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Longer Photoperiods with Adaptive Lighting Control Can Improve Growth of Greenhouse-grown 'Little Gem' Lettuce (*Lactuca sativa*)

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***Abstract*. Supplemental lighting can improve the growth of greenhouse crops, but the electricity required for supplemental lighting can be a significant expense for greenhouse growers. Lighting control strategies that use the dimmability of light-emitting diodes (LEDs) have the potential to decrease this cost. In our experiments, we tested the hypothesis that providing 'Little Gem' lettuce (*Lactuca sativa*) plants with the same daily amount of light, spread out over a longer photoperiod and at lower average photosynthetic photon flux densities (*PPFD*s), would improve growth because light is used more efficiently to drive photosynthesis at lower *PPFD*s. We conducted two greenhouse experiments wherein supplemental light was provided to reach a minimum daily light integral (DLI) of 17 mol·m^{-2}·d^{-1} with a 12, 15, 18, or 21-hour photoperiod using adaptive lighting control of LED lights. As the photoperiod for supplemental lighting was increased and supplemental light was provided at lower average *PPFD*s, plant dry weight increased. Conversion efficiency, the estimated increase in dry weight per Joule expended on supplemental lighting, increased as the photoperiod was extended from 12 to 21 hours. Leaf size and chlorophyll content index increased with longer photoperiods. The number of plants with symptoms of tipburn, including apical and marginal necrosis, also increased as the photoperiod was extended. These results demonstrate that adaptive lighting control can be used to increase the growth of 'Little Gem' lettuce and the energy use efficiency of supplemental lighting by providing supplemental light at relatively low *PPFD*s.**

Supplemental lighting is often used to improve the growth and yield of greenhouse vegetables. However, the electricity required for supplemental lighting can account for as much as 30% of the recurring cost of operating a greenhouse (van Iersel and Gianino, 2017; Watson et al., 2018). Thus, reducing the cost of greenhouse supplemental lighting or increasing the productivity of crops would be beneficial to greenhouse vegetable growers. Lighting control approaches that efficiently drive photosynthesis and growth of greenhouse vegetable crops may improve the profitability of greenhouse vegetable production.

LED lights are becoming increasingly popular in horticultural applications for a variety of reasons, including their relatively high efficacy (Nelson and Bugbee, 2014). One unique feature of LED lights is that their light output can be controlled precisely and nearly instantaneously in real time, which is not possible with high-intensity discharge lamps (van Iersel et al., 2016; Weaver et al., 2019). Dimmable LED lights can be interfaced with quantum sensors and control systems, allowing for adaptive lighting control (van Iersel and Gianino, 2017). With adaptive lighting, supplemental light is provided so that the *PPFD* of sunlight and supplemental light combined reaches a specified threshold *PPFD*, and the lights are turned off if sunlight alone exceeds this threshold *PPFD*.

Photosynthetic light responses can generally be described as concave functions of *PPFD*. The efficiency of photosynthetic light use (moles of carbon fixed per mole of photons) invariably decreases as *PPFD* increases, and hence, photosynthetic gains per unit of applied photosynthetically active radiation will always be greatest at lower *PPFD*s (Aikman, 1989; Weaver and van Iersel, 2019). The decrease in photosynthetic light use efficiency at higher *PPFD*s is due in part to photoprotective processes that convert absorbed light energy to heat, rather than allowing it to be used for electron transport in the light reactions of photosynthesis. As *PPFD* is increased, proportionally higher amounts of absorbed light energy are dissipated as heat. This prevents light-induced damage of the photosynthetic apparatus via the action of complementary photoprotective processes, which include the xanthophyll cycle and molecular rearrangement of the chlorophyll antennae and photosynthetic reaction centers (Demmig-Adams et al., 2012; Horton, 2012; Rochaix, 2014; Ruban, 2015).

Because light drives photosynthesis more efficiently at lower *PPFD*s, we have hypothesized that crop growth will be improved if light is provided at lower *PPFD*s over a longer period of time (Weaver and van Iersel, 2019). This effect has been demonstrated in growth chamber experiments for several cultivars of lettuce (*Lactuca sativa*) (Koontz and Prince, 1986; Soffe et al., 1977), as well as for other vegetable species (Soffe et al., 1977) and strawberry (*Fragaria ×ananassa)* (Tsuruyama and Shibuya, 2018). Plant growth generally increases as the same daily amount of light is provided over a longer photoperiod. Growing greenhouse crops with longer photoperiods can also be advantageous because lower electricity prices may be available at night (Albright et al., 2000). However, similar results have not yet been reported for plants grown in a greenhouse, where lighting conditions are highly variable and likely cannot be as readily controlled.

In our experiments, we grew 'Little Gem' lettuce plants in a greenhouse with supplemental light provided to reach a minimum DLI of 17 mol·m^{-2}·d^{-1} using an adaptive lighting system. We hypothesized that reaching the same DLI, with a longer photoperiod and lower average *PPFD*s, will result in increased growth for this romaine-type lettuce. Chlorophyll fluorescence measurements were used to test the hypothesis that photosynthetic efficiency decreases as *PPFD* is increased, as evidenced by a decrease in the quantum efficiency of photosystem II (Φ_{PSII}). This is a unitless measure of the efficiency with which absorbed photons are used to drive the light reactions of photosynthesis.

Materials and Methods

Experimental setup, design, and growing conditions. The experiments were conducted in a glass-covered greenhouse in Athens, GA. The first experiment was conducted from 11 Feb. to 5 Mar. 2018 (22 d), and the second experiment was conducted from 26 Mar. to 16 Apr. 2018 (21 d). Plants were grown using five ebb-and-flow trays of 1.5-m length × 90-cm width × 4-cm height (MidWest GroMaster, St. Charles, IL) covered with commercial-grade weed cloth (Weed Free Pro Fabric; DuPont, Wilmington, DE). The trays were arranged end-to-end on a single greenhouse bench with the axes of the longer sides having an east-west orientation. Each tray was divided into five (90-cm length × 30-cm width) sections separated by aluminum sheets (90-cm length × 30-cm height), and each tray was a complete block. LED light bars with a mixture of cool and warm white

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and a few red LEDs and 112-cm length × 5.1-cm width (SPYDRx with Physiospec Greenhouse spectrum; Fluence Bioengineering, Austin, TX) were mounted above four of the five sections of each bench, for a total of 20 lit sections and five unlit sections. The unlit sections served as a control treatment. The LED lights were powered using four dimmable drivers (SPYDRx; Fluence Bioengineering, Austin, TX), each of which controlled five light bars, with one light bar from each driver assigned to each of the five trays. Four supplemental lighting treatments, each having all five replications controlled by a single LED driver, and one control (no supplemental lighting), were randomized over each ebb-and-flow tray (block). Thus, the experimental design was a randomized complete block with five blocks and five treatments per block.

Quantum sensors (LI-190; LI-COR Bio-Sciences, Lincoln, NE) were positioned on the south-facing side of each section of the middle tray, ≈10 cm from the edge of the tray and 15 cm high, directly under the LED light bars in the four lit sections, and in the center of the one unlit (control) section. A datalogger (CR1000; Campbell Scientific, Logan, UT) was used to record the quantum sensor measurements and to control the dimmable LED drivers by sending a 0- to 10,000-mV signal to the driver via an analog output module (SDM-A04A; Campbell Scientific). The datalogger was also used to record temperature and relative humidity as measured by a temperature and relative humidity sensor (HMP50; Vaisala, Woburn, MA) housed in a radiation shield and positioned adjacent to the middle ebb-and-flow tray. The mean (± SD) temperature, relative humidity, and vapor pressure deficit were 23.8 ± 3.1 °C, 56 ± 17%, and 1.37 ± 0.82 kPa during the first experiment, and 24.2 ± 3.4 °C, 49 ± 17%, and 1.67 ± 0.88 kPa during the second experiment. Photosynthetic photon flux density was measured once every 2 s. Daily light integral was calculated by integrating *PPFD* measurements from the quantum sensors over each day. Photoperiod was calculated as the number of seconds during which *PPFD* was greater than zero for each day. Mean *PPFD* during the photoperiod (photoperiod *PPFD*) was calculated as the average of all nonzero *PPFD*s, from sunlight and the LED lights combined during each day. Total supplemental lighting time was calculated as the total amount of time during which the supplemental lights provided light, regardless of the *PPFD*. Because *PPFD* was only measured in one block, the exact DLI and photoperiod *PPFD* in each treatment × block combination could not be determined.

The spectrum of the LED lights was measured using a field spectroradiometer (SS-110; Apogee Instruments, Inc., Logan, UT). The LED light spectrum was measured in two positions, with the spectroradiometer positioned directly under either the white LEDs or the red LEDs of the light bars. Figure 1 shows the spectrum within the photosynthetically active region (≈400 to 700 nm), averaged over measurements taken directly under the two types of LEDs (red and white), to provide a representative illustration of the light spectrum. The spectrum of sunlight was also measured using the field spectrometer, and the red to blue ratios of the LEDs and of sunlight were calculated as the integrated *PPFD* in the 600- to 700-nm range (red) divided by the integrated *PPFD* in the 400- to 500-nm range (blue).

Seeds of 'Little Gem' lettuce were sown in 32-cell trays (27 × 53 cm) filled with a peat-perlite substrate (Fafard 2P; Sun Gro Horticulture, Agawam, MA) and thinned to one plant per cell after germination (224 plants/m^2). The plants were fertigated twice daily with a 100 mg·L^{-1} N liquid fertilizer (15N–2.2P–12.45K; 15–5–15 Cal-Mag; Everris, Marysville, OH) for the duration of each experiment. One tray was placed in each treatment × block combination (25 total trays), and the experimental unit was one tray of 32 plants.

Supplemental lighting treatments. Supplemental lighting treatments were started 1 week after germination. In each supplemental lighting treatment, a minimum DLI of 17 mol·m^{-2}·d^{-1} was provided by the LED lights and sunlight combined. The maximum output of the LED light bars at the quantum sensor position used in the experiments was 400 ± 5 µmol·m^{-2}·s^{-1}, and hence, a DLI of 17 mol·m^{-2}·d^{-1} could be reached in the absence of sunlight for all photoperiods used.

The DLI 17 mol·m^{-2}·d^{-1} was selected based on previous research on hydroponic greenhouse production of the bibb lettuce cultivar Ostinata, which showed that at this DLI, growth rates were sufficiently high to guarantee rapid production without causing excessive tipburn (Albright et al., 2000; Both et al., 1997). The treatments differed in the photoperiod allowed for providing supplemental light. In both experiments, the allowable photoperiods for supplemental lighting were 12, 15, 18, and 21 h. In the first experiment lighting treatments began at 0700 Eastern Standard Time (EST), and lighting treatments began at 0730 EST in the second experiment. The allowed photoperiod for supplemental lighting was considered to begin when the lighting treatments began, rather than at sunrise. Thus, the photoperiod to which the plants were exposed could exceed the allowed photoperiod for supplemental lighting control during the second experiment, when the natural daylength exceeded 12 h and the plants were exposed to sunlight before 0730 EST. In the case where the DLI from sunlight alone exceeded the minimum required DLI, supplemental light was not provided after the minimum DLI had been reached. Thus, in some cases, the photoperiod to which the plants were exposed was shorter than the allowed photoperiod for supplemental lighting. The interval of a 24-h period during which supplemental lighting was allowed to be provided is referred to as the "allowed photoperiod," and the actual photoperiod to which the plants were exposed is referred to as the "realized photoperiod."

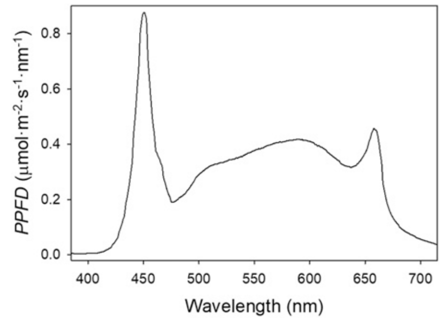

Fig. 1. Spectrum of the light-emitting diode (LED) light bars used in the experiments. Values represent the average of two measurements collected under red or white LEDs.

The LED lights were controlled using adaptive lighting control (van Iersel and Gianino, 2017). The output of the LED lights was automatically adjusted so that the *PPFD* reading of the quantum sensor associated with each treatment reached a minimum calculated threshold value using proportional control. When the measured *PPFD* exceeded the threshold *PPFD* (due to sunlight), the lights were automatically turned off. In our experiments, control to a minimum required DLI of 17 mol·m^{-2}·d^{-1} was accomplished by calculating a threshold *PPFD* once every 2 s. This threshold was calculated by first integrating all *PPFD* observations for the current photoperiod, then subtracting this running total from 17 mol·m^{-2} and dividing the difference by the time remaining in the allowed photoperiod (s). Thus, at longer photoperiods, the threshold *PPFD* for adaptive lighting control was generally lower because of the larger denominator. The control algorithm used to determine a threshold *PPFD* for adaptive lighting control can be stated in four steps (Table 3). Once a threshold *PPFD* was determined, the LED lights were automatically dimmed to reach, but not exceed, this threshold *PPFD* using proportional control by changing the voltage signal send to the driver (van Iersel and Gianino, 2017) according to

$$V_t = V_{t-1} \times (PPFD_T / PPFD_O),$$

where V is the voltage signal sent to the LED driver, t is the current time step, $PPFD_T$ is the threshold *PPFD*, and $PPFD_O$ is the observed *PPFD*. If the voltage signal at the previous time step was zero, V_{t-1} was set to the lowest value at which the LED lights were energized for each driver to allow the proportional control algorithm to operate. Likewise, in the case where the observed *PPFD* was zero, $PPFD_O$ was set to a small value (0.1 µmol·m^{-2}·s^{-1}), to avoid division by zero, and allow the control algorithm to operate. To illustrate performance of the control algorithm, simulated lighting control trajectories (Fig. 2) were created by applying the control algorithm presented in Table 3 and the adaptive lighting control rule given above to 2 d of sunlight data collected during our experiments in the control (sunlight only) treatment for a 12- and 21-h photoperiod

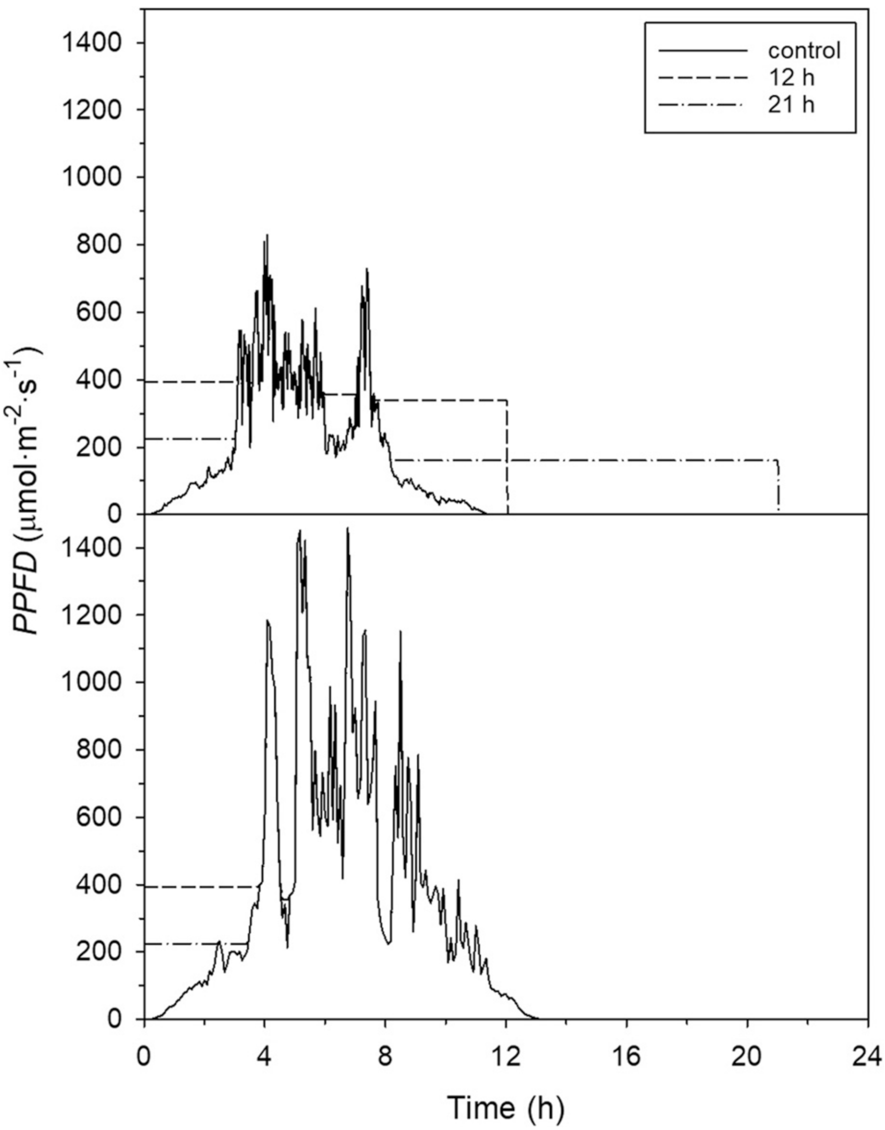

Fig. 2. Simulated operation of the control algorithm for photoperiods of 12 and 21 h (see Table 3). (**Top**) A representative day for which the daily light integral (DLI) from sunlight alone is below the required minimum DLI of 17 mol·m^{-2}·d^{-1}. Supplemental light is provided over the entirety of each allowed photoperiod, and the photosynthetic photon flux densities (*PPFD*s) at which supplemental lighting is provided are higher with the 12-h photoperiod (dashed line) than with the 21-h photoperiod (dotted dashed line). The *PPFD* from sunlight is shown with a solid line. This pattern of supplemental lighting control was typical during Expt. 1. (**Bottom**) A representative day for which the DLI from sunlight alone is greater than the required minimum DLI of 17 mol·m^{-2}·d^{-1}. Supplemental light is provided only at the beginning of each allowed photoperiod, and the *PPFD*s at which supplemental lighting is provided are higher in the 12-h photoperiod (dashed line) than in the 21-h photoperiod (dotted dashed line). This pattern of supplemental lighting control was typical during Expt. 2.

using a custom script (MATLAB R2018b; MathWorks, Natick, MA). Data from the unlit section was used for these simulations because the *PPFD* of sunlight and the LED light bars could not be measured separately in the lit sections.

Crop growth measurements. The experiments were ended when the plants had formed complete heads in all supplemental lighting treatments. At the conclusion of each experiment, chlorophyll content index (CCI) was measured on eight mature leaves for each tray (i.e., each treatment × block combination) using a handheld CCI meter (CCM-200 plus; Apogee Instruments, Inc.). The presence of tipburn was determined by visual observation, and the number of plants with symptoms of tipburn in each tray was recorded. Tipburn symptoms were defined as apical necrosis of young leaves, as well as apical or marginal necrosis on mature leaves (Collier and Tibbitts, 1982; Sago, 2016). To determine whether the treatments affected leaf elongation, 16 fully expanded, nonsenescent leaves were randomly selected from each tray and digitally photographed against a white background with a black 10-cm^2 reference disk. These images were analyzed using Image J (National Institute of Health, Bethesda, MD) to determine the mean leaf size of the harvested leaves for each tray. The remaining shoots were excised at the substrate level, dried in an oven at 80 °C for 5 to 7 d, and then weighed. The leaves used for determining leaf size were dried and weighed separately to allow for the calculation of specific leaf area (SLA). The weight of all shoot material removed from each tray was summed to determine total tray dry weight, which was divided by the number of plants to determine mean shoot dry weight (dry weight).

Energy use. Power use by each LED light fixture, one LED driver and five attached LED light bars, was calculated based on a linear relationship between the provided voltage signal from the analog output module (0–10 V) and power consumption of the fixture (40–380 W), as measured using a power meter (P3 International Corporation; New York, NY) (R^2 = 0.97). Power use was set to zero when the lights were off, even though the driver still consumed some power.

The estimated increase in dry weight per Joule used for supplemental lighting (conversion efficiency) was determined by first subtracting the mean dry weight of the controls for each experiment, averaged over all five blocks, from the dry weights observed in each supplemental lighting treatment × block combination. This was then divided by the estimated energy used per plant, assuming the total amount of supplemental light provided (and hence total Joules) was equally distributed among the five replications associated with each fixture (one supplemental lighting treatment per fixture). Thus, conversion efficiency for each treatment × experiment combination was calculated according to [(dry weight) – (mean dry weight of 5 control replications)] × 32 / [total driver energy use / 5]. The supplemental light covered a space substantially larger than the space occupied by the plants. Because not all of the provided supplemental light was directed at the crop, the calculated conversion efficiency is lower than what it would be in a commercial setting. However, this affected all treatments similarly, and conversion efficiency values can thus be used to compare treatments but should not be used for comparisons with other experiments.

Chlorophyll fluorescence monitoring. Five additional plants were seeded and grown in 10-cm square pots filled with a peat-perlite substrate (Fafard 2P; Sun Gro Horticulture), and fertigated daily with a 100 mg·L^{-1} N liquid fertilizer (15N–2.2P–12.45K; 15–5–15 Cal-Mag) using ebb-and-flow benches in the greenhouse. Chlorophyll fluorescence measurements were taken on these plants over a 20-d period (16 Mar. to 4 Apr. 2018) under ambient lighting conditions (no supplemental light). Each day, a plant was randomly selected for measurement using a chlorophyll fluorometer and attached leaf clip with quantum sensor (MINI-PAM; Heinz Walz, Effeltrich, Germany). Once every 15 min, chlorophyll fluorometry was used to measure Φ_{PSII} on the most recently fully expanded leaf. *PPFD* was measured using the built-in quantum sensor on the leaf clip, and the rate of linear electron transport through

Table 1. Greenhouse lighting conditions for Expt. 1 with only natural lighting in the control treatment and with supplemental light-emitting diode (LED) lights in the supplemental lighting (photoperiod) treatments. Allowed photoperiod indicates the photoperiod (hours) over which supplemental light was allowed to be provided for all treatments except the control. No supplemental light was provided in the control treatment. Supplemental light was provided to reach a required minimum daily light integral of 17 $mol \cdot m^{-2} \cdot d^{-1}$ in the photoperiod treatments using adaptive lighting control (see Table 3). Mean ± SD (n = 22) of realized photoperiod, daily light integral (DLI), and average nonzero photosynthetic photon flux density (*PPFD*) during the photoperiod (photoperiod *PPFD*). Total supplemental lighting hours (number of hours during which the LED lights are on at any nonzero *PPFD*), and total energy use of all five blocks for each supplemental lighting treatment are shown for the 22-d duration of the experiment.

Allowed photoperiod (h)	Realized photoperiod (h)	DLI ($mol \cdot m^{-2} \cdot d^{-1}$)	Photoperiod *PPFD* ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	Total supplemental lighting time (h)	Energy use (MJ)
Control	11.3 ± 0.3	7.9 ± 3.3	196 ± 203	0	0
12	12.0 ± 0.0	17.0 ± 0.0	395 ± 147	236	1.13
15	15.0 ± 0.0	17.0 ± 0.0	316 ± 122	292	1.05
18	18.0 ± 0.0	17.0 ± 0.0	264 ± 125	337	1.02
21	21.0 ± 0.0	17.0 ± 0.0	226 ± 106	396	1.04

Table 2. Greenhouse lighting conditions for Expt. 2 with only natural lighting in the control treatment and with supplemental light-emitting diode (LED) lights in the supplemental lighting (photoperiod) treatments. Allowed photoperiod indicates the photoperiod (hours) over which supplemental light was allowed to be provided for all treatments except the control. No supplemental light was provided in the control treatment. Supplemental light was provided to reach a required minimum daily light integral of 17 $mol \cdot m^{-2} \cdot d^{-1}$ in the photoperiod treatments using adaptive lighting control (see Table 3). Mean ± SD (n = 21) of realized photoperiod, daily light integral (DLI), and average nonzero photosynthetic photon flux density (*PPFD*) during the photoperiod (photoperiod *PPFD*). Total supplemental lighting hours (number of hours during which the LED lights are on at any nonzero *PPFD*), and total energy use of all five blocks for each supplemental lighting treatment are shown for the 21-d duration of the experiment.

Allowed photoperiod (h)	Realized photoperiod (h)	DLI ($mol \cdot m^{-2} \cdot d^{-1}$)	Photoperiod *PPFD* ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	Total supplemental lighting time (h)	Energy use (MJ)
Control	12.7 ± 0.2	16.6 ± 7.2	361 ± 385	0	0
12	12.8 ± 0.3	18.5 ± 1.7	396 ± 298	143	0.546
15	14.2 ± 1.7	18.8 ± 2.1	365 ± 314	143	0.439
18	15.6 ± 3.2	18.4 ± 1.7	326 ± 311	159	0.421
21	18.2 ± 4.5	17.7 ± 1.2	269 ± 286	207	0.435

Table 3. Control algorithm with description (left) and equations (right). Target photosynthetic photon flux density ($PPFD_T$) for adaptive lighting control of the light-emitting diode (LED) lights is calculated by dividing the difference of the required minimum, or target, daily light integral (DLI_T) and the current sum of daily photosynthetic photon flux densities, assuming units of $mol \cdot m^{-2}$, by the number of seconds remaining in the allowed photoperiod. The final time step in the photoperiod is t_f, t is the current time step, and t_0 is the initial time step, the first second of the photoperiod.

Description	Equation
If there is time remaining in the photoperiod and the target DLI has not been met:	$If\ DLI_T > \sum_{t=t_0}^{t} PPFD,\ and\ t<t_f$
The target *PPFD* for adaptive lighting control is equal to the difference between the target DLI and the current sum of *PPFD*, divided by the time remaining in the photoperiod:	$PPFD_T = \frac{(DLI_T - \sum_{t=t_0}^{t} PPFD)}{t_f - t}$
If the target DLI has been met or exceeded, or there is no time remaining in the photoperiod:	$If\ DLI_T \leq \sum_{t=t_0}^{t} PPFD,\ or\ t \geq t_f$
The target *PPFD* for adaptive lighting control is zero, the lights are powered off:	$PPFD_T = 0$

photosystem II (electron transport rate; ETR), an estimate of the rate of the light reactions of photosynthesis, was calculated from Φ_{PSII} and *PPFD* as ETR = $\Phi_{PSII} \times PPFD \times 0.42$. This equation assumes that excitation energy is evenly distributed between PSII and photosystem I, and that 84% of incident light is absorbed by a leaf (Björkman and Demmig, 1987; Genty et al., 1989). Electron transport rate and Φ_{PSII} were determined at a variety of *PPFD*s, as provided by ambient sunlight over the 20-d measuring period, to test the hypotheses that Φ_{PSII} decreases in a convex manner and ETR increases in a concave manner in response to increasing *PPFD*.

Statistical analyses. The effects of treatment, block, experiment, and the treatment × experiment interaction on dry weight, conversion efficiency, leaf size, SLA, CCI, and the number of plants with symptoms of tipburn were tested at $\alpha = 0.05$ using a mixed-model analysis of variance, where experiment and block were treated as random effects in SAS (version 9.2: SAS institute, Cary, NC). Orthogonal contrasts were used to test for significant differences between the control treatments and the mean of all four supplemental lighting treatments, as well as for linear or quadratic trends across supplemental lighting treatments at $\alpha = 0.05$ for dry weight, leaf size, SLA, CCI, and the number of plants with symptoms of tipburn. Analyses were performed using the general linear model in SAS. Dry weight and conversion efficiency were analyzed as functions of the mean realized photoperiod in each treatment × experiment combination, which differed from the allowed photoperiod for supplemental lighting in the second experiment due to high DLIs from sunlight, using linear and nonlinear regression. Leaf size and CCI were analyzed as functions of dry weight, and ETR and Φ_{PSII} were analyzed as a function of *PPFD* using nonlinear regression. Regression analyses were performed using SigmaPlot (version 14; Systat Software, Inc., San Jose, CA).

Results

Quantum yield and electron transport rate. The quantum yield of PSII decreased in an exponential (convex) manner with increasing *PPFD*, and ETR could be described as a negative exponential function of *PPFD*. Electron transport rate increased in an asymptotic (concave) manner with *PPFD* to an asymptote of 287 $\mu mol \cdot m^{-2} \cdot s^{-1}$ with an initial slope of 0.35 mol electrons transported per mol of absorbed photons.

Supplemental lighting and energy use. During the first experiment, the DLI from sunlight alone was less than 17 $mol \cdot m^{-2} \cdot d^{-1}$ on all 22 d (Table 1). In the four supplemental lighting treatments, the target 17 $mol \cdot m^{-2} \cdot d^{-1}$ DLI was met and not exceeded on all days (SD = 0.0 $mol \cdot m^{-2} \cdot d^{-1}$), and light was provided over the entirety of the allowed photoperiod. Photoperiod *PPFD* decreased with increasing photoperiod in the supplemental lighting treatments (Table 1) because the supplemental light was provided at lower *PPFD*s due to lower threshold values for adaptive lighting control with longer photoperiods. Figure 2 (top) illustrates the behavior of the control algorithm on a day for which the DLI from sunlight alone is less than the required minimum DLI, and this pattern of supplemental lighting is representative of all days during the first experiment. At the beginning of the allowed photoperiod, the threshold *PPFD* for adaptive control of the LED lights is equal to the constant *PPFD* at which light would need to be provided over the entire allowed

Table 4. Lettuce crop growth measurements. Mean ± SD (n = 5) of the average plant weight (dry weight), chlorophyll content index (CCI), area of one leaf (leaf size), and specific leaf area (SLA). Allowed photoperiod indicates the photoperiod (hours) over which supplemental light was allowed to be provided for all treatments except the control. No supplemental light was provided in the control treatment. With longer photoperiods, the average nonzero photosynthetic photon flux density (*PPFD*) from sunlight and the light-emitting diode (LED) lights combined (photoperiod *PPFD*, see Tables 1 and 2) was reduced. Supplemental light was provided to reach a required minimum daily light integral of 17 mol·m^{-2}·d^{-1} in the photoperiod treatments using adaptive lighting control. Results for Expts. 1 and 2.

Allowed photoperiod (h)	Expt.	Dry wt (g/plant)	CCI	Leaf size (cm^2)	Specific leaf area (m^2·kg^{-1})
Control	1	0.167 ± 0.023	5.1 ± 0.6	37.8 ± 2.7	46.2 ± 21.2
	2	0.478 ± 0.034	7.9 ± 0.9	89.7 ± 4.6	107.0 ± 11.8
12	1	0.528 ± 0.069	9.8 ± 0.9	57.2 ± 9.5	65.1 ± 40.7
	2	0.615 ± 0.097	9.0 ± 0.8	97.4 ± 5.7	90.3 ± 19.9
15	1	0.540 ± 0.081	10.6 ± 1.4	59.9 ± 11.5	83.1 ± 42.6
	2	0.613 ± 0.038	9.7 ± 0.9	102.8 ± 3.3	90.6 ± 13.6
18	1	0.639 ± 0.142	11.5 ± 1.9	66.2 ± 13.9	76.3 ± 42.8
	2	0.577 ± 0.029	9.7 ± 0.6	98.7 ± 9.1	94.3 ± 12.8
21	1	0.748 ± 0.090	12.0 ± 0.6	68.2 ± 2.8	79.7 ± 26.8
	2	0.712 ± 0.042	10.2 ± 0.6	105.4 ± 7.9	84.1 ± 5.8

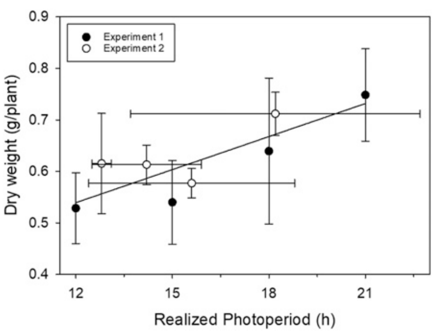

Fig. 3. Dry weight of lettuce as a function of mean realized photoperiod for the supplemental lighting treatments in Expt. 1 (closed symbols) and Expt. 2 (open symbols). At longer photoperiods within each experiment, the average nonzero photosynthetic photon flux density (*PPFD*) from sunlight and the light-emitting diode (LED) lights combined (photoperiod *PPFD*, see Tables 1 and 2) was generally reduced. Supplemental light was provided to reach a required minimum daily light integral of 17 mol·m^{-2}·d^{-1} using adaptive lighting control. The solid line represents the regression equation of dry weight vs. mean photoperiod for both experiments combined (R^2 = 0.35, P < 0.0001). Bars represent ± 1 SD, n = 5.

photoperiod to exactly reach the required minimum DLI in the absence of sunlight. The threshold *PPFD* gradually decreases when the *PPFD* from sunlight alone exceeds the calculated threshold. After sunset, the lights remain on at a final, lower target *PPFD* for the remainder of the allowed photoperiod (Fig. 2, top). Energy use varied between the four supplemental lighting treatments, ranging from 1.02 to 1.13 MJ (Table 1). This difference in power use likely occurred because uneven shading in each of the five sections with quantum sensors may have resulted in different amounts of sunlight being received in these sections. Overhead objects in a greenhouse create heterogenous shading throughout a greenhouse that may persist for longer or shorter amounts of time in a specific location depending on the time of day during which the shading occurs.

During the second experiment, the DLI from sunlight alone exceeded 17 mol·m^{-2}·d^{-1} on 14 of the 21 d. Thus, on many days, the plants received DLIs greater than 17 mol·m^{-2}·d^{-1} even without the application of supplemental lighting. On these days, more supplemental light than required to reach the required minimum DLI was generally provided by the LED lights due to the nature of the control algorithm used (Table 3). Figure 2 (bottom) illustrates the behavior of the control algorithm on a representative day on which the DLI from sunlight alone exceeded the required minimum DLI of 17 mol·m^{-2}·d^{-1}. The LED lights are on at the beginning of the photoperiod because the initial threshold *PPFD* for adaptive control is the constant *PPFD* at which light would need to be provided to exactly reach the required minimum DLI within the allowed photoperiod with no sunlight. As the day progresses, and the required minimum DLI is exceeded, the threshold *PPFD* decreases to zero and the lights are off for the remainder of the allowed photoperiod, yet some supplemental light was already provided earlier in the day. Thus, excess supplemental light was provided, but the photoperiod was not extended beyond the natural daylength, as illustrated in Fig. 2. Because the required minimum DLI was routinely exceeded by sunlight alone, the photoperiod varied daily for all supplemental lighting treatments in the second experiment, and the realized photoperiod frequently was shorter than the allowed photoperiod. Fewer hours of supplemental lighting were provided in the second experiment than in the first experiment (Tables 1 and 2). As with the first experiment, energy use also varied between treatments (Table 2), due to different daily amounts of sunlight being measured by each of the five quantum sensors. Photoperiod *PPFD* generally decreased as photoperiod was extended in the supplemental lighting treatments, and the amount of light provided at the beginning of the photoperiod was greater with shorter photoperiods than with longer ones because the initial threshold *PPFD* was higher. Hence, energy use also tended to be higher in the shorter photoperiod treatments on days for which the DLI from sunlight alone exceeded the required minimum DLI.

Dry weight and conversion efficiency. Dry weight positively correlated with photoperiod (R^2 = 0.35, P < 0.0001) and was greatest in the 21-h photoperiod treatment for both experiments. There was a significant effect of supplemental lighting treatment (P < 0.0001) and experiment (P = 0.013) on dry weight. During the second experiment, when DLIs were generally higher (Tables 1 and 2), dry weight was 0.075 g (14.3%) greater than in the first experiment, averaged over alltreatments (Table 4). Dry weight was, on average, 0.299 g (92.6%) greater in the supplemental lighting treatments than in the control treatment (P < 0.0001; Table 4). There was an increasing linear trend in dry weight with allowed photoperiod (P = 0.001). Dry weight was 0.158 g (27.6%) higher in the 21-h photoperiod treatment (0.730 g) than in the 12-h photoperiod treatment (0.572 g), averaged over both experiments. There was a significant treatment × experiment interaction (P < 0.0001), but a similar increase in dry weight with allowed photoperiod was observed in both experiments (Fig. 3).

Conversion efficiency was positively correlated with photoperiod (R^2 = 0.44, P < 0.0001) and was greatest in the 21-h photoperiod treatment for both experiments (Fig. 4). There was a significant effect (P < 0.0001) of supplemental lighting treatment on conversion efficiency, with the average conversion efficiency being 1.31 μg·J^{-1} (92%) greater in the 21-h photoperiod treatment than in the 12-h photoperiod treatment. There was also a significant effect of experiment on conversion efficiency, and it was on average 0.455 μg·J^{-1} (27.4%) greater in the first than in the second experiment (P = 0.015). There was no significant effect of treatment × experiment interaction on conversion efficiency.

Leaf size and specific leaf area. Leaf size was affected by treatment (P < 0.0001) and increased linearly across supplemental lighting treatments (P = 0.012), being on average 9.5 cm^2 (12.3%) greater in the 21-h photoperiod treatment than in the 12-h photoperiod treatment. Leaf size was 18.2 cm^2 (28.5%) greater in the supplemental lighting treatments than the control, averaged over all supplemental lighting treatments (P < 0.0001). Leaf size was on average 40.9 cm^2 (70.6%) greater in the second than in the first experiment (P < 0.0001). There was no significant effect of treatment × experiment on leaf size. Specific leaf area was not significantly affected by the supplemental lighting treatments but was 23.2 m^2·kg^{-1} (33.1%) greater in the second experiment than in the first (P = 0.0003) and

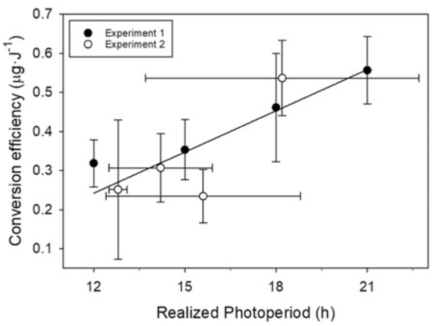

Fig. 4. Conversion efficiency of lettuce, represented as the increase in dry weight per unit energy used to provide supplemental light, as a function of mean realized photoperiod for the supplemental lighting treatments in two experiments. At longer photoperiods within each experiment, the average nonzero photosynthetic photon flux density (*PPFD*) from sunlight and the light-emitting diode lights combined (photoperiod *PPFD*, see Tables 1 and 2) was generally reduced. Supplemental light was provided to reach a required minimum daily light integral of 17 mol·m^{-2}·d^{-1} using adaptive lighting control. The solid line represents the regression equation of conversion efficiency vs. mean photoperiod for both experiments combined ($R^2 = 0.44$, $P < 0.0001$). Bars represent ± 1 SD, n = 5.

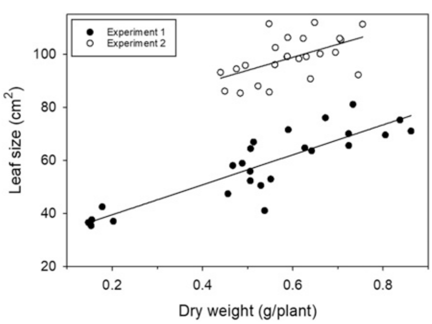

Fig. 5. Leaf size as a function of dry weight for Expt. 1 (closed symbols) and Expt. 2 (open symbols). Lines represent the regression equation of leaf size vs. dry weight for each experiment. Expt. 1: $R^2 = 0.77$, $P < 0.0001$. Expt. 2: $R^2 = 0.31$, $P = 0.0038$.

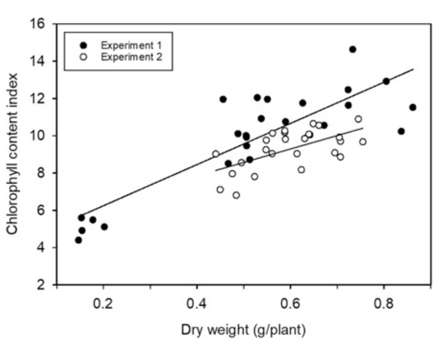

Fig. 6. Chlorophyll content index (CCI) as a function of lettuce dry weight for Expt. 1 (closed symbols) and Expt. 2 (open symbols). Lines represent the regression equation of CCI vs. dry weight for each experiment. Expt. 1: $R^2 = 0.75$, $P < 0.0001$. Expt. 2: $R^2 = 0.37$, $P = 0.0012$.

was affected by the treatment × experiment interaction ($P = 0.028$). Leaf size was positively correlated with dry weight (Fig. 5; $R^2 = 0.77$ and $P < 0.0001$ for the first and $R^2 = 0.31$ and $P = 0.0038$ for the second experiment).

Leaf chlorophyll. Chlorophyll content index was affected by photoperiod treatment ($P < 0.0001$), and CCI averaged over all supplemental lighting treatments was 3.85 units (59.3%) units greater than for the control. There was a linear increase in CCI across supplemental lighting treatments ($P < 0.0001$), with CCI being on average 1.7 units (18.1%) greater in the 21-h than in the 12-h photoperiod treatment. There was no significant difference in CCI between the two experiments. There was an effect of treatment × experiment ($P < 0.0001$), but CCI increased similarly with allowed photoperiod in both experiments. CCI was positively correlated with dry weight (Fig. 6; $R^2 = 0.75$ and $P < 0.0001$ for the first and $R^2 = 0.37$ and $P = 0.0012$ for the second experiment).

Tipburn. There was a significant treatment effect on the number of plants with tipburn ($P < 0.0001$), and a significant, positive linear trend with longer photoperiods ($P = 0.0073$). The number of plants with symptoms of leaf tipburn was on average 5.5 plants (46.6%) greater in the 21-h photoperiod treatment than in the 12-h photoperiod treatment, averaged over both experiments. On average, there were 9.7 (220%) more plants with tipburn in the supplemental lighting treatments than in the controls (Table 5). The incidence of tipburn was higher (16.5 plants, 426%) in the second experiment ($P < 0.0001$) (Table 5), during which DLIs were on average 7.9% greater in the supplemental lighting treatments than in the first experiment (Tables 1 and 2), and there was an effect of treatment × experiment ($P = 0.0097$).

Discussion

Quantum yield and electron transport rate. The asymptotic pattern of increase in ETR with *PPFD*, and attendant decrease in Φ_{PSII} (Fig. 7), is commonly observed for many plant species (Rascher et al., 2000), including lettuce (Weaver and van Iersel, 2019). Because Φ_{PSII} decreases exponentially with increasing *PPFD*, light is used more efficiently to drive photosynthesis at lower *PPFD*s. This relationship can also be observed in the response of ETR to *PPFD*; the rate of increase of ETR with increasing *PPFD* is higher at lower *PPFD*s (Weaver et al., 2019). Because light is used more efficiently to drive the light reactions of photosynthesis at lower *PPFD*s, due to the convexity of the response of Φ_{PSII} to *PPFD*, providing light over a longer photoperiod but at a lower *PPFD* should result in more photosynthesis and hence more growth if the same total amount of light is provided (Weaver and van Iersel, 2019).

Dry weight and conversion efficiency. In a previous experiment (Weaver and van Iersel, 2019), we hypothesized that lettuce growth would increase if plants are provided the same DLI with a longer photoperiod and a lower *PPFD*. This should occur because light is used more efficiently to drive the light reactions of photosynthesis at lower *PPFD*s, as evidenced by the higher Φ_{PSII} and greater slope of the ETR response at lower *PPFD*s, as reported herein (Fig. 7). The daily integral of electron transport through photosystem II will thus be greater for the same DLI if a longer photoperiod and lower average *PPFD*s are used. The daily integrated photosynthetic carbon fixation presumably would as well because electron transport through photosystem II provides the energy and reducing power required for carbon fixation via the Calvin-Benson-Basham cycle (Stanghellini et al., 2019). However, extending the photoperiod beyond some limit is not an option for all greenhouse crops, especially plants with a short-day flowering requirement, for which an uninterrupted dark period is required to initiate flowering (Taiz et al., 2018).

The increase in dry weight as the allowed photoperiod for supplemental lighting was increased may be explained by the likely increase in daily integrals of electron transport rate and photosynthesis as the allowed photoperiod was extended and light was provided at lower average *PPFD*s (Tables 1 and 2). Similar results have been reported from growth chamber experiments. Koontz and Prince (1986) showed that providing a DLI of 22.4 mol·m^{-2}·d^{-1} with a 24-h photoperiod at a constant *PPFD* of 260 µmol·m^{-2}·s^{-1} increased dry weight of five lettuce cultivars by 30% to 50% compared with a 16-h photoperiod with a constant *PPFD* of 415 µmol·m^{-2}·s^{-1} and a similar DLI of 23.9 mol·m^{-2}·d^{-1}. Similarly, Tsuruyama and Shibuya (2018) showed that in growth chambers, strawberry dry weight increases as the photoperiod is increased from 8 to 24 h (in 4-h steps), while maintaining a DLI of 10 mol·m^{-2}·d^{-1}. Likewise, Soffe et al. (1977) demonstrated that extending the photoperiod from 12 to 16 h, while holding DLI in growth chambers constant at 5 MJ·m^{-2}, increased the growth of six vegetable species; lettuce, celery (*Apium graveolens*), beet (*Beta vulgaris*), radish (*Raphanus raphanistrum* subsp. *sativus*), cabbage (*Brassica oleracea*), and canola (*Brassica napus*). However, the possible effect of photoperiod on plant growth, which may be independent of improvements in photosynthetic efficiency, must also be considered. Soffe et al. (1977) also tested the effect of extending the photoperiod from 12 to 16 h with a low *PPFD* light source (3 W·m^{-2}, ≈6 µmol·m^{-2}·s^{-1}), too weak to drive appreciable amounts of photosynthesis, using the same constant *PPFD* and DLI for the first 12 h in both treatments. They found that dry weight and leaf size of lettuce, celery, and beet increased when the photoperiod was extended from 12 to 16 h using a weak light source with the same *PPFD* in both treatments during the first 12 h. Similar effects of photoperiod extension with weak light sources have been reported for several plant species (Adams and Langton, 2005). Thus, there is likely some effect of photoperiod extension on crop growth that cannot be explained by increased photosynthetic

Table 5. Percentage of lettuce plants showing symptoms of tipburn in response to different photoperiods at the conclusion of Expts. 1 (upper rows) and 2 (lower rows). Allowed photoperiod indicates the photoperiod (hours) over which supplemental light was allowed to be provided for all treatments except the control. No supplemental light was provided in the control treatment. With longer photoperiods, the average nonzero photosynthetic photon flux density (*PPFD*) from sunlight and the light-emitting diode (LED) lights combined (photoperiod *PPFD*, see Tables 1 and 2) was reduced. Supplemental light was provided to reach a required minimum daily light integral of 17 $mol \cdot m^{-2} \cdot d^{-1}$ in the photoperiod treatments using adaptive lighting control.

Allowed photoperiod (h)	Expt.	Plants with tipburn (%)
Control	1	0
	2	27.5
12	1	6.25
	2	67.5
15	1	9.34
	2	76.9
18	1	16.2
	2	65
21	1	25.6
	2	82.5

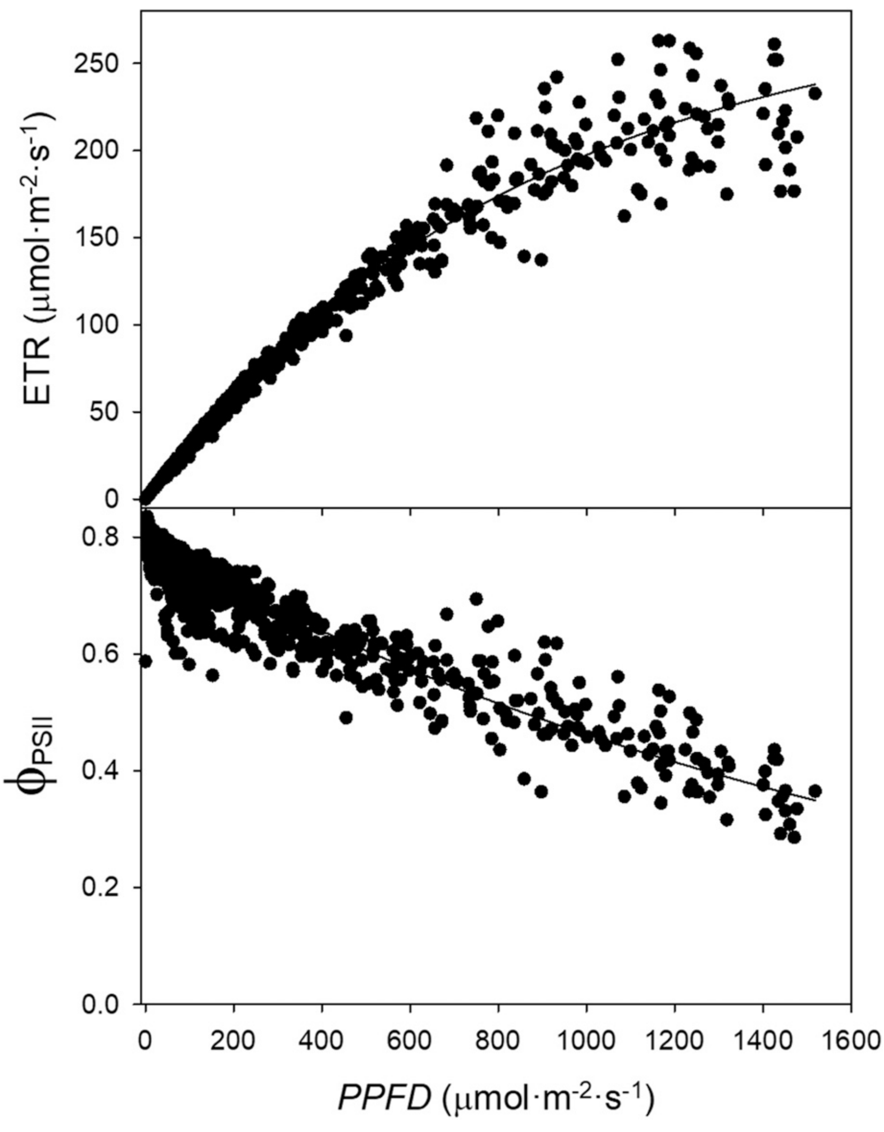

Fig. 7. Electron transport rate (ETR, **top**) and the quantum yield of photosystem II (Φ_{PSII}, **bottom**) as functions of photosynthetic photon flux density (*PPFD*). Curves represent the regression equations for ETR [ETR = 287*(1 – exp(–0.00122**PPFD*))] or Φ_{PSII} [Φ_{PSII} = 0.793 * exp(–0.00054*PPFD)] vs. *PPFD*. For ETR, $R^2 = 0.98$, $P < 0.0001$, and for Φ_{PSII}, $R^2 = 0.90$, $P < 0.0001$. Data were collected using diurnal chlorophyll fluorescence monitoring; plants were measured once every 15 min under ambient greenhouse lighting conditions for 20 d.

efficiency. However, in studies conducted with photoperiod extension using weak light sources, it is impossible to differentiate between the effects of photoperiod and possible shade acclimation induced by the photoperiod extension with low *PPFD*s. Exposure to low *PPFD*s can promote increased leaf chlorophyll, which can improve light absorption and light use efficiency (Ruban, 2015).

In our first experiment, dry weight (Fig. 3) and conversion efficiency (Fig. 4) both increased as the allowed photoperiod for supplemental lighting was extended (Table 1). In our second experiment, the photoperiod was not extended on 14 of the 21 d. However, a significant increase in dry weight and conversion efficiency was still observed as the allowed photoperiod for supplemental lighting was increased and the average realized photoperiod was longer (Fig. 4; Table 1). These results support the hypothesis that increases in growth under longer photoperiods with the same DLI are due to an increase in photosynthetic light use efficiency when the same DLI is provided at lower *PPFD*s and not due to an effect of photoperiod extension because the photoperiod was not routinely extended beyond the natural daylength in the second experiment. Although relatively little supplemental light was provided from the LED lights in the second experiment (Table 2), the supplemental light was provided at lower *PPFD*s in the longer photoperiod treatments (Fig. 2), and a large increase in conversion efficiency was observed as the allowed photoperiod was increased from 12 to 21 h (Fig. 4).

In these experiments, fresh weight was not quantified. However, it is expected that the trends observed for dry weight would be similar for fresh weight. Because lettuce is sold on a fresh weight basis, an increase in profit would be expected if the same amount of supplemental light were applied over a longer photoperiod.

Leaf size and specific leaf area. In both experiments, leaf size and dry weight increased as the allowed photoperiod for supplemental lighting was increased. Leaf size correlated positively with dry weight (Fig. 5). Larger leaf size leads to increased light interception because there is a larger surface area for absorption of light by chlorophyll antennae, and thus the larger leaves of plants grown under the longer photoperiods likely also contributed to the increase in dry weight. Soffe et al. (1977) also showed that extending the photoperiod increases leaf size in lettuce.

Specific leaf area was not significantly affected by the supplemental lighting treatments (Table 4). However, SLA was higher in the second experiment compared with the first. The thicker leaves with reduced area characteristic of plants from the first experiment (Fig. 5) may be due to the higher proportion of blue light those plants received. The ratio of red to blue light of LED lights used in these experiments is 1.08 (Fig. 1). This is relatively low compared with sunlight, which has a red to blue ratio of 1.26 on sunny days at the location of the experiments. During the first experiment, the LED lights were on for 87% of the time that plants were exposed to *PPFD*s greater than zero, averaged over the entire growing period and all supplemental lighting treatments. However, in the second experiment this was reduced to 48%. Thus, in the first experiment, the average red to blue ratio of light received by the plants was likely lower than in the second experiment. Son and Oh (2013) and Wang et al. (2016) showed that lettuce dry weight and leaf area decreased as the red to blue ratio was decreased in growth chamber experiments with plants grown under sole source LED lights.

Leaf chlorophyll. In both experiments, CCI increased as the photoperiod was extended (Tables 1 and 2). Leaf chlorophyll content has been reported to increase with photoperiod extension using weak light sources for several species (Langton et al., 2003; Lefsrud et al., 2006). Although the mechanism for this effect is not currently understood, Langton et al. (2003) hypothesized that the increase in leaf chlorophyll content observed under longer photoperiods may occur because plants can only synthesize chlorophyll in the light. Thus, the increase in CCI observed in our experiments may be due to the extended photoperiod. Leaf chlorophyll content has also been reported to increase in response to reduced *PPFD*s (shading) for some species (Niinemets et al., 1998). This occurs because many plants synthesize more chlorophyll and build larger light-harvesting antennae to capture more light energy when grown under lower *PPFD*s (Ruban, 2015). However, Kleinhenz et al. (2003) showed that applying 50% shade, compared with plants grown in full sunlight, had little effect on leaf chlorophyll concentration in four lettuce cultivars.

Tipburn. In the longer photoperiod treatments, the number of plants exhibiting symptoms of tipburn increased. This was expected because the incidence and severity of tipburn is positively correlated to the growth rate of lettuce, given that tipburn is linked to localized calcium deficiency caused by inadequate calcium transport to growing tissue when air flow is limited (Both et al., 1997; Sago, 2016). Plants in the longer photoperiod treatments grew faster than those grown in the shorter photoperiod treatments, as is evident from their greater dry weight.

Conclusions

The growth and conversion efficiency of 'Little Gem' lettuce can be improved with adaptive lighting control to provide similar amounts of light over a longer photoperiod and at lower average *PPFD*s. By extending the allowed photoperiod for supplemental lighting and using an adaptive lighting control approach that takes advantage of the dimmability of LED lights, more crop biomass is produced per Joule of electrical energy expended on providing supplemental light. However, increased growth rates are associated with a higher incidence of tipburn. Considering this, we hypothesize that with longer photoperiods, the total amount of light provided to plants (DLI) could be reduced, while maintaining a growth rate similar to that observed in the shorter photoperiod treatments, which had less tipburn. This would mean that lettuce plants could be grown with less light, and thus with a lower energy expense but with the same final dry weight and less tipburn, if the plants were grown under a longer photoperiod. Our conjecture is closely related to the idea of controlling daily crop lighting based on an integrated daily amount of photosynthetic carbon fixation, as suggested by Kjaer et al. (2011) and Clausen et al. (2015), or the daily integral of electron transport through photosystem II (Weaver and van Iersel, 2019).

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