LIGHTING STRATEGIES TO REDUCE ENERGY CONSUMPTION IN CONTROLLED ENVIRONMENT AGRICULTURE (CEA) SYSTEMS, AND CONSUMER PERCEPTION ON CEA CULTIVATED PRODUCTS

by

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(Under the Direction of Julie Campbell)

ABSTRACT

Recent advancements in light-emitting diode (LED) technology have improved the efficiency, profitability, and sustainability of controlled environment agriculture (CEA). In greenhouses, supplemental lighting compensates for limited sunlight, particularly in northern regions. LEDs have become an alternative to high-pressure sodium (HPS) fixtures because they convert electricity to light more efficiently, although they require higher initial investment. Continuous LED development has also enabled new systems such as plant factories with artificial lighting (PFALs) and indoor vertical farms, which rely entirely on artificial lighting. PFALs face high operating costs driven largely by the energy needed for artificial lighting and for removing water vapor produced by plant transpiration from enclosed spaces.

Because energy is a major component of total operating costs in both greenhouses and PFALs, this research aimed to identify ways to reduce energy requirements and lower producer costs. The first chapter developed an adaptive supplemental lighting strategy for greenhouses that adjusts supplemental light based on the amount of natural light the plants received on preceding days and the greenhouse's geographic location. Using daily optimal light levels reported in the literature, theoretical modeling indicated potential reductions in energy consumption and associated cost savings.

The second and third chapters focused on PFALs and examined whether adjusting light levels could reduce dehumidification costs. We tested whether increasing light to promote growth would affect transpiration and water use efficiency (WUE). Experiments produced notable trends in photosynthesis and transpiration at both leaf and whole-plant scales, revealing trade-offs between increased light, plant water use, and dehumidification demand. These results are promising but also point to challenges that require further study to quantify energy and economic impacts.

The final chapter investigated consumer perception of products grown under artificial lighting. We measured how information affected purchasing decisions and willingness to pay. While information influenced consumer behavior, it did not sufficiently increase willingness to pay higher prices for PFAL-grown products. These findings can inform future marketing strategies for PFAL producers.

INDEX WORDS: LED lighting, controlled environment agriculture, greenhouse, PFAL, energy efficiency, dehumidification, water use efficiency, consumer perception

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DEDICATION

A Edna Clarena Gomez Galeano, Mauricio Ricardo Mayorga Folkes, Valentina Mayorga Gomez y León, quienes son mi familia y mis amigos, que hacen lo humanamente posible por apoyarme.

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LOWERING THE TARGET DAILY LIGHT INTEGRALS FOLLOWING DAYS WITH EXCESSIVE LIGHTING CAN REDUCE LETTUCE PRODUCTION COSTS[1]

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[1] Mayorga-Gomez, A.M., van Iersel, M.W. and R.S. Ferrarezi. 2024. *Front. Plant Sci.* 15:1467443
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Abstract

Given the fluctuating availability of natural lighting throughout the year, supplemental light is frequently employed to maintain the optimal daily light integral (DLI) levels necessary for adequate plant growth. However, the use of supplemental light translates into higher operational costs. Recent reports suggest that plants can tolerate a day with low DLI following exposure to a day with high DLI from natural light. This was referred to as the 'carryover' effect. In such cases, supplemental lighting may not be necessary, resulting in energy savings. In this study, we determined if plants can withstand such DLI fluctuations over multiple days without compromising plant growth. Additionally, we calculated the energy requirements for these treatments to evaluate the potential energy savings of the carryover effect. To test this, we cultivated lettuce plants (*Lactuca sativa* cv. 'Waldmann's Dark Green' and 'Rouxai') in a walk-in grow chamber, subjecting them to six different lighting treatments. Each treatment consisted of a day with a high DLI of 22.5 $mol \cdot m^{-2} \cdot d^{-1}$ followed by a varying number of consecutive days with low DLI, ranging from 1 to 5 days, with DLIs of 7.5, 11.25, 12.5, 13.13, and 13.5 $mol \cdot m^{-2} \cdot d^{-1}$ respectively. The combined DLI for each treatment, calculated as the average DLI across high and low DLI days, was maintained at 15 $mol \cdot m^{-2} \cdot d^{-1}$. Additionally, we included a control treatment where plants were exposed to a constant DLI of 15 $mol \cdot m^{-2} \cdot d^{-1}$. We measured plant growth rate, final fresh and dry weights, leaf number, leaf area, specific leaf area, light use efficiency, and relative pigment content to assess differences in plant growth under the different lighting regimes. We observed a decrease in biomass accumulation, as indicated by a 13% reduction in final dry weight only for the treatment involving one day of high DLI followed by one day of low DLI, compared to our control. We discovered that plants can tolerate multiple days of low DLI following a day with high DLI, in contrast to the optimal values reported in the

literature. This finding can lead to reduced energy consumption for supplemental lighting and consequent operational cost savings.

Introduction

Daily light integral (DLI) refers to the amount of photosynthetically active radiation provided to plants in 24 hours (Faust et al., 2005). DLI has been used as a reference point for the required light for optimal plant growth. Runkle (2019) reported a guideline specifying the essential DLI for cultivating different crops in controlled environments. However, the availability of light varies based on geographical locations since light levels differ significantly in the northern parts of the U.S. compared to southern locations. Additionally, there is less sunlight available in winter compared to summer overall. Supplemental lighting becomes essential to ensure consistent production throughout the year (Korczynski et al., 2022). Not only supplemental light is implemented to achieve DLIs reported to be optimal. For instance, Albright et al. (2000) developed a lighting control that includes shadings and supplemental light to maintain optimal DLI for plant growth. However, the cost for supplemental lighting in a vegetable greenhouse may amount to USD $200,000 per hectare, constituting 30% of the annual farm gate value (van Iersel and Gianino, 2017). Studies have focused on reducing electricity consumption and energy pricing associated with supplemental light. In 2017, van Iersel and Gianino (2017) proposed an adaptive control system for light-emitting diode (LED) lights. This system adjusts photosynthetic photon flux density (PPFD) levels by considering the natural sunlight to achieve the target DLIs. They claim electricity consumption reductions of 20-92%. In 2021, Bhuiyan and van Iersel (2021) conducted a study testing lettuce growth under fluctuating PPFD levels every 15 minutes. They observed that when these PPFD fluctuations were not extreme, lettuce plants exhibited normal growth without significant adverse effects. This suggests that lettuce can tolerate fluctuations in PPFD levels, potentially leading to energy cost savings if paired with variable electricity prices.

Most recently, Jayalath et al. (2024). reported that plants can grow unaffectedly with extended lighting fluctuations. They conducted experiments growing lettuce in greenhouses and indoor conditions (growth chamber), varying the target DLI from one day to the next. The DLI fluctuation between two consecutive days ranged from 5 to 25 $mol \cdot m^{-2} \cdot d^{-1}$. Interestingly, plants exposed to DLI fluctuations with a difference of 10 $mol \cdot m^{-2} \cdot d^{-1}$ showed no negative effects on their growth. They propose the existence of a ‘carryover’ effect from days with high DLI (exceeding the target) to days with low DLI (falling below the target). This suggests that in agriculture setups utilizing supplemental light, it might not be always necessary to reach a specific DLI for lettuce if plants get exposed to a higher DLI than the target the day before, generating a reduction in electricity consumption.

The present study assessed whether plants can tolerate DLI fluctuations over consecutive days without compromising growth in an indoor growth chamber. Specifically, our goal was to investigate the viability of the ‘carryover’ effect for plants exposed to a high DLI for one day, followed by multiple days of a low DLI (falling below the target DLI). If plants can tolerate such lighting fluctuations, potential significant electricity savings exist. Additionally, we determined the energy requirements for these treatments to evaluate the potential energy savings of the carryover effect.

Materials and methods

Experimental set up and treatments

This research was conducted in a walk-in growth chamber (vertical farm) at the University of Georgia (College of Agriculture and Environmental Sciences, Department of Horticulture, Horticultural Physiology Laboratory), in Athens, GA, USA. The environmental conditions during the experiment, without distinguishing between light and dark periods, were: (mean ± standard deviation): temperature 24.35 ± 0.673°C, relative humidity 65.22% ± 7.56%, CO2 concentration 847.64 ± 43.52 mg/L, and vapor pressure deficit 1.0201 ± 0.235 kPa.

Inside the growth chamber, there were three metal racks (2.4 m long × 0.6 m wide × 2.2 m high), each serving as a separate replication. Each rack had three horizontal shelves, and each shelf was divided into two equal parts vertically, resulting in six growing spaces per rack and 18 growing spaces in total, each with dimensions of 1.2 m long × 0.6 m wide × 0.6 m high. Each growing space was equipped with two LED fixtures (SPYDRx Plus with PhysioSpec indoor spectrum; Fluence Bioengineering, Austin, TX, USA) (Supplementary Figure 1). Furthermore, four small fans (AD0412HB-C50; ADDA, Orange, CA, USA), evenly distributed, were positioned on the sides of each growing space to ensure proper lateral airflow.

We tested six lighting treatments randomly assigned to the growing spaces. These lighting treatments were controlled by a datalogger (CR6; Campbell Scientific, Logan, UT, USA) and six dimmable drivers (4009715; Intertek/Fluence, Arlington, VA, USA), with each driver responsible for controlling three growing spaces that shared the same lighting treatment, one space per rack or replication.

PPFD levels were assessed in the middle of every cultivation area using a quantum sensor (MQ-500; Apogee Instruments, Logan, UT, USA). Each treatment consisted of two DLI levels, called high and low, with a photoperiod of 20 hours. Plants were exposed to one day under high DLI, followed by varying numbers of days under low DLI, denoted as T0 (Control), T1, T2, T3, T4, and T5, indicating the respective number of days with low DLI in each treatment (Figure 13). DLI and PPFD for each treatment are shown in Table 1.

Plant material

Ten-cm square plastic pots were filled with soilless substrate (Metro-Mix® 830; SunGro Horticulture, Agawam, MA, USA) up to about 1 cm below the top rim. Three pelleted 'Waldmann's dark green' or 'Rouxai' (Johnny's Selected Seeds, Winslow, ME, USA) seeds were planted in each pot. The substrate was then covered with calcined clay or metakaolin (Turface MVP; Turface Athletics, Buffalo Grove, IL, USA) to avoid algae growth affecting PCS measurement. These pots were organized in trays, with fifteen pots arranged in a 5×3 configuration and placed in the designated growing spaces. Once the seeds germinated, a thinning process was carried out to keep only one seedling per pot. The plants received irrigation and nutrients through an ebb-and-flow subirrigation system, which delivered a 15N–2.2P–12.45K nutrient solution containing 100 $mg \cdot L^{-1}$ of nitrogen using a water-soluble fertilizer (15-5-15 Ca-Mg Professional LX; J.R. Peters, Allentown, PA, USA).

Data collection and calculations

- *Projected canopy size and plant growth rates*

Canopy photos of 15 plants from each tray were captured initially 7 days following seed sowing and then twice a week, employing the setup detailed in Jayalath and van Iersel (2021). These images were analyzed using a custom Python script to calculate the PCS at the time said images were taken. The PCS data was then plotted against the number of days after sowing (DAS), and a sigmoidal curve of the form PCS = a/[1 + e−(DAS−x0)/b] was applied to fit the data (SigmaPlot 11.0; Systat Software, San Jose, CA, USA). From the regression equations, we estimated the PCS for each day during the growth cycle, spanning from day 1 to day 30 for 'Waldmann's dark green' and to day 35 for 'Rouxai' (30 and 35 DAS were the harvest point respectively). Additionally, we calculated the number of days required for the crops to achieve specific sizes, such as 25%, 50%, 75%, and 100% coverage of the trays holding the plants (equivalent to 0.15 m^2), based on the estimated PCS for each day throughout the growth cycle.

- *Incident light and light use efficiency*

To determine the daily incident light received by each group of plant' canopies on each day of the growth cycle, we multiplied the daily PCS by the DLI for each light treatment, as expressed by the formula: Incident Daily Light Integral ($mol \cdot d^{-1}$) = PCS (mm^2) × DLI ($mol \cdot m^{-2} \cdot d^{-1}$). Using these values, we calculated the cumulative incident light on the canopy over the entire growth cycle. Subsequently, the cumulative incident light was divided by the final dry weight of the shoot to calculate LUE.

- *Leaf area and leaf specific area*

We measured the leaf area of three plants per cultivar per growing space using a leaf area meter (LI-3100; LI-COR Biosciences, Lincoln, NE, USA) at harvesting day. The chosen plants were located transversally in the middle of each tray containing the pots. Then, we calculated SLA as the ratio between dry weight and leaf area.

- *Pigment content*

At harvesting (30 DAS for ‘Waldmann’s dark green’ and 35 DAS for ‘Rouxai), we assessed the relative pigment content of chlorophyll and anthocyanins. The measurement involved randomly selecting 10 plants (sub-samples) per growing space per cultivar for pigment content evaluation. Measurements were taken on uppermost fully expanded leaves. The respective devices averaged the final value from each set of 10 measurements. Chlorophyll content for both cultivars was measured using a chlorophyll content meter (MC-100; Apogee Instruments, Logan, UT, USA) measuring the ratio of optical transmission at 931 to 653 nm. Anthocyanin measurement for ‘Rouxai’ was taken with an anthocyanin content meter (ACM 200 plus; Opti-sciences, Hudson, NH, USA) measuring the optical absorbency at 530 and 931 nm.

- *Fresh and dry weight*

Following the harvest of plant shoots in each cultivation area at 30 DAS for ‘Waldmann’s dark green’ and 35 DAS for ‘Rouxai’, all of the plants (15 per cultivar per treatment) were weighed to obtain their fresh weight, and subsequently, dried in an oven at 80°C for 72 hours for final dry weight determination. We computed LUE as the ratio of shoot biomass to the total incident light.

- *Energy requirement assessment*

Finally, using two hypothetical scenarios, we assessed the theoretical energy requirements of implementing the lighting strategy of reducing the target DLI for multiple days after a sunny day or day with high DLI. In the first one, we assumed that DLI was obtained only from natural light (sunlight). Here the DLI were the same as the ones provided in the treatments of this study. Days with high DLI had a DLI of 22.5 mol·m^{-2}·d^{-1}, and the days with low DLI had a DLI of 11.25, 12.5, 13.13, and 13.5 mol·m^{-2}·d^{-1} for treatments T2 to T5 respectively. Since 15 mol·m^{-2}·d^{-1} is the optimal DLI reported to grow lettuce, we calculated the DLI needed to provide during the days with low DLI to achieve said ideal number. In this case, for every day with low DLI, T2 would need an extra 3.75 mol·m^{-2}·d^{-1}, T3 would need an extra 2.5 mol·m^{-2}·d^{-1}, T4 would need an extra 1.87 mol·m^{-2}·d^{-1}, and T5 would need an extra 1.5 mol·m^{-2}·d^{-1} (Supplementary Table 1.1). To calculate the energy needed to produce the extra DLI, we followed the steps explained by Mattson (2017) and adopted the same assumptions. However, for this study, we used a light output of 1100 µmol·s^{-1}, and an energy requirement of 600 watts for this light source and area to cover one hectare during 30 days. The count of days with low DLI over 30 days, as per our lighting regimes, was as follows: 20 days of low DLI when having two days of low DLI after a day with high DLI, 22.5 days when having three days with low DLI after a day with high DLI, 24 days if there were four days with low DLI after a day with high DLI, and 25 days when having five days with low DLI after a day with high DLI.

In the second hypothetical case, days with high DLI also experienced a DLI of 22.5 mol·m^{-2}·d^{-1} naturally. However, the days with low DLI only received 10 mol·m^{-2}·d^{-1} from the sun. We chose a DLI of 10 mol·m^{2}·d-^{1} because this represents the average daily amount of light received in a northern U.S. state such as Washington, during December, January, and February when light availability is lower (Faust and Logan, 2018). The average DLI for these months in this region typically ranges between 5 and 15 mol·m^{-2}·d^{-1}. For simplicity, we used the midpoint value of 10 mol·m^{-2}·d^{-1} in our calculations. Then, the extra DLI would be provided with supplemental light either to obtain a DLI of 15 mol·m^{-2}·d^{-1} to achieve the optimal literature value, or to achieve DLI of 11.25, 12.5, 13.13, and 13.5 mol·m^{-2}·d^{-1} (depending on the number of days with low DLI) to use the ‘carryover’ effect (Supplementary Table 1.2). The energy required to produce the extra DLI to get the optimal value and to take advantage of the carryover was calculated as mentioned before.

All previous calculations were based on hypothetical DLI values provided by natural light (sunlight) and the hypothetical DLI values for each specific case using artificial lighting. The calculations considered only the DLI and did not account for the length of the day or night. It was assumed that the hypothetical DLIs from natural and supplemental light were provided over a period of 20 hours per day to provide a period of darkness even though lettuce does not respond to photoperiod.

Data analysis and experimental design

The experimental setup followed a randomized split-block design with three blocks and six lighting treatments. Each experimental unit consisted of 15 plants. We used ANOVA by using a statistical software (R version 4.1.2; R Project for Statistical Computing, Vienna, Austria) to compare differences in the number of days plants need to reach specific sizes, differences in shoot-dry weight, pigment content, leaf area, relative leaf area, dry and fresh weights, leaf number and light use efficiency.

Results

Plant growth rate

We determined the time needed to reach different coverage levels in a specific area to analyze plant growth rates by estimating the days based on the sigmoidal curves fitted to the projected canopy size (PCS) information. Plants growing under different lighting regimes needed different days to achieve specific sizes indicated by the coverage percentage of a reference area. For example, to cover 25% of the said area, plants growing with 0, 1, 2, 3, 4, and 5 days with low DLI following a day with high DLI needed an average of 11.46, 12.41, 11.81, 11.86, 11.6, and 11.54 days, respectively (Figure 1.1A). We did not find a significant interaction between the lettuce cultivars and lighting treatment (F5,24 = 0.028, P=0.99). The time taken to achieve this level of coverage showed significant differences (F5,29 = 3.91, P=0.007) between plants growing with one day of low DLI compared to the control treatment (P=0.007) (0 days with low DLI) and plants with 4 (P=0.029) and 5 (P=0.017) days with low DLI.

Likewise, to cover 50% of the reference area, plants subjected to 0, 1, 2, 3, 4 and 5 days with low DLI following a day with high DLI needed 14.25, 15.22, 14.58, 14.6, 14.26, and 14.24 days, respectively (Figure 1.1B). The interaction between cultivar and lighting treatment was not significant (F5,24 = 0.26, P=0.92). Once again, the time needed to attain this coverage level exhibited significant differences (F5, 29 = 3.62, P=0.011) when comparing plants subjected to one day of low DLI when compared with the control (P=0.017) and plants with 4 (P=0.023) and 5 (P=0.018) days with low DLI.

To achieve 75% coverage, plants growing with 0, 1, 2, 3, 4 and 5 days with low DLI following a day with high DLI needed 16.75, 17.68, 17.1, 16.97, 16.76, and 16.96 days, respectively (Figure 1.1C). Here, significant differences were found (F5,29 = 2.59, P=0.046) (Tukey’s test did not show differences when comparing means) with no interaction between lighting treatments and cultivars (F5,24 = 0.9, P=0.49). Since Tukey’s test did not show differences when comparing means, we used Fisher’s LSD test. Here, plants growing with one day of low DLI needed significantly more days to achieve 75% of coverage when compared to plants growing under 0 (P=0.005), 3 (P=0.0087), 4 (P=0.0064) and 5 (P=0.028) days with low DLI.

Finally, to cover 100% of the reference area, plants growing under 0, 1, 2, 3, 4 and 5 days with low DLI following a day with high DLI needed 19.3, 19.96, 19.5, 19.72, 19.14, and 19.27 days, respectively (Figure 1.1D). There were no significant differences among treatments regarding covering the equivalent of the entire reference area (F5,29 = 0.76, P=0.26) (F5,29 = 1.35, P=0.26). Interaction between cultivar and lighting treatments was not found (F5,24 = 1.35, P=0.29). (F5,24 = 1.304, P=0.29).

Leaf area and specific leaf area

We measured the final leaf area on three plants situated at the central transverse position of each tray, yielding a total count of six plants. The average leaf area for plants growing under the least amount of days with low DLI (T0) ascendingly to 5 days with DLI was as follows: 1436.09, 1276.86, 1342.12, 1388.37, 1409.01 and 1452.79 cm2 respectively (Figure 1.2). However, we did not find significant differences in this parameter (F5,29 = 1.65, P=0.17). Furthermore, there was no interaction between light treatment and cultivar (F5,24 = 0.36, P=0.88).

We did not find significant differences (F5,29 = 0.79, P=0.56) in specific leaf area (SLA) among plants growing under different lighting treatments, and there was no interaction between SLA and lettuce cultivar (F5,24 = 0.74, P=0.59). The average SLA per plant from treatment 0 to 5 days were as follows: 407.86, 371.18, 386.29, 370.17, 355.63, and 370.17 $cm^2 \cdot g^{-1}$ (Figure 1.3).

Pigment content

We conducted pigment content measurements on both lettuce varieties. For ‘Rouxai’, the leaf anthocyanin content varied from 7.36 to 7.46 anthocyanin content index (ACI) across treatments with varying low DLI days (Figure 1.4), with no significant differences found (F5,12 = 0.36, P=0.86). Additionally, the leaf chlorophyll content in sequence from treatment T0 to T5 were 8.36, 8.05, 8.06, 8.41, 8.11, and 7.98 chlorophyll content index (CCI) (Figure 1.5). However, no significant differences were found (F5,29 = 1.02, P=0.42) nor interaction between cultivar and treatment (F5,29 = 0.74, P=0.59).

Shoot dry weight

We averaged the final shoot dry weight for the different lighting treatments for both cultivars. The values in sequence from treatment T0 to T5 were recorded as follows: 3.91, 3.4, 3.6, 3.75, 3.87, and 3.83 g per plant (Figure 1.6). The number of days of low DLI significantly affected the final shoot dry weight (F5,29 = 3.29, P=0.017). Compared to the control treatment, plants growing with one day of low DLI showed a significant decrease in dry weight of 13% (P=0.022). The other significant differences were between plants growing under T1 and T4 (P=0.047). In addition, we did not find a significant interaction between light treatment and cultivar (F5,24 = 0.33, P=0.88).

Shoot fresh weight

On the other hand, we also assessed the final fresh weight of shoots across both cultivars. The values were the following from the treatment with less amount of days with low DLI (T0 days) to the one with more days with low DLI (T5): 80, 73, 76.07, 78.85, 80.42, and 77.95 g per plant respectively (Figure 1.7). Lighting treatments did not show significant differences (F5,29 = 1.48, P=0.22), and there was no significant interaction between cultivar type and lighting treatment (F5,24 = 0.49, P=0.77).

Light use efficiency

We calculated light use efficiency (LUE) for both cultivars for their whole growing cycle. The LUE for treatment from T0 to T5 were 0.56, 0.5, 0.51, 0.54, 0.55, and 0.54 $g \cdot mol^{-1}$, respectively (Figure 1.8). We did not find significant differences among lighting treatments on LUE (F5,29 = 1.92, P=0.121) or interaction between cultivar and treatment (F5,24 = 0.63, P=0.147). (F5,24 = 0.69, P=0.63).

Leaf number

We counted the leaf number of three plants in the middle transversely of each tray, resulting in six plants counted (three per cultivar per treatment). The average leaf count per treatment, ranging from the lowest to the highest number of days with low DLI, was as follows: 19, 18.5, 18.44, 18.77, 19.72, and 19.55 leaves (Figure 1.9). The analysis of variance (ANOVA) test showed a significant difference in leaf number (F5,29 = 2.79, P=0.035). However, Tukey's test did not show significant differences among the treatments. Additionally, we did not find an interaction between treatment and cultivar (F5,24 = 0.45, P=0.8). Then, we used the Fisher DLS test since Tukey's test did not show the significant differences announced by the ANOVA. Significant differences were found between plants growing under T1 in comparison to T4 and T5, among plants growing under T2 in comparison to T4 and T5. Finally, there was a significant difference in leaf number between plants growing under T3 and T4. However, no significant differences existed between the treatment and the control treatment or plants growing with zero days with low DLI or no DLI fluctuations.

Energy requirement

In the first hypothetical scenario about energy needs, we assessed the energy required to generate the additional DLI needed to reach the target DLI of 15 mol·m^{-2}·d^{-1} on days with low DLI, considering the number of low DLI days in our treatments over a 30-day period. The energy requirements were as follows: 113.6 MWh/ha when the additional DLI was 3.75 (1 low DLI days), 86.1 MWh/ha for an extra DLI of 2.5 mol·m^{-2}·d^{-1} (2 low DLI days), 68 MWh/ha for 1.87 mol·m^{-2}·d^{-1} (3 low DLI days), and 56.9 MWh/ha for 1.5 mol·m^{-2}·d^{-1} (1 low DLI days) (Figure 1.10).

In the second hypothetical case of energy savings, we calculated the energy required to produce an additional DLI of 5 mol·m^{-2}·d^{-1} (to reach the optimal 15 mol·m^{-2}·d^{-1}) on days with low DLI, assuming that sunlight provided a DLI of 10 mol·m^{-2}·d^{-1} over 30 days. The energy requirements were as follows: 152.7 MWh/ha for 2 days with low DLI after each day with high DLI, 171.8 MWh/ha for 3 days, 183.3 MWh/ha for 4 days, and 190.9 MWh/ha for 5 days of low DLI following a day with high DLI. Additionally, we assessed the energy needed to produce extra DLIs of 1.25, 2.5, 3.13, and 3.5 mol·m^{-2}·d^{-1} for 2, 3, 4, and 5 days of low DLI, respectively, following a day with high DLI. The resulting energy values were 38, 81.6, 114, and 133.3 MWh/ha for the additional DLI levels during the 30-day period (Figure 1.11).

Discussion

Plant growth rate

Plants growing under treatment1 day with high DLI followed only by 1 day with low DLI (T1) grew at a slower rate in comparison to plants growing with 4 (T4) and 5 days with low DLI (T5). We observed this while determining the time required for plants to reach 25%, 50%, and 75% coverage of a reference area. We assessed the plant growth rate using the PCS registered and calculated at various time points throughout the plant growth cycle. This means that when plants required more days to attain a specific coverage, they had a lower PCS, implying a slower growth rate. According to Klassen et al. (2003), plant growth is influenced by the quantity of light reaching the plant, which is directly tied to PCS and LUE (Legendre and van Iersel, 2021). Then, faster plant growth can be associated with a high PCS value. Plants with higher PCS intercept more light (Weaver and van Iersel, 2020), leading to more photosynthesis and biomass accumulation (Klassen et al., 2003). Said differences in biomass accumulation can be observed in Figure 6, what explains the differences in canopy sizes and plant growth rate in our study (Figures 1.1A–C).

As indicated by Jayalath and van Iersel (2021), LUE was one factor that plays a role in plant growth. LUE is a measure of the plant's efficiency in producing biomass with light reaching its canopy (Legendre and van Iersel, 2021). Then, differences in LUE between the plants growing under distinct light treatments are expected to contribute to differences in PCS or growing rates. However, those significant differences disappear when calculating the number of days needed to cover 100% (Figure 1.1D) of the reference area, a consequence of the overlapping canopies of the plants (Figure 1.12).

Light use efficiency

LUE (Figure 1.8) followed a similar trend to fresh and dry weight despite the absence of significant differences. This means that plants, regardless of the treatment, had the same efficiency in producing biomass with the incident light provided (Jayalath and van Iersel, 2021). The intensity of light may influence variations in LUE. Elevated light levels lead to a greater closure of the reaction centers within the photosystem II (PSII). With an increased closure of these centers, a higher proportion of absorbed light by the PSII light-harvesting complex remains unused for electron transport in PSII (van Iersel, 2017). Excess of absorbed light might be dissipated in different ways (Bassi and Dall'Osto, 2021). Consequently, when the photosynthetic machinery does not utilize light, more photons are being redirected to other routes and not used by photosynthesis, resulting in lower LUE values. On the contrary, reduced light levels produced an inverse effect and a higher LUE. The treatments in our study were made up of a combination of days with low DLI or low light intensity and days with high DLI or high light intensity, which would mean different LUE depending on the day. However, said variations in light intensities across treatments did not significantly affect the final cumulative utilization of absorbed light for electron transport or dissipation, as evidenced by the absence of significant differences in LUE.

Shoot dry weight

Plants growing under 1 day with high DLI (22.53 mol$\cdot$m$^{-2}\cdot$d^{-1}) followed by 1 day with low DLI (7.53 mol$\cdot$m$^{-2}\cdot$d^{-1}) showed the lowest final dry shoot weight, meaning that the group of plants had a lower biomass accumulation (Figure 6). Dry weight increased when the number of days with low DLI increased, and at the same time, the DLI for those days increased (11.25, 12.5, 13.17, and 13.52 mol$\cdot$m$^{-2}\cdot$d^{-1}, respectively). As far as we know, most studies that look into

DLI and biomass accumulation have grown plants under fixed DLI, even if that DLI is composed of a different combination of PPFD and photoperiod (Elkins and van Iersel, 2020). Jayalath et al. (2024) recently experimented with DLI changes only for two consecutive days. In our study, our treatments had variable DLIs for more than two following days, making it more challenging to compare results. Yan et al. (2019b) showed an increasing direct relationship between leaf dry weight and DLIs between 5.04 to 15.12 $mol \cdot m^{-2} \cdot d^{-1}$. Furthermore, Pennisi et al. (2020) reported the highest value in shoot dry weight for plants growing under a DLI of 14.4 $mol \cdot m^{-2} \cdot d^{-1}$ made of a photoperiod of 16 hours and a PPFD of 250 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Plants growing under lower DLIs (5.8, 8.6, 11.5 $mol \cdot m^{-2} \cdot d^{-1}$) and a higher DLI (17.3 $mol \cdot m^{-2} \cdot d^{-1}$) showed significantly lower final biomass values for lettuce. This relationship of higher dry weight with high light levels has been also observed on dwarf tomato (*Lycopersicon esculentum*) ‘Micro-Tom’ (Ke et al., 2023), common purslane (*Portulaca oleracea*) (Kudirka et al., 2023), petunia (Petunia × hybrida) ‘Wave Blue’, geranium (Pelargonium × hortorum) ‘Pinto Premium Orange Bicolor’, and coleus (*Solenostemon scutellariodes*) ‘Wizard Golden’ (Park and Runkle, 2018).

In addition, differences in photosynthesis rates and canopy size may explain differences in final shoot dry weight in our study. Zhou et al. (2020) observed an increase in photosynthesis rates of lettuce plants with increasing PPFD levels, ranging from 0 to 350 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (12-hour photoperiod of about DLI 15 $mol \cdot m^{-2} \cdot d^{-1}$), reaching a plateau phase at approximately 500 µmol·m-2·s-1. In our study, plants exposed to 1 day of low DLI (T1) received around 104 µmol $m^{-2} \cdot s^{-1}$, while those subjected to 5 days of low DLI (T5) received approximately 187 $\mu mol \cdot m^{-2} \cdot s^{-1}$. This difference in incident light could signify variations in photosynthesis rates, and greater photosynthesis is associated with increased biomass accumulation (Klassen et al., 2003). However, all treatments were also exposed to a day with a high DLI of approximately 14.4

mol·m^{-2}·d^{-1}, achieved by subjecting plants to PPFD of around 312 μmol·m^{-2}·s^{-1}. Specifically, plants growing with just 1 day with low DLI (T1) had a DLI of 22 mol·m^{-2}·d^{-1} during half of the growing cycle. This might suggest that these plants could have exhibited a higher photosynthetic rate during days with elevated PPFDs than other treatments (Zhou et al., 2020). However, it is crucial to note that, for the other half of the growing cycle, plants under T1 experienced lower DLI values (approximately 7.53 mol·m^{-2}·d^{-1} and PPFD of 104 μmol·m^{-2}·s^{-1}). The potential reduction in the photosynthetic rate at these lower light levels could account for a decrease in the final biomass. Zhou et al. (2020) showed reduced photosynthetic values when light intensity was low. Additionally, Pennisi et al. (2020) showed lower values of biomass accumulation for plants growing under a DLI of 8.6 mol·m^{-2}·d^{-1} and PPFD of 150 μmol·m^{-2}·s^{-1}.

When the number of days with low DLI increased, the minimum DLI also increased. Plants growing for 4 and 5 days with low DLI had an average DLI of 13.17 and 13.52 mol·m^{-2}·d^{-1}, respectively. Hence, those plants were growing most of the days under a DLI that was close to the control treatment (14.88 mol·m^{-2}·d^{-1}), which is close to the ideal DLI for lettuce between 12 and 16 mol·m^{-2}·d^{-1} depending on the cultivar (Zhang et al., 2018; Yan et al., 2019a; Kelly et al., 2020; Pennisi et al., 2020; Modarelli et al., 2022). Consequently, the photosynthetic rates, LUE, and biomass accumulation of plants growing under T4 and T5 are higher (in comparison to T1) and similar to the control treatment. Jayalath et al. (2024) reported a decrease in final dry weight when the DLI fluctuation from one day to the next is above 15 mol·m^{-2}·d^{-1}. They also explained this partly due to a lower canopy rate expansion that decreased the incident light available for photosynthesis. In our study, this lower expansion rate on the canopy can be seen in the number of days plants needed to reach different sizes (Figure 1.1).

These results corroborate the hypothesis the carryover effect exists, wherein higher photosynthesis rates during days with high DLI might compensate for the lower photosynthetic rates observed on days with lower DLI. They also indicate that plants experiencing more days with low DLI maintain similar photosynthetic rates because these lower DLI values are closely aligned with the optimal conditions required for lettuce growth.

Shoot fresh weight

Despite the significant differences observed in shoot dry weight results among the different lighting treatments, these differences were not found when measuring the final shoot fresh weight (Figure 1.7). However, the consistent trend of increasing dry weight when the number of days with low DLI increased was also observed in the fresh weight. Changes in significant differences between shoot dry and fresh weight have been reported before. Khwankaew et al. (2018) reported mismatched significant differences between shoot dry and fresh weight on Ipomoea aquatica plants growing under LED light with different spectrum combinations. Fresh weight should be assessed promptly after sampling, or plant material should be stored in hermetically sealed recipients, as fresh plant material tends to lose water rapidly (Turner, 1981). Then, if fresh weight is not taken consistently across all the samples, some variation might be induced. In our study, we measured this parameter right after cutting the shoot from the root system. Therefore, we did not expect any variability in fresh weight induced by the sampling process. A possible reason for the differences in dry weight not being reflected in the final fresh weight could be related to the water status of the plants and their water retention capacity. For instance, plants growing under our control conditions showed a fresh weight of around 80 g per plant and a dry weight of approximately 4 g per plant. We can see that the final dry weight represented only 5% of the total fresh weight of the plants. This means that the significant differences observed in dry weight are lost due to the amount of water inside the leaf. Fresh weights have been reported in other studies to be more variable for showing differences among treatments compared to dry weights (Bashan and De-bashan, 2005; Huang et al., 2017).

Leaf area and specific leaf area

No significant differences were found in final leaf area or SLA in our study (Figures 1.2, 1.3). Pennisi et al. (2020) observed an increase in leaf area for lettuce and basil with higher DLI. In contrast, the SLA for both species decreased as DLI increased. This reduction in SLA was attributed to the denser arrangement of mesophyll cells and the development of thicker and larger leaves. Similarly, Carotti et al. (2021) found that SLA decreased when lettuce plants grew under higher light intensities. However, these results were obtained for plants growing under constant DLI or light intensities. Bhuiyan and van Iersel (2021) grew lettuce plants under variable PPFD levels every 15 minutes (400/0, 360/40, 320/80, 280/120, 240/160, and 200/200 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), and observed that leaf area decreased when plants were subjected to high PPFD fluctuations but increased when the PPFD fluctuations were minimized between light levels. In contrast, SLA was higher under high PPFD fluctuations, whereas it was lower when the fluctuations were smaller at their respective light levels. They argue that extreme fluctuations in light prevent plants from reaching a steady state of photosynthesis. Consequently, this leads to reduced carbon gain by leaves, resulting in decreased dry weight and increased SLA. In our study, the DLI and PPFD fluctuations occurred over an extended period, suggesting that plants could reach a steady state of photosynthesis. This likely contributed to the production of similar biomass across treatments, resulting in comparable SLA values. Given the similar biomass production, we expected similar leaf area values regardless of our lighting treatments.

For plants growing under DLI fluctuations that happened during extended periods, specifically focusing on day-to-day variations, Jayalath et al. (2024) found that DLI fluctuations above 15 $mol \cdot m^{-2} \cdot d^{-1}$ significantly reduced leaf area. Lower PCS and LUE may explain these differences. A larger PCS captures more light, and higher LUE transforms that light more efficiently into biomass. While our study also observed differences in PCS initially, we found that PCSs became similar across all treatments once canopies started to overlap. This suggests that plants reached similar leaf area values with similar PCS and LUE. Nonetheless, our treatment involving a single day with low DLI exhibited a DLI fluctuation from one day to the next of approximately 15 $mol \cdot m^{-2} \cdot d^{-1}$, consistent with findings reported for lettuce (Jayalath et al., 2024). Despite this fluctuation, we did not observe significant differences in leaf area under the same lighting treatment.

Leaf number

Even when we found significant differences in leaf number among the treatments involving a DLI fluctuation, none showed a significant difference compared to the control treatment (Figure 1.9). Changes in leaf number depending on different light levels have been reported before. Kang et al. (2013) found a higher leaf number for lettuce plants growing under high PPFD (290 $\mu mol \cdot m^{-2} \cdot s^{-1}$) levels when their photoperiod was 6/2 (light/dark) in 3 cycles per day. On the other hand, the least number of leaves was found when the plant grew at a low PPFD (200 $\mu mol \cdot m^{-2} \cdot s^{-1}$) with a photoperiod of 18/6 (light/dark). Also, Zervoudakis et al. (2012) found a significant reduction of leaf number in common sage (*Salvia officinalis* L.) when they grew under 25% ambient light compared to plants growing under full ambient light. These results suggest that plants growing under lower light levels generally produce fewer leaves. In our study, even plants that grew under different PPFD levels depending on the number of days with low DLI; they had, on average, the same light levels when taking into account the days with DLI and the days with low DLI. This might explain the lack of differences in leaf number compared to the control treatment (T0).

Relative pigment content

- *Anthocyanins*

We did not see any differences in leaf anthocyanin content on ‘Rouxai’ plants regardless of the lighting treatment those plants were growing under (Figure 1.4). Hwang et al. (2023) demonstrated that elevating light intensity and extending the photoperiod increased anthocyanin content in Brassica juncea cultivated in a plant factory. The highest concentrations of anthocyanins were observed in plants exposed to 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for 18 hours daily. Likewise, Jones-Baumgardt et al. (2020) reported a higher concentration of anthocyanins in arugula (*Eruca vesicaria* subsp. sativa (Mill.) Thell.), cabbage (*Brassica oleracea* L.), kale (*Brassica napus* L. subsp. napus var. pabularia (DC.) Alef.), and mustard (Brassica juncea (L.) Czern) plants when cultivated under 600 $\mu mol \cdot m^{-2} \cdot s^{-1}$, as opposed to those grown under 100 $\mu mol\ m^{-2} \cdot s^{-1}$. Similar results were found on arugula (Veremeichik et al., 2023), pak-choi (*Brassica campestris* ssp. Chinensis Makino) (Zhu et al., 2017), sweet basil (*Ocimum basilicum*) ‘Opal’ and lettuce (*Lactuca sativa*) ‘Nikolaj’ (Sutulienė et al., 2022), lettuce ‘Outredgeous’ (Massa et al., 2015) and red mustard (Hwang et al., 2023). One potential role of anthocyanins in plants is safeguarding the photosynthetic machinery against high light intensities (Landi et al., 2015). Anthocyanins are believed to play a role in partially mitigating the impacts of de-epoxidation of violaxanthin within the photo-protective xanthophyll cycle (Cavender-Bares et al., 1999; Landi et al., 2015; Logan et al., 2015).

The plants in our study experienced comparable high PPFD levels during the high DLI day. Those subjected to 1 to 5 days with low DLI received approximately 312 $\mu mol \cdot m^{-2} \cdot s^{-1}$ intermittently throughout their growth cycle, potentially leading to a similar production of anthocyanins. However, under the control treatments, plants did not have days with low DLI or PPFD levels. Then, plants probably still needed protection for their photosynthetic machinery.

Temperature changes have been linked to variations in anthocyanin levels. According to Gazula et al. (2005) 'Lollo Rosso' lettuce exhibited a notable increase in anthocyanin content when grown at lower temperatures than plants cultivated under higher temperatures. Similar response was observed on Chinese cabbage (*Brassica rapa* L.) (He et al., 2020), strawberry (Fragaria × ananassa Duch. cv. Toyonoka) (Zhang et al., 2018), Japanese parsley (*Oenanthe stolonifera* DC) (Hasegawa et al., 2001), and grape (*Vitis labrusca* L. × *Vitis vinifera* L.) (Gao-Takai et al., 2019). Lower temperatures are believed to lead to elevated transcript levels for enzymes like phenylalanine ammonia-lyase and chalcone isomerase, which play a role in anthocyanin biosynthesis (Dela et al., 2003). Plants in our investigation experienced uniform temperature conditions, which could partly account for the absence of significant differences in anthocyanin content.

- *Chlorophyll*

Similar to anthocyanins in 'Rouxai' plants, we did not find significant differences in chlorophyll content for either 'Rouxai' or 'Waldmann's dark green' plants, regardless of the lighting treatment (Figure 1.5). Chlorophyll content per unit area indicates the plant's photosynthetic capacity could have been influenced by environmental factors (Palta, 1990). For instance, chlorophyll may degrade in excess light (De Carvalho Gonçalves et al., 2005) due to photo-oxidation (Kramer and Kozlowski, 1979), while under low light conditions, the content of this pigment might increase (Czeczuga, 1987). Zervoudakis et al. (2012) reported an increase of chlorophyll content on Salvia officinalis when growing under low light conditions. Similarly happened to sweet pepper (*Capsicum annuum* L.) (Sui et al., 2012). In our study, plants were subjected to varying light levels (high and low) across different days without any differences in chlorophyll content. This could indicate that the plants might have reached a balance in their suitable chlorophyll content for both conditions. Conversely, two rice (Oryza sativa) phenotypes growing under different lighting conditions, 600 and 1200 $\mu mol \cdot m^{-2} \cdot s^{-1}$, did not show significant differences in chlorophyll content despite the light intensity (Zhao et al., 2017). This suggests that variations in chlorophyll content in response to light conditions might vary among different species.

Energy requirement

DLI fluctuations only from one day to another or "carryover" effect has been reported to potentially reduce energy cost related to supplemental lighting in green houses set up (Jayalath et al., 2024). In this study, we tested how plants behave when said DLI fluctuations happen during multiple days. We proposed two hypothetical cases to assess the energy requirements for supplemental light when fluctuating DLI levels during various days. For the first case, we assumed that plants would be subjected to DLI of 11.25, 12.5, 13.13, and 13.5 $mol \cdot m^{-2} \cdot d^{-1}$ (provided by sunlight) during 2, 3, 4, and 5 days after a day with high DLI (22.5 $mol \cdot m^{-2} \cdot d^{-1}$)

respectively. Under the conditions of our study, said plants did not require a DLI of 15 mol·m-2·d-1 after a day with high DLI to not show significant differences in plant growth compared to plants growing consistently under the optimal DLI of 15 mol·m^{-2}·d^{-1}. It has been showed that plants could be allowed to get a high DLI on sunny days, and this could compensate for a day with a low DLI immediately after, and this concept was called the carryover effect (Jayalath et al., 2024). Then, if we experience one day with a high daily light integral (DLI) of 22.5 mol·m^{-2}·d^{-1}, followed by subsequent days with lower DLIs of 11.25, 12.5, 13.13, or 13.5 mol·m-2·d-1 over the next 2, 3, 4, or 5 days respectively, all under natural light conditions (as described in our first hypothetical case), the use of energy for supplemental lighting (Figure 10) to achieve an optimal DLI of 15 mol·m^{-2}·d^{-1} may not be necessary. This is due to the carryover effect from the initial high DLI day.

In our second hypothetical case, we calculated the energy requirements assuming that days with a high DLI of 22.5 mol·m^{-2}·d^{-1} (from sunlight) would be followed by periods of 2, 3, 4, and 5 days with low DLI. Additionally, we assumed that these low DLI days would receive only 10 mol·m^{-2}·d^{-1} (also from sunlight). We estimated the energy needed to supplement an extra 5 mol·m-2·d-1 to achieve the optimal 15 mol·m^{-2}·d^{-1} as well as the energy required to generate additional DLI to reach 11.25, 12.5, 13.13, and 13.5 mol·m^{-2}·d^{-1} (depending on the number of consecutive days with low DLI) to take advantage of the ‘carryover’ effect. In our study, the contrast in energy requirements between achieving the optimal DLI and the energy to use the ‘carryover’ effect could indicate potential energy savings.

Conclusions

After comparing plant responses under the lighting conditions tested in our study, we found that plants can tolerate multiple days with suboptimal DLI if they have been preceded by a day with higher-than-optimal DLI. This study suggests that plants can use the high DLI from one day to compensate for subsequent days with lower DLI. This finding implies that growers might not always need to achieve a specific DLI through supplemental lighting if similar lighting patterns are provided by sunlight. Consequently, this could reduce the need for supplemental lighting and result in economic benefits. However, the precise energy savings may vary depending on factors such as geographical location, weather conditions, and supplemental lighting systems. Additionally, determining the optimal DLI levels and acceptable DLI fluctuations for different crops is necessary if the findings of this study are to be applied more broadly.

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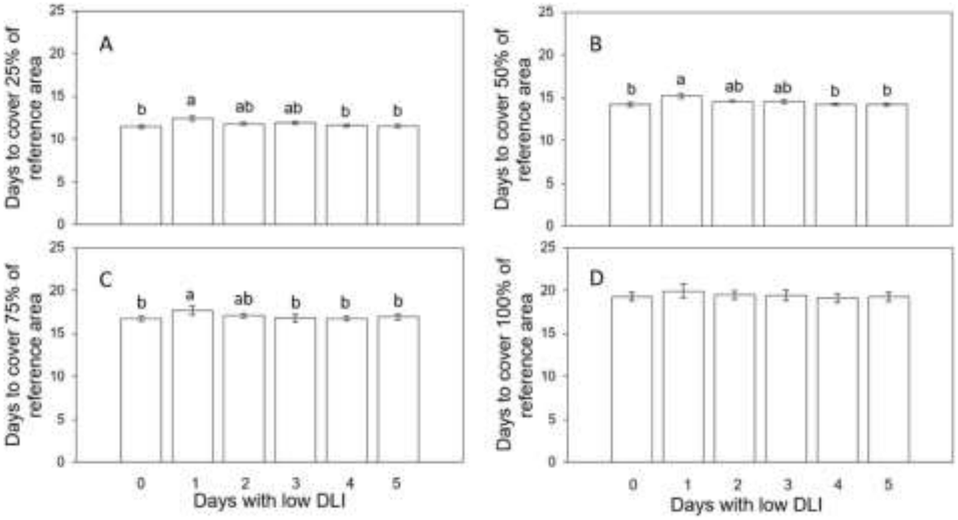


Figure 1.1. Number of days that plants growing under different daily light integral (DLI) treatments needed to achieve the coverage of a reference area of 25% (A), 50% (B), 75% (C), and 100% (D). Error bars denote standard error (n=6). Different letters on top of error bars show significant differences at α=0.05 from Tukey's test for A, B. Different letters on top of error bars show significant differences at α=0.05 from Fisher's LSD test for (C) Absence of letters on top of error bars show no significant differences.

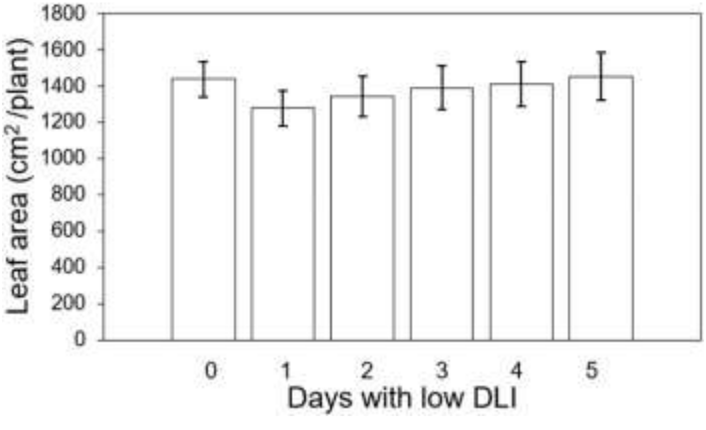


Figure 1.2. Final leaf area of 'Rouxai' and 'Walmand's dark green' lettuce plants growing under different lighting treatments. Lighting treatments are described by the number of days with low daily light integral (DLI) after a day with high DLI. Error bars denote standard

error (n=6). Absence of letters on top of error bars show no significant differences at α=0.05 from Tukey's test.

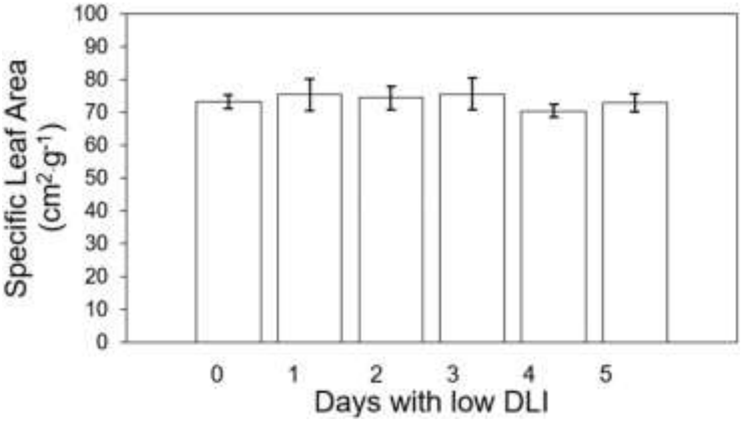


Figure 1.3. Specific leaf area of 'Rouxai' and 'Walmand's dark green' lettuce plants growing under different lighting treatments. Specific leaf area was calculated as the ratio of final leaf area and final fry weight. Lighting treatments are described by the number of days with low daily light integral (DLI) after a day with high DLI. Error bars denote standard error (n=6). Absence of letters on top of error bars show no significant differences at α=0.05 from Tukey's test.

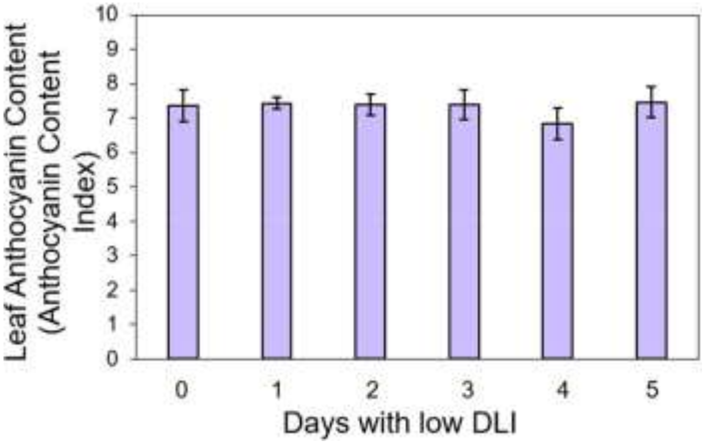


Figure 1.4. Leaf anthocyanin content of 'Rouxai' lettuce plants growing under different lighting treatments. Lighting treatments are described by the number of days with low daily light integral

(DLI) after a day with high DLI. Error bars show standard error (n=3). Absence of letters on top of error bars show no significant differences at α=0.05 from Tukey's test.

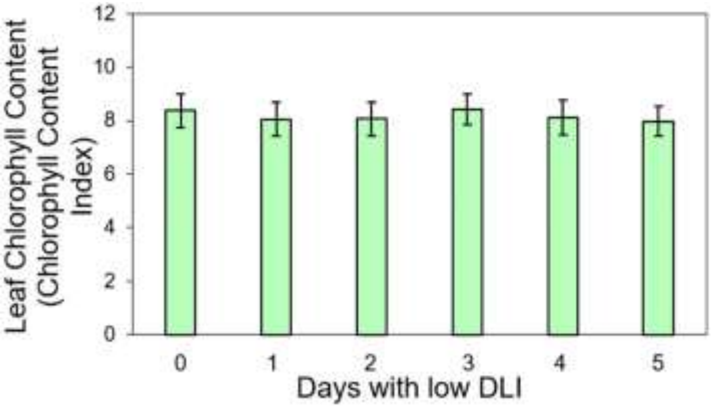


Figure 1.5. Leaf chlorophyll content in 'Waldmann's dark green' and 'Rouxai' plants (both cultivars averaged) growing under different lighting treatments. Lighting treatments are described by the number of days with low daily light integral (DLI) after a day with high DLI. Error bars show standard error (n=6). Absence of letters on top of error bars show no significant differences at α=0.05 from Tukey's test.

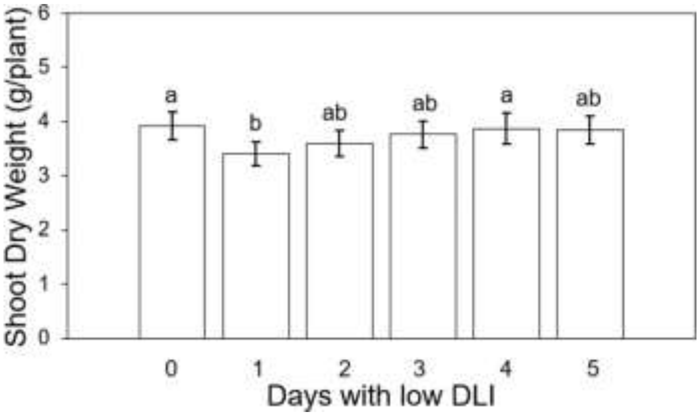


Figure 1.6. Final shoot dry weight of 'Rouxai' and 'Waldmann's dark green' lettuce plants growing under different lighting treatments. Lighting treatments are described by the number of

days with low daily light integral (DLI) after a day with high DLI. Error bars denote standard error (n=6). Different letters on top of error bars show significant differences at α=0.05.

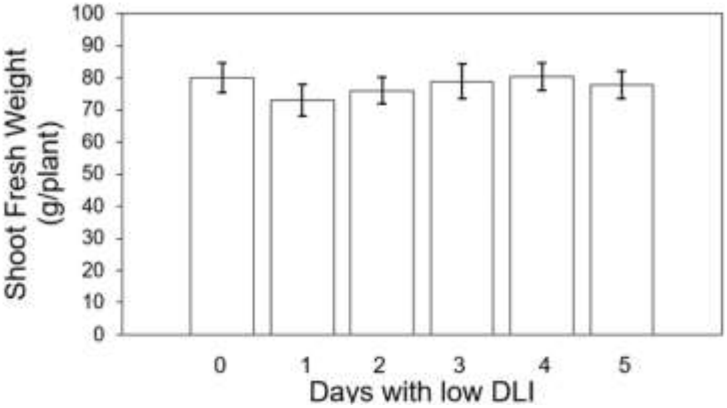


Figure 1.7. Final shoot fresh weight of ‘Rouxai’ and ‘Waldmann’s dark green’ lettuce plants growing under different lighting treatments. Lighting treatments are described by the number of days with low daily light integral (DLI) after a day with high DLI. Error bars denote standard error (n=6). Absence of letters on top of error bars show no significant differences at α=0.05 from Tukey’s test.

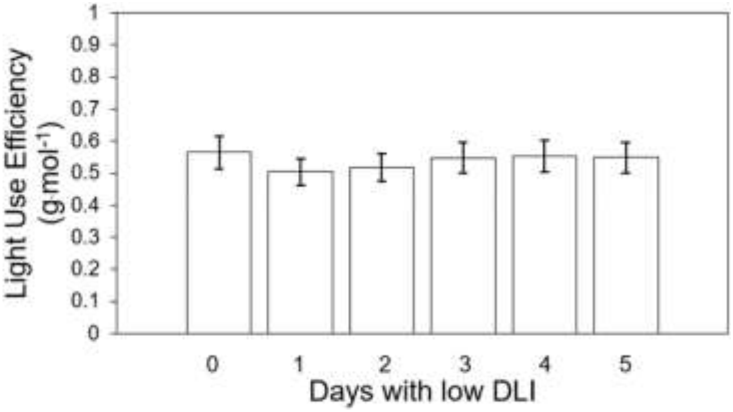


Figure 1.8. Light use efficiency of ‘Rouxai’ and ‘Waldmann’s dark green’ lettuce plants growing under different lighting treatments. Lighting treatments are described by the number of days with

low daily light integral (DLI) after a day with high DLI. Error bars denote standard error (n=6). Absence of letters on top of error bars show no significant differences at α=0.05 from Tukey's test.

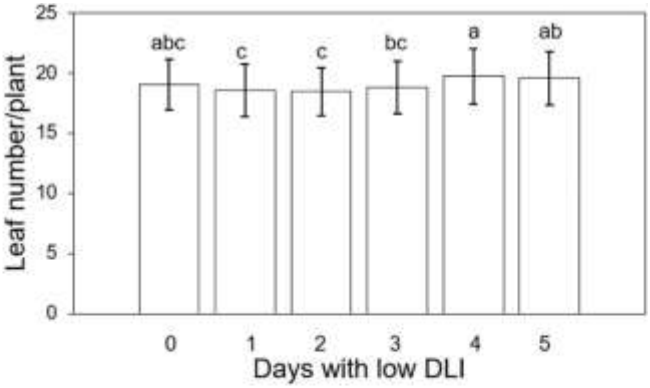


Figure 1.9. Final leaf number per plant of 'Rouxai' and 'Waldmann's dark green' lettuce plants growing under different lighting treatments. Lighting treatments are described by the number of days with low daily light integral (DLI) after a day with high DLI. Error bars denote standard error (n=6). Different letters on top of error bars show significant differences at α=0.05.

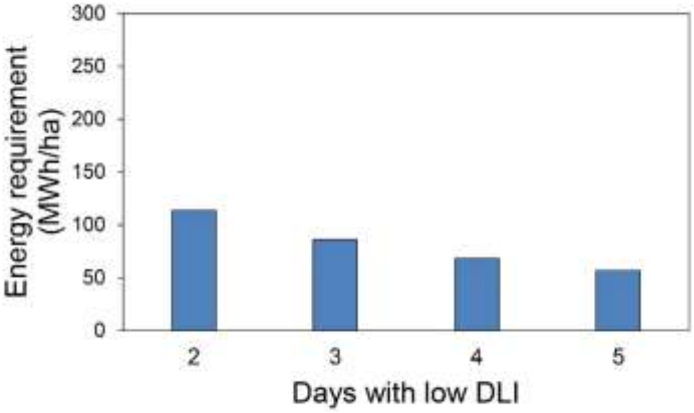


Figure 1.10. Energy requirement in 30 days used in supplemental lighting to provide extra daily light integral (DLI) to achieve a DLI of 15 $mol \cdot m^{-2} \cdot d^{-1}$ for days with low DLI for the first hypothetical case presented.

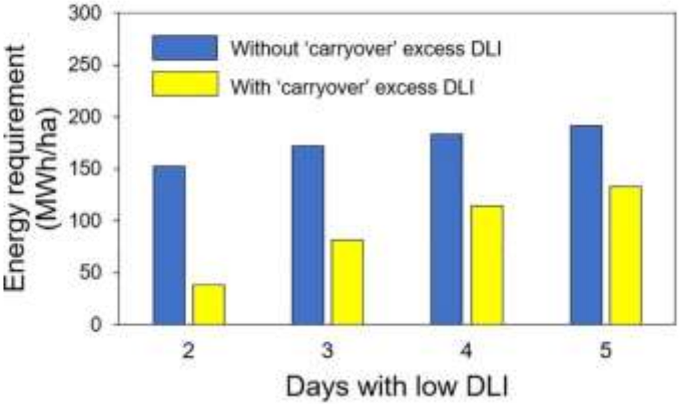


Figure 1.11. Energy requirement in 30 days used in supplemental lighting to provide extra daily light integral (DLI) to achieve a DLI of 15 mol·m^{-2}·d^{-1} (without carryover) to obtain a lower DLI (with carryover depending on the number of days with low DLI) for days with low DLI for the second hypothetical case presented.

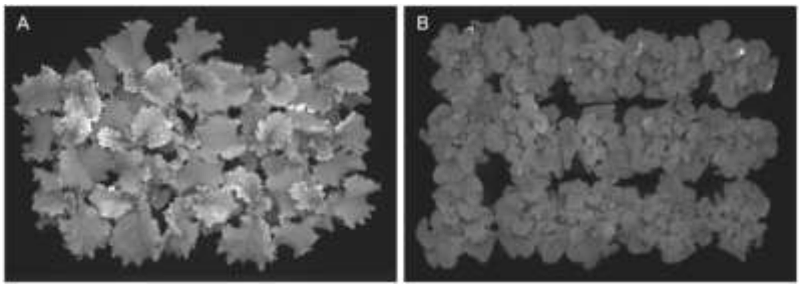


Figure 1.12. Picture of projected canopy size at 17 days after seeds were sowing shows how the canopy of individual plants overlaps with others. (A) 'Waldmann's dark green' plants. (B) 'Rouxai' plants.

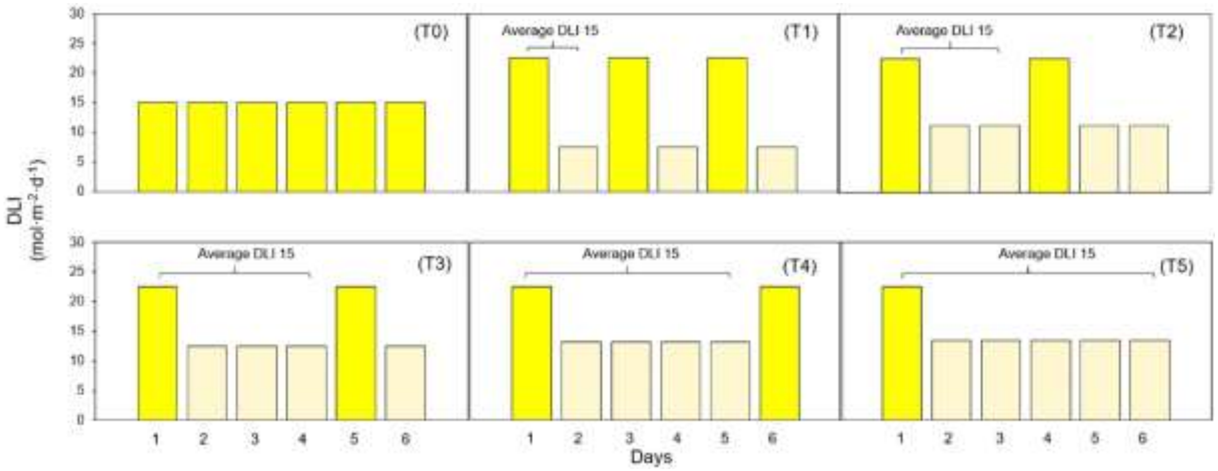
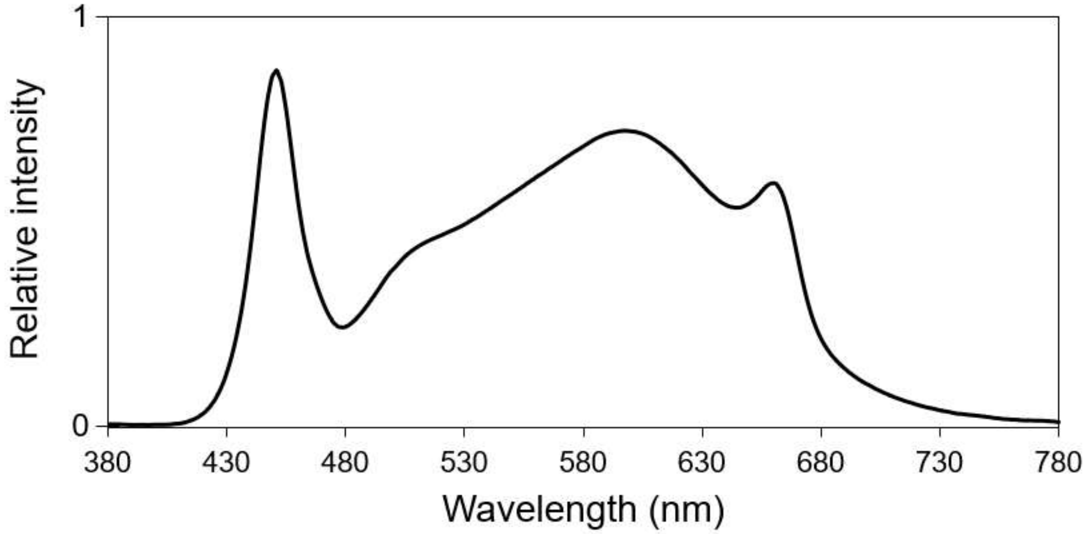


Figure 1.13. Diagram showing different lighting treatments. (T0) Treatment with zero days with low DLI. (T1) Treatment with one day with high DLI followed by one day with low DLI. (T2) Treatment with one day with high DLI followed by two days with low DLI. (T3) Treatment with one day with high DLI followed by three days with low DLI. (T4) Treatment with one day with high DLI followed by four days with low DLI. (T5) Treatment with one day with high DLI followed by five days with low DLI. The average DLI for each combination of days with high DLI and low DLI is 15 mol·m^{-2}·d^{-1}.



Supplemental figure 1.1. The electromagnetic spectrum emitted by LED fixtures (SPYDRx Plus with PhysioSpec indoor spectrum, Fluence Bioengineering, Austin, TX, USA).

Table 1.1. Photosynthetic Photon Flux Density (PPFD) levels and corresponding daily light integral (DLI). High DLI, low DLI, high PPFD, and low PPFD are averages of three lighting fixtures with ± SD. Average DLI is the average of one day with high DLI and a different number of days with low DLI, depending on the treatment.

Treatment	**High DLI**	**Low DLI**	**Average DLI**	**Days with low DLI**	**Photo-period**	**High PPFD**	**Low PPFD**
	------ (mol·m^{-2}·d^{-1}) ------				(h)	---- (μmol·m^{-2}·s^{-1}) ----	
0 (Control)	14.88±0.27	14.88±0.27	14.88	-	20	206.66±3.78	206.66±3.78
1	22.53±0.21	7.53±0.18	15.03	1	20	313±3	104.66±2.51
2	22.48±0.18	11.25±0.18	15	2	20	312.2±2.51	156.33±2.51
3	22.44±0.34	12.5±0.2	14.98	3	20	311.66±4.75	173.66±3.78
4	22.51±0.21	13.17±0.19	15.04	4	20	312.66±3.05	183±2.64
5	22.48±0.1	13.51±0.14	15.008	5	20	312.33±1.52	187.66±2.08

Supplemental table 1.1. Lighting regime for the first hypothetical case to assess energy requirement depending on the number of days with low DLI after a day with high DLI. Lines in yellow indicate the day with high DLI, and lines in white indicate days with low DLI. For each combination of days with low DLI after a day with high DLI (lighting regime), we indicate the DLI received from the sun, the extra DLI to be achieved, the DLI reported in the literature for optimal plant growth, and the extra DLI to complete a DLI to take advantage of the 'carryover' effect.

	Lighting regime											
	2 days with low DLI			3 days with low DLI			4 days with low DLI			5 days with low DLI		
Days	DLI from sun	Extra DLI to complete literature value	Extra DLI to complete carryover effect	DLI from sun	Extra DLI to complete literature value	Extra DLI to complete carryover effect	DLI from sun	Extra DLI to complete literature value	Extra DLI to complete carryover effect	DLI from sun	Extra DLI to complete literature value	Extra DLI to complete carryover effect
1	22.5	0	0	22.5	0	0	22.5	0	0	22.5	0	0
2	11.25	3.75	0	12.5	2.5	0	13.3	1.7	0	13.5	1.5	0
3	11.25	3.75	0	12.5	2.5	0	13.3	1.7	0	13.5	1.5	0
4	22.5	0	0	12.5	2.5	0	13.3	1.7	0	13.5	1.5	0
5	11.25	3.75	0	22.5	0	0	13.3	1.7	0	13.5	1.5	0
6	11.25	3.75	0	12.5	2.5	0	22.5	0	0	13.5	1.5	0
7	22.5	0	0	12.5	2.5	0	13.3	1.7	0	22.5	0	0
8	11.25	3.75	0	12.5	2.5	0	13.3	1.7	0	13.5	1.5	0
9	11.25	3.75	0	22.5	0	0	13.3	1.7	0	13.5	1.5	0
10	22.5	0	0	12.5	2.5	0	13.3	1.7	0	13.5	1.5	0
11	11.25	3.75	0	12.5	2.5	0	22.5	0	0	13.5	1.5	0
12	11.25	3.75	0	12.5	2.5	0	13.3	1.7	0	13.5	1.5	0
13	22.5	0	0	22.5	0	0	13.3	1.7	0	22.5	0	0
14	11.25	3.75	0	12.5	2.5	0	13.3	1.7	0	13.5	1.5	0

15	11.25	3.75	0	12.5	2.5	0	13.3	1.7	0	13.5	1.5	0
16	22.5	0	0	12.5	2.5	0	22.5	0	0	13.5	1.5	0
17	11.25	3.75	0	22.5	0	0	13.3	1.7	0	13.5	1.5	0
18	11.25	3.75	0	12.5	2.5	0	13.3	1.7	0	13.5	1.5	0
19	22.5	0	0	12.5	2.5	0	13.3	1.7	0	22.5	0	0
20	11.25	3.75	0	12.5	2.5	0	13.3	1.7	0	13.5	1.5	0
21	11.25	3.75	0	22.5	0	0	22.5	0	0	13.5	1.5	0
22	22.5	0	0	12.5	2.5	0	13.3	1.7	0	13.5	1.5	0
23	11.25	3.75	0	12.5	2.5	0	13.3	1.7	0	13.5	1.5	0
24	11.25	3.75	0	12.5	2.5	0	13.3	1.7	0	13.5	1.5	0
25	22.5	0	0	22.5	0	0	13.3	1.7	0	22.5	0	0
26	11.25	3.75	0	12.5	2.5	0	22.5	0	0	13.5	1.5	0
27	11.25	3.75	0	12.5	2.5	0	13.3	1.7	0	13.5	1.5	0
28	22.5	0	0	12.5	2.5	0	13.3	1.7	0	13.5	1.5	0
29	11.25	3.75	0	22.5	0	0	13.3	1.7	0	13.5	1.5	0
30	11.25	3.75	0	12.5	2.5	0	13.3	1.7	0	13.5	1.5	0
31	22.5	0	0	12.5	2.5	0	22.5	0	0	22.5	0	0
32	11.25	3.75	0	12.5	2.5	0	13.3	1.7	0	13.5	1.5	0
33	11.25	3.75	0	22.5	0	0	13.3	1.7	0	13.5	1.5	0
34	22.5	0	0	12.5	2.5	0	13.3	1.7	0	13.5	1.5	0
35	11.25	3.75	0	12.5	2.5	0	13.3	1.7	0	13.5	1.5	0
36	11.25	3.75	0	12.5	2.5	0	22.5	0	0	13.5	1.5	0
37	22.5	0	0	22.5	0	0	13.3	1.7	0	22.5	0	0
38	11.25	3.75	0	12.5	2.5	0	13.3	1.7	0	13.5	1.5	0
39	11.25	3.75	0	12.5	2.5	0	13.3	1.7	0	13.5	1.5	0
40	22.5	0	0	12.5	2.5	0	13.3	1.7	0	13.5	1.5	0
41	11.25	3.75	0	22.5	0	0	22.5	0	0	13.5	1.5	0
42	11.25	3.75	0	12.5	2.5	0	13.3	1.7	0	13.5	1.5	0
43	22.5	0	0	12.5	2.5	0	13.3	1.7	0	22.5	0	0
44	11.25	3.75	0	12.5	2.5	0	13.3	1.7	0	13.5	1.5	0
45	11.25	3.75	0	22.5	0	0	13.3	1.7	0	13.5	1.5	0
46	22.5	0	0	12.5	2.5	0	22.5	0	0	13.5	1.5	0
47	11.25	3.75	0	12.5	2.5	0	13.3	1.7	0	13.5	1.5	0
48	11.25	3.75	0	12.5	2.5	0	13.3	1.7	0	13.5	1.5	0
49	22.5	0	0	22.5	0	0	13.3	1.7	0	22.5	0	0

50	11.25	3.75	0	12.5	2.5	0	13.3	1.7	0	13.5	1.5	0
51	11.25	3.75	0	12.5	2.5	0	22.5	0	0	13.5	1.5	0
52	22.5	0	0	12.5	2.5	0	13.3	1.7	0	13.5	1.5	0
53	11.25	3.75	0	22.5	0	0	13.3	1.7	0	13.5	1.5	0
54	11.25	3.75	0	12.5	2.5	0	13.3	1.7	0	13.5	1.5	0
55	22.5	0	0	12.5	2.5	0	13.3	1.7	0	22.5	0	0
56	11.25	3.75	0	12.5	2.5	0	22.5	0	0	13.5	1.5	0
57	11.25	3.75	0	22.5	0	0	13.3	1.7	0	13.5	1.5	0
58	22.5	0	0	12.5	2.5	0	13.3	1.7	0	13.5	1.5	0
59	11.25	3.75	0	12.5	2.5	0	13.3	1.7	0	13.5	1.5	0
60	11.25	3.75	0	12.5	2.5	0	13.3	1.7	0	13.5	1.5	0

Supplemental table 1.2. Lighting regime for the second hypothetical case to assess energy requirement depending on the number of days with low DLI after a day with high DLI. Lines in yellow indicate the day with high DLI, and lines in white indicate days with low DLI. For each combination of days with low DLI after a day with high DLI (lighting regime), we indicate the DLI received from the sun, the extra DLI to be achieved, the DLI reported in the literature for optimal plant growth, and the extra DLI to complete a DLI to take advantage of the 'carryover' effect.

	Lighting regime											
	2 days with low DLI			3 days with low DLI			4 days with low DLI			5 days with low DLI		
Days	DLI from sun	Extra DLI to complete literature value	Extra DLI to complete carryover effect	DLI from sun	Extra DLI to complete literature value	Extra DLI to complete carryover effect	DLI from sun	Extra DLI to complete literature value	Extra DLI to complete carryover effect	DLI from sun	Extra DLI to complete literature value	Extra DLI to complete carryover effect

1	22.5	0	0	22.5	0	0	22.5	0	0	22.5	0	0
2	10	5	1.25	10	5	2.5	10	5	3.13	10	5	3.5
3	10	5	1.25	10	5	2.5	10	5	3.13	10	5	3.5
4	22.5	0	0	10	5	2.5	10	5	3.13	10	5	3.5
5	10	5	1.25	22.5	0	0	10	5	3.13	10	5	3.5
6	10	5	1.25	10	5	2.5	22.5	0	0	10	5	3.5
7	22.5	0	0	10	5	2.5	10	5	3.13	22.5	0	0
8	10	5	1.25	10	5	2.5	10	5	3.13	10	5	3.5
9	10	5	1.25	22.5	0	0	10	5	3.13	10	5	3.5
10	22.5	0	0	10	5	2.5	10	5	3.13	10	5	3.5
11	10	5	1.25	10	5	2.5	22.5	0	0	10	5	3.5
12	10	5	1.25	10	5	2.5	10	5	3.13	10	5	3.5
13	22.5	0	0	22.5	0	0	10	5	3.13	22.5	0	0
14	10	5	1.25	10	5	2.5	10	5	3.13	10	5	3.5
15	10	5	1.25	10	5	2.5	10	5	3.13	10	5	3.5
16	22.5	0	0	10	5	2.5	22.5	0	0	10	5	3.5
17	10	5	1.25	22.5	0	0	10	5	3.13	10	5	3.5
18	10	5	1.25	10	5	2.5	10	5	3.13	10	5	3.5
19	22.5	0	0	10	5	2.5	10	5	3.13	22.5	0	0
20	10	5	1.25	10	5	2.5	10	5	3.13	10	5	3.5
21	10	5	1.25	22.5	0	0	22.5	0	0	10	5	3.5
22	22.5	0	0	10	5	2.5	10	5	3.13	10	5	3.5
23	10	5	1.25	10	5	2.5	10	5	3.13	10	5	3.5
24	10	5	1.25	10	5	2.5	10	5	3.13	10	5	3.5
25	22.5	0	0	22.5	0	0	10	5	3.13	22.5	0	0
26	10	5	1.25	10	5	2.5	22.5	0	0	10	5	3.5
27	10	5	1.25	10	5	2.5	10	5	3.13	10	5	3.5
28	22.5	0	0	10	5	2.5	10	5	3.13	10	5	3.5
29	10	5	1.25	22.5	0	0	10	5	3.13	10	5	3.5
30	10	5	1.25	10	5	2.5	10	5	3.13	10	5	3.5
31	22.5	0	0	10	5	2.5	22.5	0	0	22.5	0	0
32	10	5	1.25	10	5	2.5	10	5	3.13	10	5	3.5
33	10	5	1.25	22.5	0	0	10	5	3.13	10	5	3.5
34	22.5	0	0	10	5	2.5	10	5	3.13	10	5	3.5
35	10	5	1.25	10	5	2.5	10	5	3.13	10	5	3.5

36	10	5	1.25	10	5	2.5	22.5	0	0	10	5	3.5
37	22.5	0	0	22.5	0	0	10	5	3.13	22.5	0	0
38	10	5	1.25	10	5	2.5	10	5	3.13	10	5	3.5
39	10	5	1.25	10	5	2.5	10	5	3.13	10	5	3.5
40	22.5	0	0	10	5	2.5	10	5	3.13	10	5	3.5
41	10	5	1.25	22.5	0	0	22.5	0	0	10	5	3.5
42	10	5	1.25	10	5	2.5	10	5	3.13	10	5	3.5
43	22.5	0	0	10	5	2.5	10	5	3.13	22.5	0	0
44	10	5	1.25	10	5	2.5	10	5	3.13	10	5	3.5
45	10	5	1.25	22.5	0	0	10	5	3.13	10	5	3.5
46	22.5	0	0	10	5	2.5	22.5	0	0	10	5	3.5
47	10	5	1.25	10	5	2.5	10	5	3.13	10	5	3.5
48	10	5	1.25	10	5	2.5	10	5	3.13	10	5	3.5
49	22.5	0	0	22.5	0	0	10	5	3.13	22.5	0	0
50	10	5	1.25	10	5	2.5	10	5	3.13	10	5	3.5
51	10	5	1.25	10	5	2.5	22.5	0	0	10	5	3.5
52	22.5	0	0	10	5	2.5	10	5	3.13	10	5	3.5
53	10	5	1.25	22.5	0	0	10	5	3.13	10	5	3.5
54	10	5	1.25	10	5	2.5	10	5	3.13	10	5	3.5
55	22.5	0	0	10	5	2.5	10	5	3.13	22.5	0	0
56	10	5	1.25	10	5	2.5	22.5	0	0	10	5	3.5
57	10	5	1.25	22.5	0	0	10	5	3.13	10	5	3.5
58	22.5	0	0	10	5	2.5	10	5	3.13	10	5	3.5
59	10	5	1.25	10	5	2.5	10	5	3.13	10	5	3.5
60	10	5	1.25	10	5	2.5	10	5	3.13	10	5	3.5

CHAPTER 2

VARYING LIGHT INTENSITIES AFFECT LETTUCE GROWTH AND PHYSIOLOGY IN CONTROLLED INDOOR ENVIRONMENTS[2]

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[2] Mayorga-Gomez, A.M., van Iersel, M.W. and R.S. Ferrarezi. 2024. *Horticulturae*, *10*, 931. Reprinted here with permission of the publisher.

Abstract

Agriculture in controlled environments has gained popularity over time. Compared to traditional agriculture, controlled environments emerge as an alternative to mitigate the negative impacts of conventional farming methods. However, controlled environment agriculture, particularly plant factories with artificial lighting, incurs higher electricity costs, primarily for supplemental lighting and dehumidification of the cultivation area. Given these high costs, it is crucial to understand how efficiently plants utilize available light to convert it into biomass. This understanding can be used to design lighting strategies to reduce electricity usage. In this study, we cultivated 'Rex' lettuce (Lactuca sativa) plants on a soilless substrate and used an ebb-and-flow system for irrigation and fertilization. Plants grew in varying photosynthetic photon flux density (PPFD) levels ranging from 125 to 375 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and were assessed for various physiological responses. Our findings revealed that plants exposed to higher light levels exhibited greater final dry weight, increased photosynthetic activity, higher water use efficiency, and accelerated growth compared to those under lower light conditions. Notably, plants subjected to higher light intensities did not show a significant increase in transpiration, suggesting a potential trade-off between energy expenditure on supplemental lighting and dehumidification. This finding opens the possibility of reducing energy consumption for dehumidification and achieving economic savings by subjecting plants to optimal growing conditions for shorter durations. This depends on whether higher savings on dehumidification are achieved compared to the energy required to maintain high PPFD levels.

Introduction

Agriculture is consistently associated with environmental problems, which have been aggravated due to the industrialization of this activity (Horrigan et al., 2022). One of the main repercussions is water pollution. Often, the fate of residuals of chemical products is waterbodies. This water is subsequently consumed by living organisms that, in the worst scenario, can cause lethal effects (Sankhla et al., 2018). Soils are also affected by agriculture. Constant tillage increases soil erosion (Lindstrom et al., 2001), and the use of heavy machinery produces soil compaction (Nawaz et al., 2013). Furthermore, the use of low-quality water and the inadequate use of fertilizers and pesticides can lead to the loss of organic matter and nutrients and increase soil salinity. This would result in a decrease in the soil's productivity (Alam 2014). Agriculture also indirectly affects the environment. Most of the time, agricultural products have to be transported over long distances from the cultivation site to the final consumer. This transportation process contributes to the emission of greenhouse gases (Wakeland et al., 2012). Additionally, in this process, close to 25–30% of global food is lost (Onwude et al., 2021).

In the last few years, controlled environment agriculture (CEA) has become popular. Contrary to traditional agriculture, CEA uses less water and does not need soil for cultivation (Ragaveena et al., 2021). As soil is not needed, the use of herbicides is completely removed from the growing system (Benke and Tomkins 2017), and the use of pesticides is considerably reduced. Further, CEA has high water use efficiency (WUE) and, in the case where a hydroponics system is used, the water consumption is 12.5 times lower when compared to traditional agriculture (Zhang et al., 2021). Additionally, by using CEA systems like plant factories with artificial lighting (PFAL), food production can take place close to urban areas (Kozai et al., 2016).

PFAL refers to a closed growing space similar to a warehouse with multiple shelves vertically stacked. To produce food in a PFAL, various components are required. The space has to be sealed because carbon dioxide (CO_2), a source of artificial light, a system that provides irrigation and fertilization to plants, fans and air conditioning, and finally, a system that controls the environment parameters is provided (Kozai et al., 2016).

Despite the benefits that PFAL has in producing food, there are some high costs in its operations. This is the case of electricity, which might account for around 60% of the total operation costs every year (Zeidler et al., 2013). Most of that energy is used to power the lighting and dehumidification systems (van Iersel 2017). Due to the high electricity cost of these agricultural systems, it is important to understand how efficiently they use the provided light to reduce electricity use associated with lighting and dehumidification.

Various studies have examined light use efficiency (LUE) under different light levels in controlled environments for different crops. Most of these studies have assessed LUE based on the total incident light in the growing area rather than the light intercepted by plants relative to their canopy area (Pennisi et al.,2002; Zou et al., 2019). In contrast, there has been less focus on transpiration and water use efficiency (WUE), two physiological parameters closely linked to the dehumidification process in indoor controlled environments.

In this study, we cultivated lettuce (*Lactuca sativa*) plants under varying photosynthetic photon flux density (PPFD) levels ranging from 125 to 375 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and assessed various physiological responses, particularly transpiration and WUE. We hypothesized that dry weight, photosynthesis, and transpiration would increase for plants subjected to higher PPFD levels.

Materials and methods

Experimental Setup and Treatments

This study was performed at the University of Georgia, Athens, GA (latitude 33°57′26.676″ N, longitude 83°22′36.48″ W), in a walk-in growth chamber measuring 4.4 × 4.1 m in (width × length) from June to August 2022. Cooling was achieved through a top-mounted refrigeration system, and a dehumidifier controlled the relative humidity within the chamber. CO_2 levels were monitored and regulated by a CO_2 transmitter (GMC20; Vaisala, Helsinki, Finland) and a datalogger (CR6, Campbell Scientific, Logan, UT, USA), which triggered a solenoid valve to release CO_2 from a compressed gas cylinder in 1 s intervals whenever concentrations fell below 800 $\mu mol \cdot mol^{-1}$. Temperature and relative humidity were recorded every ten seconds using a probe (HMP50; Vaisala, Helsinki, Finland) connected to the datalogger, and these measurements were used to calculate the vapor pressure deficit (VPD). The average experimental conditions during the whole growing period were the following (means ± standard deviation): temperature of 23.50 ± 0.2140 °C, relative humidity of 65.22% ± 8.479%, CO_2 concentration of 855.9 ± 65.48 $mg \cdot L^{-1}$, and a VPD of 1.011 ± 0.2545 kPa.

Three metal racks (each representing a block) were placed in the walk-in growth chamber. Each rack had three horizontal shelves, and each shelf was vertically divided into two equal parts to create six growing spaces per rack and 18 growing spaces in total. Two light-emitting diode (LED) fixtures (SPYDRx Plus with PhysioSpec indoor spectrum; Fluence Bioengineering, Austin, TX, USA) were placed above each growing space. Details of the light spectrum and rack layout are provided in Supplemental Figures 2.1 and 2.2. Additionally, four small fans (AD0412HB-C50; ADDA, Orange, CA, USA), evenly separated, were installed on the sides of each growing space to provide airflow. This study had six lighting treatments assigned in a randomized complete block pattern in the growing spaces. The lighting treatments were controlled using six dimmable drivers (4009715; Intertek/Fluence, Arlington, VA, USA). Each driver controlled three growing spaces (with the same lighting treatment), one per rack.

Plants were grown under six different photosynthetic photon flux density (PPFD) levels, and all treatments had a photoperiod of 20 h (Table 2.1). The different PPFD levels were controlled using a datalogger (CR6; Campbell Scientific, Logan, UT, USA), which sent dimming signals to the six LED drivers. The PPFD levels were measured at the middle of each growing space, at the pot-top level, using a quantum sensor (MQ-500; Apogee Instruments, Logan, UT, USA).

Plant Material

Ten cm square plastic pots were filled to a centimeter from the top edge with the soilless substrate (Metro-Mix® 830 Professional Growing Mix; Sun Gro Horticulture, Agawam, MA, USA). Three pelleted Butterhead 'Rex' lettuce seeds (REX MT OG-Pellet; Johnny's Selected Seeds, Winslow, ME, USA) were sowed in each pot, and subsequently, the substrate was covered with calcined clay (Turface MVP; Turface Athletics, Buffalo Grove, IL, USA). Fifteen pots were placed in trays in a 5 × 3 array and inside the growing spaces. When the seeds germinated, thinning was performed to leave one seedling per pot to finally obtain fifteen plants per growing space. This resulted in having fifteen plants sowed in a 150 cm2 area. Plants were irrigated and fertilized by using an ebb-and-flow subirrigation system that provided a nutrient solution with 100 $\mathrm{mg \cdot L^{-1}}$ of nitrogen using a 15N–2.2P–12.45K water-soluble fertilizer (Jack's Professional® LX 15-5-15 Cal-Mag LX; JR Peters, Allentown, PA, USA). Plants were harvested 30 days after sowing.

Data Collection and Calculations

Canopy images were taken the first time after 7 days of sowing the seeds and twice weekly using a chlorophyll fluorescence imaging setup. In this set up we utilized a monochrome camera (CM3-U3-31S4M-CS, Chameleon3 USB3 camera, FLIR Systems, Inc., Arlington, VA, USA) equipped with a 665 nm long pass filter (LP665 Dark Red Long pass Filter; Midopt Midwest Optical Systems, Inc., Palatine, IL, USA) coupled to the lens. The camera was positioned to face downward inside a grow tent measuring 1.2 m × 0.6 m × 1.5 m. Additionally, two blue LED panels (11GRL009-LED_v, AplusChoice, Atlanta, GA, USA) were installed inside the tent next to the camera to stimulate chlorophyll and promote fluorescence [16]. Images were analyzed using a custom Python script to determine the projected canopy size (PCS), which is a morphological measure [16]. PCS measures the plant's projected canopy area from a top view and it is used to determine the incident amount of light that plants can intercept.

The PCS was plotted against days after sowing (DAS), and the sigmoidal curve $\{PCS = a/[1 + e - (DAS - x0)/b]\}$ was fitted to the data (SigmaPlot 11.0, Systat Software, San Jose, CA, USA).

From the regression equations, the PCS for each day (DAS 1 to 30) of the growing cycle was estimated. The daily PCS was multiplied by the DLI for each light treatment to calculate the daily incident light received by the canopy of each group of plants on each day of the growing cycle [incident daily light integral ($mol \cdot d^{-1}$) = PCS (mm2) × DLI ($mol \cdot m^{-2} \cdot d^{-1}$)]. Using these values, the incident light on the canopy throughout the whole growing cycle was calculated.

Prior to harvesting the plants, we visually examined each plant tray from all treatments to assess the occurrence of tipburn in the plants and captured overhead photos to document this condition. Shoots of the plants from each growing space were harvested and placed in a drying oven at 80 °C for 72 h, and the final dry weight was measured. Light use efficiency (LUE, $g \cdot mol^{-1}$) was calculated as shoot biomass (g)/total incident light (mol). The number of days that the crops needed to reach a specific size (25%, 50%, 75%, and 100% of coverage of the trays that held the plants, 0.15 m2) was calculated based on the estimated PCS for each day of the growing cycle.

Net photosynthesis and transpiration were measured, and WUE was calculated [Assimilation ($\mu mol \cdot m^{-2} \cdot d^{-1}$)/Transpiration ($mmol \cdot m^{-2} \cdot d^{-1}$)] on one of the plants from each growing space at 28 DAS using a portable photosynthesis system (CIRAS-3; PP Systems, Amesbury, MA, USA).

Statistical Analysis

We used linear regression to determine the effect of different light levels on dry weight, total incident light, light use efficiency, efficiency of photosystem II, electron transport rate, net photosynthesis, transpiration, and water use efficiency. Also, linear regression was also used to assess the effect of total incident light on fry weight and the effect of electron transport rate on net photosynthesis. Additionally, we employed an analysis of variance (ANOVA) to evaluate the differences in the number of days required for plants to achieve specific sizes depending on the light level they grew under. For linear regression and ANOVA, we used statistical software (R version 4.1.2; R Project for Statistical Computing, Vienna, Austria).

Results

Dry Weight

The final total shoot dry weight showed a positive correlation with PPFD. Lettuce plants exhibited higher final total shoot dry weight when grown under higher PPFD levels ($p < 0.0001$) (Figure 1). Specifically, an increase of 50 $\mu mol \cdot m^{-2} \cdot s^{-1}$ from 125 to 175 $\mu mol \cdot m^{-2} \cdot s^{-1}$ resulted in a 1.5-fold increase in dry weight. Similarly, for subsequent increases of 50 μmol·m^{-2}·s^{-1} from 175 μmol·m^{-2}·s^{-1} for the remaining PPFD levels, a dry weight gain of 1.1 times was observed in comparison to the respective previous PPFD level.

Total Incident Light

The average total incident light per plant showed a positive correlation with the photosynthetic photon flux density (PPFD) (Figure 2.2). A higher PPFD level corresponded to a greater total incident light received by plants throughout their growth cycle, from germination to the harvest day ($p < 0.0001$). The PPFD levels in each treatment increased by 50 μmol·m^{-2}·s^{-1}, ranging from 125 to 375 μmol·m^{-2}·s^{-1}. Comparing the total incident light at different PPFD levels, the results showed that at a PPFD of 175 μmol·m^{-2}·s^{-1}, the total incident light increased by 1.5 times compared to a PPFD of 125 μmol·m^{-2}·s^{-1}. Similarly, at PPFDs of 225, 275, and 325 μmol·m^{-2}·s^{-1}, the total incident light increased by 1.2 times compared to the previous PPFD level. Finally, at a PPFD of 375 μmol·m^{-2}·s^{-1}, the total incident light increased by 1.1 times compared to a PPFD of 325 μmol·m^{-2}·s^{-1}.

Total Incident Light

The average total incident light per plant showed a positive correlation with the photosynthetic photon flux density (PPFD) (Figure 2.2). A higher PPFD level corresponded to a greater total incident light received by plants throughout their growth cycle, from germination to the harvest day ($P < 0.0001$). The PPFD levels in each treatment increased by 50 μmol·m^{-2}·s^{-1}, ranging from 125 to 375 μmol·m^{-2}·s^{-1}. Comparing the total incident light at different PPFD levels, the results showed that at a PPFD of 175 μmol·m^{-2}·s^{-1}, the total incident light increased by 1.5 times compared to a PPFD of 125 μmol·m^{-2}·s^{-1}. Similarly, at PPFDs of 225, 275, and 325

$\mu mol \cdot m^{-2} \cdot s^{-1}$, the total incident light increased by 1.2 times compared to the previous PPFD level. Finally, at a PPFD of 375 $\mu mol \cdot m^{-2} \cdot s^{-1}$, the total incident light increased by 1.1 times compared to a PPFD of 325 $\mu mol \cdot m^{-2} \cdot s^{-1}$.

Dry Weight in Relation to Total Incident Light

The final total shoot dry weight per plant had a positive correlation with the total incident light received by plants throughout their entire life cycle in this study from germination to harvest ($P < 0.0001$) (Figure 2.3). As the total incident light increased from approximately 1.5 mol to values approaching 5 mol, the final total shoot dry weight increased by approximately 2.6 times.

Light Use Efficiency

In this study, light use efficiency (LUE) was calculated as the ratio of total dry shoot biomass to total incident light. LUE demonstrated a negative correlation with PPFD levels ($P = 0.0002$) (Figure 2.4). Plants growing under high PPFD levels exhibited lower LUE values. Specifically, LUE decreased by around 0.9 times with each increase in the PPFD level tested in this study.

Photochemical Efficiency or Quantum Yield of Photosystem II

The photochemical efficiency or quantum yield of photosystem II ($\Phi PSII$) was indirectly correlated with PPFD levels ($P = 0.0005$). The higher the PPFD value, the lower the $\Phi PSII$ observed in plants (Figure 2.5). Specifically, the $\Phi PSII$ of plants growing under a PPFD of 125 $\mu mol \cdot m^{-2} \cdot s^{-1}$ was 1.1 times higher than the $\Phi PSII$ of plants growing under a PPFD of 375 $\mu mol \cdot m^{-2} \cdot s^{-1}$.

Photosynthesis and Electron Transport Rate

Net photosynthesis and electron transport rate exhibited a significant positive correlation with photosynthetic photon flux density ($P < 0.0001$) (Figure 2.6). As the PPFD levels increased, both net photosynthesis and electron transport rates also increased. Specifically, the electron transport rate increased by 2.7 times when comparing plants grown under a PPFD of 125 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ to those grown under a PPFD of 375 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Similarly, for the same intervals of light levels, net photosynthesis increased by 3.4 times.

We found a positive correlation between electron transport rate and net photosynthesis ($P < 0.0001$) (Figure 2.7). Increased electron transport rate corresponded to higher net photosynthesis values. Specifically, when the electron transport rate increased from approximately 40 to 100 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, net photosynthesis grew nearly 3.4 times.

Transpiration

Plant transpiration did not exhibit a linear correlation with varying light levels ($P= 0.031$) (Figure 2.8). The transpiration rate of plants exposed to a PPFD of 175 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ was 1.2 times higher than that of plants grown under a PPFD of 125 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. However, transpiration rates remained similar across the treatments, ranging from a PPFD of 175 to 375 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$.

Water Use Efficiency

WUE displayed a significant positive correlation with the various light levels under which plants were grown ($P< 0.0001$) (Figure 2.9). Plants cultivated under higher PPFD values exhibited greater WUE. For each incremental increase of 50 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in PPFD, WUE values increased by factors of 1.3, 1.2, 1.1, 1.3, and 1.6, respectively.

Plant Growth Rate

To compare plant growth rates, we calculated the number of days it would take for plants to achieve various coverage percentages on a reference area. The number of days was estimated from the sigmoidal curves fitted to the projected canopy size (PCS) data (Figure 2.10).

Plants cultivated under different PPFDs required varying durations to cover specific percentages of the reference area. For instance, to cover 25% of the reference area, plants grown under PPFDs of 125, 175, 225, 275, 325, and 375 $\mu mol\cdot m^{-2}\cdot s^{-1}$ took approximately 16.22, 15.3, 15.05, 14.95, 14.35, and 14.2 days, respectively. The number of days needed to reach this coverage was only significantly different ($F_{5,12} = 03.1$, $p = 0.05$) between plants grown under 125 and 375 $\mu mol\cdot m^{-2}\cdot s^{-1}$ ($P = 0.041$) (Figure 2.10A).

Similarly, for achieving 50% coverage, plants under 125, 175, 225, 275, 325, and 375 $\mu mol\cdot m^{-2}\cdot s^{-1}$ required an average of 18.83, 17.52, 17.3, 17.1, 16.55, and 16.39 days, respectively. The number of days needed to cover 50% of the reference area was significantly ($F_{5,12} = 3.94$, $P = 0.023$) different only between plants under 125 and 325 $\mu mol\cdot m^{-2}\cdot s^{-1}$ ($P = 0.03$) and 375 $\mu mol\cdot m^{-2}\cdot s^{-1}$ ($P = 0.019$) (Figure 2.10B).

Moreover, to achieve 75% coverage, plants under 125, 175, 225, 275, 325, and 375 $\mu mol\cdot m^{-2}\cdot s^{-1}$ took approximately 20.65, 19.1, 18.97, 18.7, 18.2, and 18.09 days, respectively. Again, the number of days required to reach this coverage was significantly different ($F_{5,12} = 3.78$, $P = 0.027$) only between plants under 125 and 325 $\mu mol\cdot m^{-2}\cdot s^{-1}$ ($P = 0.031$) and 375 $\mu mol\cdot m^{-2}\cdot s^{-1}$ ($P = 0.023$) (Figure 2.10C).

Finally, to cover 100% of the reference area, plants under 125, 175, 225, 275, 325, and 375 $\mu mol\cdot m^{-2}\cdot s^{-1}$ needed approximately 22.24, 20.54, 20.59, 20.27, 19.83, and 19.89 days, respectively. No significant differences were observed between treatments when covering the entire reference area (100% coverage) (Figure 2.10D).

Tipburn

We took top-view pictures of trays of plants growing under different light levels before they were harvested. We observed that some plants growing under 325 and 375 µmol·m^{-2}·s^{-1} presented tipburn on their leaves.

Discussion

Dry Weight, Total Incident Light, and Plant Growth Rate

The dry weight or biomass accumulation increased as the PPFD levels in our treatments increased (Figure 2.1). This relationship has been reported before in green cultivars of *Portulaca oleracea* (Kudirka et al., 2023), lettuce 'Green Salad Bowl' and mizuna (*Brassica rapa* var. japonica) (Jayalath and van Iersel, 2021), in lettuce 'Rebelina' and basil (*Ocimum basilicum* cv. 'Superbo') (Pennisi et al., 2020), and in lettuce 'Rex' and 'Rouxai' (Kelly et al., 2020). Photosynthesis rises with increasing PPFDs until reaching a saturation point, beyond which further increases in PPFDs do not increase leaf photosynthesis (Tarr et al., 2023). Then, the amount of light that reaches the plants is closely associated with plant growth (Klassen et al., 2003). This aligns with the findings of our study, where plants grown under 375 µmol·m^{-2}·s^{-1} exhibited greater biomass accumulation and consequently higher levels of photosynthesis compared to those under 125 µmol·m^{-2}·s^{-1}. Additionally, plants grown under 375 µmol·m^{-2}·s^{-1} intercepted more light throughout the crop cycle (Figure 2.2), indicating greater potential for plant growth. In fact, we observed a strong correlation between the final biomass produced by plants and the amount of light they intercepted throughout the entire crop cycle (Figure 2.3). This relationship has been reported before for sweet basil (Solbach et al., 2021). They argue that a greater amount of available light for plants was linked to increased light interception and, consequently, higher biomass production. Furthermore, Anthurium (*Anthurium andreanum*) ‘Pink Champion’ and ‘Royal Champion’ and lettuce (Jin et al., 2023) exhibited greater biomass accumulation when the intercepted light was higher (Li et al., 2016).

Plant growth is not only reflected in final biomass accumulation. In this study, we assessed plant growth rate by utilizing the PCS of plants and measuring the time taken for it to cover various percentages of a reference area. Since plants with larger a PCS intercept more light (Weaver and van Iersel, 2020), more photosynthesis can take place and produce more biomass (Klassen et al., 2003), which, at the same time, is translated into more leaf surface. This correspondence is shown in our study since plants growing under 375 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ took less amount of time to cover a reference area at different levels (25% to 75% coverage) in comparison to plants growing under 125 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Plants under 375 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ received higher light intensities, increasing biomass production. Consequently, these plants intercepted larger amounts of light and, as a result, exhibited faster growth. However, when we calculated the number of days that plants needed to cover 100% of the reference area, significant differences were absent due to canopy overlap. However, the trend of plants requiring less time to achieve the same area under higher PPFDs was consistent.

Light Use Efficiency

Light Use Efficiency (LUE) is a physiological measure of the efficiency with which plants convert incident light into biomass (Jayalath and van Iersel, 2021; Medlyn 1998). In our study, plants grown under a high PPFD (375 μmol·m^{-2}·s^{-1}) exhibited less efficient conversion of light into biomass compared to those grown under 125 μmol·m^{-2}·s^{-1}. It is not simple to compare LUE values in lettuce with other studies done on lettuce before (Pennisi et al., 2020; Zou et al., 2019). They calculated their LUE depending on their cultivation area, and LUE results were affected by the plant density in their studies. In our study, we calculated LUE with light values reaching the canopy of our plants. However, similar results were reported on lettuce 'Green Salad Bowl' that had a reduction of LUE for plants growing at a PPFD higher than 350 μmol·m^{-2}·s^{-1} and mizuna that showed a decrease in LUE for plants growing at a PPFD higher than 200 μmol·m^{-2}·s^{-1}. Their reduction in LUE with increasing PPFDs was explained as a consequence of a decrease in ΦPSII with a rise in PPFD levels. Similar results were obtained in *Lemna gibba* (Stewart et al., 2020). On the contrary, a different response has been seen in the relationship between LUE and PPFDs or light levels on lettuce 'Rebelina' and basil 'Superbo' (Pennisi et al., 2020). They found an increase in LUE between plants growing under around 5 mol·m^{-2}·d^{-1} (from 100 μmol·m^{-2}·s^{-1}) and 15 mol·m^{-2}·d^{-1} (250 μmol·m^{-2}·s^{-1}). The only reduction of LUE for both species was found for plants growing under 17 mol·m^{-2}·d^{-1} (250 μmol·m^{-2}·s^{-1}) compared to the ones growing under 15 mol·m^{-2}·d^{-1}.

LUE is reduced when the incident energy from light cannot be transferred into the photochemical process. For plants growing under high light levels, more PSIIs are closed, impeding them from accepting more excitation energy (Elkins and van Iersel, 2020). When fewer reaction centers are open in photosystem II (PSII), the incident energy has to be dissipated (Ruban 2017) and is not used for photosynthesis-reducing LUE. Additionally, the accumulation of excess excitation energy at high light conditions could lead to photoinhibition due to damage to reaction centers, which would reduce photosynthetic efficiency (Ruban 2009).

Efficiency of Photosystem II

In this study, ΦPSII decreased when the PPFD levels increased. A decrease in ΦPSII is associated with a higher dissipation of energy from absorbed light in the form of heat (non-photochemical quenching) as a consequence of PSII reaction center closure or due to photoinhibition (van Iersel 2016). In the presence of high light, the PSII reaction centers close because the main electron acceptor cannot transfer the absorbed electrons to be transported through the electron transport chain (van Iersel 2016). The electron acceptor Q_A in PSII cannot accept more electrons if it has not transferred its current electron to Q_B. Energy must be dissipated, which lowers ΦPSII (Maxwell and Johnson, 2000).

This reduction in ΦPSII with increasing PPFD has been observed in lettuce 'Green Salad Bowl' and mizuna growing under different lighting treatments from 50 to 425 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Jayalath and van Iersel, 2021). Additionally, ΦPSII was measured at different light levels (from 0 to 1600 $\mu mol \cdot m^{-2} \cdot s^{-1}$) for *Phragmites australis* and *Spartina alterniflora* plant growth under different waterlogging and salinity levels showing similar results (Li et al., 2000).

Electron Transport Rate and Photosynthesis

The electron transport rate (ETR) directly assesses the light-dependent reactions in photosynthesis, responding to variations in different light levels. ETR plays a pivotal role in driving photosynthesis and, consequently, influences crop growth (Watson et al., 2018). This relationship between ETR and photosynthesis was seen in our study. We observed that higher ETR values were positively correlated to higher photosynthesis responses (Figure 2.7). Additionally, both ETR and photosynthesis in our study increased when the PPFD values of our treatments increased (Figure 2.6). The increased ETR and the previously mentioned reduction in ΦPSII in response to higher PPFDs indicate a trade-off between photochemistry efficiency and electron transport. With higher PPFDs, more PSII reaction centers are closed, enhancing the protective mechanism against high light levels (Elkins and van Iersel, 2020). Higher ETRs as the response to higher light levels have been reported in lettuce ‘Green Towers’ (Elkins and van Iersel, 2020), moss (*Hennediella heimii*) (Pannewitz et al., 2003), and *Launaea sarmentosa* until 1000 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Guidi et al., 2006).

As mentioned, net photosynthesis also increased when plants grew with higher PPFD levels. The available PPFD primarily influences photosynthesis. Leaf photosynthetic rate rises linearly with increasing PPFDs, followed by a quadratic trend until the light saturation point is reached. Beyond this point, further increases in the PPFD do not lead to additional photosynthesis (Kelly et al., 2020). The photosynthetic response to our treatments did not display the quadratic trend described; rather, it remained linear. This suggests that the lighting treatments in our study were not sufficient to reach or approach a light saturation point. Even so, similar results have been reported previously in Romaine lettuce (Zhou et al., 2020; Zhou and Wang, 2022) and Cos lettuce (Jishi et al., 2018), sweet pepper (*Capsicum annuum* L.) (Li et al., 2020), ‘Cos’ lettuce and *Zizania latifolia* (Yan et al., 2013) and dwarf tomato (*Solanum lycopersicum* L.) ‘Micro-Tom’ (Yan et al., 2013).

Transpiration and Water Use Efficiency

In our study, plants grew under different light levels depending on the treatment. We observed that transpiration rates were higher for plants growing under 225 $\mu mol \cdot m^{-2} \cdot s^{-1}$ compared to those under 125 $\mu mol \cdot m^{-2} \cdot s^{-1}$. For the remaining treatments, transpiration did not show significant increases. Nonetheless, an overall increasing trend was noted (Figure 9). In comparison, Gavhane et al. [42] reported in increase an increase in transpiration when plants were subjected to PPFDs from around 400 to 1200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ in plants of lettuce 'Glendana' growing in greenhouse conditions with extra supplemental light and no CO_2 enrichment. Similarly, (Albornoz et al., 2014) observed an increase in transpiration with increasing PPFDs (from 400 to 2000 $\mu mol \cdot m^{-2} \cdot s^{-1}$) regardless of the nutrient solution treatments. However, their plants were grown under the same lighting conditions (greenhouse conditions) with no CO_2 enrichment, and the physiological measurements were made under different lighting levels provided by the portable photosynthesis system they used.

Transpiration is linked to blue light and its receptors, phototropins 1 and 2. Upon receiving blue light, these receptors trigger a movement of H^+ out and K^+ into guard cells, resulting in stomatal opening. More stomata opening will produce more transpiration, and at the same time, this would facilitate CO_2 fixation, increasing photosynthetic rates (Lanoue et al., 2019). Also, at high light levels or intense radiative heat, transpiration helps to cool off the leaf (Matsuda 2016). Furthermore, plants grown and developed under low light intensities have exhibited lower stomatal conductance compared to those grown under high light intensities (Hanba et al., 2020). This increase in stomatal conductance may be associated with differing transpiration rates. Finally, stomatal conductance is decreased at elevated CO_2 concentrations (Matsuda 2016), which also would have a role in the slow rise in transpiration with increasing PPFD in our study.

WUE represents the relationship between carbon biomass production and transpiration. At a leaf level, this could be calculated as the ratio of the assimilation rate and transpiration rate (Farquhar et al., 1989). This is how WUE is calculated using the equipment used in this study. We observed a linear increase in WUE with rising PPFDs (Figure 2.10). This relationship was consistent with the linear increase in assimilation or photosynthesis observed in our study, and transpiration showed a comparatively lower rate of increase. This means that photosynthesis increased at a higher rate than transpiration; in other words, plants growing under higher PPFDs had higher photosynthesis while losing less water through transpiration compared to plants growing under lower PPFDs.

Similarly, increasing WUEs with high PPFDs was found to increase lettuce 'Rebelina' and basil 'Superbo' for plans growing under different PPFDs (from 100 to 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$), producing DLIs from 5.8 to 17.3 $mol \cdot m^{-2} \cdot d^{-1}$ [14]. Also, this relationship was found in other species such as grain sorghum (*Sorghum bicolor* (L.) Moench) (Bruns, 2016) and black pine (*Pinus nigra* Arn.) for plants tested until approximately 500 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Fkiri et al., 2023) and lettuce 'partavousi' (Ghorbanzadeh et al., 2021).

Tipburn

Tipburn is manifested as necrosis at the edges of young, fast-developing leaves and is produced by a low calcium content on young and developing tissues with low transpiration rates (Lee et al., 2013). In plants, calcium moves mostly through the xylem following a transpiration flow (Clarckson 1984), which explains the incidence of this physiological disorder in said tissues with low transpiration. Tipburn presence has been reported in lettuce when growing under high light intensities. Sago 2016, reported a direct relationship between the number of leaves exhibiting tipburn and the light levels under which the plants were growing (150, 200, 250, and 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$). We found similar results in our study. Before harvesting plants, we took top-view pictures of plants growing under different light levels to document the appearance of tipburn. We observed tipburn for plants growing under 325 and 375 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Our plants grew faster when light levels were higher (Figure 2.10), which explains why plants growing under 325 and 375 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ showed more tipburn incidence.

Conclusions

There is a tradeoff between fast growth (high PPFD) and high LUE (low PPFD) since higher PPFDs result in low LUEs and high WUEs. Additionally, we observed that plants growing under high PPFD levels grow faster, which may have some economic implications. First of all, to achieve high PPFD levels, a higher energy input is required. On the other hand, if plants grow faster, they will occupy the growing space for a shorter period, thus allowing us to increase the number of crop cycles we can produce in a certain time. Additionally, at higher PPFD levels, the WUE is higher, and transpiration increases but at low rates. This suggests that the humidity to be removed from the growing space for plants exposed to high PPFD levels may not differ significantly from those under low PPFD levels. Therefore, growing plants under high PPFD levels prompts consideration of a potential tradeoff between the energy consumption for lighting and dehumidification.

This depends on whether the savings from reduced dehumidification outweigh the energy needed to sustain high PPFD levels. Additionally, it would be useful to test the same physiological parameters at the whole plant level to determine if these results can be generalized to the entire plant. If so, calculations should be made for the energy requirements to dehumidify a specific space and compare it to the energy needed to achieve specific PPFD levels. Furthermore, the issue of tipburn incidence at high PPFD levels must be fixed. Research could be conducted on developing cultivars that are less susceptible to tipburn, as well as on growing conditions that might help reduce its incidence specifically for controlled environments. Finally, lighting decisions cannot be made solely based on biomass production, LUE, or WUE (different physiological and economic factors should be considered jointly).

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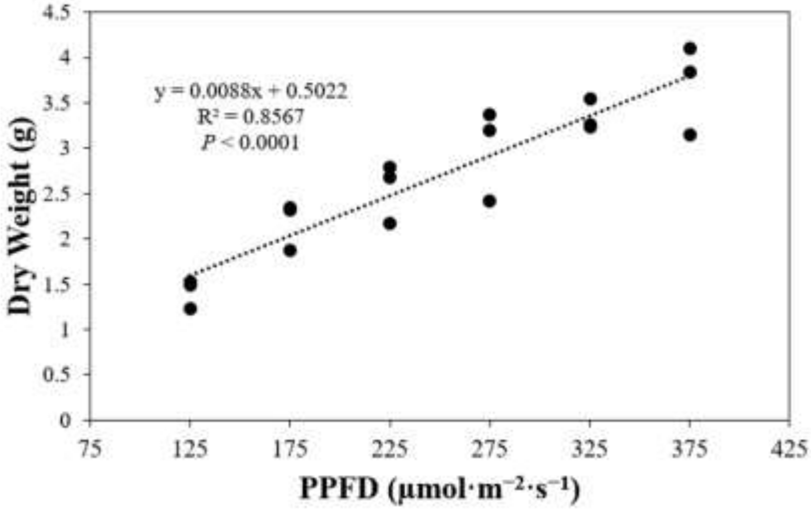


Figure 2.1. Final total shoot dry weight per plant of ‘Rex’ lettuce (*Lactuca sativa*) grown under different photosynthetic photon flux densities (PPFDs).

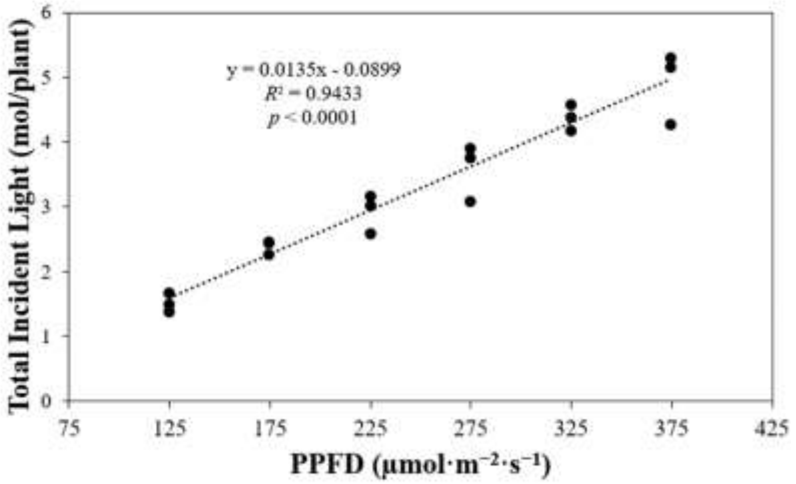


Figure 2.2. Calculated total incident light received by plants of ‘Rex’ lettuce (*Lactuca sativa*) growing under different photosynthetic photon flux densities (PPFDs) from germination to harvest.

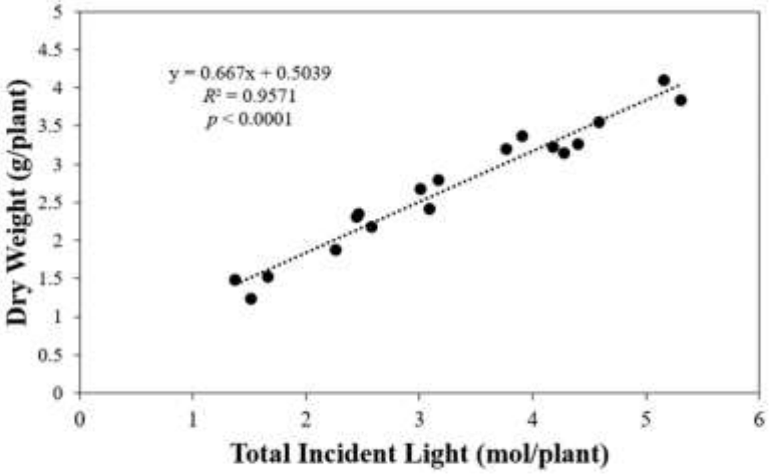


Figure 2.3. Final shoot dry weight of 'Rex' lettuce (*Lactuca sativa*) per plant in response to increasing total incident light received by a plant from germination to harvest.

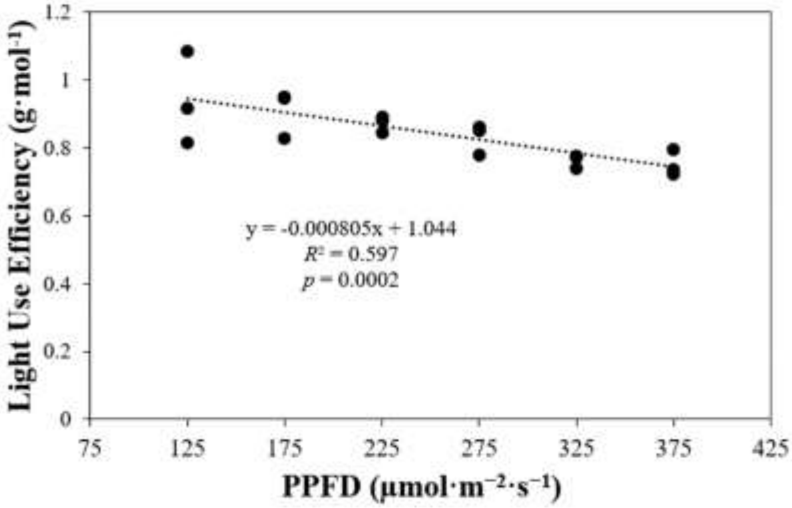


Figure 2.4. Plant light use efficiency of 'Rex' lettuce (*Lactuca sativa*) in response to increasing different photosynthetic photon flux densities (PPFDs).

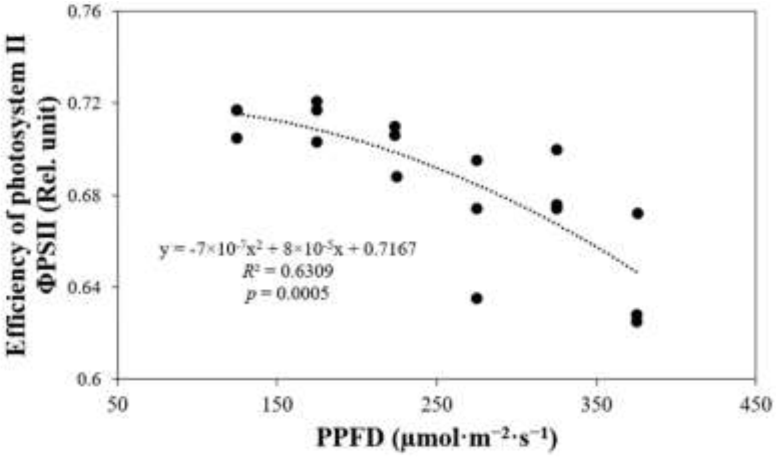


Figure 2.5. Photochemical efficiency or quantum yield of photosystem II (ΦPSII) of ‘Rex’ lettuce (*Lactuca sativa*) in response to increasing photosynthetic photon flux densities (PPFDs).

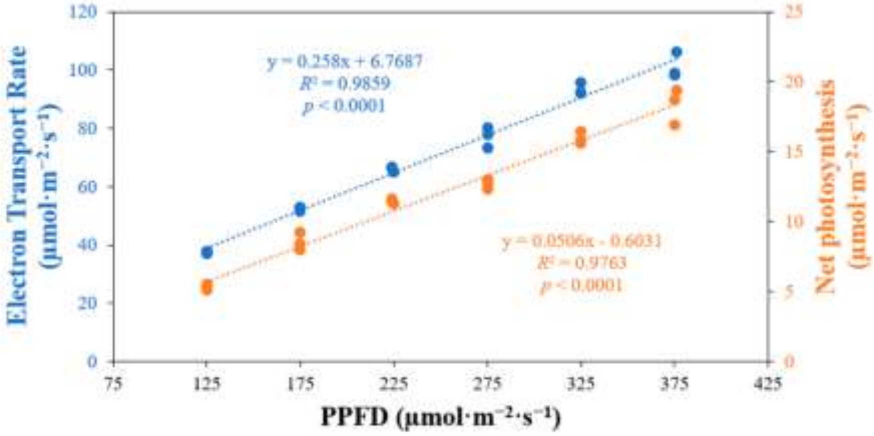


Figure 2.6. Net photosynthesis and electron transport rate of ‘Rex’ lettuce (*Lactuca sativa*) in response to increasing photosynthetic photon flux densities (PPFDs).

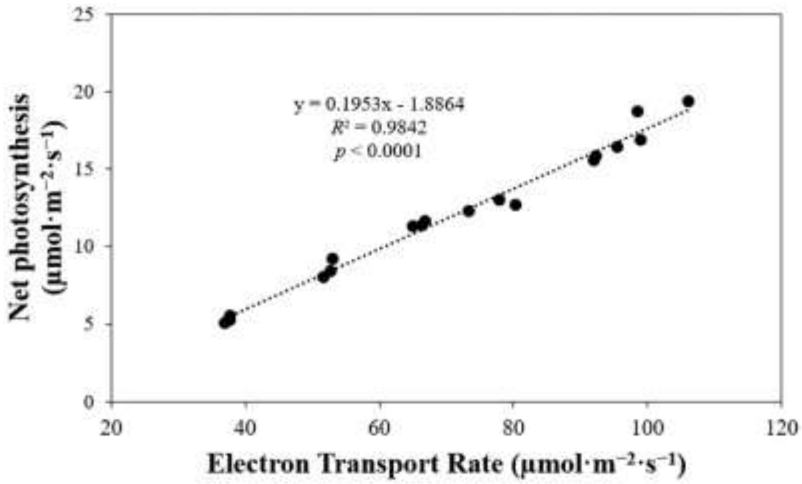


Figure 2.7. Net photosynthesis of ‘Rex’ lettuce (*Lactuca sativa*) in response to increasing electron transport rate.

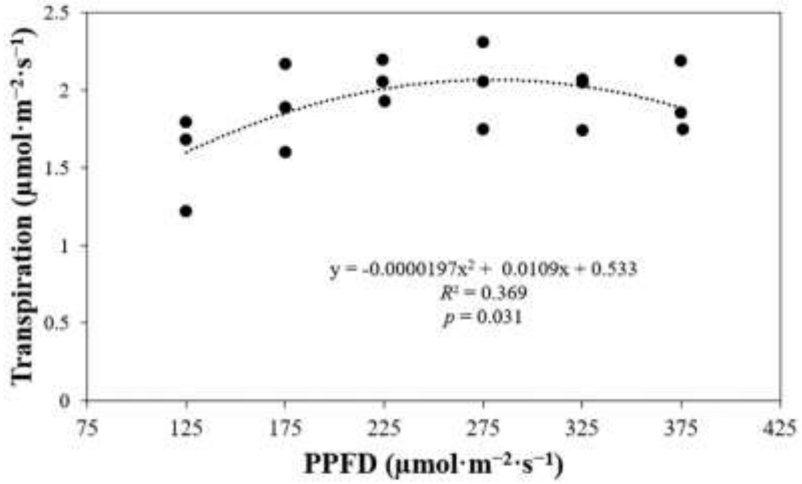


Figure 2.8. Plant transpiration of ‘Rex’ lettuce (*Lactuca sativa*) in response to increasing photosynthetic photon flux densities (PPFDs).

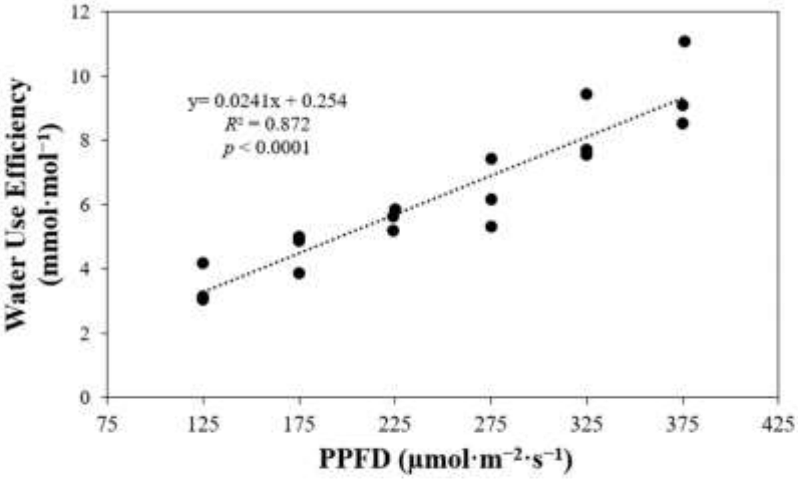


Figure 2.9. Plant water use efficiency of 'Rex' lettuce (*Lactuca sativa*) in response to increasing photosynthetic photon flux densities (PPFDs).

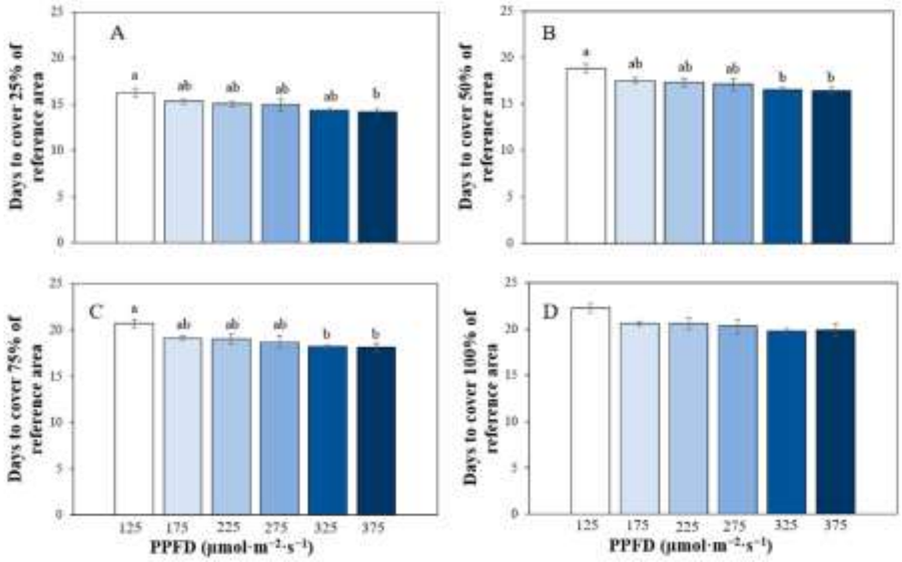
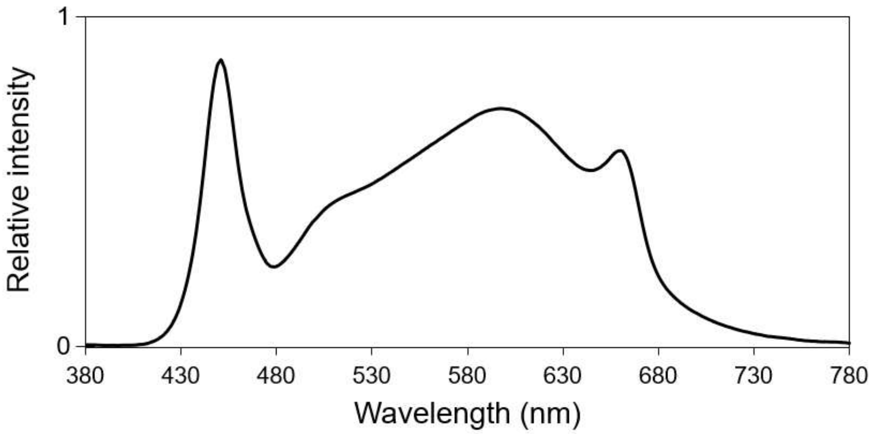
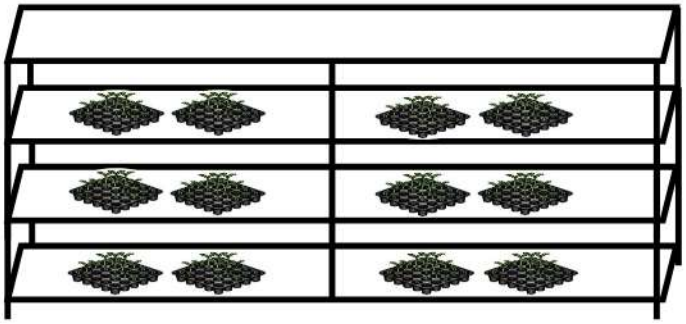


Figure 2.10. Number of days plants of 'Rex' lettuce (*Lactuca sativa*) growing under different photosynthetic photon flux densities (PPFDs) needed to cover 25% (A), 50% (B), 75% (C) and 100% (D) of a reference area (0.15 m2). Bars represent means ± standard error (n = 3), and different letters denote significant differences in means at α = 0.05.



Supplementary figure 2.1: The electromagnetic spectrum emitted by light-emitting diodes (LED) fixtures (SPYDRx Plus with PhysioSpec indoor spectrum; Fluence Bioengineering, Austin, TX, USA).



Supplementary figure 2.2: Diagram of a metal rack with three shelves divided vertically to conform six growing spaces in the walk-in growth chamber. Each growing space had a different light level to end up with six different treatments in the rack (one per growing space). Three of these racks were placed inside the walk-in growth chamber, completing 18 growing spaces in total.

Table 2.1. Six photosynthetic photon flux density (PPFD) levels and their corresponding daily light integral (DLI). Values are PPFD and DLI values averaging three growing spaces ± SD.

PPFD ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	**DLI ($mol \cdot m^{-2} \cdot d^{-1}$)**
123.3 ± 2.516	8.88 ± 0.1808
174.3 ± 1.527	12.55 ± 0.106
223.3 ± 2.081	16.41 ± 0.431
273.6 ± 1.527	19.70 ± 0.1123
324 ± 2	23.32 ± 0.1450
372 ± 2.645	26.78 ± 0.1908

CHAPTER 3

PHOTOSYNTHESIS, TRANSPIRATION AND WATER USE EFFICIENCY OF LETTUCE (*LACTUCA SATIVA*) UNDER VARYING LIGHT INTENSITIES (LEAF V.S. WHOLE PLANT)[3]

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[3] Mayorga-Gomez, A.M., van Iersel, M.W. and R.S. Ferrarezi. To be submitted to *Hort science*.

Abstract

This study examined how different light levels affect whole-plant photosynthesis, transpiration, and water use efficiency (WUE) in lettuce. Many studies use leaf-level measurements to estimate plant responses, but these often only represent a small area and may not capture what happens at the whole-plant level. We grew lettuce under two baseline light intensities and then exposed the plants to a range of increasing photosynthetic photon flux densities (PPFD), from 100 to 800 μmol·m^{-2}·s^{-1}. Using a whole-plant gas exchange system combined with load cells, we measured CO_2 uptake and water loss to estimate photosynthesis, transpiration, and WUE across the entire plant. Photosynthesis increased consistently with light intensity, with no clear saturation point even at the highest PPFD. Transpiration also increased but at a slower rate, leading to higher WUE values at higher light levels. These values began to stabilize near 800 μmol·m^{-2}·s^{-1}. Our results suggest that whole-plant responses can differ from what is observed at the leaf level and that measuring only a small leaf section may not always reflect full plant behavior. Understanding these differences can help optimize light use in indoor agriculture, improving both energy efficiency and crop performance.

Introduction

In the previous chapter (Chapter 2, VARYING LIGHT INTENSITIES AFFECT LETTUCE GROWTH AND PHYSIOLOGY IN CONTROLLED INDOOR ENVIRONMENTS), we found that higher Photosynthetic Photon Flux Density (PPFD) levels lead to greater Water Use Efficiency (WUE) and only a small increase in transpiration. This means that the amount of humidity that needs to be removed from the growing area may not be very different between plants grown under high and low PPFD. Based on this, we suggested that growing plants with high PPFD could involve a tradeoff between the energy used for lighting and for dehumidification which could produce some energy and economic savings.

In that study, WUE, photosynthesis, and transpiration were measured using a Portable Photosynthesis System, which collects data from a small area of a single leaf. Usually, a measurement taken from one spot on one leaf is used to represent the whole plant, since it is very difficult to take these kinds of measurements at the full plant level.

Because we were interested in different plant physiological parameters, especially transpiration due to its possible economic impact, we didn’t want to assume that our data, especially for transpiration, could be represented by just a small part of the canopy. Fortunately, we had access to a whole-plant gas exchange system (van Iersel and Bugbee, 2000), which allowed us to measure photosynthesis at the whole-plant level. Also, by using load cells, we could measure transpiration for the entire plant. With these two measurements, we were able to estimate other parameters like WUE at the whole-plant level.

In this chapter, we aimed to measure photosynthesis, water-use efficiency, and transpiration at the whole-plant level to determine whether measurements taken at the leaf level can accurately represent the entire plant system. Additionally, we sought to estimate the energy consumption required for lighting plants at different PPFD levels and the energy needed for dehumidification to assess the potential economic impact.

Materials and methods

Plant Material

Ten-centimeter square plastic pots were filled with a soilless mix (Metro-Mix® 830; SunGro Horticulture, Agawam, MA, USA) to about 1 cm below the top edge. Three pelleted seeds of ‘Rex’ lettuce (Johnny’s Selected Seeds, Winslow, ME, USA) were sown in each pot. To prevent algae growth from affecting PCS measurements, the substrate surface was covered with calcined clay or metakaolin (Turface MVP; Turface Athletics, Buffalo Grove, IL, USA). The pots were placed in trays, arranged in a 5×3 pattern, with 15 pots per tray in the assigned growing spaces. After the seeds germinated, a thinning process ensured only one seedling per pot. Irrigation and nutrients were provided through an ebb-and-flow sub irrigation system, delivering a 15N–2.2P–12.45K nutrient solution with 100 $mg \cdot L^{-1}$ of nitrogen, supplied via a water-soluble fertilizer (15-5-15 Ca-Mg Professional LX; J.R. Peters, Allentown, PA, USA).

Growing set up and space and lighting treatments

This investigation took place in an enclosed walk-ingrowth chamber situated in Athens, Georgia. The chamber was maintained under specific environmental conditions: 24.35 ± 0.673°C, relative humidity 64.23% ± 5.89%, CO2 concentration 826.91 ± 51.43 $mg \cdot L^{-1}$, and vapor pressure deficit 1.0451 ± 0.367 kPa. Within the growth chamber, there were three separate metal racks, each functioning as an independent block. Each rack featured three horizontal shelves, and each of these shelves was vertically divided into two equal sections, resulting in a total of six cultivation spaces per rack and a combined total of 18 growing spaces. Every one of these growing spaces was outfitted with two light-emitting diode (LED) fixtures (SPYDRx Plus with PhysioSpec indoor spectrum; Fluence Bioengineering, Austin, TX, USA) (Supplemental figure 3.1.). Furthermore, four small fans, evenly spaced, were strategically installed on the sides of each growing space to ensure proper air circulation. Each rack contained four growing spaces, used to cultivate plants at two different light levels: 215 ± 2.269 and 405 ± 3.792 PPFD ($\mu mol \cdot m^{-2} \cdot s^{-1}$), with two spaces allocated to each light level per rack. After 30 days after sowing, we moved the plants to a whole plant gas exchange system described by van Iersel and Bugbee, 2000 and Liu and van Iersel, 2023. This system consists of two growing chambers, each containing four plexiglass chambers that individually measure gas exchange.

On top of each acrylic chamber from the whole plant exchange system we placed led light fixtures (P2000; Viparspectra, Richmond, CA, USA) (Supplemental figure 3.2.). Additionally, inside each plexiglass chamber we adapted a 2 kg loading cell (LSP-2; Transducer Techniques, Temecula, CA, USA), to measure water loss and plant transpiration. Load cells were controlled by a datalogger (CR6, Campbell Scientific, Logan, UT, USA). Three plants from the walk-in growth chamber, representing the two different lighting treatments, were placed in each acrylic chamber. Aluminum foil was placed beneath the plant canopy or on top of the pot covering the substrate to prevent water evaporation.

Once the plants were added to the chambers, we provided different light levels; 100, 200, 300, 400, 500, 600, 700 and 800 $\mu mol \cdot m^{-2} \cdot s^{-1}$ two hour per light level from the lowest to the highest. To make sure that plants were receiving the corresponding light level, a photodiode calibrated by using a quantum sensor (MQ-500; Apogee Instruments, Logan, UT, USA) was placed inside each plexiglass chamber at canopy high. The light levels were controlled by datalogger (CR1000, Campbell Scientific, Logan, UT, USA).

Under this setup, we were able to measure CO^2 uptake in each chamber, which was later converted into photosynthesis rates, as well as water loss from the three pots, which was subsequently transformed into transpiration values.

Energy calculations

- *Plant transpiration*

In the previous studies described in this document, we used a walk-in growth chamber where lettuce plants were grown in pots placed on trays arranged in a 3 × 5 array, resulting in a total cultivation area of 0.15 m^2 for 15 plants. This corresponds to a plant density of 150 plants per m^2, which is the same density used in the exercise for calculating energy consumption related to dehumidification and lighting.

Previously, when plants were placed in the plexiglass chambers to measure whole-plant gas exchange, three plants were used per chamber. Therefore, we could extrapolate the transpiration data collected in that setup to estimate energy consumption for a density of 150 plants m^{-2}, based on the reference area used in the previous studies presented in this document.

Whole-plant transpiration values were obtained from plants grown under different PPFD levels before being transferred to the plexiglass chambers. Once in the chambers, transpiration rates were estimated. Based on these data, we determined the average transpiration values to be used in the energy consumption calculations for three plants, and then scaled them to the equivalent transpiration of 150 plants, representing the plant density used in our walk-in growth chamber experiment stage (Table 3.1 and Table 3.2).

- *Dehumidifier Energy Consumption*

For the dehumidification calculations, the specifications of three commercial dehumidifiers, DG-X (DryGair Energies Ltd, Herzliya, Israel), A710 (Anden, Madison, WI, US), and Quest 335 (Quest, Madison, WI, US) were used. The information extracted from these units included the energy consumed per unit volume of water removed. The average of these values was then used for the subsequent calculations (Table 3.3).

Then, by using the average water extraction efficiency and the transpiration produced by 150 plants growing in a 1m² area, and considering the 20-hour photoperiod used in the walk-in growth chamber (Table 3.4 and Table 3.5), we can calculate the energy required to remove that water per hour at each PPFD level as:

$$kWh\ needed = \frac{Water\ to\ be\ removed\ (mL)}{Water\ removed\ per\ kWh}$$

- *Lighting energy*

To estimate energy use for lighting, we selected a commercial brand and model of electric light fixture reported for use in vertical farm cultivation. The model chosen was the Mars Hydro FC-E8000, which provides a lighting output of 2240 µmol·s⁻¹ with a power input of 800 W (0.8 kW). This square fixture can illuminate the farthest corners of its coverage area (4 ft² or 1.2 m²) with a PPFD of approximately 1300 µmol·m⁻²·s⁻¹ at a height of 8 in (0.2 m), and around 1,050 µmol·m⁻²·s⁻¹ at 12 in (0.3 m). For this example, we used a value of 1000 µmol·m⁻²·s⁻¹ reaching the top of the plant canopy. With a power input of 0.8 kW delivering 1,000 PPFD to the canopy level, all subsequent energy calculations for lighting are based on a coverage area of 1 m², as defined for this exercise. *Power needed* refers to the energy required to produce a specific PPFD value based on the characteristics of the selected light fixture. *Energy per day* refers to the total energy required to maintain a given PPFD during a daily photoperiod of 20 hours (Table 3.6).

$$Power\ needed = Power\ imput \frac{PPFD\ Target}{PPFD\ Maximum}$$

$$Energy\ per\ day = \frac{Power\ needed\ \times hours}{1000}$$

Finally, we summed the total dehumidification energy and the lighting energy at each PPFD level to determine the total system energy.

Results

Plant photosynthesis

The CO_2 consumed or net photosynthesis values for plants growing under 250 PPFD (Figure 1) were as follows: When they were exposed to 100 PPFD, the Pg value was on average 5.26 µmol·h⁻¹. When exposed to 200 PPFD, the Pg was 1518.66 µmol·h⁻¹, resulting in an increase of around 188%. When exposed to 300 PPFD, photosynthesis increased to 2313.18 µmol·h⁻¹, increasing around 52% from the previous light level. When plants received 400 PPFD, photosynthesis increased to 2963.7 µmol·h⁻¹, being an increase of 28%. When receiving 500 PPFD, plants showed a photosynthesis of 3505.5 µmol·h⁻¹, meaning an increase of 18%. When plants received 600 PPFD, plant photosynthesis was 3984.3 µmol·h⁻¹, being an increase of close to 13%. When plants were exposed to 700 PPFD, photosynthesis increased roughly 10% to a value of 4419.45 µmol·h⁻¹. Finally, when plants were subjected to 800 PPFD, photosynthesis reached 4861.17 µmol·h⁻¹, meaning an increment of close to 10%.

The CO_2 consumed or net photosynthesis values for plants growing under 400 PPFD (Figure 3.1) were as follows: When they were exposed to 100 PPFD, the Pg value was on average 526.65 µmol·h⁻¹. When exposed to 200 PPFD, the Pg was 1155.96 µmol·h⁻¹, resulting in an increase of around 320%. When exposed to 300 PPFD, photosynthesis increased to 1895.76 µmol·h⁻¹, increasing around 63% from the previous light level. When plants received 400 PPFD, photosynthesis increased to 2637.45 µmol·h⁻¹, being an increase of 39%. When receiving 500

PPFD, plants showed a photosynthesis of 3398.31 μmol·h^{-1}, meaning an increase of 28%. When plants received 600 PPFD, plant photosynthesis was 4025.43 μmol·h^{-1}, being an increase of close to 18%. When plants were exposed to 700 PPFD, photosynthesis increased roughly 14% to a value of 4600.44 μmol·h^{-1}. Finally, when plants were subjected to 800 PPFD, photosynthesis reached 5139.9 μmol·h^{-1}, meaning an increment of close to 11%.

Plant Transpiration

By using load cells, we were able to measure water loss by transpiration. The transpiration for plants growing under 250 PPFD (Figure 3.2) was as follows: When they were exposed to 100 PPFD, the transpiration was on average 11.05 ml·h^{-1}. When exposed to 200 PPFD, the water loss was 12.21 ml·h^{-1}, resulting in an increase of around 10%. When exposed to 300 PPFD, transpiration increased to 13.03 ml·h^{-1}, increasing around 6% from the previous light level. When plants received 400 PPFD, water loss increased to 13.26 ml·h^{-1}, being an increase close to 2%. When receiving 500 PPFD, plants showed a transpiration of 13.39 ml·h^{-1}, meaning an increase of 0.9%. When plants received 600 PPFD, plant transpiration was 13.97 ml·h^{-1}, being an increase of close to 4%. When plants were exposed to 700 PPFD, transpiration increased roughly 8% to a value of 15.97 ml·h^{-1}. Finally, when plants were subjected to 800 PPFD, water loss reached 15.86 ml·h^{-1}, meaning an increment of close to 5%.

Similarly, we measured water loss by transpiration for plants growing under 400 PPFD (Figure) as follows: When they were exposed to 100 PPFD, the transpiration was on average 9.39 ml·h^{-1}. When exposed to 200 PPFD, the water loss was 10.2 ml·h^{-1}, resulting in an increase of around 8%. When exposed to 300 PPFD, transpiration increased to 11.76 ml·h^{-1}, increasing around 15% from the previous light level. When plants received 400 PPFD, water loss increased to 12.24 ml·h⁻¹, being an increase close to 4%. When receiving 500 PPFD, plants showed a transpiration of 14.07 ml·h⁻¹, meaning an increase of 5%. When plants received 600 PPFD, plant transpiration was 14.88 ml·h⁻¹, being an increase of close to 5%. When plants were exposed to 700 PPFD, transpiration increased roughly 8% to a value of 16.14 ml·h⁻¹. Finally, when plants were subjected to 800 PPFD, water loss reached 17.19 ml·h⁻¹, meaning an increment of close to 6%.

Plant Water Use Efficiency

Based on photosynthesis and transpiration data, we estimated WUE. The WUE for plants growing under 250 PPFD (Figure 3.3) was as follows: When they were exposed to 100 PPFD, WUE was on average 48.01 µmol·ml⁻¹. When exposed to 200 PPFD, WUE was 125.33 µmol·ml⁻¹, resulting in an increase of around 160%. When exposed to 300 PPFD, WUE increased to 179.33 µmol·ml⁻¹, increasing around 42% from the previous light level. When plants received 400 PPFD, WUE increased to 224.28 µmol·ml⁻¹, being an increase close to 25%. When receiving 500 PPFD, plants showed a WUE of 262.44 µmol·ml⁻¹, meaning an increase of 17%. When plants received 600 PPFD, the value was 285.95 µmol·ml⁻¹, being an increase of close to 9%. When plants were exposed to 700 PPFD, WUE increased roughly 2% to a value of 294.97 µmol·ml⁻¹. Finally, when plants were subjected to 800 PPFD, WUE reached 307.49 µmol·ml⁻¹, meaning an increment of close to 4%.

In the case of plants growing under 400 PPFD, we obtained the following values: When they were exposed to 100 PPFD, WUE was on average 29.05 µmol·ml⁻¹. When exposed to 200 PPFD, WUE was 113.61 µmol·ml⁻¹, resulting in an increase of around 290%. When exposed to 300 PPFD, WUE increased to 161.97 µmol·ml⁻¹, increasing around 42% from the previous light level. When plants received 400 PPFD, WUE increased to 215.66 μmol·ml^{-1}, being an increase close to 33%. When receiving 500 PPFD, plants showed a WUE of 242.24 μmol·ml^{-1}, meaning an increase of 12%. When plants received 600 PPFD, the value was 270.93 μmol·ml^{-1}, being an increase of close to 11%. When plants were exposed to 700 PPFD, WUE increased roughly 5% to a value of 285.41 μmol·ml^{-1}. Finally, when plants were subjected to 800 PPFD, WUE reached 299.44 μmol·ml^{-1}, meaning an increment of close to 4%.

Energy calculations

Based on the estimated energy requirements for dehumidification and lighting at different PPFD levels, for plants grown under two reference PPFD conditions (250 and 400 μmol·m^{-2}·s^{-1}), we calculated the total energy needed for both components. For the first group of plants, the average total energy required to produce PPFD levels from 100 to 800 μmol·m^{-2}·s^{-1}, including the corresponding dehumidification based on transpiration values, was 5.044, 7.006, 8.860, 10.533, 12.172, 13.954, 15.898, and 17.742 kWh over a 20-hour period, respectively (Figure 3.4A). For the second group, the respective values were 4.568, 6.373, 8.427, 10.216, 12.376, 14.247, 16.239, and 18.125 kWh over 20 hours (Figure 3.4B).

Discussion

Plant photosynthesis

It is not surprising that at higher light levels, plants exhibit higher photosynthesis rates, as long as the light saturation point is not reached (Kelly et al., 2020). In the previous chapter, Mayorga et al. (2014) reported an increase in photosynthesis when plants were exposed to light levels ranging from 125 to 375 μmol·m^{-2}·s^{-1}. This upward trend was also observed in lettuce plants subjected to different temperatures. Regardless of the temperature treatment, the plants increased their photosynthetic rate until they were exposed to around 500 µmol·m^{-2}·s^{-1}. After that point, the rate of photosynthesis stabilized in a plateau phase (Zhou et al., 2022).

In ‘Cos’ lettuce, photosynthetic rates also increased under different light levels, reaching a steady state near 600 µmol·m^{-2}·s^{-1} (Jishi et al., 2018). Similar results were found in lettuce plants grown under two vapor pressure deficit (VPD) conditions. When VPD was low, photosynthesis increased until the plants received a PPFD of about 800 µmol·m^{-2}·s^{-1}. Under high VPD conditions, photosynthesis increased only up to 400 µmol·m^{-2}·s^{-1} before reaching a plateau (Amitrano et al., 2021).

In all these cases where photosynthesis increased with PPFD, physiological measurements were taken using portable photosynthesis systems. This means that only a small section of a leaf was measured and used as a reference for the whole plant. In our study, for plants growing at 250 µmol·m^{-2}·s^{-1}and even more clearly for those growing at 400 µmol·m^{-2}·s^{-1} the plateau phase of photosynthesis was not clearly observed, even at 800 µmol·m^{-2}·s^{-1}. This may indicate that the light response curves at the leaf level are slightly different from those at the whole-plant level. The saturation point at the whole-plant level could be higher than what is typically accepted based on leaf-level measurements.

Plant transpiration

Plant transpiration was one of the main focuses of the previous chapter (Mayorga et al., 2024), where we hypothesized that, similar to what happens at the leaf level, plant-level transpiration may not increase significantly under higher light levels. This means that the amount of humidity that needs to be removed from the growing space may not differ much between plants grown under high and low PPFD. Based on this idea, we suggested that growing plants under high PPFD could involve a trade-off between the energy used for lighting and the energy needed for dehumidification. This could potentially lead to economic savings due to a reduced need for dehumidification, while still maintaining high photosynthesis rates and promoting faster plant growth.

We found previously that at the leaf level, transpiration increased until a certain point and then seemed to stop increasing after 325 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Pennisi et al. (2020) also studied different physiological responses to various PPFD levels. They did not report specific values for transpiration, but they did report stomatal conductance values, which can be positively correlated with transpiration (Putra et al., 2012). They showed that stomatal conductance increased when plants were growing under 100 to 250 $\mu mol \cdot m^{-2} \cdot s^{-1}$, but it seemed to start to stabilize at around 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Stomatal conductance increases with light levels; therefore, transpiration increases as well. This improves CO_2 intake for photosynthesis and also helps with leaf cooling when plants are subjected to high radiation energy, such as increasing PPFD (Matsuda, 2016). The light-dependent stomatal opening happens due to two mechanisms: one related to blue light, which is mediated by the blue light receptor phototropin, and another response dependent on photosynthesis (Shimazaki et al., 2007).

A natural question that may come up when comparing transpiration at the leaf level (when measured with portable photosynthesis systems) versus the whole plant level is: why do they behave differently? At the leaf level, when light levels increase, transpiration can increase more slowly or even decrease, but at the whole plant level, transpiration seems to keep rising at a steady rate. As a reminder, leaf-level measurements are not taken from the entire leaf but from just a small section. One possible explanation was described in a study where they found that the accumulation of sugars, produced during high photosynthesis, can activate a specific response in guard cells. This response, which involves the enzyme hexokinase (HXK) and the hormone ABA, causes the stomata to partially close. It has been suggested that this acts as a feedback system to limit water loss when photosynthesis is already high, helping to balance gas exchange and water use in the plant (Kelly et al., 2013).

Such a mechanism might be being triggered in the part of the leaf where the measurements is being taken. On the other hand, when we took measurements at the whole-plant level, the plants were placed inside a plexiglass chamber, and the physiological measurements depended on multiple whole leaves. Perhaps, the mechanism mentioned before is not being triggered in the same way at the whole-plant level. If that is the case, transpiration might continue following an increasing trend, as would be expected when light levels go up.

More than just comparing the transpiration behavior under increasing light at the plant and leaf levels, we were mainly interested in determining whether the transpiration trend we reported in our previous chapter was still present at the whole-plant level. Regardless of the reason, the pattern was not the same. As a reminder, at the leaf level, transpiration seemed to remain stable even as light and photosynthesis increased. Although we did not find the same result here, we observed that photosynthesis increased at a higher rate than transpiration. This could still suggest a potential trade-off between the energy used for supplemental lighting and the energy required for dehumidification, as we hypothesized in the previous chapter.

Plant Water Use Efficiency

Water use efficiency (WUE) can be described as the ratio of photosynthesis to transpiration, or alternatively, as the ratio of photosynthesis to stomatal conductance (Tardieu, 2013). This is how we calculated WUE, since we obtained photosynthesis values using the whole-plant gas exchange system, and estimated transpiration by measuring the weight loss of the pots containing the plants. As expected, WUE increased with PPFD and then started to stabilize when light levels reached around 800 $\mu mol \cdot m^{-2} \cdot s^{-1}$. This behavior may be explained because photosynthesis began to reach a plateau at high light levels, while transpiration continued increasing. As a result, the WUE response seemed start getting a flat trend at the highest PPFD.

Same response was found in lettuce but a leaf level (Pennisi et al., 2020). Here, the PPFD that were use for their study were between 100 and 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and WUE seemed to reach a plateau phase between 250 and 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$, which was lower PPFD values in comparison to the ones when WUE reached the same phase at a whole plant level.

Energy calculations

When analyzing the transpiration rate and pattern of plants grown under different PPFD levels in the whole-plant gas exchange system, we initially considered that since transpiration increased at a lower rate compared to whole-plant photosynthesis, this could be reflected in the total energy consumption for lighting and dehumidification when combined. We thought this might suggest potential energy savings when growing plants under higher PPFD levels. However, as shown in Figure 4, energy consumption increased linearly, indicating that higher light intensity led to higher total energy use for both lighting and dehumidification.

This suggests that a lower rate of plant transpiration alone does not necessarily result in energy savings for these two components. It is important to note that these values represent only one day of operation. Future studies should determine how many days plants require to reach harvest under each PPFD level tested (100–800 µmol·m^{-2}·s^{-1}), as well as the corresponding daily energy consumption for dehumidification throughout the growth period. Only then would it be possible to evaluate whether growing plants at higher PPFD levels throughout their entire cycle could lead to net energy savings. This would depend on the assumption that plants under higher PPFD grow faster, thus requiring fewer days to reach harvest, which could create a trade-off between the increased daily energy use for lighting and dehumidification and the potentially shorter cultivation period.

Conclusions

This study confirmed that measuring plant responses at the whole-plant level provides more detailed and accurate information, especially for parameters like transpiration. While previous work suggested that transpiration may not increase much under higher PPFD based on leaf-level data, our results showed a steady increase in transpiration at the whole-plant level. Photosynthesis also increased with light, and the plateau phase commonly observed at the leaf level was not clearly seen here, even at 800 µmol·m^{-2}·s^{-1}. As a result, WUE improved with increasing PPFD and began to stabilize only at the highest light levels. These differences between leaf-level and whole-plant measurements highlight the limitations of relying on small leaf sections to represent the entire plant. Although we did not observe the same flat transpiration trend reported previously, the fact that photosynthesis increased faster than transpiration still supports the idea of a possible trade-off between lighting and dehumidification energy. This could lead to more efficient growing strategies in controlled environments.

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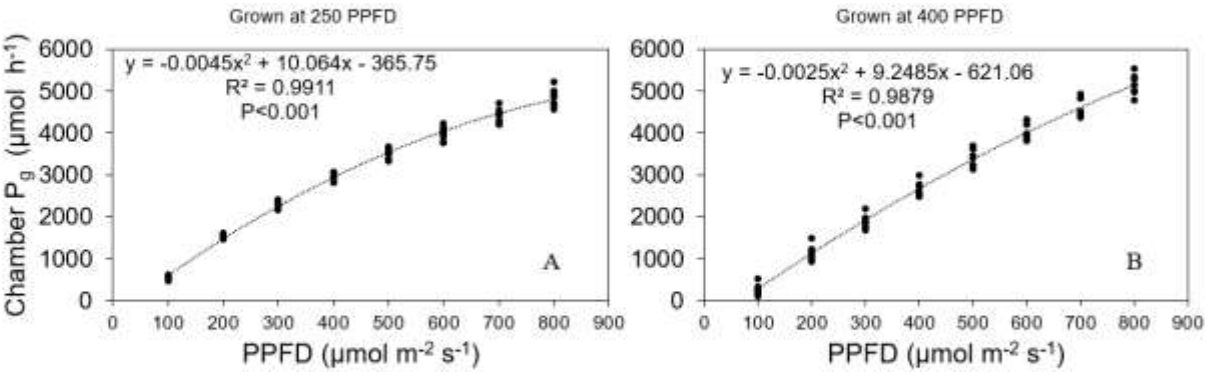


Figure 3.1. Plant net photosynthesis (µmol h^{-1}) per chamber for plants receiving different PPFD. A. Plants that grew under 250 µmol·m^{-2}·s^{-1}. B. Plants that grew under 400 µmol·m^{-2}·s^{-1}.

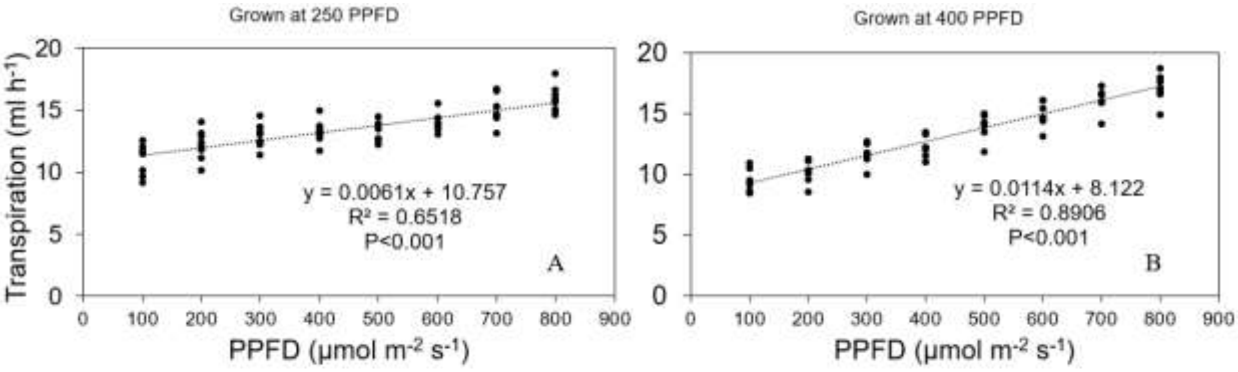


Figure 3.2. Plant transpiration (ml h^{-1}) per chamber for plants receiving different PPFD. A. Plants that grew under 250 µmol·m^{-2}·s^{-1}. B. Plants that grew under 400 µmol·m^{-2}·s^{-1}.

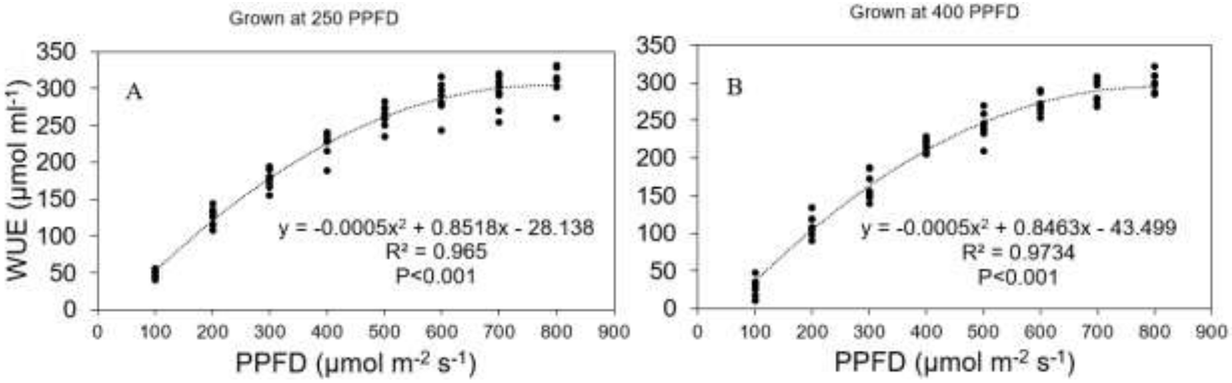


Figure 3.3. Plant water use efficiency (µmol ml^{-1}) per chamber for plants receiving different PPFD. A. Plants that grew under 250 µmol·m^{-2}·s^{-1}. B. Plants that grew under 400 µmol·m^{-2}·s^{-1}.

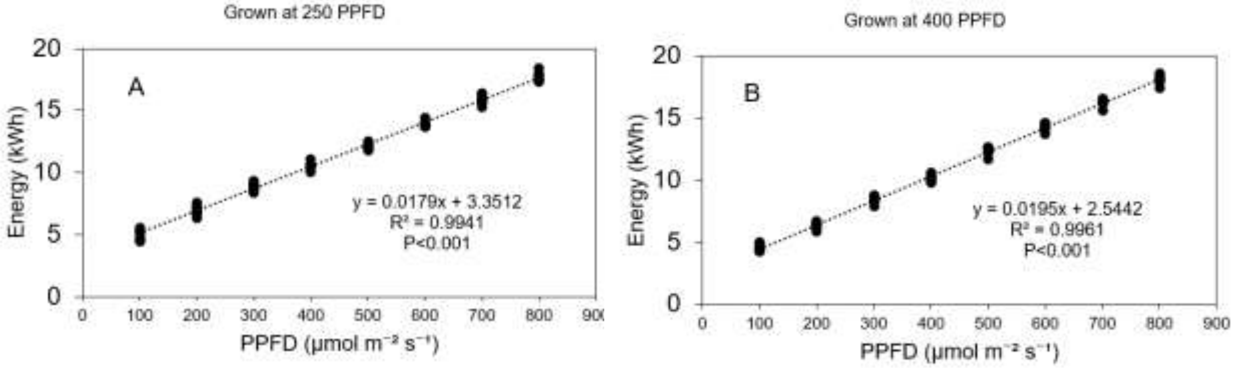
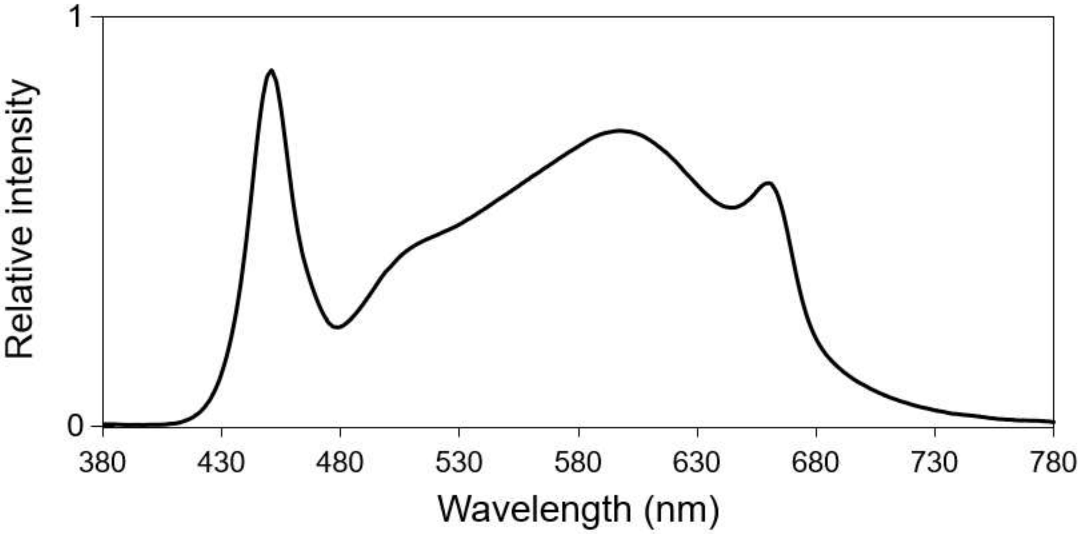
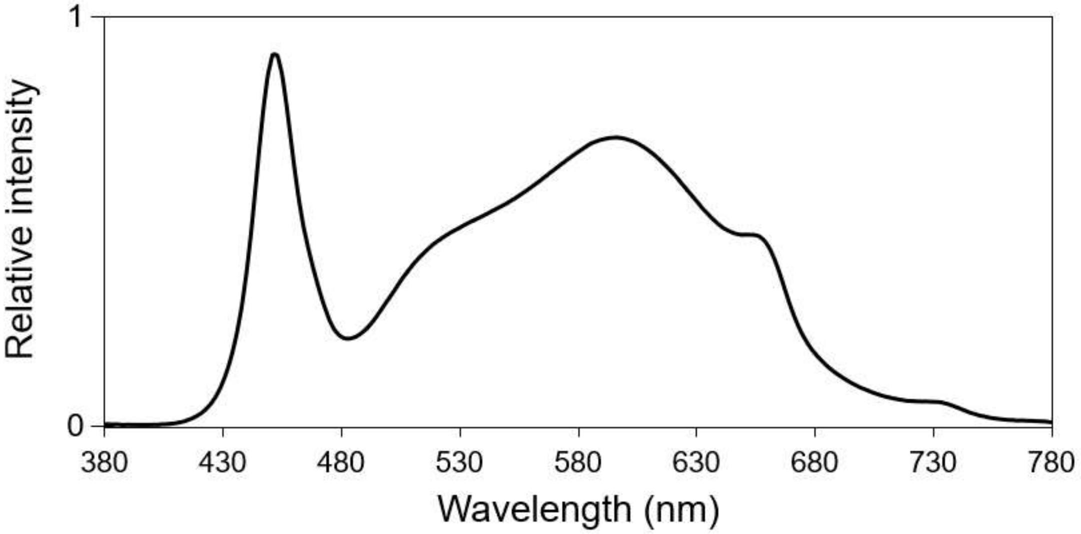


Figure 3.4. Estimated total energy consumption (kWh) for lighting and dehumidification over a 20-hour photoperiod at different PPFD levels for plants grown under 250 (A) and 400 (B) µmol·m⁻²·s⁻¹ conditions.



Supplemental figure 3.2. The electromagnetic spectrum emitted by LED fixtures (SPYDRx Plus with PhysioSpec indoor spectrum, Fluence Bioengineering, Austin, TX, USA)



Supplemental figure 3.2. The electromagnetic spectrum emitted by LED fixtures (P2000, Viparspectra, Richmond, CA, USA)

Table 3.1. Estimated water loss (ml·h^{-1}) per chamber when subjected to different PPFD for 150 plants at 30 DDA for plants that grew under 250 $\mu mol\cdot m^{-2}\cdot s^{-1}$.

PPFD ($\mu mol\cdot m^{-2}\cdot s^{-1}$)	Water loss (ml h^{1}) 150 plants							
	Ch1	Ch2	Ch3	Ch4	Ch5	Ch6	Ch7	Ch8
100	584.85	603.83	457.55	482.53	629.35	573.93	508.75	581.35
200	643.75	619.58	703.98	507.43	657.93	591.03	604.38	558.90
300	660.13	683.05	682.15	571.45	729.75	622.68	653.45	610.65
400	671.95	667.53	684.38	587.68	750.00	650.75	636.38	658.68
500	690.70	696.15	696.43	610.63	723.73	636.85	672.55	629.88
600	695.08	696.75	719.53	675.13	778.55	694.38	677.13	654.25
700	763.63	767.03	828.00	655.60	834.90	731.48	731.60	719.55
800	796.05	809.03	829.70	730.88	897.63	749.80	782.03	750.83

Table 3.2. Estimated water loss (ml·h^{-1}) per chamber when subjected to different PPFD for 150 plants at 30 DDA for plants that grew under 400 $\mu mol\cdot m^{-2}\cdot s^{-1}$.

PPFD ($\mu mol\cdot m^{-2}\cdot s^{-1}$)	Water loss (ml h^{1}) 150 plants							
	Ch1	Ch2	Ch3	Ch4	Ch5	Ch6	Ch7	Ch8
100	434.20	524.07	473.33	546.17	474.30	458.55	424.40	476.43
200	429.00	562.28	511.17	557.45	481.48	506.82	516.58	509.25
300	500.90	637.90	568.00	588.33	586.45	564.00	629.62	582.17
400	550.40	673.87	574.95	666.20	601.97	610.98	609.00	612.48
500	593.75	739.83	749.05	744.50	675.73	699.85	714.00	702.39
600	658.47	804.73	769.58	803.70	721.28	729.88	733.20	745.83
700	708.40	865.47	836.35	826.90	796.85	829.58	797.65	808.74
800	745.20	854.55	880.30	934.15	829.25	841.85	896.83	854.59

Table 3.3. Water extraction efficiency (mL/kWh) of tree commercial dehumidifiers.

Model	Water extraction efficiency (Pints/kWh)	Water extraction efficiency (mL/kWh)
DryGair DG-X	-	3800
Anden A710	6.38	3000
Quest 335	6	2830
	Average	3210

Table 3.4. Estimated energy (kWh) required to remove humidity per chamber under different PPFD levels for 150 plants at 30 DDA that were grown under 250 µmol·m^{-2}·s^{-1}, during a 20-hour daily photoperiod used as reference.

PPFD (µmol·m^{-2}·s^{-1})	kWh needed to remove water during 20 h							
	Ch1	Ch2	Ch3	Ch4	Ch5	Ch6	Ch7	Ch8
100	3.644	3.762	2.851	3.006	3.921	3.576	3.170	3.622
200	4.011	3.860	4.386	3.162	4.099	3.682	3.766	3.482
300	4.113	4.256	4.250	3.560	4.547	3.880	4.071	3.805
400	4.187	4.159	4.264	3.662	4.673	4.055	3.965	4.104
500	4.303	4.337	4.339	3.805	4.509	3.968	4.190	3.924
600	4.331	4.341	4.483	4.206	4.851	4.326	4.219	4.076
700	4.758	4.779	5.159	4.085	5.202	4.557	4.558	4.483
800	4.960	5.041	5.169	4.554	5.593	4.672	4.872	4.678

Table 3.5. Estimated energy (kWh) required to remove humidity per chamber under different PPFD levels for 150 plants at 30 DDA that were grown under 400 µmol·m^{-2}·s^{-1}, during a 20-hour daily photoperiod used as reference.

PPFD (µmol·m^{-2}·s^{-1})	kWh needed to remove water during 20 h							
	Ch1	Ch2	Ch3	Ch4	Ch5	Ch6	Ch7	Ch8
100	2.705	3.265	2.949	3.403	2.955	2.857	2.644	2.968
200	2.673	3.503	3.185	3.473	3.000	3.158	3.219	3.173
300	3.121	3.974	3.539	3.666	3.654	3.514	3.923	3.627
400	3.429	4.199	3.582	4.151	3.751	3.807	3.794	3.816
500	3.699	4.610	4.667	4.639	4.210	4.360	4.449	4.376
600	4.103	5.014	4.795	5.007	4.494	4.548	4.568	4.647
700	4.414	5.392	5.211	5.152	4.965	5.169	4.970	5.039

800	4.643	5.324	5.485	5.820	5.167	5.245	5.588	5.325

Table 3.6. Total energy required to maintain a given PPFD during a daily photoperiod of 20 hours

PPFD (μmol m^{-2} s^{-1})	Energy (kWh/day)
100	1.6
200	3.2
300	4.8
400	6.4
500	8
600	9.6
700	11.2
800	12.8
900	14.4

CHAPTER 4

CONSUMER PREFERENCES AND WILLINGNESS TO PAY FOR LETTUCE AND BELL PEPPERS GROWN UNDER DIFFERENT SUPPLEMENTAL LIGHTING SOURCES AND INFORMATION TREATMENTS[4]

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[4] Mayorga-Gomez, A.M., Campbell, J. H. and B.L. Campbell. To be submitted to *Journal of agribusiness*.

Abstract

LED lighting is increasingly used in greenhouses, especially in vertical farms, but consumer acceptance of LED-grown produce is not fully understood. This study examined consumer preferences and willingness to pay (WTP) for lettuce and bell peppers grown under LED lights, high-pressure sodium (HPS) lights, and natural sunlight. In 2021, a nationally representative survey was implemented online. A total of 915 U.S. consumers for lettuce and 890 for peppers were surveyed on their preferences and purchasing habits for these vegetables. A choice experiment was utilized to assess WTP. Participants were randomly assigned to receive positive, negative, or no information about LED lighting. Results from random parameters logit models showed that consumers preferred produce grown under natural sunlight. LED-grown produce was consistently valued lower, with WTP $2.42 less for lettuce and $1.89 less for peppers. Positive information about LED lighting slightly increased WTP, while negative information lowered it further. However, under any information treatment, WTP for LED-grown produce never reached the level of sunlight-grown produce. These results highlight that consumer perception strongly influences the market value of LED-grown vegetables. Understanding how information affects consumer preferences can help producers and marketers improve communication strategies, increase acceptance, and make LED lighting adoption in controlled environment agriculture more successful.

Introduction

Light is the primary environmental factor that controls plant growth (Bula et al., 1991), making supplemental lighting essential for various plant processes, including photosynthesis, growth, photomorphogenesis, floral induction, flower development, yield, and quality (Moe, 1997), particularly in areas where natural light is insufficient. Through the use of supplemental lighting, greenhouses can enhance the yield of their crops by extending the growing season (Demers et al., 1998).

There are several types of supplemental light sources, such as high-pressure sodium (HPS), metal halide, fluorescent, and incandescent lamps (Bula et al., 1991). However, different light sources produce light with varying spectral qualities, which can lead to differences in plant growth (Bubenheim et al., 1988). Additionally, these light sources have been found to emit high levels of thermal radiation (McCree, 1984), reducing their energy efficiency. As a result, a lighting system based on light-emitting diodes (LEDs), which offers enhanced photosynthetic and energy efficiency, has been proposed as an alternative supplemental lighting source for both research and commercial production in controlled environments (Ignatius et al., 1988).

LED technology has been shown to have superior energy conversion efficiency compared to alternative light sources (Bula et al., 1991). Despite increased efficiency, the incorporation of LED technology in greenhouses can be costly compared to other lighting sources, notably HPS lamps (Rea, 2010; Runkle, 2024). Supplemental lighting is not limited to greenhouse operations; many vertical farms or plant factories with artificial lighting (PFALs) utilize LED technology as their primary light source, though LED lighting is one of the largest cost components in these systems (Kozai et al., 2016; Zeidler et al., 2013). There has been growth in PFAL facilities throughout the United States, though multiple of these initiatives have been unsuccessful due to the inability to cover costs. Notable examples of PFAL operations that have filed for bankruptcy include Plenty (Matsuda, 2025), Aerofarms (Casey, 2023), and Fifth Season (Marston, 2023), with several other operations having ceased operations [e.g., Bowery Farms (Owens, 2014)].

As greenhouses and PFAL operations struggle to remain profitable, there are two potential solutions 1) make LED lighting more cost effective or 2) charge consumers a premium for produce grown under LED lighting. This paper assesses solution 2 by investigating consumer preferences and willingness to pay (WTP) for produce, specifically lettuce and bell peppers, grown under LED lights compared to other light sources. Furthermore, we evaluate how consumers respond when presented with negative and positive information about LED lighting.

Materials and methods

A nationwide online survey was conducted in 2021 to explore consumer preferences, awareness, and perceived challenges regarding the use of supplemental lighting in greenhouse production. Around 1,800 consumers completed the survey with 915 U.S. consumers randomly assigned to the lettuce choice experiment and 890 consumers assigned to the bell peppers choice experiment. Participants were randomly recruited from the Toluna, Inc. (Dallas, TX, USA) online panel and invited via email to complete the survey. Eligible respondents, aged 18 and older, provided informed consent before proceeding. They were then randomly assigned to an information treatment and a produce.

As noted, prior to the choice experiment, participants were randomly assigned to one of six treatment groups (Table 1). Treatment 1 included both the benefits and drawbacks of LED lighting compared to HPS and natural sunlight. Treatment 2 presented only the advantages of LED lighting over both HPS and natural sunlight. Treatment 3 provided information on the benefits of LED lighting compared to HPS alone, while Treatment 4 focused solely on LED advantages over natural sunlight. Treatment 5 conveyed only negative information about LED lighting. Lastly, Treatment 6 served as a control group and received no information.

Following their group assignments, respondents were asked to simulate a real-world purchasing scenario while considering their budget constraints.

The choice experiment included various attributes such as price, lighting type, origin, production method, and purchase location (Table 2, Table 3). To reflect price variations found across U.S. retailers, four price points were selected: \$0.99, \$1.79, \$2.99 and \$4.19 for lettuce and \$0.69, \$1.49, \$2.79 and \$3.99 for bell peppers for an 8- ounces package. The package size was determined based on an analysis of bell pepper and lettuce packaging available in Georgia grocery stores and online listings from major U.S. retailers.

These attributes were chosen based on their significance in influencing purchasing decisions for other specialty crops. Price levels were set according to market conditions at the time of the survey, as observed in local and online grocery stores. The origin attribute specified production locations: “in your state” (representing local production), “California” (signifying a domestic but non-local product), and “Mexico” (indicating an imported product). California was included because it accounts for over a third of U.S. vegetable production (California Department of Food and Agriculture, 2022). The purchase location attribute distinguished between farmers’ markets and supermarkets as potential points of sale. Additionally, the study considered organic certification as a factor, with options for organic and non-organic production (in this case no label was provided).

A key focus of this study was the inclusion of three different lighting types in the choice experiment: natural sunlight, LED lighting, and high-pressure sodium (HPS) lighting. This is because greenhouses typically rely on natural sunlight but often supplement it with HPS lighting, a widely used source, while LED lighting has recently gained popularity for this purpose (Sena et al., 2024).

In order to identify the optimal number of choices included in the choice experiment the D-efficiency criteria since it makes it possible to compare an orthogonal and balanced design with efficiency (Kuhfeld, 2010). Each participant was shown 12 choice sets, each containing three alternatives plus a "None of the above" option (Figure 1.) and they selected their preferred option in each choice set.

Econometric model

To capture potential variation in consumer tastes and preferences, a random parameters logit (RPL) model was applied. This approach allows certain model parameters to vary randomly across individuals. The utility function follows the specification described by Hensher et al. (2005).

$$U_{jsi} = \sum_{k=1}^{K} \beta_{ik} x_{jsik} + \varepsilon_{jsi}$$

In this model, x_{jsik} represents explanatory variables such as the attributes included in choice task while β_{ik} and ε_{jsi} are unobserved and stochastic components. The error term ε_{jsi} is assumed to be independently and identically distributed (i.i.d.). However, this assumption may not hold in certain cases—most notably due to clustered data. To address this, the RPL model accounts for clustering at the respondent level, which helps reduce the risk of violating the i.i.d. assumption. Within each choice set, respondents are assumed to select the option that provides the highest utility. To evaluate the influence of the information treatments and state-level effects, interaction terms were included in the model, allowing utility to be defined as follows:

$$\begin{aligned} U_{jsi} = \beta_1 + \beta_2 \text{NoneAbove} + \beta_3 F\text{armersMarket} + \beta_4 \text{State} + \beta_5 \text{Mexico} + \beta_6 \text{HPSLight} \\ + \beta_7 \text{LEDLight} + \beta_8 \text{Organic} + \beta_9 \text{TBuy} + \beta_{10} \text{TBuyOrg} + \beta_{11} \text{LEDT1} \\ + \beta_{12} \text{LEDT2} + \beta_{13} \text{LEDT3} + \beta_{14} \text{LEDT4} + \beta_{15} \text{LEDT5} + \varepsilon_{jsi} \end{aligned}$$

The variable “None of the above” takes the value of one when a respondent selected the 'none of the above' option, and zero if they chose any of the product alternatives. The variables FarmersMarket, Mexico, State, HPSLight, LEDlight, and Organic correspond to specific attribute levels used in the choice experiment. Each of these variables take the value of one if the attribute level was presented to the respondent, and zero otherwise. The variables LEDT1, LEDT2, LEDT3, LEDT4, and LEDT5 capture the interactions between the LED attribute and the different information treatments described in Table 2. The coefficients β_1 through β_{15} indicate the corresponding increase or decrease in utility associated with each attribute level. WTP was calculated individually for each attribute that was not part of an interaction term as follows:

$$WTP_{ik} = -(\frac{\beta_{ik}}{\beta_p})$$

In this expression, β_{ik} represents the coefficient for the attribute level of interest, while β_p is the coefficient associated with price (Louviere et al. 2000). For attribute levels involved in interactions, the total WTP effect was calculated as follows:

$$WTP_{ik} = -(\frac{\beta_{ik} + \beta(_n)(D)}{\beta_p})$$

Here β_{ik}, denotes the coefficient for the k-th attribute level, and β_n represents the coefficient of the n-th interaction term associated with that attribute, multiplied by the corresponding interaction dummy variable. Standard errors for the WTP estimates were computed using the Delta Method.

Results and discussion

The RPL results for lettuce are presented in Table 4, and those for peppers are shown in Table 5. Additionally, WTP estimates are reported in Table 6 for lettuce and Table 7 for peppers.

Lettuce

The price attribute has a significantly negative coefficient (-0.57), indicating a preference among the sampled population for lettuce lower prices (Table 4). This aligns with the general economic principle that lower prices increase demand (Gale, 1955), reinforcing consumer preference for affordability.

- *Lighting source*

When comparing lettuce production light sources, HPS and LED lighting systems presented negative coefficients (-1.017 and -1.387) in comparison to sun light, respectively (Table 4). This was reflected on the price people were willing to pay as consumers were willing to pay $1.772 and $2.416 for lettuce grown under HPS and LED less when compared to sunlight, respectively.

- *Purchase Point, Origin Location, and Production Method*

Consumers preferred lettuce produced in California over lettuce from their own state (-0.501) and Mexico (-0.82) (Table 4). The California finding differs from past research findings as consumers have shown to have a negative preference for some California products, which may be linked to negative perceptions of the state (Ricks et al., 2023). This trend has been observed for products like turfgrass (Campbell et al., 2021), tomatoes (Berning and Campbell, 2021), mushrooms (Chakrabarti et al., 2019), and microgreens (Ricks et al., 2023). However, this negative perception did not extend to lettuce. Given that California and Arizona are the primary lettuce-producing states in the U.S. (USDA, 2023), consumers may have a more favorable view of lettuce from California, likely influenced by its association with larger scale production within the U.S.

With respect to Mexican produce, research has shown that country of origin can significantly influence consumer preferences, with consumers generally favoring domestic products when other attributes are comparable (Elliot and Cameron, 1994). This trend aligns with the observed preference for American-produced lettuce over Mexican options. These preferences for lettuce origin are reflected in consumers' willingness to pay. Compared to lettuce from California, consumers were willing to pay $0.87 less for lettuce from their own state and $1.40 less for lettuce from Mexico.

Regarding the point of purchase, consumers showed no significant preference between buying lettuce from a farmers' market or a supermarket. Additionally, their WTP did not differ based on these purchase locations (Table 6). Furthermore, the organic production method was less preferred (-1.22) compared to traditional lettuce production. As a result, consumers were willing to pay $2.13 less for organic lettuce than for conventionally grown lettuce.

Evaluating the organic production label results indicates consumers were willing to pay $2.13 less for organic lettuce than for traditionally cultivated lettuce (Table 6). This finding contrasts with reports indicating a growing consumer shift toward organic products (Durmortier et al., 2017), often attributed to ecological, sustainability, and ethical considerations (Tandon et al., 2020).

- *Treatment and LED interaction*

LED information treatments were presented as different sets of information to survey participants, with Treatment 5 being the one providing only negative information about LED lighting and showing no effect on preferences or willingness to pay. The information in Treatments 1 to 4 influenced consumer preferences for lettuce grown under LED lighting, as indicated by the positive RPL coefficients (Table 4). This effect is also evident in the WTP results (Table 8), which show that participants who received Treatments 1 to 4 were willing to pay an additional 1.016, 0.794, 0.842, and 1.100 USD, respectively, compared with participants who were not exposed to any information. However, even though Treatments 1 to 4 showed a positive WTP effect, when this effect is compared to the baseline WTP LED effect for lettuce (−2.416 USD), the total effect of treatment along with LED lighting on WTP for Treatments 1 to 5 were −1.399, −1.621, −1.574, −1.316, and −2.369 USD (Table 8), respectively. This indicates that, even after receiving information, participants were still willing to pay less for lettuce grown under LED lighting compared with lettuce grown under natural sunlight.

Bell pepper

The price attribute exhibits a significantly negative coefficient (-0.57) (Table 5), which suggests that the sampled population showed a preference for lower prices on bell pepper.

- *Lighting source*

When comparing light sources for bell pepper production, HPS and LED lighting systems showed negative coefficients (-0.883 and -1.07, respectively) (Table 5) compared to sunlight. This preference was reflected in the price consumers were willing to pay, as they were prepared to pay \$1.558 less for lettuce grown under HPS and \$1.889 less for lettuce grown under LED, in comparison to sunlight-grown lettuce.

- *Purchase Point, Origin Location, and Production Method*

Consumers showed a preference for bell peppers grown in California over those from Mexico (-0.531), similar to the finding for lettuce (Table 5). This trend suggests that consumers tend to prefer domestic products when other characteristics of the options in the market are similar (Elliot and Cameron, 1994). Consumers exhibited a slight preference for bell peppers grown in California (-0.142, significant at α=0.1), although they preferred peppers from their own state more than they did in the case of lettuce. This may be due to the fact that other states on the East Coast, such as Georgia and Florida, also produce important quantities of bell peppers (Biswas et al., 2018).

Consumers preferred purchasing bell peppers from farmers' markets (0.299) and were willing to pay \$0.528 more than for those sold in supermarkets. Additionally, they showed a lower preference for organically produced bell peppers (-0.447), opting to pay \$0.789 less than for conventionally grown ones.

- *Treatment and LED interaction*

When presented with only positive information about LED lighting, specifically Treatment 2 (highlighting the advantages of LED light compared with HPS and natural sunlight) and Treatment 4 (showing positive information compared with natural sunlight), consumers showed a significant preference for bell peppers grown under this light source (0.464 and 0.229, respectively) (Table 5). Conversely, when exposed only to negative information (Treatment 5), their preference declined (−0.221). When looking at the WTP results (Table 7), consumers were willing to pay 0.818 and 0.405 USD more for Treatments 2 and 4, respectively. In contrast, they showed a discount of 0.883 USD after receiving the information from Treatment 5. All these values are in comparison to the group that did not receive any information.

Even though only Treatments 2, 4, and 5 showed a significant information effect on WTP, when that effect is compared to the baseline WTP LED effect for peppers (−1.889 USD), the total WTP effect of Treatments 1 to 5 combined with LED lighting effect was −1.070, −1.660, −1.484, −2.773, and −2.773 USD (Table 9), respectively. This indicates that, even after receiving information, participants were still willing to pay less for peppers grown under LED lighting compared with peppers grown under natural sunlight.

Conclusions

LED lighting is increasingly used in greenhouse and vertical farming systems, making it important for producers to understand consumer preferences and WTP for products grown partly or entirely under LEDs. Our findings show that negative information about LED-grown produce lowers consumer WTP for lettuce and peppers, while positive information increases WTP. However, under all information treatments, consumers' WTP for LED-grown products remained below the WTP for produce grown naturally under sunlight, which remained the most preferred production method. Consumers also favored produce from California and showed less interest in organic products.

These insights can guide producers in deciding whether to adopt LED lighting, how to target marketing efforts, and which labeling strategies to use. Overall, this research contributes to a better understanding of the production and marketing challenges of LED-grown vegetables in controlled environment agriculture.

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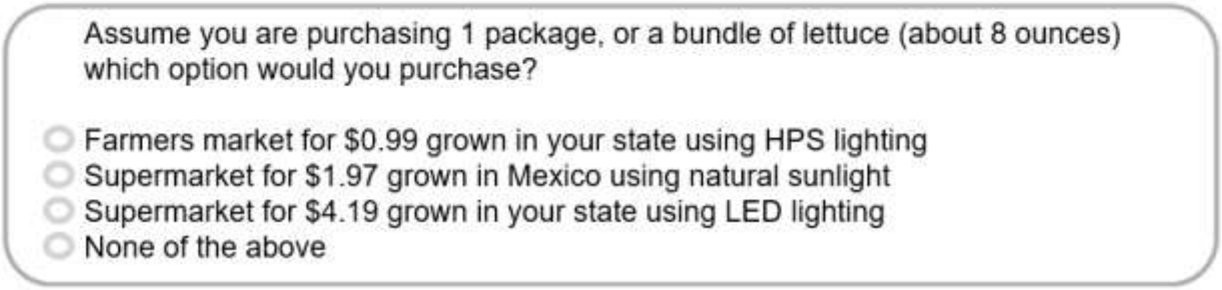

Assume you are purchasing 1 package, or a bundle of lettuce (about 8 ounces) which option would you purchase?

○ Farmers market for $0.99 grown in your state using HPS lighting
○ Supermarket for $1.97 grown in Mexico using natural sunlight
○ Supermarket for $4.19 grown in your state using LED lighting
○ None of the above

Figure 4.1. Example of a choice set presented to participants in the online survey.

Table 4.1. Descriptions of information provided to participants in a 2021 online survey on LED lighting and plant purchasing

Treatment 1: all information	Treatment 2: all LED positive information	Treatment 3: alternative information	Treatment 4: sunlight information	Treatment 5: LED negative information	Treatment 6: control (no information)
Typical lighting sources in greenhouses	Typical lighting sources in greenhouses	Typical lighting sources in greenhouses	Typical lighting sources in greenhouses	Typical lighting sources in greenhouses	Typical lighting sources in greenhouses
Natural sunlight	Natural sunlight	Natural sunlight	Natural sunlight	Natural sunlight	Natural sunlight
LED	LED	LED	LED	LED	LED
HPS	HPS	HPS	HPS	HPS	HPS
LED lighting vs. HPS					
LED lights have better energy efficiency (HPS require a lot more electricity)	LED lights have better energy efficiency (HPS require a lot more electricity)	LED lights have better energy efficiency (HPS require a lot more electricity)			
LED lights produce fewer greenhouse gases	LED lights produce fewer greenhouse gases	LED lights produce fewer greenhouse gases			
LED lights bulbs do not have to be changed as often	LED lights bulbs do not have to be changed as often	LED lights bulbs do not have to be changed as often			
LED lights do not contain mercury (potential health risk in production)	LED lights do not contain mercury (potential health risk in production)	LED lights do not contain mercury (potential health risk in production)			
LED lighting vs. sunlight					
LED lighting allows for year-round production and for production in areas where it would not be possible	LED lighting allows for year-round production and for production in areas where it would not be possible		LED lighting allows for year-round production and for production in areas where it would not be possible		

LED lighting may contain large amounts of copper (potential environmental threat), nickel (potential health risk during production), and lead (potential health risk during production)		LED lighting may contain large amounts of copper (potential environmental threat), nickel (potential health risk during production), and lead (potential health risk during production)

Table 4.2. Attributes and levels used in the choice experiment from a January 2021 online survey on LED lighting and lettuce purchasing.

Price (USD)	Lighting type	Production location	Production type	Purchase location
0.99	Natural sunlight	Own state	Organic	Supermarket
1.79	LED light	California	Non-Organic	Farmer's market
2.99	HPS	Mexico		
4.19				

LED = Light-emitting diode; HPS = high pressure sodium

Table 4.3. Attributes and levels used in the choice experiment from a January 2021 online survey on LED lighting and pepper purchasing.

Price (USD)	Lighting type	Production location	Production type	Purchase location
0.69	Natural sunlight	Own state	Organic	Supermarket
1.49	LED light	California	Non-Organic	Farmer's market
2.79	HPS	Mexico		
3.99				

LED = Light-emitting diode; HPS = high pressure sodium

Table 4.4. Random parameters logit (RPL) model results based on a 2021 online survey about LED lighting and lettuce purchases.

Variable	RPL coefficients	P value
Means of the random parameters in utility functions		
None of the above	-1.258	0.000
Purchase location		
Farmers market	0.048	0.329
Supermarket	—	—
Location produced		
Mexico	-0.825	0.000
Your state	-0.501	0.000
California	—	—
Production type		
Organic	-1.226	0.000
Nor Organic	—	—
Lighting type		
HPS	-1.017	0.000
LED	-1.387	0.000
Sunlight	—	—

Nonrandom parameters in utility functions		
Price	-0.574	0.000
LED lighting × treatment interaction		
LED × treatment 1	0.583	0.001
LED × treatment 2	0.456	0.000
LED × treatment 3	0.483	0.000
LED × treatment 4	0.631	0.000
LED × treatment 5	0.027	0.864
Standard deviations of parameter distributions		
None of the above	1.729	0.000
Farmers market	0.045	0.374
Your state	1.155	0.000
Mexico	0.543	0.000
Organic	1.610	0.000
HPS	1.139	0.000
LED	1.401	0.000
Log likelihood function: -11309.496		
Chi squared: 7785.214		
Significance level: 0		
McFadden Pseudo R-squared: 0.2560571		
Number of obs.: 10980		

Table 4.5. Random parameters logit (RPL) model results based on a 2021 online survey about LED lighting and pepper purchases.

Variable	RPL coefficients	P value
Means of the random parameters in utility functions		
None of the above	-1.418	0.000
Purchase location		
Farmers market	0.299	0.000
Supermarket	—	—
Location produced		
Mexico	-0.531	0.000
Your state	-0.142	0.081
California	—	—
Production type		
Organic	-0.447	0.000
Nor Organic	—	—
Lighting type		
HPS	-0.883	0.000
LED	-1.071	0.000
Sunlight	—	—
Nonrandom parameters in utility functions		
Price	-0.566	0.000

LED lighting × treatment interaction		
LED × treatment 1	0.168	0.211
LED × treatment 2	0.464	0.000
LED × treatment 3	0.129	0.359
LED × treatment 4	0.229	0.093
LED × treatment 5	-0.501	0.000
Standard deviations of parameter distributions		
None of the above	2.673	0.000
Farmers market	0.188	0.001
Your state	0.793	0.000
Mexico	0.46	0.000
Organic	1.071	0.000
HPS	1.072	0.000
LED	1.081	0.000
Log likelihood function: -10926.281		
Chi squared: 7758.684		
Significance level: 0		
McFadden Pseudo R-squared: 0.2620181		
Number of obs.: 10680		

Table 4.6. Estimates of willingness to pay, based on RPL model analysis of a 2021 online survey regarding LED lighting and lettuce buying behavior.

			Confidence intervals	
Variable	Willingness to pay ($)	P value	Lower limit	Upper limit
Purchase location				
Farmers market	0.084	0.330	-0.085	0.253
Supermarket	—	—	—	—
Location produced				
Mexico	-1.437	0.000	-1.58	-1.294
Your state	-0.873	0.000	-1.254	-0.492
California	—	—	—	—
Production type				
Organic	-2.136	0.000	-2.688	-1.584
Nor Organic	—	—	—	—
Lighting type				
HPS	-1.772	0.000	-1.922	-1.623
LED	-2.416	0.000	-2.799	-2.034
Sunlight	—	—	—	—

Table 4.7. Estimates of willingness to pay, based on RPL model analysis of a 2021 online survey regarding LED lighting and pepper buying behavior.

Variable	Willingness to pay ($)	P value	Confidence intervals Lower limit	Upper limit
Purchase location				
Farmers market	0.528	0	0.342	0.714
Supermarket	—	—	—	—
Location produced				
Mexico	-0.937	0	-1.091	-0.784
Your state	-0.250	0.084	-0.535	0.034
California	—	—	—	—
Production type				
Organic	-0.789	0	-1.096	-0.481
Nor Organic	—	—	—	—
Lighting type				
HPS	-1.558	0	-1.715	-1.401
LED	-1.889	0	-2.211	-1.568
Sunlight	—	—	—	—

Table 4.8. Decomposition of the willingness to pay interaction effects estimated using a random parameters logit model from an online survey on LED lighting and consumer lettuce preferences.

Variable	LED effect -(βLED/βPrice)	Information effect -(βTreatment·LED/βPrice)	Total effect -[(βLED + Treatment·LED/βPrice)]
LED, treatment 1: WTP	-2.416	1.016	-1.399
P value	0.000	0.000	0.000
Lower CI	-2.799	0.537	-1.713
Upper CI	-2.034	1.496	-1.086
LED, treatment 2: WTP	-2.416	0.794	-1.621
P value	0.000	0.001	0.000
Lower CI	-2.799	0.313	-1.948
Upper CI	-2.034	1.276	-1.295
LED, treatment 3: WTP	-2.416	0.842	-1.574
P value	0.000	0.000	0.000
Lower CI	-2.799	0.385	-1.856
Upper CI	-2.034	1.298	-1.292
LED, treatment 4: WTP	-2.416	1.100	-1.316
P value	0.000	0.000	0.000
Lower CI	-2.799	0.614	-1.636
Upper CI	-2.034	1.589	-0.995

LED, treatment 5: WTP	-2.416	0.047	-2.369
P value	0.000	0.865	0.000
Lower CI	-2.799	-0.500	-2.784
Upper CI	-2.034	0.595	-1.953

Table 4.9. Decomposition of the willingness to pay interaction effects estimated using a random parameters logit model from an online survey on LED lighting and consumer bell pepper preferences.

Variable	LED effect -(βLED/βPrice)	Information effect -(βTreatment·LED/βPrice)	Total effect -[(βLED + Treatment·LED/βPrice)]
LED, treatment 1: WTP	-1.889	0.296	-1.593
P value	0.000	2.11	0.000
Lower CI	-2.211	-0.168	-1.951
Upper CI	-1.568	0.761	-1.234
LED, treatment 2: WTP	-1.889	0.818	-1.07
P value	0.000	0.000	0.000
Lower CI	-2.211	0.388	-1.383
Upper CI	-1.568	1.249	-0.758
LED, treatment 3: WTP	-1.889	0.229	-1.66
P value	0.000	0.359	0.000
Lower CI	-2.211	-0.260	-2.045
Upper CI	-1.568	0.719	-1.275
LED, treatment 4: WTP	-1.889	0.405	-1.484
P value	0.000	0.092	0.000
Lower CI	-2.211	-0.067	-1.85
Upper CI	-1.568	0.877	-1.118
LED, treatment 5: WTP	-1.889	-0.883	-2.773
P value	0.000	0.000	0.000
Lower CI	-2.211	-1.408	-3.213
Upper CI	-1.568	-0.359	-2.333