

# Longer Photoperiods with the Same Daily Light Integral Improve Growth of Rudbeckia Seedlings in a Greenhouse

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**Abstract.** Supplemental light can increase growth and accelerate production of greenhouse crops, but it can be expensive if not provided in a way that promotes efficient use of the light. Dimmable light-emitting diode (LED) fixtures have the potential to reduce lighting costs because the output can be precisely controlled to meet crop needs. Because light is used more efficiently to drive photosynthesis at lower photosynthetic photon flux densities (PPFDs), we hypothesized that providing *Rudbeckia fulgida* var. *sullivantii* ‘Goldsturm’ seedlings with the same daily light integral (DLI), spread out over a longer photoperiod and at lower PPFDs, should improve growth. A DLI of 12 mol·m<sup>-2</sup>·d<sup>-1</sup> was provided in a greenhouse over 12, 15, 18, or 21-hour photoperiods from a combination of sunlight and supplemental light from LEDs, using adaptive lighting control. Plants grown without supplemental light had an ≈12-hour photoperiod and received an average DLI of 5 mol·m<sup>-2</sup>·d<sup>-1</sup>, ≈58% less light than the four lighting treatments. Lengthening the photoperiod from 12 to 21 hours increased shoot dry mass (30%), root dry mass (24%), plant height (14%), leaf area (16%), and chlorophyll content index (48%), and decreased specific leaf area (26%). There was no significant effect of photoperiod on root mass fraction or compactness. Growth parameters of plants without supplemental light were 26% to 90% smaller compared with those in the 12-hour photoperiod treatment. Treatment effects on canopy size, seen as early as 2 weeks into the study, were correlated with final shoot dry mass. Longer photoperiods did not induce a shade-avoidance response, based on specific leaf area and compactness data. The 24% increase in root dry mass for the plants in the 21-hour photoperiod suggests that cropping cycles can be shortened by 1 to 2 weeks compared with the 12-hour photoperiod. This could result in more crop turns per year and increased profits. In addition, fewer lights would be needed for adequate growth, reducing the capital cost of the lighting system.

There are more than 2000 farms engaged in seedling (plug) and cutting (liner) production in the United States, with 345 ha under protection and annual sales of \$644 million (U.S. Department of Agriculture, 2019). Many greenhouse operations use supplemental lighting to improve growth and yield of crops. At higher latitudes, where larger seasonal fluctuations in the DLI occur, supplemental light is vital for year-round production (Albright et al., 2000). However, supplemental lighting costs can be high. Electricity alone can account for ≈30% of total production costs (van Iersel and Gianino, 2017; Watson et al., 2018). One way to offset supplemental lighting costs is to shorten cropping cycles and increase the number of crop turns per year. To achieve this, effective lighting strategies should be developed that result in efficient use of the supplemental light to speed up growth.

Dimmable LED fixtures can be used to develop improved lighting strategies because their light output can be precisely controlled and programmed to respond to environmental parameters (e.g., sunlight) in real time (van Iersel and Gianino, 2017; van Iersel et al., 2016; Weaver et al., 2019). Our adaptive lighting control system measures the PPFD of the overall light environment (sunlight + supplemental light) at the canopy level and uses those data to adjust the amount of supplemental light provided. The PPFD of supplemental light is continually adjusted so that sunlight combined with supplemental light reaches, but does not exceed, a target DLI at the end of a specified photoperiod. On overcast or seasonally low DLI days, more supplemental light will be provided to reach the target DLI.

To develop effective lighting strategies, it is important to understand how plants absorb and use light to provide energy for growth. This process starts with plants absorbing photons, which depends on canopy size. Because of their small canopy, seedlings often intercept little of the total light available to them. Growing seedlings at high densities (up to 4000 plants/m<sup>2</sup>) can make supplemental lighting more cost-effective (Graper et al., 1989; van Iersel, 2017). The energy from photons absorbed by photosynthetic pigments can be used for electron transport in the light reactions of photosynthesis (photochemistry), dissipated as heat, or reemitted as chlorophyll fluorescence. Chlorophyll fluorescence can be used to measure the quantum yield of photosystem II (Φ<sub>PSII</sub>). This is the ratio between electrons transported through photosystem II (PSII) and absorbed photons, a measure of photochemical efficiency (Maxwell and Johnson, 2000). With Φ<sub>PSII</sub> and known PPFD, the electron transport rate (ETR) through PSII can be estimated (Maxwell and Johnson, 2000). High PPFDs are needed for high ETRs, but that also means low Φ<sub>PSII</sub> values due to excess light energy being dissipated as heat to prevent photoinhibition (Demmig-Adams et al., 2012; Ruban, 2015). Light drives photochemistry more efficiently at lower PPFDs (Koontz and Prince, 1986; Soffe et al., 1977; Weaver and van Iersel, 2019). The photochemistry of plants acclimates to the light conditions plants are exposed to. When measured at the same PPFD, plants grown under lower PPFD have a lower Φ<sub>PSII</sub> than plants grown under higher PPFD conditions (Zhen and van Iersel, 2017). In addition to PPFD effects on photochemistry, PPFD has a direct effect on plant photomorphogenesis. Plants grown under low light may develop shade acclimation characteristics, including increased leaf size which in turn increases light interception. Other morphological responses in response to shade include stem, petiole, and leaf elongation (Evans and Poorter, 2001; Franklin, 2008; Franklin and Whitelam, 2005; Gommers et al., 2013) and changes in pigment composition. For example, high PPFD increases the relative leaf chlorophyll and anthocyanin content of lettuce leaves, whereas increasing far-red light can decrease pigmentation (Meng and Runkle, 2019).

Previously, Weaver and van Iersel (2020) observed that lettuce (*Lactuca sativa* ‘Green Towers’) growth increased when the same DLI was provided over a longer photoperiod. Kelly et al. (2020) reported similar results for lettuce under sole-source lighting. However, this approach has not yet been tested for ornamental species.

This led to our hypothesis that the same DLI, provided over a longer photoperiod and hence a lower instantaneous PPFD, would increase growth of *Rudbeckia fulgida* var. *sullivantii* ‘Goldsturm’ via increased light interception (larger canopy size) and more efficient photochemistry. *Rudbeckia fulgida* var. *sullivantii* ‘Goldsturm’ is one of the most popular perennial landscape plants, native to the Eastern United States (Missouri Botanical Garden, n.d.). It is an obligate long day

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plant (Yuan et al., 1998) that grows best in full sun but can grow in partial shade. In addition, it is one of the few perennial plants still grown from seed.

## Materials and Methods

**Experimental setup, plant material, and growing conditions.** An adaptive lighting system was used to study the effect of providing a DLI of  $12 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$  over four photoperiods (12, 15, 18, and 21 h). The study was conducted in a glass-covered greenhouse at the University of Georgia in Athens. The adaptive lighting system consisted of five ebb-and-flow trays with inside dimensions of  $1.5 \text{ m} \times 0.9 \text{ m} \times 4 \text{ cm}$ , covered with landscape fabric (Scotts Pro Weed Control; Greenscapes Inc., Calhoun, GA), and placed side-by-side on a single greenhouse bench. Each tray was a separate block and divided into five sections, for a total of 25 growing sections. Each section was  $0.9 \text{ m}$  long  $\times$   $0.3 \text{ m}$  wide and separated by aluminum sheet metal dividers,  $0.9 \text{ m}$  long  $\times$   $0.3 \text{ m}$  high, to prevent light contamination among neighboring sections. Black shade cloth,  $3 \text{ m}$  wide  $\times$   $12 \text{ m}$  long was draped over the top and sides of the adaptive lighting system to mimic winter DLI (but not daylength) conditions. The shade cloth blocked  $\approx 80\%$  of the solar radiation.

One cool-white LED light bar (SPYDRx with PhysioSpec greenhouse spectrum; Fluence Bioengineering, Austin, TX) was mounted  $38 \text{ cm}$  above the tray bottom in the center of four of the five sections in each block. The LED light bars were connected to and powered by four separate dimmable drivers (SPYDRx; Fluence Bioengineering). Each driver controlled five light bars, with one light bar from each driver assigned to one section in each of the five trays. The dimming inputs of the drivers were connected to an analog output module (SDM-A04A; Campbell Scientific, Logan, UT) that was connected to a datalogger (CR1000; Campbell Scientific). This resulted in four treatments with and one treatment without supplemental light. Quantum sensors (LI-190; LI-COR BioSciences, Lincoln, NE) were placed in the five growing sections of the center block and connected to the datalogger. The sensors were positioned  $\approx 10 \text{ cm}$  from the southern edge of the tray,  $15 \text{ cm}$  above the bottom of the tray and centered between the two aluminum dividers. In the four lit sections, the quantum sensors were directly under the light bar. The datalogger measured the quantum sensors every  $2 \text{ s}$  and collected averages every  $15 \text{ min}$ . The datalogger also controlled the dimmable LED drivers by sending a  $0$  to  $10,000 \text{ mV}$  signal to the drivers via the analog output module. This allowed for precise control of the supplemental *PPFD*, using the approach described in detail by Weaver and van Iersel (2020). Briefly, every  $2 \text{ s}$  the datalogger used the *PPFD* measurements to calculate how much light had been received at any time during a day, determined how much additional light was needed to reach a

DLI of  $12 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ , and determined the average *PPFD* required during the remainder of the photoperiod. The datalogger then adjusted the voltage signal to the dimmable driver to ensure the plants received the appropriate *PPFD*. The datalogger also recorded temperature and relative humidity as measured by a combined probe (HMP50; Vaisala, Helsinki, Finland) housed in a radiation shield placed on the bench adjacent to the middle block.

Supplemental lighting treatments consisted of four photoperiods (12, 15, 18, and 21 h). The DLI in each section with a quantum sensor was  $12.0 \pm 0.0 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$  (mean  $\pm$  SD) from a combination of sunlight plus supplemental light. The section without supplemental light received an average DLI of  $5.0 \pm 1.7 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$  from sunlight only. To reach the target DLI for the different photoperiods, supplemental lights turned on at 0000, 0300, 0600, or 0900 HR for photoperiods of 21, 18, 15, and 12 h, respectively, and all lights turned off at 2100 HR. The natural photoperiod (sunrise to sunset) decreased from 12 h 55 min on 30 Aug. to 11 h 22 min on 14 Oct.

On 20 Aug. 2019, seeds of *R. fulgida* were sown in 72-cell trays ( $25 \text{ cm} \times 50 \text{ cm}$ ) filled with a soilless propagation medium (Fafard germinating mix with RSi; SunGro Horticulture, Agawam, MA). The trays were cut in half, creating an experimental unit of 36 plants per tray. Seed trays were covered with a clear plastic humidity dome and placed on a five-shelf stainless steel cart retrofitted with white LED lights (225 LED ultrathin grow light panel; Apluschoice, La Puente, CA), small fans, and dataloggers (HOBO U12; Onset Computer Corp., Bourne, MA). Seeds germinated under these conditions for 10 d under a 10-h photoperiod, *PPFD* of  $279 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , and air temperature of  $24.3 \pm 2.2 \text{ }^\circ\text{C}$  (mean  $\pm$  SD). The seeds were fertigated, as needed, by overhead misting with a  $100 \text{ mg}\cdot\text{L}^{-1}$  N water-soluble fertilizer solution (15N–2.2P–12.5K, Peters Excel 15–5–15 Cal-Mag Special; ICL Fertilizers, Dublin, OH). On 30 Aug. 2019, 25 of the 36-cell trays were thinned to one plant per cell, resulting in a plant density of  $600 \text{ plants}/\text{m}^2$ , and moved to the 25 separate sections of the adaptive lighting system in the greenhouse.

During the study period, 30 Aug. to 14 Oct. 2019, plants were subirrigated as needed (every 2 to 3 d) with a  $100 \text{ mg}\cdot\text{L}^{-1}$  N water-soluble fertilizer solution (15N–2.2P–12.5K, Peters Excel 15–5–15 Cal-Mag Special; ICL Fertilizers), the air temperature was  $27.0 \pm 1.1 \text{ }^\circ\text{C}$  (mean  $\pm$  SD), and the vapor pressure deficit was  $1.35 \pm 0.13 \text{ kPa}$ .

**Experimental design, data collection, and analysis.** A custom-made imaging system was used to nondestructively measure projected canopy size over the course of the study. The imaging system consisted of a grow tent,  $0.6 \text{ m}$  wide  $\times$   $0.6 \text{ m}$  long  $\times$   $1.2 \text{ m}$  high with a mylar reflective interior lining, with a LED light fixture (Pro 325e; LumiGrow, Emeryville, CA) mounted inside at the top of the tent. A digital monochrome camera

(CM3-U3-31S4M-CS; FLIR Systems, Wilsonville, OR) with a band-pass filter ( $680$  to  $740 \text{ nm}$ ; Omega Optical, Brattleboro, VT) was mounted inside at the top of the grow tent. Chlorophyll fluorescence images of each 36-cell tray were taken weekly, beginning 30 Aug. and ending 11 Oct. 2019, for a total of 7 weeks. To collect each image, the blue LEDs (peak wavelength of  $440 \text{ nm}$ ) in the light fixture were turned on and the camera with the band-pass filter captured leaf fluorescence from the chlorophyll in the plant tissue. The chlorophyll fluorescence images were analyzed using ImageJ (National Institutes of Health, Bethesda, MD) software to determine projected canopy size. Taking images of chlorophyll fluorescence makes the process of separating canopy from background simple (Narayanan et al., 2019).

On 14 Oct. 2019, 55 d after sowing, plants in most treatments had reached a marketable transplant size and were harvested. The number of viable plants (four or more true leaves) per 36-cell tray were counted. Chlorophyll content index (CCI) was measured on five fully expanded leaves per experimental unit using a handheld meter (CCM-200 plus; Apogee Instruments Inc., Logan, UT). The CCI is a quantitative measure of leaf chlorophyll concentration (Parry et al., 2014). Because we did not quantify the relationship between CCI and leaf chlorophyll concentration, we report only CCI values. Five representative plants were selected from each tray, and height was measured (from media surface to tallest leaf). Additionally, shoots were cut at the substrate level, leaves were counted, and total leaf area was measured (LI-3100, LI-COR Biosciences). Finally, foliage was dried in an oven at  $80 \text{ }^\circ\text{C}$  for 7 d and then weighed. Roots of these plants were washed, dried in an oven at  $80 \text{ }^\circ\text{C}$  for 7 d, then weighed. Shoots from the remaining plants were cut at substrate level, leaf area measured, dried in an oven at  $80 \text{ }^\circ\text{C}$  for 7 d, then weighed. Leaf area was calculated as the sum of leaf area of the five representative plants and the leaf area of the remaining plants divided by the total number of plants harvested. Compactness was calculated as shoot dry mass divided by height. Using data from the five representative plants, specific leaf area (SLA) was calculated as leaf area divided by shoot dry mass and root mass fraction was calculated as root dry mass / (shoot + root dry mass).

This study was designed as a randomized complete block with five blocks (replications) and five treatments per block. JMP Pro (version 14.1.0; SAS Institute, Cary, NC) was used to analyze the data, using analysis of variance to test for differences among the treatment without supplemental light and other treatments using Dunnett's test ( $\alpha = 0.05$ ). Effects of the four photoperiods were tested using mixed model regression analyses (linear and quadratic,  $\alpha = 0.05$ ) with photoperiod as a continuous variable and block as a random variable. Quadratic effects are shown only when the regression parameter was statistically significant ( $P < 0.05$ ). SigmaPlot

(version 11.0; Systat Software, Inc., San Jose, CA) was used to analyze the relationship between projected canopy size and final dry mass.

## Results and Discussion

The calculated threshold *PPFDs* at the start of the photoperiod were 158.7, 185.2, 222.2, and 275.2  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  for the 21, 18, 15, and 12 h photoperiods, respectively. These thresholds were recalculated constantly throughout the day so that when the *PPFD* from the sun exceeded these thresholds, the threshold *PPFD* decreased to ensure the target DLI was not exceeded by the end of the photoperiod. Thus, early in the day, *PPFD* remained at the initial calculated threshold. As the sunlight became more intense, the supplemental lights were dimmed or completely turned off, and the threshold *PPFD* decreased. This decrease in threshold *PPFD* was more pronounced on sunny than overcast days (Fig. 1). This resulted in precise control, and all supplemental lighting treatments received a DLI of  $12.0 \pm 0.0 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$  every day.

*Rudbeckia fulgida* can be difficult to germinate with variable germination rates (Fay et al., 1993). Although initial germination percentage was good and there were seedlings in each cell, some seedlings simply failed to thrive, resulting in nonviable transplants. The number of viable plants (four or more true leaves) per 36-cell tray ranged from 26 to 35, with an average of  $29.8 \pm 2.3$  plants, and this was unaffected by treatment (data not shown). Shoot and root dry mass of plants without supplemental light averaged 0.04 and 0.007 g/plant, 83% and 90% lower, respectively, than plants in the 12-h photoperiod treatment (Fig. 2). The difference in shoot and root dry mass between the plants without supplemental light and those in the 12-h photoperiod treatment was much greater than the difference in DLI ( $\approx 58\%$ ). Randall and Lopez (2015) also reported disproportionate increases in shoot and root dry mass for seedlings in response to supplemental light (control DLI  $6.6 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ , DLI with supplemental light  $10.6 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ ). This 38% increase in DLI increased shoot

dry mass of vinca (*Catharanthus roseus*), impatiens (*Impatiens walleriana*), and geranium (*Pelargonium xhortorum*) seedlings by 50% to 74% and root dry mass by 81% to 104%. The disproportionate increase in dry mass with increasing DLI is likely not the result of effects on leaf photosynthesis. Leaf photosynthesis increases asymptotically with increasing *PPFD*, i.e., a doubling of *PPFD* will generally increase leaf photosynthesis less than 2-fold. Instead, the disproportionate increase in growth with increasing DLI may be related to the carbon use efficiency, the efficiency with which plants convert carbohydrates into biomass. Carbon use efficiency is a direct function of relative growth rate (van Iersel, 2003). When *PPFD* and photosynthetic rates are low, plants use a large fraction of their carbohydrate supply for maintenance respiration, rather than growth and growth respiration (Nemali and van Iersel, 2004).

Shoot and root dry mass increased linearly, from 0.23 to 0.30 g/plant (30% increase) and from 0.071 to 0.088 g/plant (24% increase), respectively, as photoperiod increased from 12 to 21 h, while maintaining a DLI of  $12 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$  (Fig. 2A and B). Other studies have reported a similar increase in plant dry mass in response to extending the photoperiod while maintaining the total amount of light delivered daily. Soffe et al. (1977) determined that by extending the photoperiod in growth chambers from 12 to 16 h while maintaining a constant  $5 \text{ MJ}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ , plant dry mass increased by 20% for radish (*Raphanus sativus*), cabbage (*Brassica oleracea capitata*), and oilseed rape (*Brassica napus*); 40% for spinach beet (*Beta vulgaris*), beetroot (*Beta vulgaris*), and celery (*Apium graveolens*); and 100% for lettuce. Koontz and Prince (1986) reported a 30% to 50% increase in dry mass of four loose-leaf lettuce cultivars by extending the photoperiod from 16 to 24 h, while providing about the same DLI ( $22.4$  and  $23.9 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ , respectively). Recently, Weaver and van Iersel (2020) used a similar approach to the one used in this study to extend photoperiods without changing the DLI ( $17 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ ) and found a 28% increase in dry mass of lettuce grown under a 21-h vs. a 12-h photoperiod. Differences in dry mass among plants

in the different treatments in this study were clearly visible; plants grown without supplemental light were small, whereas plants grown with a 12-h photoperiod were visibly smaller than those grown with an 18- or 21-h photoperiod (Fig. 3).

There was no indication that photoperiod treatments influenced root mass fraction (Fig. 2C). Average root mass fraction with the four photoperiods was 0.23, 26% higher than that of the plants without supplemental light (0.17).

Plant height increased linearly from 12.8 to 14.6 cm (14%) as photoperiods increased from 12 to 21 h (Fig. 4A). This suggests

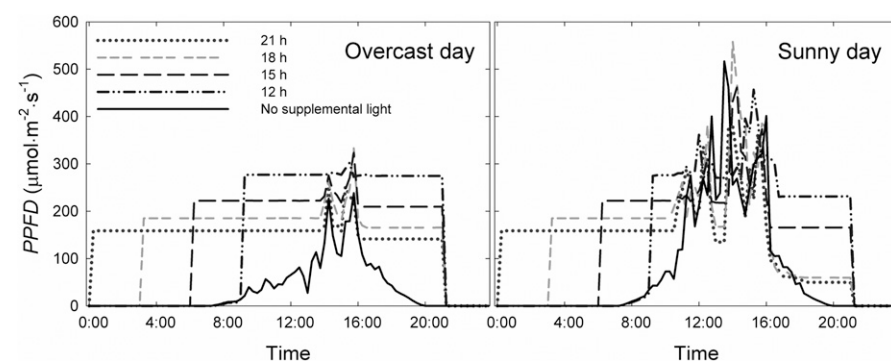


Fig. 1. Photosynthetic photon flux density (*PPFD*) over the course of a 24-h period on an overcast day (left) compared with a sunny day (right) as measured by a quantum sensor. The four photoperiod (12, 15, 18, and 21 h) treatments all had a daily light integral of  $12 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ .

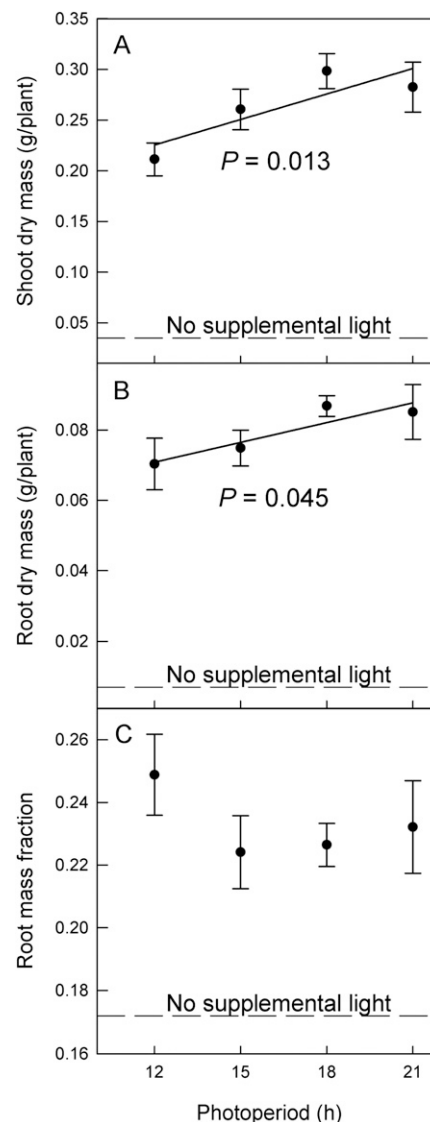


Fig. 2. Shoot dry mass (A), root dry mass (B), and root mass fraction (root dry mass / total plant dry mass) (C) of *Rudbeckia fulgida* var. *sullivantii* as a function of photoperiod. All plants received a daily light integral (DLI) of  $12 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ , except for plants that received no supplemental light (dashed line, mean DLI of  $5.0 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ ). Plants without supplemental light differed from the four other treatments for all three parameters ( $P \leq 0.02$ ). Data represent the mean  $\pm$  SE. Regression lines indicate significant effects of photoperiod.

plants elongated as a shade response to lower *PPFD* associated with longer photoperiod. However, compactness was not significantly affected by photoperiod (Fig. 4B), suggesting that increased height was not caused by more elongation but rather increased growth. Plants without supplemental light had an average height of 5.8 cm and a compactness of 1.0 g·m<sup>-1</sup>, 53% shorter and 59% less compact, respectively, compared with plants grown under the 12-h photoperiod.

Leaf area increased in a quadratic manner from 56 to 65 cm<sup>2</sup>/plant (16% increase) as photoperiod increased from 12 h to 15 or 18 h

and then decreased back to 56 cm<sup>2</sup>/plant with a 21-h photoperiod (Fig. 4C). Leaf area for the plants without supplemental light was 15 cm<sup>2</sup>/plant. The number of leaves per plant was similar in all treatments and averaged 5.0 (data not shown). However, SLA decreased linearly from 266 to 197 cm<sup>2</sup>·g<sup>-1</sup> (26% decrease) as photoperiod increased from 12 to 21 h (Fig. 4D). This contradicts the initial hypothesis that lower *PPFDs* associated with the longer photoperiods would induce a shade acclimation response resulting in larger, thinner leaves and increased SLA. Plants without supplemental light had a much

higher SLA (428 cm<sup>2</sup>·g<sup>-1</sup>) than any of the other treatments with higher DLIs, which is consistent with a shade acclimation response (Evans and Poorter, 2001; Gommers et al., 2013; Gong et al., 2015). Leaf elongation in response to shade is often controlled through phytochrome (Stutte, 2009). However, the spectrum of the supplemental light was identical in all four photoperiod treatments.

Increased projected canopy size with increasing photoperiod was evident early in the study and remained until the end of the study. Despite a decrease in SLA with longer photoperiods, projected canopy size increased linearly from 42.6 to 69.1 cm<sup>2</sup> (week 3) and from 240 to 358 cm<sup>2</sup> (week 5) as photoperiod increased from 12 to 21 h, and in a quadratic manner from 769 to 911 cm<sup>2</sup> for week 7 (Fig. 5). Plants without supplemental light consistently had a small projected canopy size compared with plants in all other treatments; compared with the 12-h treatment, this difference widened from 28% after 3 weeks to 65% after 7 weeks. Canopy size is directly related to light interception and canopy photosynthesis, which in turn drives growth (Klassen et al., 2003).

Variation in projected canopy size, which determines how much light is captured by plants and thus important for growth, helps explain differences in final plant dry mass among treatments. The importance of canopy size for growth is evident from the positive correlation between weekly projected canopy size and final shoot dry mass (Fig. 6). Plants with greater projected canopy size as early as week 2 had a larger final shoot dry mass. Thus, early differences in projected canopy size were indicative of plant growth over the entire study. Other studies also found that differences in projected canopy size early during the growing cycle were predictive of differences in final biomass of leafy greens (Kim and van Iersel, 2019; Palmer, 2020). The correlation between projected canopy size and shoot dry mass became stronger over time. The strong positive correlation between early leaf area suggests that it may be possible to expose plants to different lighting treatments for a relatively short period and use those results to predict the outcome of longer trials. Shorter trials would make it easier to test a wider range of different lighting strategies.

Chlorophyll content index increased from 15.5 to 23.0 (48% increase) as photoperiod increased from 12 to 21 h (Fig. 7). Increased chlorophyll content, a common shade acclimation response, can increase light absorption (Evans and Poorter, 2001; Givnish, 1988; Nemali and van Iersel, 2004), which may result in increased photosynthesis and growth. In our study, the increase in CCI may have been a direct consequence of the decrease in SLA with longer photoperiods. CCI is indicative of the chlorophyll concentration per unit leaf area (Parry et al., 2014). Therefore, a decrease in SLA would be expected to increase CCI if the concentration per unit dry mass is unaffected.

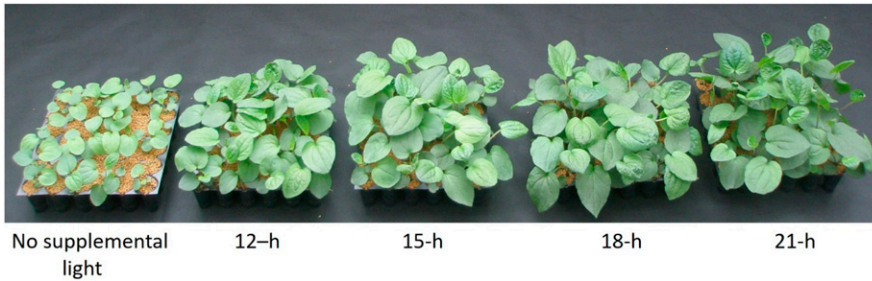


Fig. 3. Appearance of *Rudbeckia fulgida* var. *sullivantii* plants as a function of photoperiod. All plants received a daily light integral (DLI) of 12 mol·m<sup>-2</sup>·d<sup>-1</sup>, except for plants that received no supplemental light (mean DLI of 5.0 mol·m<sup>-2</sup>·d<sup>-1</sup>).

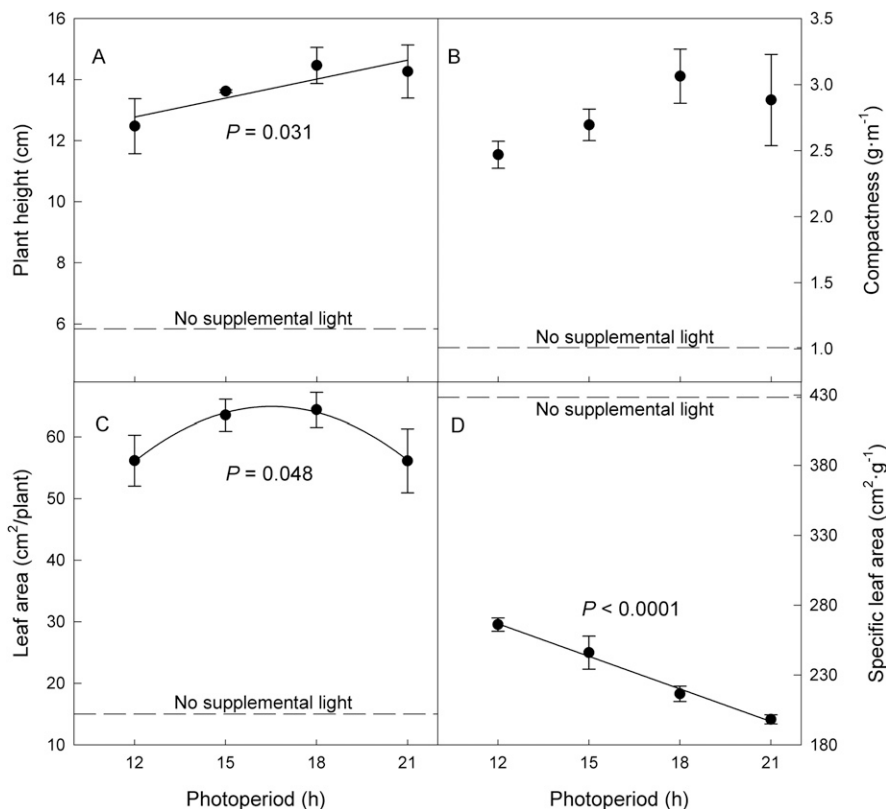


Fig. 4. Plant height (A), compactness (B), leaf area (C), and specific leaf area (D) of *Rudbeckia fulgida* var. *sullivantii* plants as a function of photoperiod. All plants received a daily light integral (DLI) of 12 mol·m<sup>-2</sup>·d<sup>-1</sup>, except for plants that received no supplemental light (dashed line, mean DLI of 5.0 mol·m<sup>-2</sup>·d<sup>-1</sup>). Plants without supplemental light differed from the four other treatments for all four parameters ( $P < 0.0001$ ). Data represent the mean  $\pm$  SE. Regression curves indicate significant effects of photoperiod.

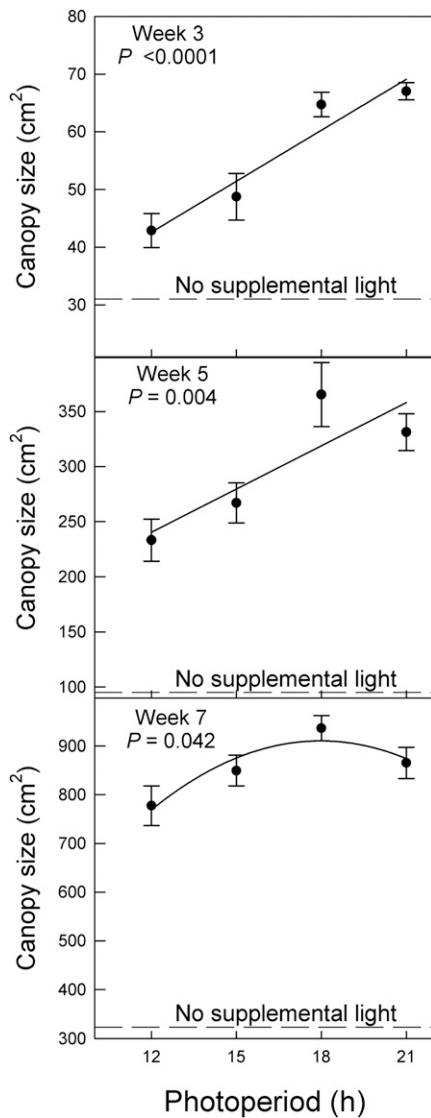


Fig. 5. Projected canopy size of *Rudbeckia fulgida* var. *sullivantii* plants as a function of photoperiod for weeks 3, 5, and 7 of the study period. All plants received a daily light integral (DLI) of  $12 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ , except for the plants that received no supplemental light (dashed line, mean DLI of  $5.0 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ ). Plants without supplemental light had a significantly smaller projected canopy size than plants in any of the other treatments at any of these time points ( $P \leq 0.006$ ).

Hurd (1973) observed a 34% increase in chlorophyll in tomato (*Lycopersicon esculentum*) grown with a 16-h day compared with an 8-h day, with the same DLI. Based on research by Gabrielsen (1948) on chlorophyll concentration and photosynthetic efficiency, Hurd (1973) estimated the 34% increase in chlorophyll would yield a 6% increase in photosynthesis under low light treatment(s). Plants without supplemental light had an average CCI of 9, 53% lower than plants grown under a 12-h photoperiod. Overall, plants that did not receive supplemental light performed poorly (Figs. 2–5) and may not have had adequate resources to acclimate to and thrive in their low-light environment.

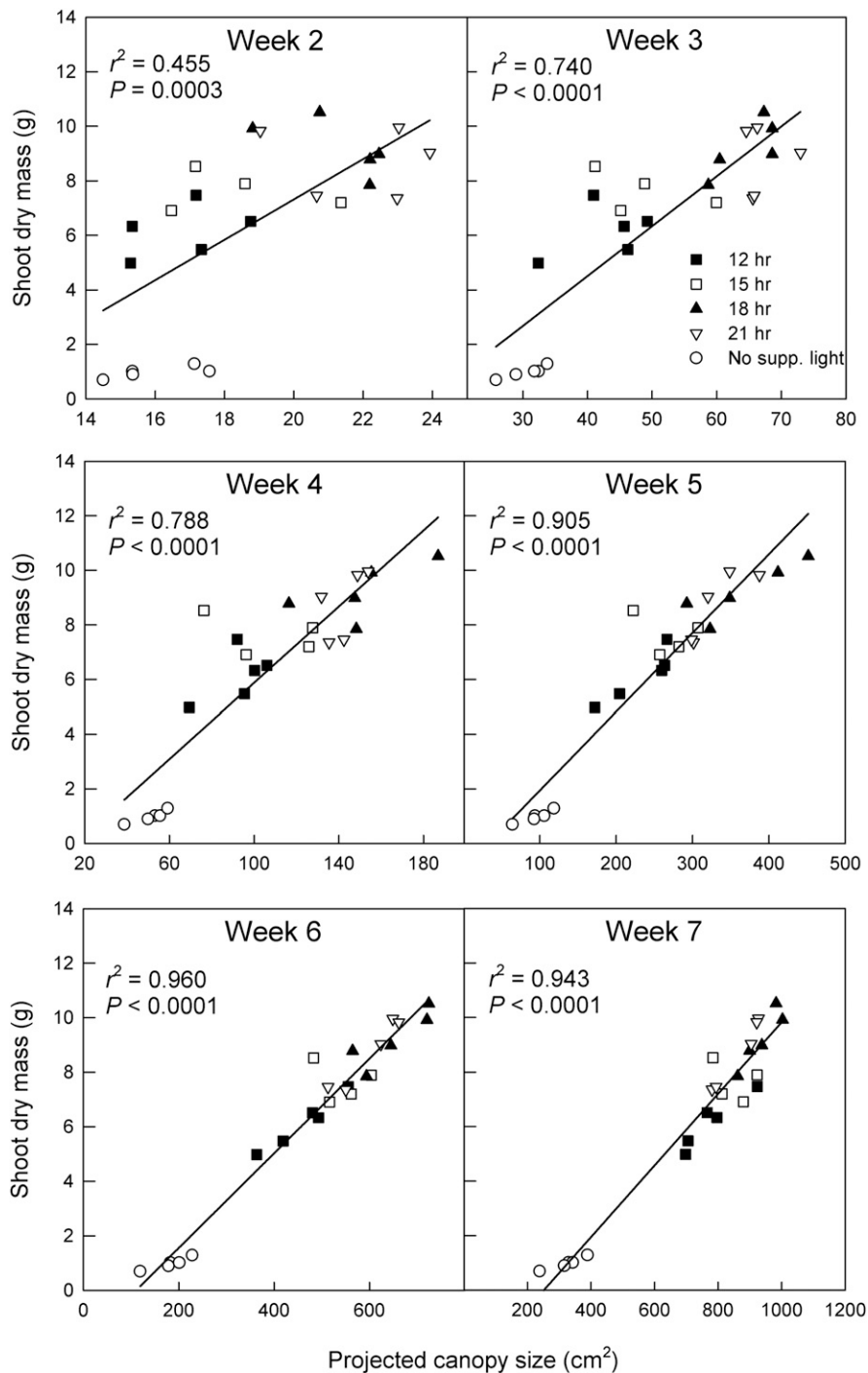


Fig. 6. Total final shoot dry mass of *Rudbeckia fulgida* var. *sullivantii* plants as a function of projected canopy size at different times during the growing cycle. The treatments included photoperiods of 12, 15, 18, and 21 h, each receiving a daily light integral (DLI) of  $12 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$  and a treatment without supplemental light that received a mean DLI of  $5 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ . Note that the x-axis scales differ among graphs.

Several factors may contribute to increased plant growth in response to an extended photoperiod delivered using methods such as daylength extension, night break, or providing the same DLI over a longer photoperiod. These include increased leaf expansion, higher chlorophyll content, and more photosynthesis (Adams and Langton, 2005). Previous studies reported increased leaf expansion with extended photoperiods and a

constant DLI (Langton et al., 2003; Milford and Lenton, 1976; Soffe et al., 1977). Increased leaf expansion is often accompanied by an increase in SLA, an indication of larger, thinner leaves (Adams and Langton, 2005). However, we saw a decrease in SLA with longer photoperiods, while leaf area was greatest with 15 and 18 h photoperiods. However, the strong correlation between projected canopy size and final dry mass,

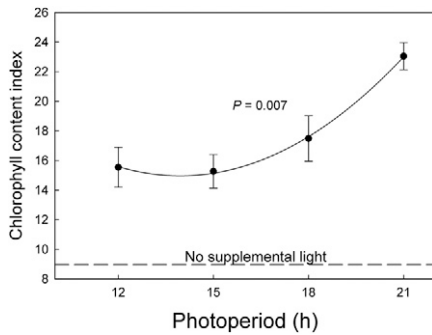


Fig. 7. Chlorophyll content index of *Rudbeckia fulgida* var. *sullivantii* plants as a function of photoperiod. All plants received a daily light integral (DLI) of 12 mol·m<sup>-2</sup>·d<sup>-1</sup>, except for plants that received no supplemental light (dashed line, mean DLI of 5.0 mol·m<sup>-2</sup>·d<sup>-1</sup>). Plants without supplemental light had a lower chlorophyll content index than plants in any of the other treatments ( $P=0.004$ ). Data represent the mean ± SE. The regression curve indicates significant effect of photoperiod.

especially from week 3 onward, suggests that light interception played a critical role in determining growth differences.

However, the efficiency with which plants use light is also important. Under low *PPFD*, plants have a higher  $\Phi_{PSII}$ , but lower ETR (Weaver and van Iersel, 2019, 2020; Zhen and van Iersel, 2017; Zou et al., 2019). At low *PPFDs*, more of the reaction centers of PSII are open, allowing for more efficient photochemistry. Therefore, a longer photoperiod with lower *PPFD*, will result in greater electron transport through PSII when integrated over the entire photoperiod. In a recent study, Elkins (2020) reported a 74% and 109% increase in lettuce integrated electron transport as the photoperiod increased from 7 to 22 h, with DLIs of 15 and 20 mol·m<sup>-2</sup>·d<sup>-1</sup>, respectively. Increased daily photochemistry may increase daily photosynthesis and growth. That can increase leaf area, which in turn increases light capture and canopy photosynthesis, thus perpetuating a positive feedback mechanism. Finally, increased chlorophyll as a result of longer photoperiods can increase light absorption and photochemistry. These factors likely combined to result in increased growth with longer photoperiods.

### Conclusion

Supplemental lighting can increase growth of *R. fulgida* seedlings, especially when supplied over longer photoperiods at a lower *PPFD*. In plug production, root system size is an important indicator of plug quality and primary determinant of transplant readiness. Based on the observed 24% increase in root dry mass of *R. fulgida*, we estimate supplemental light with a DLI of 12 mol·m<sup>-2</sup>·d<sup>-1</sup> and 21-h photoperiod can shorten cropping cycles by 1 to 2 weeks (55 d in the study period × 0.24 = 13.2 d) compared with a 12-h photoperiod. Although statistical analyses suggest a linear increase in shoot dry mass, root dry

mass, and plant height, those growth parameters had similar values in the 18- and 21-h photoperiod treatments, and it is possible that extending the photoperiod beyond 18 h does not provide any additional benefits. Whether other species respond similarly is to be determined. Shortening the cropping cycle can allow for more crops (turns) per year and increased profits. In addition, growers could install fewer lights to achieve adequate growth responses, reducing the capital expense of the lighting system.

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