.; writing—review and editing, J.X. and N.M.; visualization, J.X.; supervision, N.M.;

project administration, N.M.; funding acquisition, N.M. All authors have read and agreed to the published version of the manuscript.

Funding: This work was supported by joint research under Project No. 1237650 and extension program funded by the Cornell University Agricultural Experiment Station (Hatch/Multistate funds) and Cornell Cooperative Extension (Smith Lever funds) received from the National Institutes of Food and Agriculture (NIFA), U.S. Department of Agriculture (USDA). Any opinions, findings, conclusions, or recommendations expressed in this publication are those of the author(s) and do not necessarily reflect the view of the USDA.

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

Acknowledgments: We wish to express our sincere gratitude to Matthew Moghaddam, Nicholas Kaczmar and Kendra Hutchins for their valuable technical support. Without their assistance, this paper and the research behind it would not have been possible. We would also like to thank all other members of Mattson lab and greenhouse staff at Guterman Bioclimatic Research Lab at Cornell University.

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

References

1. Kang, S.; Kim, S.; Ha, S.; Lee, C.; Nam, S. Biochemical components and physiological activities of ice plant (*Mesembryanthemum crystallinum*). *J. Korean Soc. Food Sci. Nutr.* **2016**, *45*, 1732–1739. [CrossRef]
2. Loconsole, D.; Murillo-Amador, B.; Cristiano, G.; De Lucia, B. Halophyte Common Ice Plants: A Future Solution to Arable Land Salinization. *Sustainability* **2019**, *11*, 6076. [CrossRef]
3. Gómez, C.; Currey, C.J.; Dickson, R.W.; Kim, H.-J.; Hernández, R.; Sabeh, N.C.; Raudales, R.E.; Brumfield, R.G.; Laury-Shaw, A.; Wilke, A.K.; et al. Controlled environment food production for urban agriculture. *HortScience* **2019**, *54*, 1448–1458. [CrossRef]
4. Shamshiri, R.; Kalantari, F.; Ting, K.; Thorp, K.R.; Hameed, I.A.; Weltzien, C.; Ahmad, D.; Shad, Z.M. Advances in greenhouse automation and controlled environment agriculture: A transition to plant factories and urban agriculture. *Int. J. Agric. Biol.* **2018**, *11*, 1–22. [CrossRef]
5. Benke, K.; Tomkins, B. Future food-production systems: Vertical farming and controlled-environment agriculture. *Sustain. Sci. Pract. Policy* **2017**, *13*, 13–26. [CrossRef]
6. Goto, E. Plant production in a closed plant factory with artificial lighting. *Acta Hortic.* **2012**, *956*, 37–49. [CrossRef]
7. Kozai, T.; Niu, G.; Takagaki, M. *Plant Factory: An Indoor Vertical Farming System for Efficient Quality Food Production*, 2nd ed.; Academic Press: London, UK; San Diego, CA, USA, 2019.
8. Kerslake, N. *Indoor Crop Production: Feeding the Future*; Newbean Capital: Reno, NV, USA, 2017.
9. Nicholson, C.F.; Harbick, K.; Gómez, M.I.; Mattson, N.S. An Economic and Environmental Comparison of Conventional and Controlled Environment Agriculture (CEA) Supply Chains for Leaf Lettuce to US Cities. In *Food Supply Chains in Cities*; Aktas, E., Bourlakis, M., Eds.; Springer: Berlin, Germany, 2020; pp. 33–68.
10. Yang, J.; Liu, M.; Lu, J.; Miao, Y.; Hossain, M.A.; Alhamid, M.F. Botanical internet of things: Toward smart indoor farming by connecting people, plant, data and clouds. *Mob. Netw. Appl.* **2018**, *23*, 188–202. [CrossRef]
11. Lee, K.; Elliott, c.; Pattison, P. *Energy Savings Potential of SSL in Agricultural Applications*; Guidehouse Inc.: Washington, DC, USA, 2020.
12. Snowden, M.C.; Cope, K.R.; Bugbee, B. Sensitivity of seven diverse species to blue and green light: Interactions with photon flux. *PLoS ONE* **2016**, *11*, e0163121.
13. Kusuma, P.; Pattison, P.M.; Bugbee, B. From physics to fixtures to food: Current and potential LED efficacy. *Hortic. Res.* **2020**, *7*, 56. [CrossRef]
14. Massa, G.D.; Kim, H.-H.; Wheeler, R.M.; Mitchell, C.A. Plant productivity in response to LED lighting. *HortScience* **2008**, *43*, 1951–1956. [CrossRef]
15. Stutte, G.W.; Edney, S.; Skerritt, T. Photoregulation of Bioprotectant Content of Red Leaf Lettuce with Light-emitting Diodes. *Hortscience* **2009**, *44*, 79–82. [CrossRef]
16. Dou, H.; Niu, G.; Gu, M. Pre-harvest UV-B radiation and photosynthetic photon flux density interactively affect plant photosynthesis, growth, and secondary metabolites accumulation in basil (*Ocimum basilicum*) plants. *Agronomy* **2019**, *9*, 434. [CrossRef]
17. Park, Y.; Runkle, E.S. Far-red radiation and photosynthetic photon flux density independently regulate seedling growth but interactively regulate flowering. *Environ. Exp. Bot.* **2018**, *155*, 206–216. [CrossRef]
18. Jones, H.G. Limiting factors in photosynthesis. *New Phytol.* **1973**, *72*, 1089–1094. [CrossRef]
19. Cammarisano, L.; Donnison, I.S.; Robson, P.R. Producing enhanced yield and nutritional pigmentation in lollo rosso through manipulating the irradiance, duration, and periodicity of LEDs in the visible region of light. *Front. Plant Sci.* **2020**, *11*, 598082. [CrossRef] [PubMed]
20. 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]

21. 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]
22. Elkins, C.; van Iersel, M.W. Longer photoperiods with the same daily light integral increase daily electron transport through photosystem II in lettuce. *Plants* **2020**, *9*, 1172. [CrossRef]
23. Kim, Y.J.; Kim, H.M.; Kim, H.M.; Jeong, B.R.; Lee, H.-J.; Kim, H.-J.; Hwang, S.J. Ice plant growth and phytochemical concentrations are affected by light quality and intensity of monochromatic light-emitting diodes. *Hortic. Environ. Biotechnol.* **2018**, *59*, 529–536. [CrossRef]
24. Mattson, N.S.; Peters, C. A recipe for hydroponic success. In *Inside Grower*; Ball Publishing: Chicago, IL, USA, 2014; pp. 16–19.
25. Xia, J.; Mattson, N. Response of Common Ice Plant (*Mesembryanthemum crystallinum* L.) to Sodium Chloride Concentration in Hydroponic Nutrient Solution. *HortScience* **2022**, *57*, 750–756. [CrossRef]
26. Agarie, S.; Shimoda, T.; Shimizu, Y.; Baumann, K.; Sunagawa, H.; Kondo, A.; Ueno, O.; Nakahara, T.; Nose, A.; Cushman, J.C. Salt tolerance, salt accumulation, and ionic homeostasis in an epidermal bladder-cell-less mutant of the common ice plant *Mesembryanthemum crystallinum*. *J. Exp. Bot.* **2007**, *58*, 1957–1967. [CrossRef] [PubMed]
27. Atzori, G.; de Vos, A.C.; van Rijsselberghe, M.; Vignolini, P.; Rozema, J.; Mancuso, S.; van Bodegom, P.M. Effects of increased seawater salinity irrigation on growth and quality of the edible halophyte *Mesembryanthemum crystallinum* L. under field conditions. *Agric. Water Manag.* **2017**, *187*, 37–46. [CrossRef]
28. Jackson, S.D. Plant responses to photoperiod. *New Phytol.* **2009**, *181*, 517–531. [CrossRef] [PubMed]
29. Koontz, H.; Prince, R. Effect of 16 and 24 hours daily radiation (light) on lettuce growth. *HortScience* **1986**, *21*, 123–124.
30. Velez-Ramirez, A.I.; van Ieperen, W.; Vreugdenhil, D.; Millenaar, F.F. Plants under continuous light. *Trends Plant Sci.* **2011**, *16*, 310–318. [CrossRef]
31. Demers, D.; Gosselin, A. Growing greenhouse tomato and sweet pepper under supplemental lighting: Optimal photoperiod, negative effects of long photoperiod and their causes. *Acta Hortic.* **2000**, *580*, 83–88. [CrossRef]
32. Murage, E.N.; Watashiro, N.; Masuda, M. Leaf chlorosis and carbon metabolism of eggplant in response to continuous light and carbon dioxide. *Sci. Hortic.* **1996**, *67*, 27–37. [CrossRef]
33. Barber, J.; Andersson, B. Too much of a good thing: Light can be bad for photosynthesis. *Trends Biochem. Sci.* **1992**, *17*, 61–66. [CrossRef]
34. Müller, P.; Li, X.-P.; Niyogi, K.K. Non-photochemical quenching. A response to excess light energy. *Plant Physiol.* **2001**, *125*, 1558–1566. [CrossRef]
35. Xu, D.-Q.; Shen, Y.-K. Light stress: Photoinhibition of photosynthesis in plants under natural conditions. In *Handbook of Plant and Crop Stress*, 4th ed.; Mohammad, P., Ed.; Marcel Dekker, Inc.: New York, NY, USA, 1999; pp. 483–497.
36. Flexas, J.; Ribas-Carbó, M.; Bota, J.; Galmés, J.; Henkle, M.; Martínez-Cañellas, S.; Medrano, H. Decreased Rubisco activity during water stress is not induced by decreased relative water content but related to conditions of low stomatal conductance and chloroplast CO_2 concentration. *New Phytol.* **2006**, *172*, 73–82. [CrossRef]
37. Givnish, T.J. Adaptation to sun and shade: A whole-plant perspective. *Funct. Plant Biol.* **1988**, *15*, 63–92. [CrossRef]
38. Terashima, I.; Miyazawa, S.-I.; Hanba, Y.T. Why are sun leaves thicker than shade leaves?—Consideration based on analyses of CO_2 diffusion in the leaf. *J. Plant Res.* **2001**, *114*, 93–105. [CrossRef]
39. Walters, K.J.; Currey, C.J. Effects of nutrient solution concentration and daily light integral on growth and nutrient concentration of several basil species in hydroponic production. *HortScience* **2018**, *53*, 1319–1325. [CrossRef]
40. Gent, M.P. Effect of daily light integral on composition of hydroponic lettuce. *HortScience* **2014**, *49*, 173–179. [CrossRef]
41. Mansfield, T.; Jones, R.J. Effects of abscisic acid on potassium uptake and starch content of stomatal guard cells. *Planta* **1971**, *101*, 147–158. [CrossRef]
42. Nu-may, R.R.; Bonner, B.A. The effect of abscisic acid on the uptake of potassium and chloride into Avena coleoptile sections. *Planta* **1974**, *116*, 173–185.
43. Desikan, R.; Cheung, M.K.; Bright, J.; Henson, D.; Hancock, J.T.; Neill, S.J. ABA, hydrogen peroxide and nitric oxide signalling in stomatal guard cells. *J. Exp. Bot.* **2004**, *55*, 205–212. [CrossRef]
44. Kriedemann, P.; Loveys, B.; Fuller, G.; Leopold, A. Abscisic acid and stomatal regulation. *Plant Physiol.* **1972**, *49*, 842–847. [CrossRef]
45. Winter, K.; Foster, J.G.; Edwards, G.E.; Holtum, J.A. Intracellular localization of enzymes of carbon metabolism in *Mesembryanthemum crystallinum* exhibiting C3 photosynthetic characteristics or performing Crassulacean acid metabolism. *Plant Physiol.* **1982**, *69*, 300–307. [CrossRef]
46. Chu, C.; Dai, Z.; Ku, M.S.; Edwards, G.E. Induction of Crassulacean acid metabolism in the facultative halophyte *Mesembryanthemum crystallinum* by abscisic acid. *Plant Physiol.* **1990**, *93*, 1253–1260. [CrossRef]