Urban Agriculture
& Regional Food Systems

Minimum Light Requirements for Indoor Gardening of Lettuce

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CORE IDEAS

- Lettuce grown under LEDs produced more shoot fresh and dry mass than those grown under fluorescent lamps. However, all lamp types resulted in comparable growth and quality attributes.
- Growth, aesthetic quality, and nutritional quality increased with higher daily light integrals.
- A minimum daily light integral of 6.5 to 9.7 $mol \cdot m^{-2}\ d^{-1}$ is recommended for indoor gardening of red-leaf lettuce plants.

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Abbreviations: Chla, Chlorophyll-a; Chlb, chlorophyll-b; DLI, daily light integral; DM, dry mass; DMSO, dimethyl sulfoxide; EC, electrical conductivity; LED, light emitting diode; PPF, photosynthetic proton flux; RH, relative humidity; SPAD, Soil Plant Analysis Development; YPF, yield proton flux.

ABSTRACT Indoor food-gardening is an important trend in horticulture. However, most research-based light recommendations are oriented towards commercial production, with recommended daily light integrals (DLI) significantly higher than those found inside a home environment. The objective was to evaluate growth (fresh and dry mass), accumulation of key phytochemical constituents (leaf photosynthetic pigment and nitrate content), and aesthetic quality (elongation and pigmentation) of red-leaf lettuce (*Lactuca sativa*) grown from transplant to a harvest stage in an indoor environment using different (i) light sources (light-emitting diode [LED] vs. fluorescent lamps), and (ii) light quantities (from 1.6 to 9.7 mol $m^{-2}\ d^{-1}$). In the first experiment, four broadband white light sources were compared in a growth chamber using 5.2 $mol \cdot m^{-2} \cdot d^{-1}$: (i) 'neutral-white' 4000-K LED lamps, (ii) 'day-white' 5000-K LED lamps, (iii) 'neutral-white' 4100-K fluorescent lamps, or (iv) 'daylight' 6500-K fluorescent lamps. Lettuce grown under LED lamps produced more shoot fresh and dry mass than those grown under fluorescent lamps. However, all light sources resulted in comparable growth and quality attributes. In two separate experiments, plants were grown under one of four DLI. As DLI increased, plants had more growth, higher aesthetic quality (more compact leaves and higher pigment content), and superior nutritional quality (increased leaf concentrations of anthocyanin and carotenoid, and reduced nitrate). Based on these results, a minimum DLI of 6.5 to 9.7 mol $m^{-2}\ d^{-1}$ is recommended when designing indoor gardening systems for red-leaf lettuce plants.

The US sales value of urban food systems, which includes the indoor farming industry in warehouse-based "plant factories," rooftop greenhouses on top of city buildings, public community gardens, and residential food gardens, is estimated to reach $20 billion in 2019 (USDA, 2016). Residential food gardens are small, private spaces used by individual households to grow edible produce (Kirkpatrick and Davison, 2018). Compared with gardening in public spaces, residential food gardens have received little research attention despite the fact that they can help increase access to fresh fruit and vegetables (Kortright and Wakefield, 2011). Furthermore, an increasing body of empirical evidence suggests that residential food gardening (here onwards referred

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to as "gardening") may provide health and well-being benefits through physical activity, healthier diet, and mental acuity (Kortright and Wakefield, 2011; Nicklett et al., 2014).

Consumer interest in gardening is an important urban trend, and a growing market for companies supplying plant products. In 2014, one in three US households participated in some type of gardening activity and had a total spending budget of $3.5 billion (NGA, 2014). Sales of vegetable bedding plants from the top 15 floriculture states in the nation increased from 47 to 55 million units from 2011 to 2014, and the wholesale value of the industry increased from $75 to $99 million (USDA, 2012, 2015). Until recently, gardening was primarily an outdoor activity, heavily dependent on climatic seasons and vulnerable to unpredictable weather, weed pressure, animals, insects, and diseases. However, limited space, soil, and water in urban settings are bringing attention to indoor gardening, which was recently ranked as the fastest-growing trend in horticulture by an industry group (GMG, 2017).

As part of the gardening experience, consumers typically purchase vegetable bedding plants at a transplant or preharvest stage to grow on to harvest. Nonetheless, information on conditions required to successfully finish vegetable bedding plants is lacking to support consumers interested in indoor gardening. For example, although numerous studies have evaluated growth and development of lettuce under different light qualities and quantities in controlled environments (Chen et al., 2016; Dougher and Bugbee, 2001; Johkan et al., 2010; Kim et al., 2004; Li and Kubota, 2009; Lin et al., 2013; Son and Oh, 2013), most research-based recommendations for indoor plant production typically aim to maximize yield under optimal environmental conditions. In contrast, research to support non-commercial, small-scale indoor gardening should seek to identify environmental set points that can satisfy human comfort and function, and can ensure a successful harvest without compromising aesthetic and nutritional quality. This is because consumers are not likely to change the environmental set points within their home environment to maximize plant yield at the expense of comfort.

To our knowledge, no published studies have evaluated growth and quality of lettuce grown under DLI that are significantly below the typical recommended ranges for commercial production. Nonetheless, light quantity used for commercial lettuce production is considerably higher than the typical DLI within a residential environment. Both et al. (1997) recommended 17 mol m^{-2} d^{-1} to produce a 150-g lettuce head. Similarly, Fu et al. (2012) measured the highest lettuce yield (158 to 163 g) with 20 to 30 mol m^{-2} d^{-1}. Recommended light intensities for human comfort in a residential indoor environment are ~7 μmol m^{-2} s^{-1}, if using cool-white fluorescent lamps (adapted from U.S. General Services Administration, 2013). At that light intensity, lamps would only provide 0.6 mol m^{-2} d^{-1} if operated for 24 h. Therefore, supplementing light within a residential indoor environment is necessary to sufficiently support indoor gardening.

Rapid advancements of light-emitting diode (LED) lamps have made it possible to evaluate various aspects of plant growth and development indoors. To date, most studies using LED lamps for lettuce production have compared a combination of red (600 to 700 nm) and blue (400 to 500 nm) light (Johkan et al., 2010; Li and Kubota, 2009; Liu et al., 2016; Son and Oh, 2013; Stutte et al., 2009), with some studies evaluating the addition of far-red or broadband white light (Kubota et al., 2011; Lin et al., 2013; Park and Runkle, 2018). Stutte et al. (2009) found that lettuce grown with ~19 mol m^{-2} d^{-1} under red or red and blue LED lamps produced approximately 30% more biomass than plants grown under the same DLI using fluorescent lamps. However, plants grown under red and blue LED lamps appear purplish gray to the human eye and are not aesthetically pleasing. In addition, broadband white lamps are more readily available as off-the-shelf products for consumers interested in indoor gardening.

The objective of this study was to evaluate growth, accumulation of key phytochemical constituents, and aesthetic quality of red-leaf lettuce grown from the transplant-to-harvest stage indoors using different (i) light sources (LED vs. fluorescent lamps), or (ii) light quantities (from 1.6 to 6.5 mol m^{-2} d^{-1} or from 2.5 to 9.7 mol m^{-2} d^{-1}). Our goal was to compare lamps that were readily available for indoor gardening, rather than horticultural-grade lamps. Therefore, the light intensities evaluated in our study were below the recommended ranges for commercial production, considering that the feasible light intensity within a residential indoor environment would be limited by the number of fixtures within a small area, as well as the output limitations when using off-the-shelf lamps that are readily available for consumers. The tested cultivar, Red Salad Bowl, was selected because it is a pick-and-eat variety, rather than a head-lettuce type, that allows multiple partial harvests and has high aesthetic quality for salad use. We hypothesized that growth and quality of plants would be similar under the different broadband white lamps, and that increasing DLI would increase biomass production and quality attributes. We further hypothesized that a DLI <10 mol m^{-2} d^{-1} would satisfy consumer requirements for indoor gardening, which we defined as achieving active growth at the end of the experiment, and with a lack of etiolated growth (measured by chlorophyll and anthocyanin content and leaf elongation).

MATERIALS AND METHODS

Light Quality Experiment

In Experiment 1, seeds of 'Red Salad Bowl' (Johnny's Selected Seeds, Fairfield, ME) lettuce, which require 50 days to maturity, were germinated in a 102-cell tray filled with horticultural grade substrate composed of 7 to 10% (v/v) perlite, 70 to 65% peat moss, and 23 to 25% coir (Pro-Mix MP Mycorrhizae Organik, Premier Tech Horticulture, Quakertown, PA) and topped with coarse vermiculite. Plants were propagated for one week in a germination room at a constant temperature of 23 °C and 80% relative humidity (RH), with

fluorescent light providing a DLI of 5.7 mol $m^{-2}d^{-1}$ (100 µmol m^{-2} s^{-1} for 16 h d^{-1}). One week after sowing, trays were moved to an even-span glass-glazed greenhouse located at the University of Florida in Gainesville, FL (30 ° N. lat). Four weeks after sowing, five uniform seedlings with four true leaves were transplanted into 16-cm diameter, 6-cm tall containers filled with 700 mL of an Irish *Sphagnum* peat substrate with no fertilizer charge (Bulrush Horticulture LTD, Magherafelt, UK), amended with 30% coarse perlite by volume, and 5.5 kg m^{-3} (0.4 g L^{-1} N) of 8–1.75–3.32 N–P–K (Sustane 8-4-4, Sustane Natural Fertilizer, Inc., Cannon Falls, MN). The day, night, and average air temperatures during that period were 24.3 ± 2.2 °C, 20.7 ± 1.2 °C, and 22.5 ± 2.9 °C, respectively, and the average DLI was 17 ± 4.3 mol m^{-2} d^{-1}. The initial production phase ended 5 wk after sowing, when transplants were considered a prefinished vegetable bedding plant product suitable for sale to indoor gardeners (with 6 to 8 fully extended leaves). At that point, containers were moved to a growth chamber to compare growth under different light sources.

The walk-in growth chamber (C6 Control System with ECoSys Software, EGC, Chagrin Falls, OH) was equipped with four shelving units (1.8-m tall, 0.9-m wide, and 0.6-m deep), each with four shelves. Each shelving unit was considered a block, providing a total of four blocks. The four replicate shelves (0.4-m tall, 0.6-m wide, 0.6-m deep) had a randomly assigned light treatment replication within each shelving unit resulting in a randomized complete block design. Each shelf was surrounded with white plastic with black backing, to prevent light pollution, and had a 2.5-cm thick foam board at the bottom to provide heat insulation. Four containers, each with five plants, were placed on each replicate shelf. Four off-the-shelf broadband white light sources were compared as treatments: (i) 'neutral-white' 4000-K LED lamps (4000LED [Model 97743, Green Creative, San Bruno, CA]), (ii) 'day-white' 5000-K LED lamps (5000LED [Model 40803, Green Creative]), (iii) 'neutral-white' 4100-K fluorescent lamps (4100FLR [Model 64234, GE Lighting, Cleveland, OH]), or (iv) 'daylight' 6500-K fluorescent lamps (6500FLR [Model 64243, GE Lighting]). All lamps were retrofitted to a 0.6-m long T8 strip light (Metalux SNF217R, Cooper Lighting, Peachtree City, GA). The spectral distribution of each light source was measured with a spectroradiometer (SS-110, Apogee Instruments Inc., Logan, UT) and is shown in Figure 1 and described in Table 1.

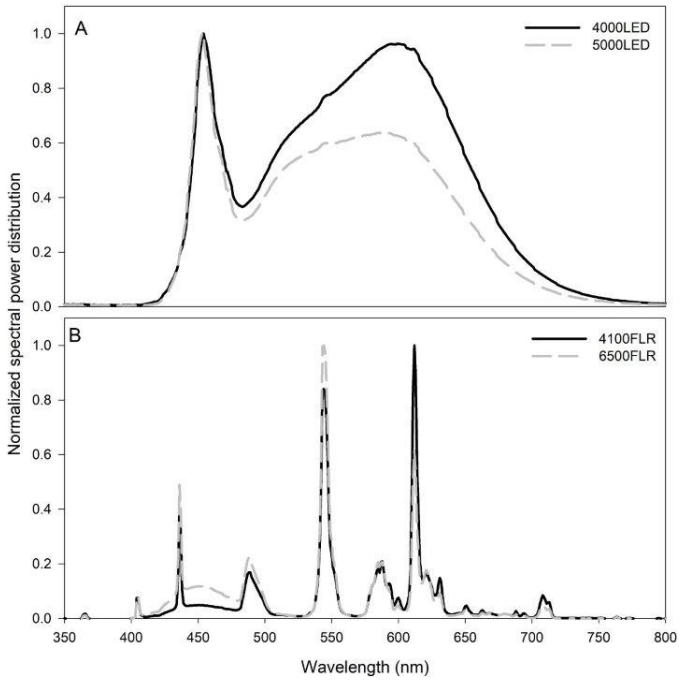

Fig. 1. Normalized spectral power distribution of 4000-K (4000LED) or 5000-K (5000LED) light-emitting diode (LED) lamps (A), and 4100-K (4100FLR) or 6500-K (6500FLR) fluorescent lamps (B). Photon flux (µmol m^{-2} s^{-1}) was measured for every 1 nm.

Prior to starting the experiment, a quantum sensor (LI-COR LI-250A, LI-COR, Lincoln, NE) was used to measure photosynthetic photon flux (PPF) to ensure that plants received an average of DLI of 5.2 mol m^{-2} d^{-1} (120 µmol m^{-2} s^{-1} for 12 h d^{-1} from 0600 to 1800 h). The set point for ambient CO_2 and RH were 400 ppm and 70%, respectively. Temperature was set at 22 °C, which is a common temperature set point within residential environments. The recorded air temperature (day/night) during the experiment was 24.7 ± 1.6 °C/22.2 ± 1.4 °C , measured with a temperature logger (WatchDog A Series, Spectrum Technologies, Aurora, IL) placed at the center of each compartment. Plants were watered every other day with 150 mL tap water. Tap water had an electrical conductivity (EC) of 0.4 mS cm^{-1}, pH of 8.3, and 40 mg L^{-1} $Ca–CO_3$ alkalinity.

Table 1. Photosynthetic photon flux (PPF), total photon flux per broadband waveband, and yield photon flux (YPF) provided by different lighting treatments.

Treatment†	PPF (400-700 nm)	Ultraviolet (340-400 nm)	Blue (400-500 nm)	Green (500-600 nm)	Red (600-700 nm)	Far-red (700-800 nm)	YPF‡
				µmol m^{-2} s^{-1}			
4000LED	120 ± 2	0.3	25 (21%)§	55 (46%)	40 (33%)	3	105
5000LED	120 ± 2	0.5	32 (27%)	55 (46%)	34 (27%)	2	103
4100FLR	120 ± 1	0.2	28 (23%)	51 (43%)	42 (34%)	4	107
6500FLR	120 ± 1	0.3	43 (36%)	51 (42%)	26 (22%)	1	102

† 4000-K light-emitting diode (LED) lamps (4000LED), 5000-K LED lamps (5000LED), 4100-K fluorescent lamps (4100FLR), or 6500-K fluorescent lamps (6500FLR).

‡ YPF is the product of PPF and relative quantum efficiency calculated based on McCree (1971) and Sager et al. (1988).

§ Numbers in parenthesis represent the percentage of each waveband from total PPF.

Data Collected

Two weeks after the light treatments started (7 wk after sowing), the temperature of the fourth true leaf was measured for the middle plant in each container using a hand-held infrared thermometer (Model IRT4, Mannix Testing and Measurement, Lynbrook, NY). Chlorophyll content (Soil Plant Analysis Development [SPAD] index) was measured with a chlorophyll meter (SPAD-502, Konica Minolta Sensing Inc., Osaka, Japan) in all plants on the first lobe of the fourth true leaf, and the average SPAD index per container was recorded. Length of the middle rib of the fourth true leaf of the middle plant within each container was measured. For each treatment replication (shelf), two containers with five plants each were harvested by cutting the shoots at substrate level. After measuring fresh mass per container, tissue was oven-dried to a constant mass at 80 °C for 72 h for dry mass determination. Samples for dry mass per container were ground, and used to determine nitrate content. Plants within the remaining two containers per shelf were used to quantify content of key phytochemicals from fresh tissue.

Chlorophyll and carotenoids were measured following the dimethyl sulfoxide (DMSO) extraction method described in Richardson et al. (2002). Glass vials were wrapped in aluminum foil to protect samples from light exposure. The vials contained 7 mL DMSO and were preheated in a 65 °C water bath. A 3.1 cm^2 disk was cut for the middle plant within each container and placed in the vial and extracted for 30 min in the dark. Samples were removed from the water bath, the extracted liquid was brought to a volume of 10 mL with DMSO, and 2.5 mL of each extract were transferred to a disposable polystyrene cuvette. Pure DMSO was used as the blank. The absorbance of both blank and samples were measured with a spectrophotometer (SpectraMax Plus 384, Molecular Devices, Sunnyvale, CA) at 480, 649, and 665 nm. Chlorophyll-a (Chla), chlorophyll-b (Chlb), and carotenoids were calculated using the equations from Wellburn (1994).

Anthocyanins were measured using the methanol extraction method described in Gould et al. (2000). A 10-mm diameter disk was cut as a sample from the distal half of each leaf lamina. The samples were agitated gently in the dark for 24 h at 4 °C in 1 mL of 3 M HCl, water, and methanol (1:3:16 by volume). Samples were then placed in a centrifuge for 15 min. The absorbance of the extracts were measured with a spectrophotometer at 530 (A530) and 653 (A653) nm, with methanol used as the blank solution. Anthocyanin concentration was calculated as A530–(0.24 × A653). Nitrate was analyzed using the methods described in Cataldo et al. (1975) and Lin et al. (2013). Standard solutions were made containing approximately 60 µg of nitrate nitrogen (NO_3–N). Dried samples were ground to a 35-mesh size and 100 mg were suspended in 10 mL of deionized water. The suspension was incubated at 45 °C for 1 h. Samples were then mixed, placed in the centrifuge at 5000 g_n for 15 min, and 0.2 mL of the extracts were pipetted into a 50 mL Erlenmeyer flask. The samples were mixed with 0.8 mL of 5% (w/v) salicylic acid in concentrated, pure sulfuric acid. After 20 min at room temperature, 19 mL of 2M NaOH were slowly added to the samples, then left to cool (for ~30 min) to room temperature before being transferred to cuvettes. Absorbance was measured with a spectrophotometer at 410 nm. The blank was 0.2 mL of water in the reagents.

The experiment was replicated a second time, following the same procedures with the exception that seedlings were transplanted into the containers 1 wk earlier (i.e., 3 wk after sowing), treatments began 4 wk after sowing, and plants were harvested 2 wk later (i.e., 6 wk after sowing). Day, night, and average air temperature while plants were grown in the greenhouse (2 to 4 wk after sowing) averaged 22.5 ± 0.8 °C, 21.3 ± 0.2 °C, and 21.9 ± 0.5 °C, and the average DLI was 7.6 ± 3.8 mol m^{-2} d^{-1}. The air temperature (day/night) recorded in the growth chamber during the second experimental run was 23.6 ± 1.4 °C/22.0 ± 0.8 °C. Data from both replications were analyzed in a combined analysis using analysis of variance (ANOVA) as a randomized complete block design using SAS PROC GLIMMIX (SAS Institute, 2012). Random effects for the model were experimental replication and its interaction with block. Treatment means were separated using Tukey's test at $P < 0.05$.

Light Quantity Experiments

In Experiment 2, lettuce seeds were propagated and transplanted following the same procedures as previously described, with the exception that due to excessive ambient temperature in the greenhouse (>27°C), plants were propagated, transplanted, and grown in a growth room for 4 wk without a greenhouse phase. Set points for DLI and air temperature (day/night) during that period were 6.9 mol m^{-2} d^{-1} (120 µmol m^{-2} s^{-1} for 16 h d^{-1}) and 23 °C/22 °C, respectively. Five weeks after sowing, containers with five plants were transferred into a walk-in growth chamber and experimental treatments were initiated. The growth chamber had the same setup as previously described, with four blocks (shelving units), each with four replicate shelves that differed in light treatment. Based on findings from Experiment 1, 4000LED lamps were used to provide the following DLI treatments: 1.6, 2.2, 3.7, or 6.5 mol m^{-2} d^{-1} (37, 52, 85, or 150 µmol m^{-2} s^{-1} for 12 h d^{-1} from 0600 to 1800h). Target PPF was achieved by adjusting the number of lamps per fixture. The set point for ambient CO_2 and RH were 400 ppm and 70%, respectively. Ambient temperature was set at 22 °C, and the recorded air temperature (day/night) during the experiment was 22.8 ± 1.9/21.6 ± 1.0 °C. In order to avoid a confounding effect of substrate moisture level on light level, plants were irrigated with 150 mL tap water every time their container weighed less than 350 g (approx. average weight at which containers were at 50% container capacity). Plants in containers under 1.6, 2.2, 3.7, and 6.5 mol m^{-2} d^{-1} received 450, 750, 1050 and 1500 mL of water, respectively. The experiment was terminated 9 wk after sowing (i.e., 4 wk of treatment). Data collected included: leaf temperature, SPAD index, leaf length, shoot fresh and dry mass, and concentrations of Chla, Chlb, carotenoids, anthocyanins, and nitrate, following the same protocols as previously described.

Table 2. Effect of light source on growth, leaf temperature, and quality attributes of 'Red Salad Bowl' grown for two weeks under different lighting treatments.

Treatment†	Leaf length‡	Fresh mass	Dry mass	Leaf temperature	SPAD index	Chl a‡	Chl b‡	Carotenoids	Anthocyanin	Nitrate
	mm	g		°C				µg/g FM		µg/g DM
4000LED	182 a§	59 a	3.7 a	21.7 ab	28 a	1.02 a	0.42 a	0.26 a	0.53 a	34.91 a
5000LED	174 a	56 a	3.6 a	21.5 b	29 a	1.13 a	0.45 a	0.27 a	0.62 a	28.73 a
4100FLR	180 a	51 b	3.1 b	22.8 a	27 a	1.15 a	0.47 a	0.27 a	0.65 a	32.90 a
6500FLR	172 a	49 b	3.0 b	21.8 ab	28 a	1.16 a	0.47 a	0.27 a	0.51 a	32.70 a

† 4000-K light-emitting diode (LED) lamps (4000LED), 5000-K LED lamps (5000LED), 4100-K fluorescent lamps (4100FLR), or 6500-K fluorescent lamps (6500FLR).

‡ FM, fresh mass; DM, dry mass; Chla, chlorophyll-a; Chlb, chlorophyll-b.

§ Mean within columns with different letters are significantly different by Tukey's HSD test at $P \leq 0.05$.

A follow-up experiment (Experiment 3) was conducted, which eliminated the lowest DLI from the previous experiment, and included a higher DLI of 9.7 mol m^{-2} d^{-1} to compare a broader range of DLIs. Lettuce seeds were propagated under the same conditions described for Experiment 2, with the exception that seedlings were transferred to a greenhouse 1 wk after sowing. Three weeks after sowing, three seedlings were transplanted to 15.2-cm in diameter, 9.5-cm tall containers filled with Irish *Sphagnum* peat amended with 30% coarse perlite (by volume) and 5.5 kg m^{-3} of 8–1.75–3.32 N–P–K Containers were immediately moved inside two walk-in growth chambers. The day, night, and average air temperature in the greenhouse for that period (1 to 3 wk after sowing) was 22.3 ± 0.6 °C, 21.3 ± 0.2 °C, and 21.8 ± 0.4 °C, respectively, and average DLI was 7.8 ± 3.7 mol m^{-2} d^{-1}.

In Experiment 3, commercial horticultural-grade LED modules (GreenPower, Philips Lighting, Somerset, NJ; 150-cm long) were used to provide the following DLI treatments: 2.2, 3.7, 6.5, or 9.7 mol m^{-2} d^{-1} (52, 85, 150, or 225 µmol m^{-2} s^{-1} for 12 h d^{-1} from 0600 to 1800 h). The experiment was conducted in two growth chambers, each with two shelving units (1.8-m tall, 1.8-m wide, and 0.6-m deep). Each shelving unit had four shelves (individual replicates, 0.4-m tall, 1.4-m wide, and 0.6-m deep), and each shelf had one of four randomly assigned DLI. The broadband LED modules had peak wavelengths of 660 and 450 nm and provided 12% blue, 18% green (500–600 nm), and 70% red light (measured with a spectroradiometer). Target PPF was achieved by varying the number of energized lamps within a compartment. The set point for ambient CO_2 and RH were 400 ppm and 70%, respectively. Ambient temperature was set at 22 °C, and the recorded air temperature (day/night) during the experiment was 24.7 ± 1.2 °C/21.7 ± 0.8 °C, measured with a temperature logger. Plants were irrigated with 280 mL tap water every time their container weighed less than 380 g (approx. average weight at which containers were at 50% container capacity). Plants in containers under 2.2, 3.7, 6.5, and 9.7 mol m^{-2} d^{-1} received 1040, 1040, 1320, and 1880 mL of water, respectively. The experiment was terminated 7 wk after sowing (i.e., 4 wk of treatment), and data collected were the same as previously described.

Because of differences in DLI and other details between Experiments 2 and 3, regression analysis was performed by experiment on data for leaf temperature, SPAD index, leaf length, and shoot fresh and dry mass using SAS. Data for chlorophyll, carotenoid, anthocyanin, and nitrate content were analyzed by experiment with ANOVA as a randomized complete block design using SAS PROC GLIMMIX (SAS Institute, 2012). Random effects for the model in Experiment 2 were experimental replication and its interaction with block. Random effects for the model in Experiment 3 were growth chamber and its interaction with block. Treatment means were separated using Tukey's test at $P < 0.05$.

RESULTS AND DISCUSSION

Experiment 1

Light quality from the different lamps had no significant effect on leaf length, SPAD index, Chla and Chlb, carotenoids, anthocyanin, and nitrate content (Table 2). However, shoot fresh and dry mass were up to 20 and 23% higher in plants grown under LED compared with those grown under fluorescent lamps, which corresponds with the findings of others (Lin et al., 2013; Son and Oh, 2013; Stutte et al., 2009). Several studies have evaluated the effect of spectral quality on lettuce growth. Although Snowden et al. (2016) suggested that lettuce is highly sensitive to light intensity, but minimally sensitive to spectral quality, others have reported higher biomass accumulation under red or far-red enriched light (Chen et al., 2016; Mickens et al., 2018; Son and Oh, 2013; Wang et al., 2016). Similarly, green-light supplementation has been shown to enhance lettuce growth under sole-source lighting (Kim et al., 2004; Mickens et al., 2018). In our study, plants grown under 4000LED and 4100FLR were exposed to the highest percentages of red and far-red light (Table 1). However, both LED lamps emitted more green light than fluorescent lamps, which has been shown to penetrate deeper into leaves, resulting in higher CO_2 fixation of inner chloroplasts and thus, higher overall leaf photosynthesis compared to red or blue light (Sun et al., 1998; Terashima et al., 2009). Green light has also been shown to penetrate deeper into the foliar canopy when applied with other wavebands, and can therefore increase whole-plant photosynthesis by stimulating CO_2 fixation of inner- and lower-leaves when foliar canopies close (Frantz et al., 2000; Kim et al., 2004). We grew five plants in each container, which could have induced premature canopy closure. Canopy closure

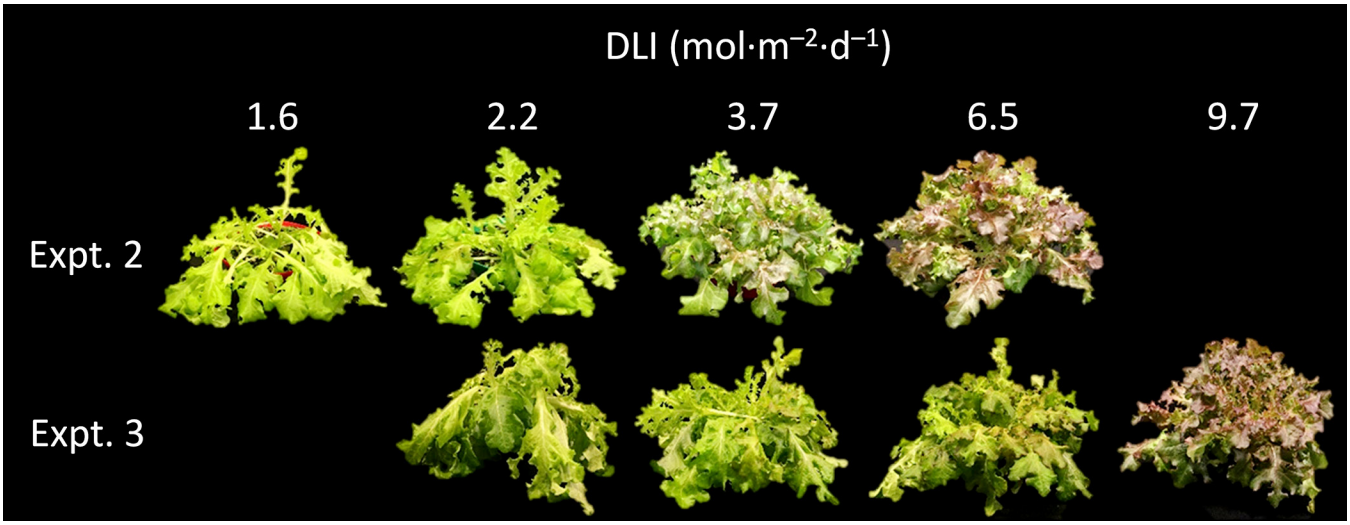

Fig. 2. Morphology of 'Red Salad Bowl' lettuce at harvest after exposure to 4 wk of different daily light integral (DLI) treatments provided by 4000-K light-emitting diode (LED) lamps (Expt. 2) or GreenPower LED production modules (Expt. 3).

coupled with the absorption of green photons by lower leaves might have increased the photosynthetic capacity of inner leaves,and thus, potentially increased biomass production under higher green light. Therefore, the higher percentage of green light emitted by both LED lamps may partially explain the highest fresh and dry mass accumulation of plants grown under LED compared with fluorescent lamps.

The LED lamps used in our study also emitted slightly higher ultraviolet radiation compared with the two fluorescent lamps (Table 1). Ultraviolet radiation has been shown to reduce plant biomass accumulation in lettuce, most likely as a response to the high metabolic cost of accumulating photoprotective compounds such as anthocyanins, which tend to increase in response to high energy radiation (Tsormpatsidis et al., 2008). Anthocyanins, which are responsible for the red pigmentation in red-leaf lettuce cultivars, have been suggested to offer an array of health-promoting benefits to consumers and are therefore considered to be a desirable qualitative trait in lettuce (Gazula et al., 2007; Owen and Lopez, 2015). However, the lack of differences in anthocyanin content measured in our study suggest that fresh and dry mass accumulation were not likely affected by low percentages of ultraviolet radiation levels in this experiment (Table 2). Furthermore, the lack of treatment differences for phytochemical constituents was unexpected, as plants grown under 65000FLR were exposed to ~10% more blue light compared to those grown under other treatments. Several studies have shown a positive correlation between blue light and anthocyanin and carotenoid content in lettuce leaves (Johkan et al., 2010; Li and Kubota, 2009; Owen and Lopez, 2015; Stutte et al., 2009; Tsormpatsidis et al., 2008). However, most of these studies have used monochromatic light applied as treatments. In contrast, all four of the treatments in our study provided broadband white light, which may have saturated the light-quality response of phytochemicals in leaves. Furthermore, potential specific waveband interactions within each light source may explain the lack of treatment differences in the concentration of anthocyanins, carotenoids, and Chla and Chlb measured in our study.

Yield photon flux (YPF), which weighs photons in the range from 360 to 760 nm according to plant photosynthetic responses, was highest under 4100FLR (Table 1) (McCree, 1971; Sager et al., 1988). In addition, leaves of plants grown under 4100FLR were ~1 °C warmer than those grown under other treatments (Table 2). Warmer leaves may be indicative of partial stomatal closure (Blonquist et al., 2009), which reduces transpiration and photosynthesis and may explain the lower growth under 4100FLR compared with the two LED treatments, even though YPF was highest under 4100FLR. Moreover, the highest percentage of blue light in 6500FLR might explain the growth reduction measured in plants grown under this treatment. Because approximately 20% of blue photons are absorbed by inactive pigments, their energy is not efficiently transferred to reaction centers, significantly reducing the quantum yield of absorbed blue photons (Barnes and Bugbee, 1992). The lower quantum yield is most likely responsible for the lowest fresh and dry mass accumulated under 6500FLR.

Experiments 2 and 3

For both experiments, increasing DLI resulted in higher shoot fresh and dry mass (Fig. 2, 3), which demonstrates that active growth occurred after plants were transferred to an indoor environment for 4 wk. Many studies have reported that increasing DLI promotes lettuce growth (Both et al., 1997; Fu et al., 2012; Johkan et al., 2010; Stagnari et al., 2015; Yanagi et al., 1996). It is typically assumed that a 1% reduction in light intensity will reduce production (harvestable yield) of edibles by 1% (Dorais, 2004), and lettuce growth therefore tends to be highly correlated with DLI. The ratios from high to low DLI of 4.1 (6.5/1.6 mol m^{-2} d^{-1}) and 4.4 (9.7/2.2 mol m^{-2} d^{-1}) in Experiments 2 and 3, respectively, resulted in six- and threefold increases in shoot dry mass (3.4/0.6 and 10.0/3.0 g). However, in both experiments, the increase in shoot fresh and dry mass was

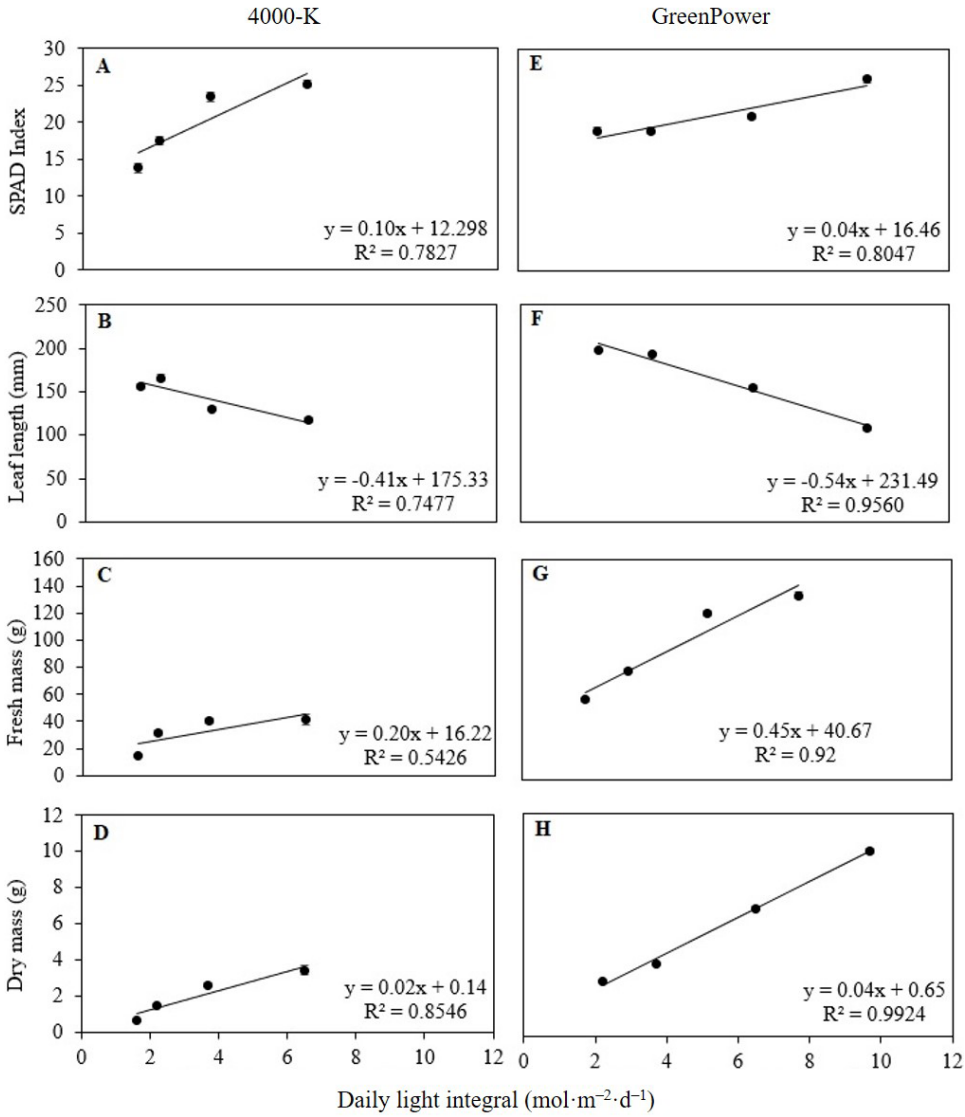

Fig. 3. Effect of daily light integral (DLI) provided by 4000-K light-emitting diode (LED) lamps in Experiment 2 (A-D) or GreenPower LED production modules in Experiment 3 (E-H) on chlorophyll content in leaves by the chlorophyll meter (Soil Plant Analysis Development, SPAD index), leaf length, shoot fresh and dry mass of 'Red Salad Bowl' lettuce. Each data point shows the mean of four treatment replicates (n = 4).

higher from the second to the third DLI, relative to the values measured from the third to the fourth DLI, which suggests that growth became limited under the highest DLI. Light interception, nutrient availability, and/or plant age may have contributed to reducing the extent of dry mass accumulation under the highest DLI. The combination of high planting density (five plants in each container for Experiment 2, and three plants in each container for Experiment 3), in addition to more growth produced under higher DLI, might have induced premature mutual shading which could have affected the growth rate under the highest DLI. Light interception plays a critical role in radiation capture, and limiting radiation interception due to mutual shading has been shown to significantly reduce growth (Bugbee, 2016). Additionally, the fact that a single dose of fertilizer was preplant incorporated to the substrate might have resulted in premature nutrient depletion under the highest DLI, where plants grew at a faster rate compared with those grown under other treatments. Furthermore, because the light treatments started 5 (Experiment 2) or 3 (Experiment 3) wk after sowing, it is likely that plants grown under the highest DLI approached the end of their exponential growth phase faster than those grown under smaller DLI. Therefore, potential growth may have been limited by the time the experiments were terminated.

Increasing DLI with higher PPF decreased leaf length in both experiments (Fig. 2, 3). Galieni et al. (2015) reported a similar decrease in lettuce leaf length with an increase in PPF from 200 to 1300 μmol m^{-2} s^{-1}. Kitaya et al. (1998) also measured shorter lettuce leaves with higher PPF. Similar to blue-light responses, high light intensities have been shown to reduce leaf area expansion, which could be related to leaf elongation (Hogewoning et al., 2010). In contrast, leaf elongation under low-light intensities can be the result of a shade-avoidance response, in an effort to increase radiation capture by plants (Snowden et al., 2016). Also, leaves grown under low

Table 3. Quality attributes of 'Red Salad Bowl' lettuce grown for four weeks under different daily light integrals (DLI) provided by 4000-K light-emitting diode (LED) lamps.

DLI	Total chlorophyll	Carotenoids	Anthocyanin	Nitrate
mol m^{-2} d^{-1}		µg/g FM†		µg/g DM†
1.6	0.94 c‡	0.12 c	0.01 b	110 a
2.2	1.42 b	0.20 b	0.10 b	95 a
3.7	1.79 ab	0.24 ab	0.17 b	24 b
6.5	1.92 a	0.27 a	0.42 a	15 b

† FM = fresh mass; DM = dry mass.

‡ Mean within columns with different letters are significantly different by Tukey's HSD test at $P \leq 0.05$.

Table 4. Quality attributes of 'Red Salad Bowl' lettuce grown for four weeks under different daily light integrals (DLI) provided by Philips GreenPower LED production modules.

DLI	Total chlorophyll	Carotenoids	Anthocyanin	Nitrate
mol m^{-2} d^{-1}		µg/g FM†		µg/g DM†
2.2	0.90 b‡	0.14 c	0.04 c	94 a
3.7	0.85 b	0.14 c	0.08 bc	106 a
6.5	1.05 b	0.17 b	0.17 b	57 b
9.7	1.28 a	0.22 a	0.65 a	32 c

† FM = fresh mass; DM = dry mass.

‡ Mean within columns with different letters are significantly different by Tukey's HSD test at $P \leq 0.05$.

light tend to be thinner than those grown under high light to maximize photosynthetic light harvesting by positioning chloroplasts closer to the epidermis (Vogelmann, 1993). Although leaf area and thickness were not measured in our study, plants grown under lower DLI had visibly larger and thinner leaves compared to those grown under high light (Fig. 2). Despite apparent adaptive efforts to maximize radiation capture under lower DLI, increasing PPF increased growth rates of plants to a larger extent than the ability of plants to adapt to lower DLI.

Lettuce aesthetic and nutritional quality was significantly improved as DLI increased in both experiments (Table 3, 4). As shown in Figure 2, regardless of the experiment, plants grown under the lowest DLI were chlorotic and etiolated, which is typically the result of light starvation. In contrast, firmness and red pigmentation of leaves were visibly enhanced under the highest DLI. Gaudreau et al. (1994) reported that low light levels result in the formation of loose lettuce heads with low fresh mass, which correspond with our visual assessment and quantitative results (Fig. 2, 3). Furthermore, red pigmentation of lettuce leaves is a key component that influences consumer perception of product quality, as it is typically associated with higher anthocyanin content in the foliage (Gazula et al., 2007; Owen and Lopez, 2015; Ryder, 1999). When comparing results for the lowest and highest DLI evaluated in our study, anthocyanin content increased with increasing DLI by 4100% in Experiment 2, and by 1525% in Experiment 3. Similarly, total chlorophyll and carotenoid content increased by 104 and 125%, and by 42 and 57%, respectively, in Experiments 2 and 3. In addition, SPAD index linearly increased in response to DLI. In contrast, nitrate content generally decreased with decreasing DLI from 110 to 15 µg mL^{-1} in Experiment 2, and from 106 to 32 µg mL^{-1} in Experiment 3.

Darker leaves tend to result in higher SPAD index readings and are commonly associated with higher chlorophyll concentration per unit leaf area (León et al., 2007). As mentioned before, leaf color can influence consumer perception of lettuce quality. Therefore, darker leaves with higher SPAD index and more total chlorophyll content, as the ones produced under the highest DLI, are most likely to satisfy the indoor-gardening experience (Fig. 2, 3; Table 3, 4). Similar to our findings, Snowden et al. (2016) reported a significant increase in lettuce chlorophyll content with higher light intensities, and explained that under low light conditions, plants typically adapt by reducing chlorophyll concentration per unit leaf area. Moreover, others have shown that carotenoid and anthocyanin content of lettuce increase in response to light intensity, increasing the plant's nutritional value (Richards et al., 2004; Stagnari et al., 2015; Voipio and Autio, 1995). Like anthocyanins, higher carotenoid concentration is an important quality attribute, as it has been shown to delay age-related eye diseases (Mou, 2005). In contrast, high nitrate content is a negative nutritional quality factor of lettuce and has been implicated with increasing the risk of methemoglobinemia and gastric cancer (Bruning-Fann and Kaneene, 1993). As found in our study, nitrate accumulation in lettuce leaves tends to increase under low light conditions (Bian et al., 2018; Blom-Zandstra and Lampe, 1985; Escobar-Gutierrez et al., 2002; Samuolienė et al., 2009). As suggested by Blom-Zandstra and Lampe (1985), nitrate serves as an osmotic regulator under low light intensities, which helps compensate for the shortage of carbohydrates resulting from suboptimal photosynthesis. A recent European Food Safety report stated that the recommended nitrate content in lettuce is <500 µg g^{-1} dry mass (DM), which is above the nitrate content measured in any of our treatments. Overall, phytochemical constituents and nitrate content were negatively affected with decreases in DLI. However, nitrate values under the highest DLI were within ranges that have been commonly reported in the literature under higher DLI (Bian et al. 2018; Li and Kubota, 2009).

CONCLUSIONS

Although lettuce grown under LED lamps produced more shoot fresh and dry mass than those grown under fluorescent lamps, all the light sources evaluated in our study resulted in comparable growth and quality attributes. Based on our findings, consumers interested in indoor gardening could install different kinds of off-the-shelf broadband white lamps to provide adequate aesthetic and nutritional quality of pick-and-eat lettuce plants, assuming that the distribution of spectral quality of the lamps is similar to the ones used in our experiment. In addition, our results suggest that consumers should provide at least 6.5 mol m^{-2} d^{-1} of photosynthetic light to grow lettuce plants indoors, although 9.7 mol m^{-2} d^{-1} would be preferable to increase growth, nutritional attributes, and

visual appeal. Daily light integrals below 6.5 mol m^{-2} d^{-1} could greatly compromise growth and quality of pick-and-eat lettuce, potentially leading to an unsuccessful consumer experience. In an effort to address the needs of an emerging trend for indoor-food gardening, we have begun to characterize the minimum light requirements to grow lettuce plants indoors. Further work is needed to provide baseline information about minimum environmental requirements compared to commercial standards, and market research is needed to identify consumer preferences for acceptable yield and quality when finishing vegetable transplants in an indoor environment. Further work should also track consumer attitude towards using different DLI and light sources within a residential setting.

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