

Growth and Photosynthetic Capacity of Basil Grown for Indoor Gardening under Constant or Increasing Daily Light Integrals

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ADDITIONAL INDEX WORDS. hydroponics, noncommercial production, *Ocimum basilicum*, pick-and-eat, sole-source lighting

SUMMARY. In the quest to identify minimum daily light integrals (DLIs) that can sustain indoor gardening, we evaluated DLIs less than the recommended ranges for commercial production of basil (*Ocimum basilicum*). Experiments were conducted for 8 weeks to evaluate the effect of providing a constant vs. an increasing DLI over time (DLI_{Inc}) on growth and photosynthetic capacity of green ('Genovese Compact') and purple ('Red Rubin') basil grown hydroponically under a constant ambient temperature of 21 °C. Plants were grown under a 14 h·d⁻¹ photoperiod and were subjected to the following DLI treatments: 4 (DLI₄), 6 (DLI₆), 8 (DLI₈), or 10 (DLI₁₀) mol·m⁻²·d⁻¹ (80, 119, 159, and 197 μmol·m⁻²·s⁻¹, respectively); DLI_{Inc} was used as a fifth treatment and was achieved by transitioning hydroponic systems systematically to treatments with greater DLIs every 2 weeks. In general, regardless of cultivar, leaf area, leaf number, and overall growth [shoot fresh weight (SFW) and shoot dry weight (SDW)] were similar for plants grown under DLI_{Inc} to DLI₄ and DLI₆ during weeks 2, 4, and 6. However, plants grown under DLI_{Inc} produced the same leaf area as those grown under DLI₁₀ at week 8. Nonetheless, across weeks, growth was significantly less under DLI_{Inc} compared with DLI₁₀, but similar to that produced by DLI₈ at week 8. Photosynthetic responses were significant only at week 8, for which leaves of plants grown under DLI₈, DLI₁₀, and DLI_{Inc} had 15% to 25% greater maximum gross carbon dioxide (CO₂) assimilation (A_{max}) than plants grown under DLI₄. The light saturation point of photosynthesis was unaffected by DLI, but showed a general increasing trend with greater DLIs. Overall, our results suggest that providing a constantly high DLI results in greater growth and yield than increasing the DLI over time. In addition, we found that changes in A_{max} and the light saturation point are not good indicators of the capacity of whole plants to make use of the available light for photosynthesis and growth. Instead, morphological and developmental traits regulated by DLI during the initial stages of production are most likely responsible for the growth responses measured in our study.

The increasing preference for living within city limits poses unique challenges for the continued development of productive green spaces. Indoor food gardening,

which integrates edible production with indoor farming at a noncommercial scale, provides an opportunity to support the gardening experience for consumers with limited access to production resources such as space and fertile soil. According to an industry group, indoor food gardening is one of the fastest growing trends in horticulture (Garden Media Group, 2017). Compared with outdoor gardening in

public spaces, indoor food gardening has received limited research attention despite its potential to help overcome common challenges affecting outdoor food gardening (e.g., unpredictable weather, weeds). In addition, indoor food gardening may increase access to fresh fruits and vegetables and can help foster a positive shift toward healthier food choices (Kalich et al., 2009; Kortright and Wakefield, 2011). Information is lacking to support small-scale indoor food gardening, as research-based recommendations for commercial indoor plant production typically aim to maximize productivity under optimal environmental conditions, which are difficult to replicate in an indoor environment designed for human comfort.

Consumers interested in indoor food gardening (from now on referred to as "indoor gardeners") tend to produce leafy greens (e.g., salad greens and microgreens) and culinary herbs, because they are fast-growing crops that require fewer inputs (e.g., fertilizer and water) and less maintenance compared with most fruiting crops (Di Gioia and Santamaria, 2015). Among them, basil is the most popular culinary herb because it can be cultivated for fresh, dry, or processed consumption. In addition, basil can be used as an ornamental or medicinal plant, increasing its appeal to indoor gardeners (Barbalho et al., 2012; Dou et al., 2018).

Recommended DLIs for commercial basil production range between 13 and 35 mol·m⁻²·d⁻¹ (Beaman et al., 2009; Dou et al., 2017; Moya et al., 2014; Somerville et al., 2014; Walters and Currey, 2018). However, when using cool-white fluorescent lamps in an indoor environment not designed for plant production, the recommended light intensity for human comfort and function

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Units

To convert U.S. to SI, multiply by	U.S. unit	SI unit	To convert SI to U.S., multiply by
29.5735	fl oz	mL	0.0338
3.7854	gal	L	0.2642
2.54	inch(es)	cm	0.3937
6.4516	inch ²	cm ²	0.1550
0.0254	mil(s)	mm	39.3701
1	mmho/cm	dS·m ⁻¹	1
1	mmho/cm	mS·cm ⁻¹	1
28.3495	oz	g	0.0353
1	ppm	mg·L ⁻¹	1
(°F - 32) ÷ 1.8	°F	°C	(°C × 1.8) + 32

is $\approx 7 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, resulting in a DLI of $0.6 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ using a 24 h·d⁻¹ photoperiod [adapted from U.S. General Services Administration (2013)]. Similarly, based on data we collected in multiple strategic locations within office, residential, and classroom environments, indoor light intensities using common electric lamps [e.g., fluorescent or light-emitting diode (LED) bulbs] can range from 5 to $1500 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, depending on the time of day and proximity to a lamp or sunlit location (e.g., window). These examples illustrate the need to supplement light for indoor food gardening of crops like basil, if grown in spaces that do not receive continuous direct sunlight.

Although studies have compared growth and quality responses of edible plants grown with sole-source lighting under different DLIs (Beaman et al., 2009; Dou et al., 2017, 2018; Ferreira Fernandes et al., 2013; He et al., 2001; Walters and Currey, 2018), most research has been conducted to address the needs of commercial growers who aim to maximize yield. Therefore, leafy greens for commercial production are typically grown with target DLIs in the range of 10 to $20 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$, whereas $30 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ are commonly targeted when producing fruiting crops like tomato [*Solanum lycopersicum* (Beaman et al., 2009; Dorais et al., 2017; Kang et al., 2013)]. However, providing DLIs in those ranges is not likely to be a feasible strategy by indoor gardeners because 1) the recommended light intensity for human comfort results in less than $1 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ of light and 2) the cost for fixture installation and maintenance to provide sole-source lighting is not expected to result in an economic return and may limit the willingness of consumers to invest in lamps and electricity (Halleck, 2018; U.S. General Services Administration, 2013). Moreover, it is important to understand that most indoor gardeners are motivated by their desire to be actively involved in the growing and harvesting process and, thus, may be satisfied with having a reliable harvest for their personal use (Gao et al., 2009; Kortright and Wakefield, 2011). Therefore, DLIs that result in a constant supply of high-quality fresh produce, as opposed to those that maximize yield and profits, may be adequate to

satisfy the motivation for indoor gardeners. Paz et al. (2019) recently showed that less than half the recommended DLI for commercial lettuce (*Lactuca sativa*) production is sufficient to maintain pick-and-eat plants with adequate nutritional qualities. Thus, through the use of DLIs below the recommended ranges for commercial production, one of our goals was to identify minimum DLIs that could sustain basil production for indoor gardeners.

Changes in DLI over time

Typically, the lighting strategy for commercial plant production indoors consists of adjusting the DLI during different plant stages, such as seedling, flowering, fruiting, or finish (Currey et al., 2017). However, the duration of these stages and the DLI requirements are crop specific and not always reported in the literature. Limited research has been conducted that evaluates the effect of a DLI_{Inc}. Studies with ornamental plugs have shown that providing a DLI_{Inc} can result in similar SDW and leaf number compared with providing a constantly high DLI (Lopez and Runkle, 2008; Oh et al., 2010). However, few studies report plant growth under changing DLIs for edible crop production. Brechner and Both (2013) suggested that to maximize hydroponic lettuce yield indoors, a seedling stage of 11 d requires $22 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ using a 24 h·d⁻¹ photoperiod, whereas a finish stage of 24 d requires $17 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ using a 20 h·d⁻¹ photoperiod. However, van Iersel (2017) proposed that tailoring the intensity of light according to crop-specific photosynthetic efficiency could prove to be more beneficial than providing a set photosynthetic photon flux (PPF) at predefined developmental stages. The author described the use of dynamic lighting by controlling PPF precisely with dimming in response to certain physiological parameters, ultimately providing an opportunity for energy savings when producing high-value crops indoors. Similarly, Poulet et al. (2014) found that increasing DLI systematically as lettuce plants grow and develop can help reduce energy costs associated with sole-source lighting. Both aforementioned studies suggest that manipulating the light environment during the crop cycle can help optimize energy

efficiency and plant productivity using electric lamps. Therefore, another goal of this study was to evaluate the use of DLI_{Inc} to determine whether plants grown under limited DLIs during the initial stages of production could be as productive as those grown constantly under higher DLIs.

Based on our two goals, the objective of this study was to quantify and compare growth and photosynthetic capacity over time of two basil cultivars grown hydroponically under constant (4, 6, 8, or $10 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) or increasing (from 4 to $10 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) DLIs. We hypothesized that basil plants grown under DLI_{Inc} would have a similar yield compared with those grown under a constant DLI of $10 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$. We further hypothesized that plants produced under lower DLIs (4 or $6 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) would make more efficient use of the available light than those grown under higher DLIs (8 or $10 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$), for which light-response curves were measured to determine the light saturation point of photosynthesis and A_{max} , as two potential indicators of the photosynthetic capacity of leaves.

Materials and methods

PLANT MATERIAL AND GROWING CONDITIONS. Seeds of green ‘Genovese Compact’ and purple ‘Red Rubin’ basil (Johnny’s Selected Seeds, Winslow, ME) were sown into 98-plug sheets (individual cell volume, 55 mL) of rockwool (A-Ok starter plugs; Grodan, Roermond, The Netherlands) and germinated inside a walk-in growth chamber (C6 Control System with EcoSys Software; Environmental Growth Chambers, Chagrin Falls, OH) at 21 °C, 400 ppm of CO₂, and 70% relative humidity (RH). Until germination occurred, plants were irrigated as needed with tap water that had an electrical conductivity (EC) of $0.4 \text{ mS}\cdot\text{cm}^{-1}$, a pH of 8.3, and $40 \text{ mg}\cdot\text{L}^{-1}$ calcium carbonate alkalinity.

At 15 d after sowing, uniform seedlings were selected and the experiment was initiated. Four seedlings were transplanted into a single deep-water culture hydroponic system using 2-inch-diameter net cups. Each 2-gal hydroponic system (23 cm wide × 23 cm long × 19 cm tall) was rust colored and had a white plastic lid with four openings (20 cm apart) that

held one net cup each. A clear plastic tube attached to an air pump (320 GPH, Dual Diaphragm Air Pump; General Hydroponics, Santa Rosa, CA) provided continuous aeration. Bamboo stakes (40 cm tall) were used to provide physical support for the plants, which were secured as needed with twist ties. Plants were grown for 8 weeks inside two walk-in growth chambers (C6 Control System), each equipped with two opposite shelving units with two experimental compartments (61 cm wide \times 183 cm long \times 94 cm tall). Each compartment had a unique lamp setup to create different light intensities. For each constant DLI treatment, four hydroponic systems (two per cultivar) were maintained permanently within each compartment. For the DLI_{inc} treatment, four systems (two per cultivar) were moved to different compartments every 2 weeks (as described under “Treatments”). Within each chamber, constant ambient temperature, CO₂ concentration, and RH were set at 21 °C, 400 ppm, and 70%, respectively.

TREATMENTS. The light treatments consisted of four target DLIs: 4 (DLI₄), 6 (DLI₆), 8 (DLI₈), and 10 (DLI₁₀) mol·m⁻²·d⁻¹, which were achieved by using *PPFs* of 80, 119, 159, and 197 \pm 5 μ mol·m⁻²·s⁻¹, respectively, and a constant 14 h·d⁻¹ photoperiod (0600 to 2000 HR). DLI_{inc} was used as a fifth treatment, which was achieved by moving two hydroponic systems per cultivar systematically to a treatment with a greater DLI every 2 weeks (starting with DLI₄ and ending with DLI₁₀). A light map was generated before treatment initiation to determine the maximum *PPF* at mid-canopy height using a spectroradiometer (SS-110; Apogee Instruments, Logan, UT). The target *PPFs* were provided by broad-spectrum LED lamps, where 93% of the *PPF* was delivered by lamps with a fixed output (GreenPower; Signify United States, Somerset, NJ) and 7% by lamps with dimmable settings (RAY66 lamps; Fluence Bioengineering, Austin, TX). The light output to achieve a target *PPF* and a uniform spectral distribution was controlled by adjusting the number of lamps and/or the dimmer settings (Fig. 1). Light pollution (<5 μ mol·m⁻²·s⁻¹) within treatments was minimized by covering the sides and

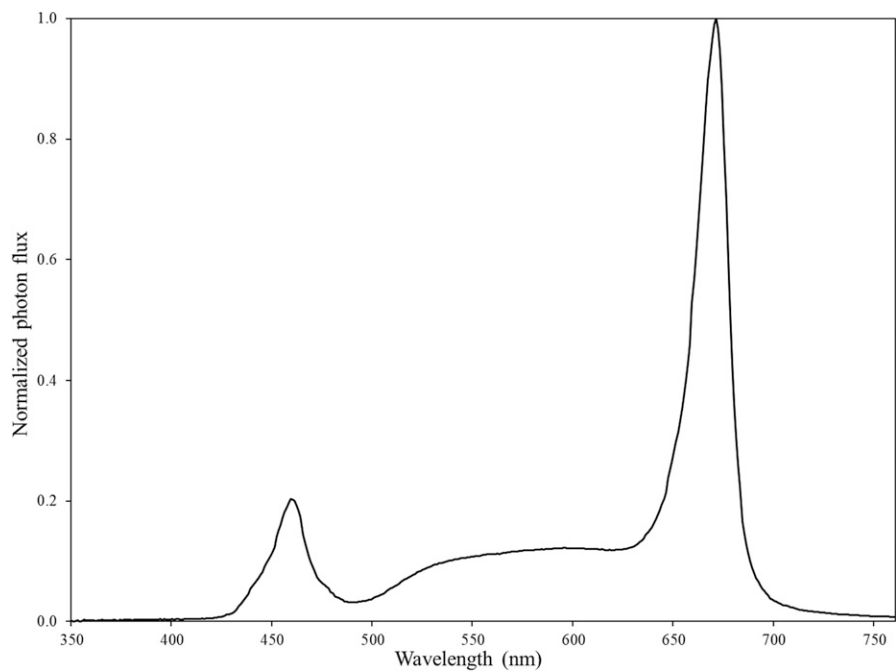


Fig. 1. Normalized spectral power distribution of the lamps used in the experiment. Photon flux (μ mol·m⁻²·s⁻¹) was measured for every 1 nm.

back of the shelves with a double layer of 6-mil-thick black and white polyethylene film (white side facing the plants). A black and white polyethylene film curtain (215 cm long \times 200 cm tall) was used to prevent light pollution between the two opposite shelves (black side facing the plants). The curtain was placed in the middle of each chamber, 30 cm apart from the shelves to allow for sufficient air circulation. In addition, a foam board was placed at the bottom of each compartment to provide insulation from the metallic shelves. All hydroponic systems within each treatment were rotated randomly daily to minimize location effects within the experimental area.

Plants had a complete nutrient solution replacement 4 weeks after treatment initiation. The nutrient solution consisted of a two-part liquid fertilizer mix with different nitrogen (N), phosphorous (P), and potassium (K) quantities. Plants within one system were fertilized with 20 mL 4N-0P-0.8K and 20 mL 2N-1.3P-5.8K (Root Farm Nutrients; Hawthorne Gardening Co., Marysville, OH) to obtain a concentration of 231 mg·L⁻¹ N. EC and pH of the nutrient solution were monitored weekly with an EC and pH meter (HI 9813-6N waterproof; Hanna Instruments, Carrollton, TX) to ensure that values

were maintained within recommended ranges for basil (1.0–1.6 dS·m⁻¹ EC and 5.5–6.5 pH) (Moya et al., 2014; Somerville et al., 2014). Near-canopy air temperature was measured with one type-K thermocouple (diameter, 0.1 mm) placed in the middle of every compartment underneath a leaf located at mid-canopy height. Thermocouples were interfaced to a multiplexer (AM16/32B; Campbell Scientific, Logan, UT) and data were recorded with a data logger at 10-min intervals (CR1000; Campbell Scientific). The mean \pm SD of near-canopy air temperature values recorded throughout the experiment and averaged across replications were 20.8 \pm 1.2, 21.1 \pm 1.1, 21.3 \pm 1.1, and 21.5 \pm 1.3 °C for DLI₄, DLI₆, DLI₈, and DLI₁₀, respectively.

DATA COLLECTED. Photosynthetic light–response curves were measured before destructive harvests at weeks 4, 6, and 8 after treatment initiation. Because leaves were too small (<6 cm²) to measure at week 2, light–response curve data were not collected. Measurements were made on one plant per system per treatment. Data were collected using a portable photosynthesis system (LI-6400xt; LI-COR Biosciences, Lincoln, NE) under six different *PPFs* (600, 400, 200, 100, 75, and 0 μ mol·m⁻²·s⁻¹). The reference CO₂

concentration, leaf temperature, and flow rate inside the chamber were $400 \pm 5 \mu\text{mol}\cdot\text{mol}^{-1}$, $21 \text{ }^\circ\text{C}$, and $500 \text{ mL}\cdot\text{min}^{-1}$, respectively. Data were fitted to the following model equation (Jurik et al., 1988):

$$A_{\text{net}} = -R_d + \frac{\theta \times PPF + A_{\text{max}} - \sqrt{(\theta \times PPF + A_{\text{max}})^2 - 4\theta \times PPF \times k \times A_{\text{max}}}}{2k}$$

where A_{net} is the net CO_2 assimilation rate, R_d is dark respiration, θ is the quantum use efficiency, PPF is the incident irradiance, A_{max} is the maximum gross CO_2 assimilation (light-saturated net CO_2 assimilation + R_d), and k is the curvature factor describing the convexity of the curve (range, 0–1). The light compensation point and light saturation point were calculated as the PPF -associated photosynthetic rates when $A_{\text{net}} = 0$ and $A_{\text{net}} = A_{\text{max}} \times 0.90$, respectively (Jurik et al., 1988).

For each cultivar, one plant per system per treatment was harvested destructively every 2 weeks. Shoots were cut at the base of the stem near the substrate plug. The number of leaves (>1 cm) per plant was counted and total leaf area was measured using a leaf area meter (LI-3100C, LI-COR Biosciences). Shoots (stem and leaves) and roots were weighed separately with an electronic balance to obtain SFW and root fresh weight (RFW), respectively. Tissue was oven-dried at $70 \text{ }^\circ\text{C}$ for 72 h to determine SDW and root dry weight (RDW), respectively.

DATA ANALYSIS. Within each chamber, data from the two hydroponic systems per cultivar per treatment were pooled and averaged to be used as a single data point. Each treatment \times cultivar combination was replicated two times in space (once within each growth chamber) and twice over time. All lighting treatments were rerandomized within each chamber before the start of the second replication over time. In our statistical model, random effects were experimental replication and its interaction with treatment and cultivar. The treatment \times cultivar interaction was not significant ($P > 0.05$); thus, pairwise comparisons for the main effect treatment means were used for the analyses ($n = 8$). A regression analysis was conducted to compare growth trends measured for plants

grown under all constant DLI treatments (DLI_4 , DLI_6 , DLI_8 , and DLI_{10}) using SigmaPlot (version 13.0; Systat Software, San Jose, CA). For each response variable, we evaluated both a linear and a quadratic fit; a linear fit was chosen as the appropriate model based on the r^2 value. A nonrectangular hyperbola was used to fit the light–response curve data using the nonlinear fitting procedure of SAS (version 9.4; SAS Institute, Cary, NC). However, because we were unable to measure light–response curves at week 2 and thus, only three data points were available, we chose not to use a regression analysis. Growth and light–response curve data comparing DLI_{Inc} to all other treatments were analyzed using a Dunnett test with JMP (version 12, SAS Institute). Graphs for week 2 are not shown in Fig. 2 because data points were orders of magnitude less than those at weeks 4, 6, and 8. However, where appropriate, trends for week 2 are described throughout the Results section.

Results

GROWTH RESPONSES. Except for leaf number at week 2 and RDW at week 4, all growth variables increased linearly in response to DLI_{Inc} (Fig. 2). There were no significant differences in leaf number between DLI_{Inc} and all other treatments at week 2 (data not shown). However, DLI_8 and DLI_{10} had 71%, 48%, and 36%; and 107%, 116%, and 163% more leaves than DLI_{Inc} at weeks 4, 6, and 8, respectively. In addition, DLI_6 produced significantly more leaves than DLI_{Inc} at week 4, and plants grown under DLI_{10} had 156%, 140%, and 198% larger leaves than DLI_{Inc} at weeks 2, 4, and 6, respectively. Leaf area was significantly smaller for plants grown under DLI_{Inc} compared to those grown under DLI_8 and DLI_{10} at week 2. However, at week 8, leaf area was similar among DLI_6 , DLI_8 , DLI_{10} , and DLI_{Inc} . In addition, DLI_{Inc} produced 73% larger leaves than DLI_4 at week 8.

Except for week 2, responses for SFW and SDW showed similar trends across weeks (Fig. 2). We found that, in general, DLI_{10} produced significantly more SFW and SDW than DLI_{Inc} , with percentage increases ranging from 40% to 181% and 45%

to 227%, respectively. Similarly, except for SDW at week 2, plants grown under DLI_8 were generally larger than those grown under DLI_{Inc} at weeks 2, 4, and 6. Nonetheless, DLI_4 produced 62% and 53% less SFW and SDW, respectively, compared with DLI_{Inc} at week 8. No significant differences were measured for RDW between DLI_{Inc} and all other treatments at weeks 2, 4, and 8. However, DLI_{10} produced almost three times the RDW than DLI_{Inc} at week 6.

PHYSIOLOGICAL RESPONSES. Except for week 8, no treatment differences were measured for dark respiration, A_{max} , and the light compensation point (Table 1). At week 8, dark respiration for plants grown under DLI_8 and DLI_{10} was up to 56% and 78% greater than that for plants grown under DLI_4 and DLI_6 , respectively. Also at week 8, plants grown under DLI_8 , DLI_{10} , and DLI_{Inc} had 25%, 20%, and 15%, respectively, greater A_{max} values compared to those grown under DLI_4 . In addition, at week 8, the light compensation point for plants grown under DLI_8 , DLI_{10} , and DLI_{Inc} was significantly greater than that measured for plants grown under DLI_4 , ranging from 21.5 to $24.4 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. No treatment differences were measured for the light saturation point across weeks.

Discussion

Young plants with small leaves are not expected to have the same capacity for photosynthesis as mature plants with larger leaves that can capture radiation more efficiently (Nobel et al., 1975). Therefore, guidelines typically recommend lower DLIs to be used during propagation compared with production (Brechtner and Both, 2013; Currey et al., 2017; Poulet et al., 2014). Based on this general recommendation, one of our goals was to measure growth and development over time to evaluate the effects of DLI_{Inc} throughout the 8-week production cycle.

Our data indicate that by providing a DLI_{Inc} , basil plants were ultimately as productive as those grown under DLI_8 , with overall SFW and SDW ranging from 120 to 151 g and 10 to 12 g, respectively (Fig. 2). However, values for SFW and SDW of plants grown under

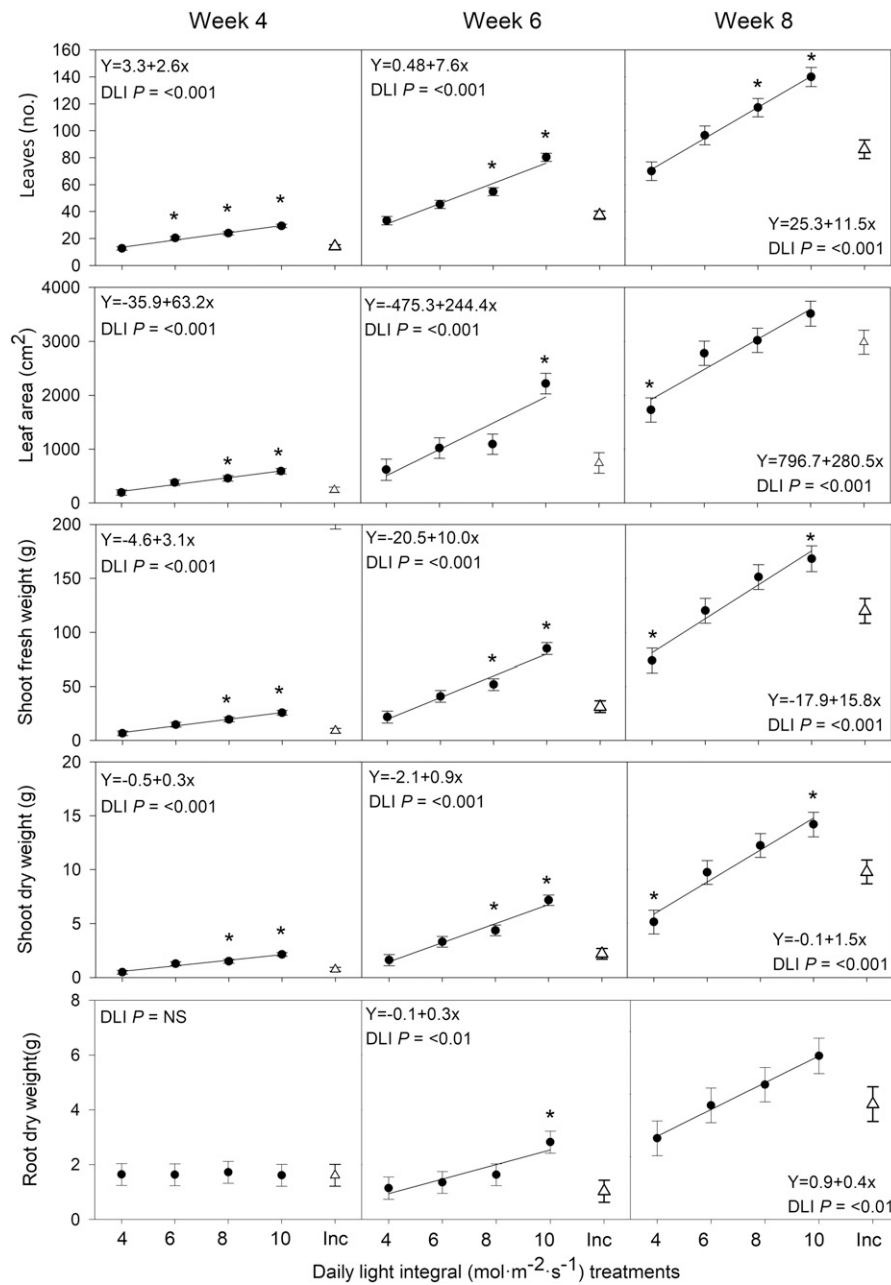


Fig. 2. Effect of daily light integral (DLI) on growth parameters for basil at different harvest dates. Plants were grown under one of four constant DLI treatments: 4, 6, 8, or 10 mol·m⁻²·d⁻¹, or an increasing DLI (Inc) (from 4 to 10 mol·m⁻²·d⁻¹, increased every 2 weeks). Black circles represent the mean ±SE of four replications and two cultivars: Genovese Compact and Red Rubin (n = 8). Asterisks (*) depict significant differences between Inc (white triangle) and all other treatments according to the Dunnett test (P ≤ 0.05); 1 cm² = 0.1550 inch², 1 g = 0.0353 oz.

DLI_{Inc} were consistently less than those of plants grown under DLI₁₀, even if at week 8, leaf area was similar between both treatments. Surprisingly, across weeks, plants grown under DLI₈ and DLI₁₀ had significantly fewer leaves than those grown under DLI_{Inc}. In addition, although not measured in our study, leaves of

plants grown under DLI_{Inc} were visibly thinner than those grown under DLI₁₀. In agreement with our observation, leaves that develop under light-limited environments tend to be irreversibly thin, which is an acclimation response that maximizes radiation captured across the leaf surface (Castro-Díez et al., 2000; Oguchi

et al., 2003; Peralta et al., 2002; Sims and Pearcy, 1992; Yamashita et al., 2000). Considering that shoot biomass production is, in general, directly proportional to leaf area, leaf thickness, and sometimes leaf number (Aranda et al., 2004), the DLI effect on leaf number and leaf thickness is most likely responsible for the biomass responses measured in our study.

Although it is likely that toward the end of the experiment, newly developed leaves of plants grown under DLI_{Inc} had similar traits (e.g., leaf area and thickness) as those grown under constantly greater DLIs, the limited DLI provided during the initial growth stages affected the overall growth capacity of plants grown under DLI_{Inc} (Fig. 2). Frak et al. (2001) showed that mature leaves developed under light-limited environments are able to adjust their photosynthetic capacity when exposed to high PPF values. Nonetheless, developmental limitations in response to low-light environments, such as leaf thickness, chloroplast abundance, and chlorophyll content, ultimately drive the capacity of plants to photosynthesize and produce biomass (Terfa et al., 2013). Therefore, in our study, providing constantly high DLIs was more beneficial than increasing the DLI over time, because it enabled plants to produce ultimately more biomass.

The regression analysis indicates that, in general, as DLI increased, growth increased linearly (Fig. 2). Across weeks, plants grown under DLI₈ and DLI₁₀ consistently produced more and larger leaves than those grown under lower DLIs (<6 mol·m⁻²·d⁻¹). Similar to our results, Ferreira Fernandes et al. (2013) reported linear or quadratic increases in the number of inflorescences, leaves, and RDW of basil plants when comparing growth under 10 vs. 20 mol·m⁻²·d⁻¹. Walters and Currey (2018) also found that edible yield of basil can increase linearly, with DLIs ranging from ≈7 to 19 mol·m⁻²·d⁻¹. However, Chang et al. (2008) reported no differences in biomass production for basil plants grown in a greenhouse under 13 or 25 mol·m⁻²·d⁻¹, but SFM, SDM, and leaf area were lowest under a DLI of 5 mol·m⁻²·d⁻¹. Similarly, Beaman et al. (2009) showed that basil grown under DLIs from 17 to 23 mol·m⁻²·d⁻¹ had no differences in plant height, canopy diameter,

Table 1. Photosynthetic parameters estimated from light-response curves measured at week (W) 4, 6, and 8 for basil plants grown in a growth chamber under one of five lighting treatments.

DLI treatment (mol·m ⁻² ·d ⁻¹) ^z	Dark respiration			Maximum gross CO ₂ assimilation			Light compensation point			Light saturation point		
	W4	W6	W8	W4	W6	W8	W4	W6	W8	W4	W6	W8
4	0.8 ^y	0.9	0.9	9.6	10.6	11.9*	12.8	16.4	17.9*	392.4	415.9	468.7
6	0.9	0.9	1.0	10.0	11.3	12.8	13.9	19.2	19.1	427.3	458.7	487.9
8	1.0	0.9	1.4	10.9	11.9	14.9	15.6	21.7	23.2	459.2	497.2	545.1
10	1.0	0.9	1.6	11.3	12.4	14.3	17.0	21.1	24.4	485.8	528.5	518.5
DLI _{Inc}	0.9	0.9	1.2	9.9	11.7	13.7	13.1	18.8	21.5	416.8	479.5	527.2

^zFour constant daily light integrals (DLIs): 4, 6, 8, or 10 mol·m⁻²·d⁻¹ or an increasing DLI [DLI_{Inc} (from 4 to 10 mol·m⁻²·d⁻¹, increased every 2 weeks)].

^yData represent the mean of four replications and two cultivars: Genovese Compact and Red Rubin (n = 8). Means within a column marked with an asterisk (*) are different from DLI_{Inc} based on the Dunnett test (P ≤ 0.05).

or yield. In our study, the *PPFs* used for the DLI treatments were significantly lower than those used by Beaman et al. (2009) and Chang et al. (2008). It is likely that the *PPF* values used in the aforementioned studies approached the light saturation point, and thus further increases in DLI had no positive effects in growth. In contrast, our results indicate that the *PPF* values used in our different DLI treatments were less than half the intensity that would saturate photosynthesis (Table 1), suggesting that growth and yield could increase further with greater *PPF* values.

Our findings are in agreement with studies indicating that DLI increases growth and yield linearly for crops with high-harvest indexes, such as leafy greens and herbs (Chang et al., 2008; Walters and Currey, 2018). Nonetheless, our data describe basil growth under DLIs less than those typically used for commercial production (Fig. 2). Therefore, our results are not directly comparable with most of the literature, which tends to report significantly greater yields as a result of greater DLIs. For example, Dou et al. (2017) produced 23 g fresh weight per plant when ‘Genovese Compact’ basil plants were grown for 3 weeks under DLIs in the range of 12 to 18 mol·m⁻²·d⁻¹. Similarly, Majkowska-Gadomska et al. (2017) reported that ‘Genovese’ basil plants grown in northern Europe inside a greenhouse without supplemental lighting from April through May can yield up to 330 g fresh weight per plant. In addition, Omobolanle Ade-Ademilua et al. (2013) reported that clove basil (*Ocimum gratissimum*) grown under full sunlight can yield 38 g fresh weight per

plant, which is almost double the yield of plants grown under 50% shade (20 g; duration of treatment not reported). Results from these studies indicate that greater DLIs can increase growth and yield of basil significantly, which is in agreement with our findings. However, our data are reflective of the limited DLI ranges used in our study.

In a study that compared two DLI treatments (7 vs. 15 mol·m⁻²·d⁻¹), Walters and Currey (2018) reported that ‘Red Rubin’ basil grown under 7 mol·m⁻²·d⁻¹ produced ≈143 and 9 g SFW and SDW, respectively, during a 4-week production cycle. Nonetheless, to our knowledge, no other studies have reported data that would support growth and yield of basil plants grown under DLIs less than those typically used for commercial production (<10 mol·m⁻²·d⁻¹). Thus, considering human comfort and limitations within spaces not designed for plant production purposes, our findings are relevant to consumers interested in producing edible crops for indoor gardening. In view that consumers typically purchase commercial packages of fresh sweet basil containing 20 to 55 g on average (based on locally available products), the SFW of plants produced under DLI_{Inc}, DLI₈, and DLI₁₀, which ranged from 120 to 168 g, could satisfy the needs of indoor gardeners who are likely to grow basil for pick-and-eat purposes. Furthermore, gradually increasing the DLI, as opposed to using a constant DLI of 8 mol·m⁻²·d⁻¹, might help reduce the energy costs associated with the use of electric lamps for indoor gardening (Poulet et al., 2014). However, this strategy could be considered time-consuming or

burdensome, because it may increase the effort of growing basil for indoor gardening.

Although not measured in our study, we observed that plants grown under DLI₁₀ produced more inflorescences than those grown under lower DLIs (<8 mol·m⁻²·d⁻¹). This is similar to what Ferreira Fernandes et al. (2013) reported, in that basil grown under 4, 7, 11, and 20 mol·m⁻²·d⁻¹ had an inflorescence dry weight of ≈0.5, 2.2, 9.3, and 14.7 g, respectively. Moccaldi and Runkle (2007) showed that by reducing *PPF* values, growers can delay flowering and extend the vegetative stage of *Salvia splendens* and *Tagetes patula*. Flowering of basil plants can accelerate the decline in quality attributes by inducing bitterness and reducing aroma (Barbalho et al., 2012; Raimondi et al., 2006). Considering that indoor gardeners tend to grow basil for edible purposes, lower DLIs might help prolong the vegetative stage of basil plants while maintaining visual appeal, which was considered acceptable across all treatments evaluated in our study (e.g., no chlorotic or etiolated tissue and adequate plant firmness).

Although the photosynthetic capacity of a single leaf cannot be extrapolated to our growth data, light-response curves were measured to help elucidate whether leaves developed under constantly high DLIs had a greater photosynthetic capacity compared to those grown under DLI_{Inc} (Table 1). In addition, calculated values from light-response curves helped determine the minimum light requirement to grow basil for indoor gardening. According to McDonald (2003), leaves developed under high light tend to have greater metabolic requirements than those

developed under low light. Therefore, to sustain the photosynthetic demand from high organelle activity, leaves acclimated to greater *PPF* values have greater dark respiration than those acclimated to lower *PPF* values (McDonald, 2003). Accordingly, our results show that at week 8, dark respiration for DLI_8 and DLI_{10} was up to 40% and 78% greater than that of plants grown under DLI_4 and DLI_6 , respectively (Table 1). Our findings are similar to those of Nemali and van Iersel (2004), who found a significant increase in dark respiration of wax begonia (*Begonia semperflorens-cultorum*) with greater *DLIs*. They suggested that a decrease in dark respiration in response to low *DLI* is an acclimation response that increases the net carbon gain of plants grown under limited light (Nemali and van Iersel, 2004).

As indicated by A_{max} , the photosynthetic capacity of plants was similar across treatments during weeks 4 and 6 (Table 1). Because no significant differences were measured at the leaf level for A_{max} throughout production, we can infer that morphological and developmental traits (e.g., leaf thickness, leaf number, and leaf area) regulated by *DLI* during the initial production stages are most likely responsible for the growth responses measured in our study. Thus, A_{max} is not a good indicator for the capacity of whole plants to make use of the available light for photosynthesis (Fig. 2). Nonetheless, our results show that at week 8, plants grown under DLI_8 , DLI_{10} , and DLI_{Inc} had 15% to 25% greater A_{max} than those grown under DLI_4 . Similar to our findings, Oguchi et al. (2003) reported that if herbs are transferred from low ($70 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) to high ($700 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) *PPF* values, A_{max} increases; however, values are not comparable to those from leaves developed under high *PPF* values. In addition, although new growth may adapt to greater *PPF* values, leaf thickness and leaf area of preexisting leaves do not change (Oguchi et al., 2003). Therefore, increases in photosynthetic capacity for leaves of plants transferred from a low to high *PPF* do not necessarily contribute to more growth, because increases in overall photosynthetic capacity of whole plants may be limited by anatomical, morphological, and physiological

characteristics of preexisting leaves (Baille et al., 1996; Fan et al., 2013; Sims and Pearcy, 1992).

Typically, values for the light compensation point and the light saturation point for plants grown under high light intensities are greater than those for plants grown under low light intensities, indicating that when grown under low *PPF* values, plants have a limited capacity to process absorbed light into photosynthetic products (Gu et al., 2008). Therefore, it was not surprising that the light compensation point at week 8 was the lowest for leaves developed under DLI_4 (Table 1). Although we found that the light saturation point was unaffected by *DLI*, the general trends indicate an increase in the light saturation point with greater *DLIs*, suggesting that as plants mature, their capacity to use light for photosynthesis increases. This corresponds with the findings of Nemali and van Iersel (2004), who showed that both the light compensation and light saturation points of wax begonia increased with greater *DLIs*, but the increases were not statistically significant. Similar to our results, Park et al. (2016) found that the light saturation point for basil grown under $200 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ is $\approx 500 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Photosynthesis at *PPF* values beyond the light saturation point is typically limited by CO_2 concentration, metabolism of triose phosphates, and/or rubisco activity, all of which can limit the efficiency of plants to use light (Ehleringer and Sandquist, 2010; von Caemmerer and Farquhar, 1981). This is in agreement with studies indicating that, although growth and yield continue to increase with *DLI*, light use efficiency is greater when plants are grown under lower *DLIs* (He et al., 2001; van Iersel, 2017). Accordingly, van Iersel (2017) showed that dynamic lighting (i.e., lighting adapted to crop-specific photosynthetic capacity) can help optimize energy use efficiency and plant productivity when plants are grown indoors with electric lamps. Low values for the light compensation point and the light saturation point could be beneficial for indoor gardening, because the *PPF* values required to promote photosynthesis could be provided by electric lamps at levels that are comfortable for the human eye (Halleck, 2018).

In conclusion, considering the differences in growth and development across weeks, providing a constantly high *DLI* is more beneficial for basil grown for indoor gardening than increasing the *DLI* over time because it increases yield. Because, in general, the light saturation point and A_{max} were unaffected by *DLI* throughout most of the production cycle, the capacity of individual leaves to photosynthesize is not a good indicator of the capacity of whole plants to make use of the available light for photosynthesis and growth. Instead, developmental and morphological traits regulated by *DLI* during the initial stages of production are most likely responsible for the biomass responses measured in our study.

Addressing the needs of the emerging indoor food gardening movement, we have begun to characterize the minimum light requirements to grow basil plants indoors. To ensure a positive experience for indoor gardeners, further work is needed to identify minimum *DLI* requirements for other crops, keeping in mind that fruiting crops may require significantly greater *DLIs* than leafy greens and culinary herbs. In addition, market studies would help elucidate consumer preferences for acceptable yield and quality, as well as knowledge gaps that limit a successful indoor food gardening experience. Well-established recommendations for commercial food production in controlled environments may not be appropriate or relevant for small-scale, noncommercial indoor gardeners. Instead, new approaches and strategies should be developed to help expand niche market opportunities for indoor plant production.

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