LIGHTING CONTROL STRATEGIES FOR IMPROVED PHOTOCHEMICAL EFFICIENCY IN CONTROLLED-ENVIRONMENT AGRICULTURE

by

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(Under the Direction of Marc van Iersel)

ABSTRACT

Supplemental lighting can be used in greenhouses to improve the growth, quality, and yield of greenhouse crops. However, the electricity cost associated with providing supplemental light can be high. The concave response of electron transport rate (ETR), an indicator of the overall rate of the photosynthetic light reactions, to photosynthetic photon flux density (*PPFD*) provides a valuable means for formulating supplemental lighting control strategies which reduce this energy expense by accounting for crop light use efficiency. The ETR response of 'Little Gem' lettuce (Lactuca sativa) was evaluated in a greenhouse over a 35-day production cycle, and the resulting information was used to propose energy-efficient supplemental lighting strategies. One means of improving crop supplemental light use efficiency is to provide the same quantity of supplemental light over a longer period of time at lower *PPFDs*, which is hypothesized to result in greater amounts of photosynthesis and increased plant growth. Greenhouse trials with 'Little Gem' lettuce demonstrate that this approach can be implemented in a greenhouse effectively using dimmable light-emitting diode lights, leading to improved growth and improvements in crop growth per Joule of energy expended on supplemental lighting. For a fixed photoperiod, simulations and numerical optimization demonstrate that the most efficient way to apply greenhouse supplemental light is to apply light in the most consistent possible manner over the course of a day. Simulations based on the ETR response of 'Green Towers' lettuce suggest that this approach can reduce energy use for supplemental lighting by as much as 10%. Because the response of ETR to *PPFD* can generally be described as an exponential rise to a maximum with only two parameters, it is possible to describe this response using only two measurements. This approach was tested and compared to data collected in a greenhouse and growth chamber for six annual bedding plant species. The two-point approximation generally somewhat over-estimates ETR but is reasonably accurate.

INDEX WORDS: adaptive lighting, chlorophyll fluorescence, electron transport rate, greenhouse, light-emitting diodes, nonlinear optimization, photochemistry, photoperiod, quantum yield of photosystem II

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DEDICATION

This work is dedicated to Sylvia, Madelyn, Perry, and Alden.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

The hallmark of controlled-environment agriculture is that it allows plants to be grown under regulated environmental conditions, thereby improving growth and allowing crops to be grown at times of year and in locations where they otherwise could not be. In greenhouses, many environmental variables are highly controlled and maintained within an ideal range for a crop (Jones, 2005; van Straten et al., 2010). Light, however, is generally poorly controlled, and in the greenhouse environment, light intensity is spatially and temporally heterogeneous, and reduced compared to outside conditions (Morrow, 2008). Vegetable crops, in particular, are often grown in greenhouses during the winter months or at Northern latitudes, and under these conditions the overall amount of light received by the plants from sunlight alone may be too low for adequate plant growth and development. Thus, supplemental lighting is often necessary for greenhouse vegetable production (Gruda, 2005; Lu & Mitchell, 2016). Similarly, production of ornamental bedding plants often occurs in the winter for sale in spring, and during this time light can be limiting to crop growth (Currey et al., 2012; Hutchinson et al., 2012). Thus, supplemental lighting can be used to improve the growth and productivity of greenhouse crops. However, the electricity required for providing supplemental light can be a significant expense, and it has been estimated that the electricity required for greenhouse 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).

Light-emitting diode (LED) lights are becoming increasingly popular for horticultural applications, and the advent of LED technology for horticultural lighting has facilitated the development of innovative approaches to providing and controlling greenhouse supplemental lighting (Morrow, 2008; Pinho et al., 2012; Singh et al., 2015). Light-emitting diode fixtures have several distinct advantages over the high-intensity discharge (HID) lamps traditionally used for greenhouse lighting, including their relatively high efficacy, low radiant heat load, and variable spectra. Another unique feature of LEDs is that the intensity of their light output can be controlled precisely and rapidly in a manner that is not possible with HID lamps. Lighting control systems that utilize this dimmability have the potential to reduce the electricity costs associated with providing supplemental light, and to increase the efficiency with which supplemental light is used for promoting plant growth. Adaptive supplemental LED lighting control systems operate by keeping the LED lights off when the ambient photosynthetic photon flux density (*PPFD*) exceeds a predefined threshold *PPFD*. When ambient *PPFD* falls below this level, supplemental light is provided so that the combined PPFD of the LED lights and sunlight reaches, but does not exceed, the threshold. This ensures that supplemental light is provided only when the overall *PPFD* is relatively low, and the supplemental light can be used more efficiently by plants, since plant light use efficiency invariably decreases at higher *PPFDs* (Pinho et al., 2013; van Iersel and Gianino, 2017). This strategy was proposed as early as 1993 by Ishii et al. (1993) but would have been impractical to implement at the time since only HID lamps were available for supplemental lighting. In a recent study, Schwend et al. (2016) demonstrated that using adaptive lighting control reduced electricity costs by 21% without compromising crop

quality of sunflower (*Helianthus annuus*), when compared to simple threshold control (i.e., turning lights on or off at prescribed *PPFD*s).

During the light reactions of photosynthesis, some of the light energy absorbed by chlorophylls and accessory pigments migrates to photosystem II (PSII) reaction centers, resulting in the splitting of water molecules, liberating electrons and protons. The freed electrons are used to regenerate NADPH via the electron transport chain, and a proton gradient across the thylakoid membrane drives ATP synthase, regenerating ATP. These energy-rich molecules, NADPH and ATP, provide the reducing power and chemical energy for carbohydrate production in the Calvin-Benson-Bassham cycle. However, not all light absorbed by photosynthetic pigments is used to drive the light reactions; a significant amount is dissipated as heat. This occurs because the accumulation of excess light energy in the light-harvesting complexes can lead to light-induced damage of PSII reaction centers (photoinhibition). Plants have evolved a variety of interrelated photoprotective mechanisms by which excess absorbed light energy can be safely dissipated as heat, including molecular re-organization of PSII and the xanthophyll cycle (Demmig-Adams et al., 2012; Horton, 2012; Rochaix, 2014; Ruban, 2015). The xanthophyll cycle is the process by which the accumulation of protons, due to high *PPFDs*, leads to acidification of the thylakoid lumen, activating violaxanthin deepoxidase which catalyzes the de-epoxidation of violaxanthin to form antheraxanthin and zeaxanthin. This chemical conversion of the xanthophyll pigments facilitates the dissipation of excess light energy as heat. It reverses relatively slowly through epoxidation catalyzed by zeaxanthin epoxidase.

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, 2018). The decrease in photosynthetic light-use efficiency at higher *PPFDs* is due in part to photoprotective processes (Demmig-Adams et al., 2012; Horton, 2012; Rochaix, 2014; Ruban, 2015). The decrease in photosynthetic efficiency with increasing *PPFD* is most clearly evidenced by a decrease in the quantum yield of photosystem II (Φ_{PSII}), a unitless measure of the efficiency with which absorbed photons are used to drive the light reactions of photosynthesis. The quantum yield can be directly quantified using chlorophyll fluorometry (Baker, 2008; Genty, 1989; Rasher et al., 2000; Weaver and van Iersel, 2019). Chlorophyll fluorometry is a powerful method for assessing the photosynthetic responses to *PPFD*. When light energy is absorbed by a leaf, a small fraction is reemitted as fluorescence. By measuring the fluorescence emitted by chlorophyll *a* before and during a brief pulse of light with sufficient intensity to completely saturate the reaction centers of photosystem II (PSII), Φ_{PSII} can be directly measured (Baker and Rosenqvist, 2004; Genty et al, 1989; Maxwell and Johnson, 2000). When PPFD is also measured, chlorophyll fluorometry can be used to estimate the rate of linear electron transport through PSII (electron transport rate; ETR), a measure of the rate of the light reactions of photosynthesis. While ETR can be a useful indicator of overall photosynthetic rates, an exact correlation between ETR and CO₂ fixation rates may be difficult to establish. This is because the products of the light reactions can be used to

drive processes other than the Calvin-Benson-Bassham Cycle. Photorespiration is a major sink for NADPH and ATP in C3 plants (Krall and Edwards, 1992), and NADPH may be used as an electron donor for nitrate reduction (Tischner, 2000). Freed electrons may reduce O₂ at photosystem I (Mehler reaction, or water-water cycle) rather than be used to produce NAPDH (Polle, 1996), and ATP can be used for chloroplast functions such as protein repair and nucleotide metabolism (Murata and Nishiyama, 2018; Spetea et al., 2004). Thus, the relationship between ETR and CO_2 fixation depends on many factors including temperature, relative humidity, CO₂ concentration, and water and nutrient availability. However, ETR can be taken as a relative indicator of overall photosynthetic rates, and hence plant growth. Furthermore, compared to gas exchange, ETR of C3 plants is relatively insensitive to changes in environmental variables other than light (Murchie and Lawson, 2013). In addition to their usefulness for directly probing the light reactions of photosynthesis, chlorophyll fluorometers are small and portable, have simple operation, and require no re-calibration. Thus, chlorophyll fluorometry is an ideal tool for studying crop light responses in the field.

Providing supplemental light in a manner that allows it to be used most efficiently by a crop, such as using adaptive lighting control to limit the *PPFD* at which supplemental light is provided, has the potential to decrease the amount of supplemental light, and thus the total amount of electricity required for crop growth. For example, using simulations based on historical weather data and cultivar-specific light responses, Weaver and van Iersel (2018) estimated that the amount of supplemental light required for early-season production can be reduced by 24% for *Petunia* × *hybrida* 'Daddy Blue' and 37% for *Impatiens walleriana* 'Super Elfin XP Violet' using an adaptive lighting

control approach that accounts for crop light use efficiency. Similarly, Kjaer et al. (2011) controlled high-pressure sodium (HPS) lamps to reach a daily sum of net carbon fixation, as approximated by a nonlinear model, and accounted for variable electricity prices. They demonstrated that providing supplemental light when *PPFD*s from sunlight alone are low and electricity is cheap, can reduce electricity costs by 25% without compromising the overall quality of two ornamental *Campanula* species. Several other approaches to controlling greenhouse supplemental lighting in a manner which accounts for crop light use efficiency supplemental lighting in optimal control of greenhouse environments or crop growth have been developed, primarily in the context of optimal control. These include approaches that utilize proportional-integral-derivative (PID) control with data clustering (Mahdavian et al., 2017), fuzzy logic (Kolokotsa et al., 2010), and hierarchical control (Bozchalui et al., 2010) with on/off control of supplemental lights, and moveable shades (Kolokotsa et al., 2010).

The focus of this dissertation is developing and testing lighting control strategies which improve crop light use by accounting for the ETR response to PPFD and using adaptive control of greenhouse supplemental lights. In chapter two, ETR is evaluated and analysed as a function of *PPFD*, in a greenhouse, using a crop of 'Green Towers' lettuce (*Lactuca* sativa) plants and chlorophyll fluorometry. This information is then used to formulate and describe methods for improving crop light use efficiency using dimmable LED's in greenhouses. One means of improving crop supplemental light use efficiency is to provide the same quantity of supplemental light over a longer period of time at lower *PPFD*s, which will result in greater amounts of photosynthesis and increased plant growth. This effect has been demonstrated for several species (Aikman, 1989; Craker et

al., 1983; Koontz and Prince, 1986; Soffe et al., 1977; Tsuruyama and Shibuya, 2018). In chapter four, the effect of extending the photoperiod (the continuous interval within a 24hour period during which plants are exposed to light) and providing the same overall amount of light using lower PPFDs is tested in a greenhouse using adaptive lighting control with 'Little Gem' lettuce. Growth is improved as the photoperiod increases, as predicted in chapter two. However, extending the photoperiod is not always an option because some crops have a strictly limited photoperiod requirement. In this case, the simulations presented in chapter two suggest that the greatest crop light use efficiency will be achieved if light is provided in the most uniform manner possible. In chapter three, the problem of improving crop light use efficiency is approached as a nonlinear optimization problem. The goal is to minimize the total amount of supplemental light provided, and thereby minimize the amount of electricity required, subject to achieving a specified minimum integrated sum of ETR during a photoperiod, based on the ETR response from chapter two. The results show that the optimizer is indeed equivalent to providing supplemental light in the most uniform possible manner over a photoperiod, which can be achieved using adaptive lighting. Chapter five explores the possibility of describing the response of ETR to *PPFD* for specific crops using only two measurements. This approach is hypothesized to be feasible because the ETR response can generally be described as a negative exponential function of PPFD with only two parameters; the initial slope and the asymptote of ETR as a function of PPFD. The method is tested using six annual bedding plant species and is shown to be more or less successful.

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CHAPTER 2

PHOTOCHEMICAL CHARACTERIZATION OF GREENHOUSE-GROWN LETTUCE (*LATUCA SATIVA* L. 'GREEN TOWERS') WITH APPLICATIONS FOR SUPPLEMENTAL LIGHTING CONTROL¹

¹ Weaver, G. M. and van Iersel, M. W. 2019. *HortScience*. 54:317-322. Reprinted here with permission of the publisher.

Abstract

Plant light use efficiency decreases as light intensity is increased, and a better understanding of crop-specific light responses can contribute to the development of more energy-efficient supplemental lighting control strategies for greenhouses. In this study, diurnal chlorophyll fluorescence monitoring was used to characterize the photochemical responses of 'Green Towers' lettuce (Lactuca sativa L.) to photosynthetic photon flux density (*PPFD*) and daily light integral (DLI) in a greenhouse over a production cycle. Plants were monitored continuously for 35 days with chlorophyll fluorescence measurements collected once every 15 minutes. Quantum yield of photosystem II decreased exponentially with PPFD, while electron transport rate (ETR) increased asymptotically to 121 μ mol·m⁻²·s⁻¹. Daily photochemical integral (DPI) is defined as the integral of ETR over a 24-hour period; DPI increased asymptotically to 3.29 mol·m⁻²·d⁻¹ with increasing DLI. No effects of plant age or prior days' DLIs and a negligible effect of PPFDs 15 or 30 minutes before measurements within days were observed. Simulations were conducted using the regression equation of ETR as a function of PPFD (ETR = 121(1-exp(-0.00277PPFD))) to illustrate methods of increasing photochemical light use efficiency for improved supplemental lighting control strategies. For a given DLI, DPI can be increased by providing light at lower *PPFD*s over a longer period of time and maximized by providing light with a uniform *PPFD* over the entire photoperiod. Similarly, the DLI required to achieve a given DPI is reduced using these same methods.

Introduction

Supplemental lighting can improve the profitability of greenhouse crop production, and a better quantitative understanding of plant responses to photosynthetic photon flux density (PPFD) can facilitate the development of more efficient, crop-specific control strategies for greenhouse supplemental lighting (van Iersel, 2017). Chlorophyll fluorescence measurements are a rapid and reliable means of directly probing the light reactions of photosynthesis (Baker, 2008). During the light reactions, some of the light energy absorbed by chlorophylls and accessory pigments migrates to photosystem II (PSII) reaction centers, resulting in the splitting of water molecules, liberating electrons and protons. The freed electrons are used to regenerate NADPH via the electron transport chain, and a proton gradient across the thylakoid membrane drives ATP synthase, regenerating ATP. These energy-rich molecules, NADPH and ATP, provide the reducing power and chemical energy for carbohydrate production in the Calvin-Benson-Bassham cycle. However, not all light absorbed by photosynthetic pigments is used to drive the light reactions; a significant amount is dissipated as heat, and a small fraction is reemitted as fluorescence. By measuring the fluorescence emitted by chlorophyll a molecules before and during short exposure to a beam of light with sufficient intensity to completely saturate the PSII reaction centers (a "saturating pulse"), the quantum yield of photosystem II (Φ_{PSII}) can be directly quantified; Φ_{PSII} is a unitless measure of the efficiency with which absorbed light is used to drive photochemistry in the light-adapted state of PSII. The dark-adapted value of the quantum efficiency of PSII (F_v/F_m) is an indicator of maximum potential photochemical efficiency. Combined with PPFD, Φ_{PSII} is used to calculate the rate of linear electron transport through PSII (electron transport rate,

ETR), an estimate of the overall rate of the light reactions of photosynthesis (Baker and Rosenqvist, 2004; Genty et al., 1989; Maxwell and Johnson, 2000). To distinguish measurements based on chlorophyll fluorescence from other measures of photosynthesis such as gas exchange or oxygen evolution, data related to Φ_{PSII} and ETR are referred to as *photochemical* rather than *photosynthetic* herein.

Chlorophyll fluorescence is an ideal tool for understanding crop-specific photochemical responses to PPFD. Chlorophyll fluorometers are generally small and portable, with simple operation that requires no re-calibration. Measurements can be collected quickly in situ, and are non-invasive and accurate (Baker and Rosenqvist, 2004; Maxwell and Johnson, 2000). An exact correlation between ETR and CO_2 fixation rates may be difficult to establish because the products of the light reactions can be used to drive processes other than the Calvin-Benson-Bassham Cycle. Photorespiration is a major sink for NADPH and ATP in C3 plants (Krall and Edwards, 1992), and NADPH may be used as an electron donor for nitrate reduction (Tischner, 2000). Freed electrons may reduce O₂ at photosystem I (Mehler reaction, or water-water cycle) rather than be used to produce NAPDH (Polle, 1996), and ATP can be used for chloroplast functions such as protein repair and nucleotide metabolism (Murata and Nishiyama, 2018; Spetea et al., 2004). Thus, the relationship between ETR and CO₂ fixation depends on many factors including temperature, relative humidity, CO₂ concentration, and water and nutrient availability. However, ETR can be taken as a relative indicator of overall photosynthetic rates, and hence plant growth. Furthermore, compared to gas exchange, ETR of C3 plants is relatively insensitive to changes in environmental variables other than light (Murchie

and Lawson, 2013). Thus, chlorophyll fluorescence measurements provide a convenient, rapid, accurate, and robust means of evaluating photochemical responses to *PPFD*. Light response curves collected using chlorophyll fluorescence measurements are typically performed over a relatively brief period (often just a few minutes) with a highlyfocused light source and may not accurately represent photochemical responses under variable ambient light conditions (Rascher et al., 2000). Photoprotective processes affect photochemical light use efficiency by reducing the amount of absorbed light energy transferred to PSII reaction centers and may operate over longer time scales. Because the accumulation of excess light energy in the light-harvesting complexes can lead to lightinduced damage of PSII reaction centers (photoinhibition), plants have evolved a variety of interrelated photoprotective mechanisms by which excess absorbed light energy can be safely dissipated as heat, including molecular re-organization of PSII and the xanthophyll cycle (Demmig-Adams et al., 2012; Horton, 2012; Rochaix, 2014; Ruban, 2015). As PPFD increases, a larger fraction of absorbed light is dissipated as heat, resulting in a decrease in Φ_{PSII} (Baker, 2008; Maxwell and Johnson, 2000). Fluctuations in *PPFD* over the course of a day can lead to variations in Φ_{PSII} due to the up or down-regulation of the xanthophyll cycle. The xanthophyll cycle is the process by which the accumulation of protons leads to acidification of the thylakoid lumen, activating violaxanthin deepoxidase which catalyzes the de-epoxidation of violaxanthin to form antheraxanthin and zeaxanthin. This chemical conversion of the xanthophyll pigments facilitates the dissipation of excess light energy as heat. It reverses relatively slowly, over a scale of several minutes, through epoxidation catalyzed by zeaxanthin epoxidase. Because of this slow relaxation, transient exposure to high light levels may lead to decreases in
photochemical efficiency (relative decreases in Φ_{PSII} and ETR) for several minutes even if *PPFD*s subsequently decrease to much lower levels (Demmig-Adams et al., 2012; Kaiser et al., 2018; Ruban, 2015). Photochemistry-induced acidification of the thylakoid lumen can further affect rates of electron transport by inhibiting plastohydroquinone oxidation by the cytochrome b_6f complex, thereby decreasing the rate of linear electron transport through PSII, in a process known as photosynthetic control (Foyer et al., 2012).

Light response curves collected over a short period of time may also be inadequate to describe photochemical responses for an entire growing period because photosynthetic rates can vary with leaf or plant age (Locke and Ort, 2014; Salmon et al., 2011), and can be affected by slow acclimation to light intensities. Acclimation to light intensities over the course of hours or days can lead to changes in the overall light response through mechanisms such as chlorophyll antennae re-arrangement or changes in cellular metabolism and translation, and nuclear transcription, induced by chloroplast signaling (Dietz, 2015; Ruban, 2015). If factors such as ontogeny or acclimation significantly impact the overall photochemical light response, light response curves collected over only a few minutes may not sufficiently describe realistic photochemical responses for a crop, and longer-term monitoring would be needed to characterize the photochemical response over a production cycle. Diurnal chlorophyll fluorescence monitoring can be used to gain a more detailed understanding of the photochemical light response under greenhouse lighting conditions (Weaver and van Iersel, 2016). This method consists of measuring chlorophyll fluorescence and PPFD over the course of several days, with measurements taken at regular intervals. Generally, a 15-min interval between chlorophyll fluorescence measurements is sufficiently long to avoid

measurement-induced photoinhibition due to the repeated application of saturating light pulses (van Iersel et al., 2016).

While supplemental lighting can improve the growth, quality, and profitability of greenhouse-grown crops, the electricity requirement of supplemental lights can account for as much as 30% of the operating cost of a greenhouse (van Iersel and Gianino, 2017; Watson et al., 2018). The advent of LED technology for horticultural lighting has facilitated the development of innovative approaches to providing and controlling greenhouse supplemental lighting (Morrow, 2008; Pinho et al., 2012; Singh et al., 2015). Light-emitting diode fixtures have several distinct advantages over the high-intensity discharge (HID) lamps traditionally used for greenhouse lighting, including their relatively high efficacy, low radiant heat load, and variable spectra. Another unique feature of LEDs is that the intensity of their light output can be controlled precisely and rapidly in a manner that is not possible with HID lamps. Lighting control systems that utilize this dimmability have the potential to reduce the electricity costs associated with providing supplemental light, and to increase the efficiency with which supplemental light is used for promoting plant growth. These adaptive, or dynamic, supplemental LED lighting control systems operate by keeping the LED lights off when ambient *PPFD* exceeds a predefined threshold *PPFD*. When ambient *PPFD* falls below this level, supplemental light is provided so that the combined *PPFD* of the LED lights and sunlight reaches, but does not exceed, the threshold. This ensures that supplemental light is provided only when the overall *PPFD* is relatively low, and the supplemental light can be used more efficiently by plants, since plant light use efficiency invariably decreases at higher *PPFDs* (Pinho et al., 2013; van Iersel and Gianino, 2017).

Providing supplemental light in a manner that allows it to be used most efficiently by a crop has the potential to decrease the amount of supplemental light, and thus the total amount of electricity required, for crop growth. For example, using simulations based on historical weather data and cultivar-specific light responses, Weaver and van lersel (2018) estimated that the amount of supplemental light required for early-season production can be reduced by 24% for *Petunia* × *hybrida* 'Daddy Blue' and 37% for *Impatiens walleriana* 'Super Elfin XP Violet' using an adaptive lighting control approach that accounts for crop light use efficiency. Thus, understanding species- or cultivarspecific photosynthetic or photochemical responses to *PPFD* can facilitate the implementation of lighting control strategies that fully utilize the dimmability of LEDs and reduce electricity costs by providing supplemental light according to a specific crop's ability to use that light efficiently.

Lettuce is an important greenhouse crop because there is a continuous demand for a supply of fresh leafy greens, production cycles are relatively short, and lettuce can be produced year-round in greenhouses if appropriate environmental conditions (*e.g.*, light, temperature) are provided. Supplemental lighting for hydroponic greenhouse lettuce production has been the subject of a great deal of research, and some of the most advanced supplemental lighting strategies developed to date have focused on lettuce production (Albright et al., 2000; Bumgarner and Buck, 2016; Seginer et al., 2006). In our study, in situ diurnal chlorophyll fluorescence monitoring was used to evaluate the photochemical performance of a greenhouse-grown crop of a romaine-type lettuce cultivar (*Lactuca sativa* L. 'Green Towers') under growing conditions comparable to a commercial production environment. Specific hypotheses tested were whether the current

ETR is affected by previous *PPFD*s during a day, and whether photochemical efficiency is affected by plant age or previous days' DLIs. In addition to quantifying instantaneous photochemical responses to *PPFD*, the integral of ETR over individual measurement days was calculated and defined as the daily photochemical integral (DPI; mol·m⁻²·d⁻¹), the integral of ETR over a 24-h period. Finally, we conducted simulations to demonstrate how these data can be used to develop energy-efficient supplemental lighting strategies, and outline general methods for using adaptive lighting control to improve crop light use efficiency by decreasing the DLI required to achieve a given DPI, or increasing the resulting DPI for a fixed DLI.

Materials and Methods

The study was conducted in a glass-covered greenhouse in Athens, GA during March and April of 2015. The mean relative humidity ($\pm \sigma$) was 66.3 \pm 16.3 %, the mean temperature was 21.4 \pm 1.7 °C, and the mean daily light integral (DLI) was 13.9 \pm 6.8 mol·m⁻²·d⁻¹ (Fig. 2.1). Seeds of 'Green Towers' lettuce were sown in 10-cm square pots filled with a peat-perlite substrate (Fafard 2P; Sun Gro Horticulture, Agawam, MA). Fifteen plants were grown on ebb-and-flow benches and fertigated daily with a 100 mg·L⁻¹ N liquid fertilizer (15N:2.2P:12.45K; 15-5-15 Cal-Mag; Everris, Marysville, OH). The plants were grown without shading to ensure that measurements could be taken under the widest range of DLIs and *PPFD*s possible.

Chlorophyll fluorescence monitoring was initiated two weeks after germination and performed using a chlorophyll fluorometer and attached leaf clip with quantum sensor (JUNIOR-PAM, Heinz Walz; Effeltrich, Germany). The most recently fullyexpanded leaf was measured until the onset of head formation, after which the youngest

fully-expanded leaf exterior to the head was measured. Leaves were placed in the leaf clip and positioned such that the quantum sensor was fully exposed to the south side of the greenhouse and not shaded by other leaves. Chlorophyll fluorescence measurements were taken once every 15 min to determine Φ_{PSII} , and *PPFD* was measured using the built-in quantum sensor on the leaf clip. Electron transport rate (ETR), an estimate of the rate of the light reactions of photosynthesis, was calculated from Φ_{PSII} and *PPFD* as ETR $= \Phi_{PSII} \times PPFD \times 0.84 \times 0.5$. 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). After 48 h, a different plant was randomly selected for measurement, and measurements using the new plant commenced at least one hour after sunset in order to verify that the F_v/F_m of the new leaf section was within an acceptable range; at least 0.78, with a theoretical maximum of around 0.85. Observations of F_v/F_m below 0.78 indicate that the leaf is experiencing some type of stress and may be senescing. Values exceeding 0.85 are usually due to measurement error, especially improper positioning of the fluorometer sensor head. This initial value was recorded and used as the value of F_v/F_m for subsequent analysis. Chlorophyll fluorescence monitoring continued in this fashion for 35 d and was terminated when the plants had formed a head and reached a salable size. Only one plant was measured at any given time because no treatments were applied or compared, and replications were not needed for a statistical analysis of the data.

Daily light integral was calculated by integrating *PPFD* over each 24-h period, with *PPFD* assumed to be constant for each 15-min increment of the 24-h period. Daily photochemical integral was calculated by integrating ETR over each 24-h period, with

ETR assumed to be constant for each 15-min increment of the 24-h period. The 24-h period was defined as beginning and ending at midnight. The apparent saturating *PPFD* for ETR was calculated as the *PPFD* at which 90% of the asymptote of ETR was reached. The apparent saturating DLI for DPI was calculated as the DLI at which 90% of the asymptote of DPI was reached.

Regression analyses were performed using SigmaPlot (version 13; Systat Software, Inc., San Jose, CA). Regression analysis was used to evaluate ETR and Φ_{PSII} as functions of *PPFD* for all days pooled and for individual days, and to evaluate F_v/F_m as a function of measurement day and preceding day's DLI. Electron transport rate was fit as a function of *PPFD* using the equation ETR=a(1- $e^{-b(PPFD)}$), Φ_{PSII} was fit as a function of *PPFD* using the equation $\Phi_{PSII} = c + a(e^{(-b(PPFD))})$, and DPI was fit as a function of DLI using the equation $DPI=a(1-e^{-b(DLI)})$, where a, b, and c are regression coefficients. To test the hypothesis that plant age affected photochemical capacity, daily asymptotes of ETR were analyzed as a function of plant age for all measurement days with at least two observations of PPFD above 831 µmol·m⁻²·s⁻¹, the apparent saturating PPFD for the pooled ETR response. The analysis was restricted to days on which saturating PPFDs were observed to ensure that an accurate approximation of the asymptote could be obtained. These asymptotes were also analyzed as a function of previous day's DLI to test whether acclimation to the previous day's DLI impacted the current day's photochemical capacity. To test the hypothesis that previous *PPFD*s impacted current photochemistry within days, Φ_{PSII} was analyzed as a quadratic function of current *PPFD* and the observed PPFDs 15 and 30 min prior (PPFD₁₅ and PPFD₃₀, respectively) for all days, using polynomial regression with a general linear model (Proc GLM; SAS version

9.2: SAS Institute, Cary, NC), according to the model: $\Phi_{PSII} = a_0 + a_1 \times PPFD + a_2 \times PPFD$ $PPFD^{2} + a_{3} \times PPFD_{15} + a_{4} \times PPFD_{30}$, where a_{0}, \ldots, a_{4} are regression coefficients. Significance was tested at p = 0.05. To further test the effect of within-day variations in *PPFD* on ETR and Φ_{PSII} , observations of ETR and Φ_{PSII} occurring before and after solar noon for non-zero PPFDs were compared and tested for significant differences at p =0.05 using a mixed-model analysis of covariance, where day of experiment was treated as a random effect, time of day (before/after solar noon) was a fixed effect, and PPFD was a covariate. Analysis was performed using the general linear model in SAS (Proc GLM). The covariate effect was approximated using a ninth-order polynomial for ETR and a sixth-order polynomial for Φ_{PSII} , according to the model: $y = a_0 + a_1 \times PPFD + ... + a_n \times PPFD$ PPFDⁿ, where y is the dependent variable, n is the highest order of the polynomial, and a_0, \ldots, a_n are regression coefficients. Polynomial order for each dependent variable was selected by using Taylor's theorem to determine the lowest-order polynomial needed to accurately replicate the function values of the exponential equations fitted via regression analysis over at least 90% of the range of the PPFD data. Polynomial fit was verified using regression analysis in SAS with model significance tested at p = 0.001. Data from five measurement days were excluded from the analyses and graphs because observations of F_v/F_m recorded more than one hour after sunset following the first photoperiod of diurnal measurement fell outside of the acceptable range (0.78 to 0.85), the same criteria used for the initial measurement of F_v/F_m at the onset of diurnal monitoring. Additionally, observations were missing from 3 measurement days, and thus DPI and DLI were not calculated for these days.

Simulations were conducted based on the relationship between ETR and PPFD. A set of simulations was conducted in which the objective was to reach a DLI of 17 mol·m⁻ ²·d⁻¹ with nine photoperiods (8-24 h, 2 h intervals) with a constant *PPFD*. The required constant *PPFD* for each photoperiod was determined by dividing 17 mol·m⁻² by the photoperiod. Electron transport rates corresponding to these PPFDs were calculated using the regression equation of ETR as a function of *PPFD*. Calculated ETRs were integrated over the photoperiod to obtain the DPI. Further simulations were conducted in which the objective was to reach a DLI of 17 mol·m⁻²·d⁻¹ with a 12-h photoperiod using two PPFDs, each for half of the photoperiod, with a range of differences (0 to 700 μ mol·m⁻²·s⁻¹) between the two *PPFD*s (Δ *PPFD*). The constant *PPFD* for the 0 μ mol·m⁻ 2 ·s⁻¹ difference scenario was calculated as described above to be 394 μ mol·m⁻²·s⁻¹. For the remaining scenarios, the required PPFD for each half of the photoperiod was calculated by increasing or decreasing 394 µmol·m⁻²·s⁻¹ by one half of the required difference in *PPFD*. For each half of the photoperiod, ETR was calculated using the regression equation of ETR versus PPFD, and DPI was obtained by integrating these values over the whole photoperiod. A third set of simulations was conducted in which the objective was to reach a DPI of 2.89 mol·m⁻²·d⁻¹ with nine photoperiods (8-24 h, 2 h intervals) with a constant ETR (which corresponds to a constant *PPFD*). The required constant ETR was calculated for each photoperiod by dividing 2.89 mol·m⁻² by the photoperiod. The corresponding *PPFD* was calculated using the inverse function of the regression equation of ETR as a function of *PPFD*: *PPFD*=ln(a/a-ETR)/b, where a and b are regression coefficients. Daily light integral was obtained by integrating this *PPFD* over the photoperiod.

Results and Discussion

Quantum yield of PSII decreased exponentially ($R^2 = 0.89$, p < 0.0001) as *PPFD* increased from 0 to $\approx 1500 \ \mu mol \cdot m^{-2} \cdot s^{-1}$, the highest *PPFD* observed during this study (Fig. 2.2, top). This decrease in Φ_{PSII} was observed because, as *PPFD* increases, a greater proportion of absorbed light energy is dissipated as heat due to the operation of the xanthophyll cycle and other photoprotective processes, leaving a smaller fraction of the light to drive photochemistry (Demmig-Adams et al., 2012; Horton, 2012; Rochaix, 2014; Ruban, 2015). The response of ETR to *PPFD* was an exponential rise to a maximum (Fig. 2.2, bottom) with an asymptote of 121 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and an initial slope of 0.335 moles of electrons per mole of incident photons ($R^2 = 0.95$, p < 0.0001). The apparent saturating *PPFD* (reached at 90% of the asymptote of ETR) was 831 $\mu mol \cdot m^{-2} \cdot s^{-1}$.

There was no significant change in the daily asymptotes of ETR over the course of the study (data not shown). This suggests that, for this cultivar, plant age has little impact on maximum photochemical capacity. Some of the variability in these data may have been due to leaf, rather than plant age, which was not documented. Similarly, F_v/F_m did not change significantly with plant age (data not shown). This could be due to the short duration of the study, or the relative insensitivity of F_v/F_m to leaf ontogeny; while some chlorophyll fluorescence parameters may change with plant age, F_v/F_m is known to vary little with leaf age, except during senescence (Mauromicale et al., 2006; Šesták, 1999). Because plant age did not affect photochemical characteristics, it is likely that diurnal chlorophyll fluorescence monitoring conducted over a much shorter period of time than the 35-d used in this study would be adequate to describe the photochemical

light response of this cultivar over a production cycle. However, because only a small part of one leaf was measured at any given time, these results may not be indicative of entire canopies or the effect of aging on whole canopy photochemistry. Fluctuating light levels can impact overall daily rates of photochemistry because photoprotective processes such as the xanthophyll cycle (Demmig-Adams et al., 2012), as well as photosynthetic control (Foyer et al., 2012), can inhibit photochemical light use for several minutes after transient exposure to high light intensities (Kaiser et al., 2018; Slattery et al., 2018). To test the hypothesis that previous light levels impact current photochemistry, Φ_{PSII} was analyzed as a quadratic function of current *PPFD* and linear effects of the *PPFD*s observed 15 and 30 min prior. Overall, the model fit well ($R^2 =$ 0.86, p < 0.0001) and both PPFD₁₅ and PPFD₃₀ were highly significant (p < 0.0001) but contributed little to the overall model R^2 (partial $R^2 = 0.008$ and 0.005, respectively). Thus, *PPFDs* from the previous 15 and 30 min had a negligible effect on Φ_{PSII} (and hence ETR). Furthermore, there was no significant difference in observations of either Φ_{PSII} or ETR taken before versus after solar noon (Fig. 2.2). These results are likely due to the time resolution of our measurements; the 15-min interval needed to avoid measurementinduced photoinhibition is likely a sufficient span of time for xanthophyll cycle activity to almost completely relax after transient high light exposure. Zeaxanthin is converted back to the non-photoprotective violaxanthin by zeaxanthin epoxidase on a scale of several minutes (Demmig-Adams et al., 2012; Kaiser et al., 2018). Daily light integrals of individual measurement days also had no significant effect on F_v/F_m measured during the subsequent dark period, or on the following day's asymptote of ETR (data not shown),

and the study was conducted under a wide range of DLIs (Fig. 2.1). Thus, photochemical acclimation over a timescale of days was not observed in this study.

Daily photochemical integral, the integral of ETR over a 24-h period, was evaluated as a function of DLI. Like the response of ETR to PPFD, DPI increased exponentially to a maximum with DLI (Fig. 2.3; $R^2 = 0.82$, p < 0.0001), with an asymptote of 3.30 mol·m⁻²·d⁻¹; 90% of this asymptote was reached at a DLI of 18.9 mol·m⁻²·d⁻¹ (apparent saturating DLI). Previous research showed that the ideal DLI for hydroponic greenhouse production of the bibb lettuce cultivar 'Ostinata' is 17 mol·m⁻²·d⁻ ¹. At this daily light integral, growth rates were sufficiently high to guarantee rapid production without causing excessive leaf tip burn (Albright et al., 2000; Both et al., 1997). Interestingly, although a different cultivar was used, the saturating DLI found in our study deviates by only 11% from the recommended DLI based on growth trials (Both et al., 1997). This points to the potential utility of chlorophyll fluorescence monitoring for developing crop-specific DPI or DLI recommendations. However, it is important to recognize that DPI is not a direct function of DLI, but rather of the integral of ETR over a day. Electron transport rate in turn is a non-linear function of *PPFD*, and hence DPI does not simply depend on DLI, but also on how observations of *PPFD* are distributed over the course of a day. Because of this, seasonal variation in daily distributions of *PPFD* would be expected to influence the observed response of DPI to DLI.

Lighting recommendations for greenhouse crops are currently made based on estimates of the range of DLIs required for ideal production of specific crops (*e.g.*, Torres and Lopez, undated). However, with the same DLI, different DPIs can result from providing the same quantity of light with different distributions of *PPFD*, due to the

nonlinearity of the ETR response. Although a clear correlation between DPI and crop growth has not yet been established, quantifying DPI provides a means of assessing the effectiveness of greenhouse supplemental lighting control strategies, assuming that an increase in DPI will result in higher growth rates. One means of increasing DPI for a given DLI is to extend the photoperiod, allowing supplemental light to be provided at lower PPFDs, thereby increasing the efficiency of photochemical light use and leading to higher DPIs. Figure 2.4 shows the *PPFD* required to reach a DLI of 17 mol·m⁻²·d⁻¹ using a constant *PPFD* at a range of photoperiods (8-24 h), with the corresponding calculated ETR and resultant DPI based on the regression equation of ETR as a function of *PPFD*. As the photoperiod is increased and the constant PPFD decreased, DPI increases from 2.81 mol·m⁻²·d⁻¹ with an 8-h photoperiod to 4.39 mol·m⁻²·d⁻¹ with a 24-h photoperiod (Fig. 2.4). This occurs because the rate of increase in ETR decreases exponentially as *PPFD* increases, since ETR as a function of *PPFD* is an exponential rise to a maximum. Evidence from previous research indicates that these simulated increases in DPI do indeed correspond to improved plant growth. Koontz and Prince (1986) showed that providing the same DLI with a 24-h photoperiod increased lettuce weight by 30-50% compared to a 16-h photoperiod. Soffe et al. (1977) demonstrated that extending the photoperiod from 12 to 16 h, while holding DLI constant at 5 MJ·m⁻², increased growth rates of seven vegetables; lettuce, celery (Apium graveolens), beetroot (Beta vulgaris), spinach beet (Beta vulgaris), radish (Raphanus raphanistrum subsp. sativus), cabbage (Brassica oleracea), and oilseed rape (Brassica napus). Since altering the photoperiod may have unintended consequences for flowering of many daylength-sensitive crops, extending the photoperiod may not always be an option. Another means of increasing

DPI for a fixed DLI is to provide supplemental light with a more uniform (less variable) distribution over the photoperiod. Figure 2.5 illustrates this principle. If light is provided to reach a DLI of 17 mol·m⁻²·d⁻¹ with a 12-h photoperiod, a constant *PPFD* of 394 μ mol·m⁻²·s⁻¹ would be required, resulting in a DPI of 3.47 mol·m⁻²·d⁻¹. If the distribution of *PPFD* is altered such that light is provided to reach a DLI of 17 mol \cdot m⁻²·d⁻¹ in 12 h, with a higher PPFD for half of the photoperiod and a lower PPFD for the other half (with the difference between these denoted as $\Delta PPFD$), DPI will decrease with increasing $\Delta PPFD$, and at a $\Delta PPFD$ of 700 µmol·m⁻²·s⁻¹ DPI is reduced to 2.58 mol·m⁻ 2 ·d⁻¹ (Fig. 2.5). Uniform distributions of *PPFD* are associated with higher DPIs than more variable distributions due to the nonlinearity of the ETR response; as PPFD is decreased or increased by the same amount from some initial value, the decrease in ETR at the lower *PPFD* will be greater than the increase in ETR at the higher *PPFD*, and the magnitude of this difference increases as the change in PPFD increases. The hypothesis that an increase in DPI due to improved uniformity of *PPFD* will improve crop growth is supported by past research. Aikman (1989) demonstrated the effect of lighting uniformity on tomato growth. Tomatoes were grown in growth chambers at a constant DLI with a consistent light level of 58 W·m⁻², and with two variable light distributions, where the light was provided at 103 W·m⁻² first half of the day and 13 W·m⁻² for the second, or vice versa. Dry weight of plants grown under the uniform light intensity was on average 33% greater than in the other treatments. While the simulations presented herein do not account for the interactions of supplemental LED lights and sunlight, adaptive lighting control can be used to improve the uniformity of PPFDs from LED lights and sunlight

combined, and to minimize the *PPFD* provided by LED lights, thereby achieving equivalent increases in DPI (van Iersel and Gianino, 2017).

In a manner analogous to increasing DPI for a given DLI, the DLI required to reach a particular DPI can be reduced by providing supplemental light at lower *PPFD*s and/or with a more uniform *PPFD* distribution. Reducing the required DLI will decrease the total amount of supplemental light provided, which results in electricity savings. According to the regression equation of DPI versus DLI (Fig. 2.3), a DPI of 2.89 mol·m⁻ ²·d⁻¹ corresponds to the recommended DLI of 17 mol·m⁻²·d⁻¹ for lettuce (Both et al., 1997). If light is provided to reach a DPI of 2.89 mol·m⁻²·d⁻¹ with a continuous *PPFD* over a range of photoperiods (8-24 h), the required DLI decreases as the photoperiod is extended (Fig. 2.6). The highest DLI requirement, 18.4 mol·m⁻²·d⁻¹, occurs with an 8-h photoperiod, while the DLI required for a 24-h photoperiod is only 10.1 mol·m⁻²·d⁻¹, a 45% decrease. Similarly, for a fixed photoperiod and DPI, DLI will be reduced if supplemental light is provided with a more uniform distribution of *PPFD* (Weaver and van Iersel, 2018).

Control strategies for greenhouse supplemental lighting which account for daily requirements of photosynthesis or photochemistry have been developed with the goal of reducing electricity costs by decreasing the amount of supplemental lighting required, or providing supplemental lighting when electricity is less expensive (Clausen et al., 2015; Wang et al., 2018; Watson et al, 2018; Weaver and van Iersel, 2018). Kjaer et al. (2011) demonstrated that the electricity cost associated with supplemental lighting can be reduced by 25% without affecting the overall quality of two ornamental *Campanula* species when supplemental lights are controlled by the DynaLight system. This system

accounts for electricity prices and photosynthetic rates to achieve a specified daily photosynthetic integral with the lowest possible electricity cost, using a canopy photosynthesis model based on *PPFD*, temperature, and CO₂ concentration (Aaslyng et al., 2003; Clausen et al., 2015; Kjaer et al., 2012). Implementing such strategies requires evaluating crop-specific light response and establishing recommendations for daily photosynthesis or photochemistry for individual crops. The results of our paper demonstrate that the response of ETR to *PPFD*, as determined using diurnal chlorophyll fluorescence monitoring, is robust to plant age, within-day fluctuations in *PPFD*, and previous days' DLIs for the lettuce cultivar studied. Additional research, including greenhouse growth trials, is needed to evaluate the relationship between DPI and crop growth, and to establish methods for determining crop-specific DPI requirements.

Conclusions

The photochemical responses of 'Green Towers' lettuce were found to be consistent over the course of this study, being unaffected by plant age or previous *PPFD*s or DLIs, within or across days. This suggests that, while diurnal chlorophyll fluorescence monitoring over a production cycle provides valuable insight, photochemical light response curves collected over a shorter period of time should be adequate for characterizing crop-specific photochemical responses to develop supplemental lighting control strategies. Electron transport rate is an asymptotically-increasing function of *PPFD*, and therefore daily photochemical light use efficiency can be improved by providing supplemental light at relatively low *PPFD*s over an extended period of time, or by providing supplemental light in a uniform manner. For a given DLI, DPI can be increased by applying these principles. Similarly, the DLI required to achieve a given

DPI can be reduced. Further research is needed to assess the effectiveness of supplemental lighting control strategies which account for these dynamics and determine whether greenhouse crop production can be improved by providing supplemental light in a photochemically-efficient manner.

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Figure 2.1. Daily light integral (DLI) over the course of the study.



Figure 2.2. Quantum yield of photosystem II (Φ_{PSII}) of 'Green Towers' lettuce as a function of *PPFD* based on 35 d of constant diurnal monitoring. Closed symbols represent measurements taken before solar noon, open symbols represent measurements taken after solar noon. The regression line represents the equation $\Phi_{PSII} = 0.171 \pm 0.643e^{-0.00178PPFD}$, with $R^2 = 0.89$ and p < 0.0001 (top). Electron transport rate (ETR) of 'Green Towers' lettuce as a function of *PPFD* based on 35 days of constant diurnal monitoring. Closed symbols represent measurements taken before solar noon, open symbols represent measurements taken after solar noon. The regression line represents the equation $\Phi_{PSII} = 0.171 \pm 0.643e^{-0.00178PPFD}$, with $R^2 = 0.89$ and p < 0.0001 (top). Electron transport rate (ETR) of 'Green Towers' lettuce as a function of *PPFD* based on 35 days of constant diurnal monitoring. Closed symbols represent measurements taken before solar noon, open symbols represent measurements taken after solar noon. The regression line represents the equation ETR = $121(1-e^{-0.00277PPFD})$, with $R^2 = 0.95$ and p < 0.0001 (bottom).



Figure 2.3. Daily photochemical integral (DPI) of 'Green Towers' lettuce as a function of DLI based on 35 d of diurnal chlorophyll fluorescence monitoring. The regression line represents the equation DPI = $3.30(1-e^{-0.122\text{DLI}})$, with $R^2 = 0.82$ and p < 0.0001.



Figure 2.4. Daily photochemical integral (DPI) resulting from reaching a DLI of 17 $mol \cdot m^{-2} \cdot d^{-1}$ with a constant *PPFD* over a range of photoperiods required (top); required *PPFD*, and corresponding ETR (calculated from equation in Fig. 2.2, bottom).



Figure 2.5. Daily photochemical integral (DPI) resulting from reaching a DLI of 17 mol·m⁻²·d⁻¹ with a 12-h photoperiod using two *PPFD*s, each for half of the photoperiod, with a range of differences between the two *PPFD*s ($\Delta PPFD$) (top). Required *PPFD*s

(bottom), and corresponding ETRs (middle) are shown. For $\Delta PPFD=0$, only one *PPFD* is used.



Figure 2.6. Daily light integral (DLI) needed to reach a calculated DPI of 2.89 mol·m⁻²·d⁻¹ with a constant *PPFD* over a range of photoperiods (top); required ETR, and corresponding *PPFD* (bottom) based on the regression equation in Fig. 2.2 (bottom).

CHAPTER 3

A PHOTOCHEMISTRY-BASED METHOD FOR OPTIMISING GREENHOUSE SUPPLEMENTAL LIGHT INTENSITY²

² Weaver, G. M., van Iersel, M. W., and Mohammadpour Velni, J. 2019. *Biosystems Engineering*. 182:123-137. Reprinted here with permission of the publisher.

Abstract

Supplemental lighting in greenhouses can increase crop growth, improving rates of greenhouse production. The advent of light-emitting diodes (LEDs) for photosynthetic lighting presents new opportunities for optimising greenhouse supplemental lighting control. Because LED light intensity can be controlled rapidly and precisely in real time, these lights can be controlled such that supplemental light is provided when it will be most efficiently used to drive photosynthesis. This approach to supplemental lighting control has the potential to reduce the electricity cost associated with greenhouse lighting while retaining the beneficial effects on crop growth, thereby decreasing the financial cost and improving the sustainability of greenhouse crop production. In this paper, an optimisation problem is formulated to minimise the total amount of electricity used by supplemental LED lights, subject to achieving a specified daily amount of photochemistry. An algorithm to solve the problem explicitly based on sufficient conditions for a global minimiser is developed. This method represents a computationally simple and broadly applicable means for minimizing the amount of electricity required for supplemental lighting in greenhouses.

1. Introduction

1.1. The need for optimal supplemental lighting control in greenhouses and physiological basis for optimal control. Plants are photoautotrophs that synthesise carbohydrates through a light-dependent pathway, photosynthesis, and hence light is an absolute requirement for plant growth (Taiz, Zeiger, Møller, & Murphy, 2015). Greenhouse production of many plant species can be improved by using supplemental lights to increase the amount of photosynthesis and corresponding plant growth, thereby shortening production cycles and improving crop yields (Gómez Morrow, Bourget, Massa, & Mitchell, 2013; Nelson & Bugbee, 2014; Singh, Basu, Meinhardt-Wollweber, & Roth, 2015). In highly-controlled greenhouse environments, other limiting factors for plant growth, such as water and fertiliser availability, temperature, CO₂ concentration, and relative humidity are typically controlled and maintained within an ideal range for a specific crop (Jones, 2005; van Straten, van Willigenburg, van Henten, & van Ooteghem, 2010). Light, however, is generally poorly controlled, and in the greenhouse environment, light intensity is spatially and temporally heterogeneous, and reduced compared to outside conditions (Morrow, 2008). Inconsistencies and deficiencies in greenhouse light levels can limit overall crop growth and quality (Dorais & Gosselin, 2000; Faust, Holcombe, Rajapakse, & Layne, 2005). Vegetable crops are often grown in greenhouses during the winter months or at Northern latitudes, and under these conditions the overall amount of light received by the plants from sunlight alone may be too low for adequate plant growth and development. Thus, supplemental lighting is often necessary for greenhouse vegetable production (Gruda, 2005; Lu & Mitchell, 2016). Although there is a long history of optimisation for greenhouse cultivation (van Straten et al., 2010), relatively little work has focused on

optimising supplemental lighting. The electricity use of supplemental lighting can account for as much as 30% of the operating cost of a greenhouse (van Iersel & Gianino, 2017; Watson, Boudreau, & van Iersel, 2018). Thus, there is a critical need for optimal decision making in greenhouse lighting control to reduce the cost and energy expense associated with supplemental lighting, thereby improving the profitability and sustainability of greenhouse crop production.

Photosynthesis is a photon-driven process. Thus, for plant physiological research, photosynthetic light levels are measured and quantified as the photosynthetic photon flux density (PPFD, μ mol m⁻² s⁻¹), the number of photons of light in the photosynthetically-active wavelength range (400-700 nm) per square meter per second. The integral of PPFD during a 24-hour period is known as the daily light integral (DLI, mol m⁻² d⁻¹). Photoperiod is defined as the interval of a 24-hour period during which plants are exposed to light (see Table 3.1).

Currently, lighting recommendations for greenhouse crops are made in terms of DLI, and the correlation between DLI and overall crop growth is generally assumed to be linear (Albright, Both, & Chiu, 2000; Lopez & Runkle, 2008). However, photosynthetic responses to PPFD are nonlinear, and plant light use efficiency invariably decreases at higher light intensities (Rascher, Liebig, & Lüttge, 2000; Sharkey, Bernacchi, Farquhar, & Singsaas, 2007). As PPFD increases, more light is absorbed by leaves than can be used by the photosynthetic pathway. This leads to an accumulation of excess excitation energy which can damage the photosynthetic apparatus. To avoid light-induced damage, plants have evolved a series of pathways through which excess absorbed light energy is safely dissipated as heat (Horton, 2012; Rochaix, 2014; Taiz et al., 2015). Thermal losses

become proportionally higher as PPFD increases, thus, light is used more efficiently to drive photosynthesis at lower PPFDs (van Iersel et al., 2016). The nonlinear response of photosynthesis to light intensity presents one means by which to formulate optimisation problems for controlling greenhouse supplemental light intensity; because light is used more efficiently for photosynthesis at lower PPFDs, preferentially providing the same quantity of supplemental light over time at lower PPFDs will result in greater amounts of photosynthesis and increased plant growth. This effect has been demonstrated for several species (Soffe, Linton, & Milford, 1977; Craker, Seibert, & Clifford, 1983; Koontz & Prince, 1986; Aikman, 1989; Tsuruyama & Shibuya, 2018).;

1.2. *Literature review on greenhouse lighting control and optimisation*. Early efforts towards dynamic, real-time control of greenhouse supplemental lighting used rule-based decision making to control daily light levels to a specific DLI. Carrier, Gosselin, and Gauthier (1994) described a rule-based system designed to achieve a user-defined DLI within a specified photoperiod. This system utilised a daily sunlight forecast and incorporated a crop growth model for tomato to estimate the profitability of providing supplemental light. A later, well-known example of rule-based greenhouse lighting control is the system first described by Albright et al. (2000) which has since become known as LASSI (light and shade system implementation). The system uses supplemental lights in combination with moveable shades and a sunlight prediction to achieve a consistent target DLI of 17 mol m⁻² d⁻¹, which was determined to be ideal for lettuce (*Lactuca sativa* L.) production based on previous research (Both, Albright, Langhans, Reiser, & Vinzant, 1997; Both, Albright, & Langhans, 1998). Although this approach does not, in principle, constitute optimisation in that no objective function is being minimised or maximised, part

of the LASSI decision-making framework is to delay supplemental lighting until as late as possible, when off-peak pricing is more likely to be available. Later work showed that the overall electricity cost could be reduced by considering the 3-day average DLI rather than individual DLIs (Seginer, Ioslovich, & Albright, 2005), or by using an improved sunlight prediction (Seginer, Albright, & Ioslovich, 2006). Recent simulations by Harbick, Albright, and Mattson (2016) showed that the LASSI system could reduce overall energy consumption for tomatoes, lettuce, and floricultural crops as compared to simple threshold control where lights are turned on when PPFD falls below some specified level and shades are deployed when it exceeds some higher level. While controlling light to a consistent DLI across seasons would ensure consistent, year-round production, the use of shading is likely not beneficial for all crops because shading eliminates what would otherwise be cost-free photosynthetic gains from sunlight. Shading to restrict DLI below an upper bound may be beneficial in the special case of lettuce because the physiological disorder known as leaf tipburn is more likely to occur with higher DLIs (Both et al., 1997; 1998).

Most previous approaches to controlling greenhouse lighting were based on the use of high-intensity discharge (HID) lamps (particularly, high-pressure sodium lamps) since these were the primary type of greenhouse horticultural light available for many years. Light-emitting diode (LED) lights are gradually replacing HID lamps as the preferred type of greenhouse supplemental lighting. Several features of LED lights have contributed to their adoption by the greenhouse industry, including their high energy-use efficiency, relatively low heat load, and narrow spectra (Bourget, 2008; Morrow, 2008; Gómez et al., 2013; Pocock, 2015; van Iersel, 2017). Another unique feature of LED lights is that the intensity of their light output can be quickly, precisely, and automatically controlled in real time via several methods including pulse-width modulation (PWM) and current control (Narra & Zinger, 2004; Nishikawa, Ishizuka, Matsuo, & Shigematsu, 2006). Compared to LED lights, HID lamps have limited dimming capability and cannot be cycled on and off rapidly, and thus the ability to control the intensity of these lamps' light output is limited (Nehdi et al., 2014; Nsibi et al., 2017).

The dimmability of LED lights has enabled the development of lighting control strategies that would not be possible with simple on/off control (van Iersel et al., 2016). A rule-based approach to controlling supplemental light intensity that utilises the controllability of LED lights is known as dynamic, or adaptive, lighting control (Pinho, Hytönen, Rantanen, Elomaa, & Halonen, 2013; van Iersel & Gianino, 2017). The basic principle of this type of control is that supplemental light is provided up to, but not exceeding some specified threshold PPFD, and the lights are turned off if this threshold level is exceeded by sunlight alone. Adaptive lighting control can be used to take advantage of the nonlinearity of the photosynthetic light response by preferentially providing supplemental light at lower PPFDs which will be used more efficiently to drive photosynthesis. This strategy was proposed as early as 1993 by Ishii, Murata, and Tanaka (1993) but would have been impractical to implement at the time since only HID lamps were available for supplemental lighting. In a recent study, Schwend, Beck, Prucker, Peisl, and Mempel (2016) demonstrated that using adaptive lighting control reduced electricity costs by 21% without compromising crop quality of sunflower (Helianthus annuus), when compared to simple threshold control (i.e., turning lights on or off at prescribed PPFDs).

While rule-based methods such as adaptive lighting control or LASSI can reduce electricity costs and improve crop growth, few optimally-controlled greenhouse lighting strategies have been implemented to date. Perhaps the best example of real-time implementation of an optimal control strategy for greenhouse supplemental lighting is the DynaLight system (Maersk-Møller & Jørgensen, 2011; Clausen et al., 2015). With this system, the objective is to minimise the total daily cost of running the supplemental lights, subject to achieving a minimum daily amount of photosynthesis (daily photosynthetic integral). It considers real-time electricity prices, daily weather forecasts, and a crop photosynthesis model, and thereby accounts for the efficiency with which supplemental light is used by plants to drive photosynthesis, as well as the cost of providing supplemental light. The general operation of the DynaLight system is such that the lights are turned on when electricity prices and ambient PPFDs are both relatively low, if supplemental lighting is required to meet the minimum daily photosynthetic integral for a given 24-hour period. Kjaer, Ottosen, and Jørgensen (2011) demonstrated that this system can reduce electricity costs by 25% without compromising the overall quality of two ornamental Campanula species. The DynaLight system was developed for use with HID lamps, but recent improvements considered LED lights as part of an integrated multiobjective greenhouse environment optimisation strategy and demonstrated that electricity costs can be reduced further by replacing HID lamps with LED lights (Sørensen, Kjaer, Ottosen, & Jørgensen, 2016). Several other approaches to including supplemental lighting in optimal control of greenhouse environments or crop growth have been developed. These include proportional-integral-derivative (PID) control with data clustering (Mahdavian, Sudeng, & Wattanapongsakorn, 2017), fuzzy logic (Kolokotsa, Saridakis, Dalamagkidis, Dolianitis, & Kaliakatsos, 2010), and hierarchical control (Bozchalui,
Cañizares, & Bhattacharya, 2015), using on/off control of supplemental lights, and moveable shades (Kolokotsa et al., 2010).

Recently, dimmable LED lights have been included in greenhouse lighting optimisation strategies. Chang, Chang, and Song (2016) developed a cloud-based fuzzy control method for controlling LED lights using image sensors and a plant physiological database which uses pulse-width modulation to control the intensity of the LED lights. Light intensity was decreased as plants grew closer to the lamps, and spectral composition of the red, blue, and white LED lights was also altered over the course of the growth cycle. Fuzzy control was compared to a rule-based "automatic mode" in which LED light intensity was decreased and spectral composition was altered in a pre-defined manner at fixed time intervals and tested using lettuce. The cloud-based fuzzy control reduced the energy cost of LED lights by 19.3% over a 31-day growing period, but total shoot fresh mass was similarly reduced (on average, 17.8% lower in the fuzzy control treatment). Dimmable LED lighting control has also been considered within the context of optimal greenhouse environmental control for maximizing profit based on crop growth models for tomatoes (Wang, Wei, & Xu, 2018) and lettuce (Xu, Du, & van Willigenburg, 2018).

1.3. *Description of current* work. The direct physiological impact of incident photons (PPFD) is that they provide the energy to drive electron transport in the light reactions of photosynthesis. We therefore choose electron transport rate as the most relevant physiological process to be considered in our optimisation problem. The response of photochemical electron transport to PPFD can generally be described as an exponential rise to a maximum (Rascher et al., 2000). Due to the asymptotic nature of the photochemical light response, identical daily amounts of daily photochemistry can be

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achieved with infinitely many different combinations of PPFDs. Thus, the amount of supplemental light provided, and corresponding energy cost can be minimised by using a control strategy which takes advantage of the nonlinear relationship between PPFD and photochemistry. In our current work, an optimisation problem is formulated to minimise the total amount of light provided from supplemental LED lights with variable intensity to reach a specified daily amount of photochemistry within a specified photoperiod. This approach minimises the total amount of electricity required because light (PPFD) output of LED lights is directly proportional to their electricity consumption when dimming is accomplished using PWM. A computationally-simple (explicit form) solution to this problem is presented that can facilitate real-time implementation. This problem is similar to that presented by Clausen et al. (2015) and solved using DynaLight. Our present work differs in that we do not consider variable electricity pricing, but rather expand on the basic principle by taking advantage of the controllability of LED light intensity, leading to greater reductions in the objective (cost) function value than would be possible with binary control (Wang et al., 2018). For this problem to be implemented in real time, a prediction of daily sunlight levels would be needed, and the accuracy of this prediction would likely correlate to the realised reductions in energy use (Seginer et al., 2006; Clausen et al., 2015; Sørensen et al., 2016).

2. Materials and Methods

2.1. *Evaluating photochemistry as a function of* irradiance. Functions describing the photochemical light response of greenhouse-grown lettuce ('Green Towers') were taken from previous research conducted by Weaver and van Iersel (2019) which utilised diurnal chlorophyll fluorescence monitoring with a 15-minute measurement interval over a 35-day

production cycle. Measuring chlorophyll fluorescence is a means by which the light reactions of photosynthesis can be directly probed. During the light reactions, some of the energy from absorbed photons is used to move electrons through photosystem II. A small fraction of the absorbed light energy is re-emitted from chlorophyll molecules and the amount of fluorescence depends on the efficiency of electron transport. By measuring this fluorescence under ambient light and during a brief saturating pulse of light, the quantum yield of photosystem II can be directly measured (Φ_{PSII}). This is a unitless measure of the proportion of absorbed light that is used to drive the light reactions of photosynthesis (*i.e.*, the proportion that is not dissipated as heat). Based on Φ_{PSII} and PPFD, the rate of electron transport through photosystem II can be calculated (electron transport rate; ETR, μ mol m⁻² s^{-1}) (Genty, Briantais, & Baker, 1989; Baker & Rosenqvist, 2004). Electron transport rate is expressed as a function of PPFD based on regression analysis of the data presented in Fig. 3.1 (ETR = $A(1-\exp(-k*PPFD))$), with A = 121 and k = 0.00277). To formulate the optimisation problem based on photochemical light use efficiency, the daily photochemical integral (DPI, mol m⁻² d⁻¹) is defined as the integral of daily ETR per square meter of crop canopy. Daily photochemical integral for this crop was evaluated as a function of DLI as measured in a greenhouse under ambient lighting conditions, with no supplemental lighting (Fig. 3.2).

2.2. Tools to solve underlying optimisation problem. To solve the defined optimisation problem (see section 3.3), we will utilise tools from nonlinear optimisation theory and derive an explicit form solution and search method based on satisfying the Karush-Kuhn-Tucker (KKT) conditions (Karush, 1939; Kuhn & Tucker, 1951; Hanson, 1981). In order to develop an efficient algorithm for finding the optimal x^* explicitly using the KKT conditions, the problem is re-written to express the variables in units of ETR rather than PPFD (section 3.3) by solving the regression equation from Fig. 3.1 for PPFD; PPFD = (ln(A/(A-ETR))/k). By formulating the problem in this way, all constraints become linear, allowing for an effective and simple iterative search for the global minimiser, x^* , to be conducted based on the vector of Lagrange multipliers, λ , using a scalar threshold descent method.

2.3. *Optimal solutions and simulations*. The optimal solution was found using light data from three different sources. The problem was solved manually (sections 4.1 and 4.2) using data obtained from a weather station in Watkinsville, GA. The problem was solved with MATLAB (R2018b) using a custom script which performed the search algorithm given in sections 3.5 and 3.6, and also simulated an on/off supplemental lighting control strategy. Comparisons of the optimal control and on/off strategy were made by applying these algorithms to typical meteorological year (TMY3) irradiance data for Kalamazoo, MI, an important greenhouse production area in the Northern U.S. (section 4.3). Typical meteorological year data was obtained from the national solar radiation database website at https://rredc.nrel.gov/solar/old_data/nsrdb/1991-2005/tmy3/. Photosynthetic photon flux density was calculated from the gross horizontal irradiance given in the TMY3 dataset by multiplying by a conversion factor of 2.02 μmol J⁻¹ (Faust and Logan, 2018). The optimisation problem was also solved using the custom MATLAB script and greenhouse PPFD data collected during a previous study (Weaver and van Iersel, 2019) (section 4.4).

3. Theory/Calculations

3.1. *Plant physiological* rationale. In the underlying optimisation problem (see section3.3), the general strategy is to minimise the amount of electricity used by the LED lights,

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subject to achieving a specified DPI within a defined photoperiod. The cost function is the sum of daily PPFDs from the supplemental LED lights, which corresponds to the total amount of electricity used by the supplemental LED lights, because energy use of LED lights is directly proportional to their light output. Thus, there is no need to explicitly quantify the amount or cost of energy associated with using the LED lights. The underlying assumption is that the marginal benefits of providing enough supplemental light to reach the selected target DPI outweigh the minimised energy costs. For the example problem and simulations, the goal is to minimise the total light output of the LED lights while achieving a DPI equal to 3 mol $m^{-2} d^{-1}$ if sunlight alone does not provide sufficient light to reach this target. This target DPI (DPI_T) of 3 mol m⁻² d⁻¹ corresponds to approximately 90% of the asymptote of DPI, based on the regression model (Fig. 3.2), and is consistent with current lighting recommendations for greenhousegrown lettuce, which specify an ideal DLI of 17 mol m⁻² d⁻¹ (Both et al., 1997; 1998). From a physiological perspective, the 24-hour period is a rational choice of time span for integrating photochemical rates because plant growth processes are coupled to circadian patterns of gene expression. Circadian patterns oscillate with a period of approximately 24 hours, and in the case of higher plants, certain growth processes occur only during the subjective "night" (Bendix, Marshall, & Harmon., 2015; Covington, Maloof, Straume, Kay, & Harmer, 2008; Greenham & McClung, 2015). Kjaer, Ottosen, and Jørgensen (2012) demonstrated that controlling supplemental lighting to a specified daily photosynthetic integral using different lighting regimes resulted in similar amounts of crop growth in two Campanula species. Extrapolating from these results, and considering the DLI recommendation for lettuce, the problem can be stated as: "minimise the

electricity use of supplemental LED lights, subject to achieving a specific amount of daily crop growth". The lower bound on DPI was selected based on the established DLI recommendations and the asymptotic behaviour of DPI as a function of DLI, evaluated in a greenhouse under natural lighting conditions for the lettuce cultivar considered. However, further work is needed to establish methods for determining species or varietyspecific DPI bounds for other greenhouse crops.

3.2. Constraints and limitations. In addition to the lower bound on DPI (section 3.1), the optimisation problem is constrained by the minimum and maximum light output (U_{LED}) of the LED lights (0 and 200 µmol m⁻² s⁻¹, respectively). The upper bound is consistent with a realistic PPFD output at plant level using currently available greenhouse LED lights. The vector of PPFDs from the supplemental LED lights is denoted as x, while s is the vector of PPFDs from sunlight ($s \ge 0$). To solve the optimisation problem, we assume that s is known, or has been predicted with 100% accuracy. For practical applications, a prediction of s with reasonable accuracy would be needed to effectively implement an optimal control strategy of this type. The entries of x and s are average PPFDs for each *n*-second interval. The continuous period during which plants are exposed to nonzero PPFDs over a 24-hour period (photoperiod) may be limited to less than 24 hours because in many realistic scenarios shorter photoperiods yield desirable morphological results. For example, many varieties of lettuce flower more quickly under longer photoperiods, and upon flowering lettuce stops producing edible biomass (Waycott, 1995). To account for this restriction, the number of entries of x and s is made equal to the number of seconds in the photoperiod divided by *n* (this quotient is denoted as τ), and the i^{th} entry of x corresponds to the i^{th} entry of s. For the example problem and simulations

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using greenhouse PPFD data, a 16-hour (57,600-second) photoperiod is used (n = 900, and $\tau = 64$) and days were selected for which the 16-hour photoperiod exceeds the natural photoperiod (sunrise to sunset), PPFDs from sunlight alone would not result in a DPI greater than or equal to 3 mol m⁻² d⁻¹ and at least some supplemental light from the LED lights will be needed (i.e., x > 0), and for which achieving a DPI greater than or equal to DPI_T is possible given the selected $U_{LED} = 200 \ \mu\text{mol m}^{-2} \ \text{s}^{-1}$. For practical implementation, if the DPI from sunlight alone is predicted or known to exceed the lower bound, the LED lights would either be turned off for the entire day or kept on at an arbitrarily low intensity when PPFD from sunlight is zero to maintain a consistent photoperiod. Likewise, for any day during which the selected DPI_T cannot be reached, the LED lights would be powered on at maximum intensity for the entire photoperiod in order to come as close as possible to achieving the required DPI_T .

3.3. *Optimisation problem* statement. The goal of the optimisation is to minimise the total amount of light provided by the LED lights $(\sum_{i=1}^{\tau} nx_i)$, subject to achieving a specified target amount of daily photochemistry $(\sum_{i=1}^{\tau} n\bar{x}_i)$, where *x* is the vector of PPFDs from the LED lights and \bar{x} is the vector of ETRs from the LED lights. The problem is further constrained by the lower (zero) and upper (U_{LED}) bounds on the entries of *x*. The optimisation is conducted over a predetermined $n\tau$ -second photoperiod.

Strictly speaking, ETR is a concave nonlinear function of PPFD. However, for the purpose of formulating an optimisation problem, PPFD can be expressed as a convex nonlinear function of ETR, and the PPFD from the LED lights over each discrete time interval (x_i) thus be written as $x_i = (ln(A/(A - \bar{x}_i - \bar{s}_i))/k) - s_i$, where \bar{s} is the vector of ETRs from sunlight and \bar{x} is the vector of ETRs from the LED lights. The advantage of writing

the problem in this form is that it results in a nonlinear optimisation problem with all constraints being linear. The problem is solved with a search method that exploits the specific structure of the optimisation problem (see sections 3.4 and 3.5) to find the unique (global) minimiser which satisfies the sufficient (KKT) conditions. Because all constraints are linear, the unique global minimiser that yields the vector of optimal Lagrange multipliers (λ^*) can be found efficiently using a simple linear approximation from an initial guess which satisfies certain conditions outlined in section 3.5. Generally, indirect solution methods based on exploiting the specific structure of a problem are computationally more efficient than direct nonlinear programming methods (van Straten et al., 2010), and for this particular problem the accuracy of linear approximation to λ^* due to the strict linearity of the constraint functions guarantees fast convergence.

The optimisation problem is written as follows:

Minimise
$$f(\bar{x}) = \sum_{i=1}^{\tau} ln(a/(a - \bar{x}_i - \bar{s}_i))/k$$
 (1)

subject to:

$$\sum_{i=1}^{\tau} (\bar{x}_i + \bar{s}_i) \ge DPI_T/n \tag{2}$$

$$\bar{x}_i \ge 0 \tag{3}$$

$$-\bar{x}_i \ge -\bar{U}_{LED,i} \tag{4}$$

$$i \in \{1, ..., \tau\}$$

where the upper bound of \bar{x}_i ($\bar{U}_{LED,i}$) is calculated for each of the τ elements of \bar{x} as follows:

$$\overline{U}_{LED,i} = a \left(1 - e^{-k(U_{LED} + s_i)} \right) - a \left(1 - e^{-k(s_i)} \right).$$
(5)

The objective function is nonlinear, all constraints are linear, the Hessian of the objective function is positive definite for all feasible \bar{x} , and the problem is convex:

$$\frac{\partial^2 f(\bar{x})}{\partial \bar{x}_i^2} = 1/((a - \bar{x}_i - \bar{s}_i)^2 k) > 0; \forall 0 \le (\bar{x}_i + \bar{s}_i) < a$$

$$\frac{\partial^2 f(\bar{x})}{\partial \bar{x}_i \partial \bar{x}_j} = 0; \forall i \ne j$$

$$(6)$$

$$(7)$$

If $(\bar{x}_i + \bar{s}_i) \ge A$, the cost function $f(\bar{x})$ (Eq. (1)) is undefined and the problem is infeasible because there is no solution. Thus, $\nabla^2_{\bar{x}\bar{x}} f(\bar{x})$ is a positive definite, diagonal matrix with all diagonal entries being strictly positive for any feasible \bar{x} and \bar{s} (Eq. (6)) and the sufficient conditions for a global minimiser \bar{x}^* are (Griva, Nash, & Sofer, 2009):

 $C\bar{x}^* \ge b$ $\nabla f(\bar{x}^*) = C^T \lambda^*$ $\lambda^* \ge 0$ $\lambda^{*T} g(\bar{x}^*) = 0$

The constraint functions and partial derivatives of the objective function are:

$$g_1(\bar{x}) = \sum_{i=1}^{\tau} (\bar{x}_i + \bar{s}_i) - DPI_T / n$$
(8)

$$g_{i+1}(\bar{x}) = \bar{x}_i \tag{9}$$

$$g_{i+\tau+1}(\bar{x}) = \overline{U}_{LED,i} - \bar{x}_i \tag{10}$$

$$\frac{\partial f(\bar{x})}{\partial \bar{x}_i} = 1/((a - \bar{x}_i - \bar{s}_i)k) > 0; \ \forall \ 0 \le (\bar{x}_i + \bar{s}_i) < a.$$
(11)

3.4. Existence of a scalar threshold-type solution. For a global minimiser, \bar{x}^* , $g_1(\bar{x})$

in (8) must be active because, if it is not active, the objective function value will be decreased by decreasing one or more \bar{x} ; assuming that $\sum_{i=1}^{\tau} \bar{s}_i < DPI_T/n$ and a feasible solution exists. Thus, to satisfy the condition $\lambda^{*T}g(\bar{x}^*) = 0$, λ_1^* must be positive for a global minimiser \bar{x}^* , Considering this, and the sufficient conditions $\nabla f(\bar{x}^*) = C^T \lambda^*$ and $\lambda^* \ge 0$, it is concluded that for the global minimiser \bar{x}^* , considering only positive values of λ^*_{i+1} and $\lambda^*_{i+\tau+1}$:

$$\frac{\partial f(\bar{x}^*)}{\partial \bar{x}_i^*} = \begin{cases} \lambda_1^*, & \text{for } \overline{U}_{LED,i} > \bar{x}_i^* > 0\\ \lambda_1^* + \lambda_{i+1}^*, & \text{for } \bar{x}_i^* = 0\\ \lambda_1^* - \lambda_{i+\tau+1}^*, & \text{for } \bar{x}_i^* = \overline{U}_{LED,i} \end{cases}$$
(12)

Thus, for an optimal solution $\bar{\mathbf{x}}^*$ there must exist some scalar value \bar{y}_i^* such that:

$$\lambda_1^* = 1/((a - \bar{y}_i^*)k) > 0; \quad \forall \ 0 \le \bar{y}_i^* < A.$$
(13)

Since the partial derivatives of the objective function, for any feasible sum of \bar{x} and \bar{s} , are strictly positive and monotonically increasing in $(\bar{x}_i + \bar{s}_i)$ (Eq. (11)), it is concluded that:

$$\bar{x}_{i}^{*} = \begin{cases} \bar{y}_{i}^{*} - \bar{s}_{i}, \text{ for } \overline{U}_{LED,i} \geq (\bar{y}_{i}^{*} - \bar{s}_{i}) > 0 \\ 0, & \text{ for } (\bar{y}_{i}^{*} - \bar{s}_{i}) \leq 0 \\ \overline{U}_{LED,i}, & \text{ for } \overline{U}_{LED,i} < (\bar{y}_{i}^{*} - \bar{s}_{i}) > 0 \end{cases}$$
(14)

and equivalently, for positive values of λ_{i+1}^* and $\lambda_{i+\tau+1}^*$;

$$\frac{\partial f(\bar{x}^*)}{\partial \bar{x}_i^*} = \begin{cases} \lambda_1^*, & \text{for } \overline{U}_{LED,i} \ge (\bar{y}_i^* - \bar{s}_i) > 0\\ \lambda_1^* + \lambda_{i+1}^*, & \text{for } (\bar{y}_i^* - \bar{s}_i) \le 0\\ \lambda_1^* - \lambda_{i+\tau+1}^*, & \text{for } \overline{U}_{LED,i} < (\bar{y}_i^* - \bar{s}_i) > 0 \end{cases}$$
(15)

Thus, the entries of \bar{x}^* can be determined using a single scalar value, \bar{y}_i^* , which is equivalent to a threshold value of ETR for adaptive LED lighting control.

3.5. Search method for global minimiser. Let \bar{y} be a τ -long vector with all entries

equal. The global minimiser x^* can be found by solving for \overline{y}_i^* starting from an initial feasible guess of \overline{y} . Rewriting $g_1(\overline{x})$ gives (see Eq. (8)):

$$g_1(\bar{x}) = \sum_{i=1}^{\tau} \bar{x}_i + \sum_{i=1}^{\tau} \bar{s}_i - DPI_T/n$$
(16)

Defining $h(\bar{x}) = \sum_{i=1}^{\tau} \bar{x}_i$ results in (for $\sum_{i=1}^{\tau} \bar{s}_i \leq DPI_T/n$):

$$h(\bar{x}) = \sum_{i=1}^{\tau} \bar{x}_i \ge (DPI_T/n - \sum_{i=1}^{\tau} \bar{s}_i)$$
(17)

For a global minimiser, $\lambda_1^* > 0$ and $g_1(\bar{x}^*) = 0$. Therefore, the optimal value of $h(\bar{x}^*)$ must satisfy:

$$h(\bar{x}^*) = DPI_T / n - \sum_{i=1}^{\tau} \bar{s}_i.$$
 (18)

Assume that $\bar{y}_i^* < \bar{U}_{LED,i}$ (all constraints $g_{i+\tau+1}(\bar{x})$ are inactive) (Eq. (10)) and a global minimiser \bar{x}^* exists for which the upper bound will not be reached for any \bar{x}_i^* . If $\bar{x}_i > 0$, then $g_{i+1}(\bar{x})$ is inactive (Eq. (9)) and $\bar{x}_i = \bar{y}_i - \bar{s}_i$. Let \hat{H} represent the $\tau \times \tau$ submatrix of active constraints consisting of rows 2 through $\tau+1$ of the matrix of active constraints; the $(i,i)^{\text{th}}$ elements of \hat{H} are equal to one for any $\bar{x}_i = 0$, and all other entries are equal to zero. Thus, for any $\bar{y}, p^T \bar{y} = p^T \bar{x} + p^T \bar{s}$, where p is a null space vector for \hat{H} (i.e., $\hat{H}p = 0$). If p is chosen such that $p^T \bar{x} = h(\bar{x})$, the optimal \bar{y}^* can be estimated from an initial feasible guess of \bar{y} and $h(\bar{x})$ according to the following:

$$\hat{p}^T \, \overline{\mathbf{y}}^* \approx \hat{p}^T \, \overline{\mathbf{y}} \left[(h(\overline{\mathbf{x}}^*) + \hat{p}^T \overline{\mathbf{s}}) / (h(\overline{\mathbf{x}}) + \hat{p}^T \overline{\mathbf{s}}) \right] \tag{19}$$

$$\bar{y}^* \approx \bar{y} [(h(\bar{x}^*) + \hat{p}^T \bar{s})/(h(\bar{x}) + \hat{p}^T \bar{s})], \text{ or equivalently}$$
 (20)

$$\bar{y}_i^* \approx \bar{y}_i [(h(\bar{x}^*) + \hat{p}^T \bar{s}) / h(\bar{x}) + \hat{p}^T \bar{s})]; \text{ where}$$
(21)

$$\hat{p}^T \bar{\mathbf{x}} = h(\bar{\mathbf{x}}) = \sum_{i=1}^{\tau} \bar{\mathbf{x}}_i,\tag{22}$$

and $\hat{p}^T \bar{s}$ is assumed to be constant. Generally, $\hat{p}^T \bar{s}$ decreases with a decrease in \bar{y} , and hence the assumption that this quantity remains constant prevents the estimate from failing erroneously low and leading to an infeasible solution. If the assumption that $\bar{y}_i^* < \bar{U}_{LED,i}$ is not correct, and some \bar{x}_i^* must be equal to $\bar{U}_{LED,i}$, the above identities remain useful, but the estimate will be less accurate. Although in this case $p^T \bar{y}$ will not necessarily be equal to $(p^T \bar{x} + p^T \bar{s})$. However, these quantities will always be proportional; $p^T \bar{y} \propto p^T \bar{x} + p^T \bar{s}$. Furthermore, it can be shown that for any global minimiser where one or more \bar{x}_i^* equals $\bar{U}_{LED,i}$, the objective function value would be decreased if U_{LED} were increased such that all \bar{x}_i^* are less than $\bar{U}_{LED,i}$; the solution for the problem with a lower U_{LED} is in the feasible set for the problem re-stated with the higher U_{LED} but is not the global minimiser (see Appendix).

3.6. Search algorithm and solution to the optimisation problem. The algorithm to solve for \bar{y}^* is as follows:

(*i*) Specify an initial guess, \bar{y} . All entries of \bar{y} are equal, and the scalar value \bar{y}_i is not bounded by any $\bar{U}_{LED,i}$.

(*ii*) Calculate \bar{x} and $h(\bar{x})$ based on \bar{y} according to (see Eq. (14)):

$$\bar{x}_{i} = \begin{cases} \bar{y}_{i} - \bar{s}_{i}, \text{ for } \overline{U}_{LED,i} \geq (\bar{y}_{i} - \bar{s}_{i}) > 0 \\ 0, & \text{ for } (\bar{y}_{i} - \bar{s}_{i}) \leq 0 \\ \overline{U}_{LED,i}, & \text{ for } \overline{U}_{LED,i} < (\bar{y}_{i} - \bar{s}_{i}) > 0 \end{cases}$$

$$(iii) \text{ If } h(\bar{x}) = h(\bar{x}^{*}), \text{ stop, } \bar{y} = \bar{y}^{*} .$$

$$(iv) \text{ If } h(\bar{x}) > h(\bar{x}^{*}), \text{ update the estimate of } \bar{y}^{*} \text{ by (see Eq. (21)):}$$

$$\bar{y}^{*} \approx \bar{y}[(h(\bar{x}^{*}) + \hat{p}^{T}\bar{s})/(h(\bar{x}) + \hat{p}^{T}\bar{s})].$$

$$(v) \text{ Iterate until the solution converges to an optimal } \bar{y}^{*} \text{ for which } h(\bar{x}) = h(\bar{x}^{*}).$$

Once an optimal solution \overline{y}^* is found, the global minimiser for x is determined by solving for x^* from:

$$x_i^* = (\ln(a / (a - \bar{x}_i^* - \bar{s}_i))/k) - s_i.$$
⁽²⁴⁾

Alternately, x^* can be found by converting the optimal threshold scalar ETR \bar{y}_i^* to an optimal threshold PPFD (y_i^*) from:

$$y_i^* = \ln(a/(a - \bar{y}_i^*))/k$$
(25)

and calculating the entries of x^* according to the scalar value of y_i^* in a manner analogous to the calculation of \bar{x}_i^* in (14).

While x^* is the global minimiser for supplemental lighting intensities (PPFDs from the LED lights), for implementing this solution with an adaptive lighting control system, only the scalar threshold value y_i^* is required (Eq. (25)). This value corresponds to the maximum combined PPFD of the LED lights and sunlight for which supplemental light will be provided; if the PPFD from sunlight alone exceeds this value the LED lights are de-energised, otherwise light is provided up to but not exceeding this PPFD if this is within the capability of the LED lights, and up to the maximum PPFD of the LED lights if this threshold (y_i^*) cannot be reached. The search algorithm converges to the optimal \overline{y}^* and the threshold PPFD is calculated according to (25). Hence, the ultimate optimal control rule is:

$$x_{i}^{*} = \begin{cases} y_{i}^{*} - s_{i}^{*}, \text{ for } U_{LED} \geq (y_{i}^{*} - s_{i}^{*}) > 0\\ 0, & \text{for } (y_{i}^{*} - s_{i}^{*}) \leq 0\\ U_{LED}, \text{ for } U_{LED} < (y_{i}^{*} - s_{i}^{*}) > 0 \end{cases}$$

$$(26)$$

4. Results

4.1. *Example* problem. An example problem was formulated based on current recommendations and existing data for the lettuce cultivar 'Green Towers' (see sections 2.1 and 3.1). The parameter values used for the example problem are given in Table 3.2. The vectors of PPFDs (s) and ETRs (\bar{s}) from sunlight were:

These vectors represent a day with a DLI of 9.30 mol m⁻² d⁻¹ and a DPI of 2.00 mol m⁻² d⁻¹ if no supplemental lighting were provided, with each observation of PPFD (entries of s^T) and ETR (entries of \bar{s}^T) assumed to be constant over each 15-minute (*n*) interval. Photosynthetic photon flux density data for sunlight (*s*) was obtained from an outdoor weather station in Watkinsville, GA (for January 4, 2017), with an assumed 60% transmittance applied to simulate greenhouse conditions. Electron transport rates for sunlight (\bar{s}) were calculated from the PPFDs according to the regression equation shown in Fig. 3.1 (see section 2.1).

4.2. Solution of example problem with described search method. Using the described algorithm to solve the problem explicitly (section 3.6), the solution converged to the optimal \bar{y}^* , where $h(\bar{x}^*) = DPI_T/n - \sum_{i=1}^{\tau} \bar{s}_i$ with 3-digit accuracy in only 3 iterations. The convergence of this algorithm is illustrated in Fig. 3.3. and the optimal solution x^* is shown in Fig. 3.4.

For the search algorithm (see sections 3.5 and 3.6), an initial guess of $\bar{y}_i = 52$ was chosen because this corresponds to the value of \bar{y} that would be required in the case where $\bar{s} = 0$ to satisfy $\lambda_1 > 0$, $g_1(\bar{x}) = 0$, and $h(\bar{x}^*) = DPI_T/n = 3,330$. With the parameter values used for this example problem, $\bar{U}_{LED,i} = 51.5$ for $s_i = 0$ ($\bar{U}_{LED,i}$ is the upper bound on the ETR that can be provided from the LED lights at a particular sunlight PPFD, for the given upper bound on PPFD from the LED lights, $U_{LED} = 200$). Calculations were performed manually with \hat{p} chosen such that:

$$\hat{p_I} = \begin{cases} 1, \text{ for } \bar{x_i} > 0, \\ 0, \text{ for } \bar{x_i} = 0, \end{cases}$$

thereby satisfying $\hat{p}^T \bar{x} = h(\bar{x}) = \sum_{i=1}^{\tau} \bar{x}_i$, and $\hat{H}\hat{p} = 0$, where \hat{H} is the submatrix of active constraints consisting of rows 2 through $1+\tau$ of the matrix of active constraints. Fig. 3.3 illustrates the convergence of this algorithm.

At the first iteration:

 $h(\bar{x}^*) = 1102$

 $h(\bar{x}) = 1670$

 $\hat{p}^T \bar{s} = 396$, and the new estimate of \bar{y}_i^* is:

 $\bar{y}_i^* \approx 37.7$

At the second iteration:

$$h(\bar{x}) = 1148$$

 $\hat{p}^T \bar{s} = 247$, and the new estimate of \bar{y}_i^* is:

$$\bar{y}_i^* \approx 36.5$$

At the third iteration, $h(\bar{x}) = 1104 \approx h(\bar{x}^*) = 1102$. The algorithm was terminated and the final entries of x^* (Fig. 3.4) were calculated according to (24). This corresponds to a total DLI of 12.9 mol m⁻² d⁻¹, with 3.6 mol m⁻² d⁻¹ provided by the supplemental lights, and a total DPI of 3.00 mol m⁻² d⁻¹. The required DPI (*DPI_T*) has been met.

4.3. *Comparison of the optimal solution to an on/off control* strategy. To evaluate the potential economic benefit of this optimisation method, simulations were conducted using MATLAB (see section 2.3) to compare the optimal lighting control strategy presented in this paper to an on/off lighting control strategy. With the on/off strategy, the

supplemental LED lights are turned on at maximum intensity ($U_{LED} = 200 \ \mu mol \ m^{-2} \ s^{-1}$) for the number of seconds required to exactly reach the specified $DPI_T = 3 \text{ mol m}^{-2} \text{ d}^{-1}$, with all supplemental light provided at the end of the photoperiod. For these simulations, the photoperiod is defined as beginning at sunrise, and thus, with the on/off control strategy, the application of supplemental light is delayed until as late in the evening as possible, and hence supplemental light will also generally be applied when PPFDs from sunlight are lowest. While there is no extant industry standard for supplemental lighting control with which the optimal solution presented in this paper can be compared, this on/off control approach bears similarities to the LASSI (Albright et al., 2000) and DynaLight (Clausen et al., 2015) control systems described in section 1.2. Simulations were conducted using all 365 days of the typical meteorological year data for Kalamazoo, MI, an area with many commercial greenhouses where supplemental lighting is common. In both scenarios, sunlight intensities are known, and exactly enough supplemental light is provided to reach DPI_T if the DPI from sunlight alone does not reach or exceed this target value; no light is provided otherwise. The simulations used an assumed 70% greenhouse transmittance and were conducted using both a 16-hour (57,600-second) and 20-hour (72,000-second) photoperiod, with parameters A and k the same as those given in Table 3.2, and $\tau = 16$ for the 16-hour photoperiod and $\tau = 20$ for the 20-hour photoperiod

With the optimal control strategy, the annual amount of light required was 798 mol m⁻² for the 16-hour photoperiod and 732 mol m⁻² for the 20-hour photoperiod. The on/off strategy used 861 and 809 mol m⁻² for the 16- and 20-hour photoperiods, respectively. The optimal control strategy reduced the total amount of supplemental light required by 7.28% with a 16-hour photoperiod and 9.55% with a 20-hour photoperiod,

compared to the on/off strategy. Applying these results to one ha of greenhouse growing area, and assuming an LED efficacy of 1.66 μ mol J⁻¹ (Nelson and Bugbee, 2014) and a fixed electricity price of \$0.12 per kWh, results in the annual electricity costs shown in Table 3.3. The optimal control strategy reduces annual electricity costs by \$12,591 for the 16-hour photoperiod and \$15,530 for the 20-hour photoperiod.

4.4. Solutions with greenhouse PPFD data. The optimisation problem was solved for three days of PPFD data collected in a research greenhouse in Athens, GA during Weaver and van Iersel's (2019) study, with MATLAB using a custom script (sections 2.3 and 4.3) with all parameters the same as given in Table 3.2. The results are shown in Fig. 3.5 for (top to bottom) March 25, April 2, and April 10, 2015. On these days, sunlight PPFDs were relatively low and highly variable. In all cases, the optimal solution is equivalent to providing supplemental LED light up to, but not exceeding, some threshold value of PPFD for sunlight and the LED lights combined (*y**). This optimal threshold PPFD varies day-to-day because of differences in sunlight among days but is constant over each individual photoperiod and is found using the search method described in sections 3.4 through 3.6. Thus, the optimal solution can easily be implemented in real time using previously-described adaptive LED light control methods (van Iersel & Gianino, 2017).

5. Discussion

5.1. *Significance of current work*. Controlling supplemental light based on a daily amount of photosynthesis is a straightforward alternative to the more common approach of controlling based on DLI which affords the opportunity to minimise the total amount of light required, and hence total electricity use. The explicit solution presented herein

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provides a computationally simple means of implementing this approach using adaptive control of supplemental LED lights. By solving this optimisation problem, a specified amount of daily photochemistry is achieved using the lowest possible amount of electricity to power the LED lights. In practice, the solution is equivalent to controlling supplemental LED light intensity (PPFD) to a constant threshold PPFD (y_i) over a single photoperiod. The optimal value of this threshold PPFD (y_i^*) is determined by the individual values of PPFDs from sunlight (s_i) for a given day, the specified target DPI (DPI_T) , and the length of the photoperiod, and found using a simple iterative search (sections 3.5 and 3.6). Thus, our current work provides an effective means of determining an optimal threshold PPFD for dimmable LED lights that minimise total electricity use and can be easily programmed and implemented. The current limitation to applying this strategy in real time is the need for a reasonably accurate prediction of the PPFDs of sunlight over the course of a day. Furthermore, to apply this strategy to a specific crop, an estimate of that crop's DPI requirement would be needed. This is one of many possible approaches to optimising supplemental LED lighting control in greenhouses. Since dimmable LED lights can easily be incorporated into existing greenhouses, and control is easily and precisely accomplished in real time, there is ample opportunity for developing crop, site, greenhouse, and objective-specific control strategies for supplemental LED lighting.

5.2. *Further considerations for optimising greenhouse lighting*. Other strategies for optimising greenhouse supplemental lighting have been formulated in terms of the financial return associated with using supplemental lights, based on crop growth models. Models can be used to describe crop growth as a function of optimally-controlled inputs,

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and the greenhouse environment can be optimised to maximise profits. Several greenhouse growth models for common crops including tomatoes (Jones, Dayan, Allen, van Keulen, & Challa, 1991; Heuvelink, 1999; van Straten et al., 2010) and lettuce (van Henten, 2003; Seginer, Linker, Buwalda, van Straten, & Bleyaert, 2004) have been developed. Another consideration for optimising supplemental light intensity in terms of financial gain arises in the case of variable electricity prices. If off-peak or real-time pricing is available, the monetary cost of providing supplemental light can be accounted for. The applicability of real-time pricing depends on the photoperiod requirement of a specific crop and the pricing structures available at a specific site. For example, if a crop has a short photoperiod flowering requirement, and off-peak pricing is available later in the evening, variable pricing may be unimportant. However, if a crop is grown with a longer photoperiod and real-time pricing is available, it would be advantageous to consider variable electricity costs.

Early work by Heuvelink and Challa (1989) used a crop growth and photosynthesis model, and estimates of market prices for various crops, to calculate "break-even points" for supplemental lighting control; defined as the light intensities for which the increase in economic gain from providing additional light equals the electricity cost of providing that light. These "break-even points" could be used as guidelines to help growers decide when to turn on supplemental lights, or could be incorporated into realtime control strategies, although it is unclear whether this approach was ever implemented by the greenhouse industry (van Iersel, 2017). Mahdavian and Wattanapongsakorn (2017) used an iterative search, as well as a genetic algorithm, to solve a related optimisation problem: maximise profit, considering the market price of tomatoes, real-time electricity prices, a photosynthetic model for fruit production, and the cost of providing supplemental light. They showed that optimal control of supplemental lighting over a 120-day growing cycle for cherry tomatoes over 20-ha of greenhouse could increase overall profits by \$2,157,580.

Recently, dimmable LED lighting control has been incorporated into growth model-based optimal control strategies for maximizing profit. Wang et al. (2018) considered this problem for tomatoes with both overhead and intracanopy lighting and demonstrated that adaptive lighting control could increase profits compared to an on/off control strategy in which the lights are turned on when the economic benefit of using the LED lights outweighs the cost of running them, similar to the "break-even point" of Heuvelink and Challa (1989). Xu et al. (2018) evaluated the economic impact of incorporating dimmable LED lights into existing Chinese and Dutch solar greenhouse with two time-scale receding horizon optimal control of the greenhouse environment and a lettuce growth model (van Henten, 2003). They determined that the addition of LED lighting can increase profits and crop growth in both types of greenhouses over multiple time scales. The estimated increase in profit over a 50-day growing period was \$2.08 to \$2.50 per square meter of growing area (119-137% increase), with a 10.8 to 11.5-fold increase in dry weight per square meter. These findings demonstrate the potential benefit of implementing optimised adaptive lighting control with LED lights in greenhouses.

6. *Conclusions*

Supplemental lighting is valuable for improving and accelerating the growth of greenhouse crops. However, the electricity required to power supplemental lights can yield a significant cost. This work presents an optimal solution method to address this

problem by minimizing the total amount of supplemental light provided, based on a cropspecific photochemical response. This is formulated as a convex nonlinear optimisation problem: minimise the amount of supplemental LED lighting provided, subject to achieving a required integral of daily photochemistry (DPI). A solution method and search algorithm for the global minimiser are described, and the optimisation problem was solved using this method. Simulations demonstrate that the annual electricity cost and total amount of supplemental LED light can be reduced by as much as 9.55% using this optimal control method. This approach represents a broadly applicable method closely related to the current practice of controlling light to a specified DLI, with cropspecific DLI recommendations. The optimal solution is equivalent to controlling LED light intensity to a constant threshold PPFD over an individual photoperiod using previously-described adaptive lighting control methods. The simplicity of the calculations and accessibility of the required lighting control method is expected to facilitate real-time implementation.

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Appendix. Statement of optimisation problem with nonlinear constraints

The optimisation problem may be formulated with ETR being a concave nonlinear function of PPFD. In this case, the objective function is linear, and the first constraint function is nonlinear. Doing so precludes the possibility of employing the search method given in sections 3.4 through 3.6. However, this formulation may be seen as being more explicitly representative of the problem as stated, because PPFD is not transformed into a nonlinear function of ETR. The solution is unchanged when the problem is re-stated in this manner. The optimisation problem is written as follows:

Minimise
$$f(x) = \sum_{i=1}^{\tau} x_i$$
 (27)

subject to:

$$\sum_{i=1}^{\tau} a\left(1 - e^{-k(x_i + s_i)}\right) \ge DPI_T/n \tag{28}$$

$$x_i \ge 0 \tag{29}$$

$$-x_i \ge -U_{LED} \tag{30}$$

$$i \in \{1, ..., \tau\}$$

where *x* is the vector of PPFDs from the LED lights and *s* is the vector of PPFDs from sunlight.

The optimisation problem can be solved explicitly by writing optimality conditions. The explicit solution is found by analysing the objective and constraint functions, identifying the sufficient conditions for a minimiser, and identifying the set of active and inactive constraints that would be necessary to satisfy the sufficient conditions for a given *s*. The objective function is linear, with nonlinear inequality constraints, and hence the sufficient conditions for a local minimiser are (Griva et al., 2009):

$$\nabla_{x}\mathcal{L}(x^{*},\lambda^{*})=0,$$

$$\lambda^* \geq 0$$

 $\lambda^{*T}g(x^*) = 0$, and

 $Z_{+}(x^{*})^{T} \nabla^{2}_{xx} \mathcal{L}(x^{*},\lambda^{*}) Z_{+}(x^{*})$ is positive definite, where Z_{+} is a null space basis matrix for the Jacobian of the nondegenerate constraints at x^{*} (Griva et al., 2009).

The Lagrangian function, the i^{th} entry of its gradient with respect to x, and the constraint functions are:

$$\mathcal{L}(x,\lambda) = \sum_{i=1}^{\tau} x_i - \lambda_1(g_1(x)) - (\sum_{i=1}^{\tau} \lambda_{i+\tau+1}(g_{i+\tau+1}(x))), \qquad (31)$$

$$\frac{\partial \mathcal{L}(x,\lambda)}{\partial x_i} = 1 - \lambda_1 \left(\frac{\partial g_1(x)}{\partial x_i}\right) - \lambda_{i+1} + \lambda_{i+\tau+1}$$
(32)

$$g_{1}(x) = \sum_{i=1}^{\tau} a \left(1 - e^{-k(x_{i}+s_{i})} \right) - DPI_{T}/n$$
(33)

$$g_{i+1}(x) = x_i \tag{34}$$

$$g_{i+\tau+1}(x) = U_{LED} - x_i,$$
 (35)

where
$$\frac{\partial g_1(x)}{\partial x_i} = ka(e^{-k(x_i+s_i)}).$$
 (36)

The minimiser is global because the problem is convex, and $\nabla_{x x}^2 \mathcal{L}(x, \lambda)$ is always positive definite for any feasible *x*. We have:

$$\frac{\partial^2 \mathcal{L}(x,\lambda)}{\partial x_i^2} = k^2 A(e^{-k(x_i+s_i)}) > 0; \ \forall \ (x_i+s_i) \ge 0,$$

$$(37)$$

$$\frac{\partial^2 \mathcal{L}(x,\lambda)}{\partial x_i \partial x_j} = 0; \ \forall \ i \neq j.$$
(38)

Thus, $\nabla \mathcal{L}_{x x}^2(x, \lambda)$ is a positive definite, diagonal matrix with all diagonal entries being positive (Eqs. (37) and (38)), and the final sufficient condition can be ignored. Considering the above, the optimality conditions are now reduced to:

$$\frac{\partial \mathcal{L}(x,\lambda)}{\partial x_{i}} = 1 - \lambda_{1} \left(\frac{\partial g_{1}(x)}{\partial x_{i}} \right) - \lambda_{i+1} + \lambda_{i+\tau+1} = 0; \forall i$$

$$\lambda_{1} > 0$$
(39)

 $\lambda^* \ge 0$ $\lambda^{*T} g(x^*) = 0.$

For simplicity, let all constraints $g_{i+\tau+1}(x)$ be inactive. The constraint $g_1(x^*)$ must be active for a global minimiser, since for any inactive $g_1(x)$ and feasible $x \neq 0$, the objective function value will be decreased by decreasing one or more x_i such that $g_1(x)$ becomes active. Furthermore, the partial derivative $(\partial g_1(x)/\partial x_i)$ is strictly positive and monotonically decreasing in $(x_i + s_i)$ (Eq. (36)). Considering this and the sufficient conditions for a minimiser, for an optimal solution x_i^* , either $\lambda_1(\partial g_1(x^*)/\partial x_i) = 1$ and $g_{i+1}(x^*)$ is inactive for x_i^* (thus, $\lambda_{i+1} = 0$), or $\lambda_1(\partial g_1(x^*)/\partial x_i) < 1$ and $g_{i+1}(x^*)$ is active for x_i^* (thus, $\lambda_{i+1} = 0$), for all x_i^* (Eq. (39)). Therefore, there must exist some feasible vector y^* that satisfies: $\lambda_1(ka(\exp(-ky_i))) = \lambda_1(\partial g_1(x^*)/\partial x_i) + \lambda_{i+1} = 1$, where all entries of y^* are equal because λ_1 is a scalar (according to (13)). If $s_i > y_i$, then $x_i = 0$ ($g_{i+1}(x)$ is active for one or more i, $x_i = (s_i + U_{LED}) < y_i$, and $\lambda_{i+\tau+1} > 0$. The optimal solution x^* can be found by solving for the critical value of y^* using an iterative search with gradient-based descent.

The assumption that all constraints $g_{i+\tau+1}(x)$ are inactive (*i.e.*, the PPFD of the LED lights never reaches its maximum, U_{LED}) is useful in formulating a search method for the optimiser (section 3.5). While the validity of this assumption depends on the specific values of *s*, DPI_T , *n*, τ , and U_{LED} used to formulate the problem, it can be shown that for any $\sum_{i=1}^{\tau} a(1 - exp(-ks_i)) < DPI_T/n$, where the elements of *x* can be increased such that $\sum_{i=1}^{\tau} a(1 - exp(-k(s_i + x_i))) = DPI_T/n$, with a variable U_{LED} , and constant DPI_T , *n*, and τ , the objective function value will be lowest if U_{LED} is sufficiently high such that

 $(y^* - s_i) < U_{LED}$ for all s_i , and no $g_{i+\tau+1}(x)$ is active. From an initial optimal solution, where $y^* < U_{LED}$, if U_{LED} were decreased such that at least one $(y-s_i) > U_{LED}$, one or more x_i must be decreased from $(y-s_i)$ to U_{LED} , and the value of y^* increased, in order for the problem to remain feasible. Assuming that an optimal solution exists with the reduced U_{LED} , this solution will be in the feasible set of solutions for the problem with the original, higher, upper bound. Since the solution obtained with a lower U_{LED} is in the feasible set of solutions for the higher U_{LED} , but is not the global minimiser, it necessarily has a higher objective function value than the solution obtained with a higher U_{LED} . The magnitude of increase of y^* , and resulting increase in all x_i with inactive $g_{i+\tau+1}(x)$, must be greater than the magnitude of decrease in U_{LED} due to the nonlinearity of the constraint function $g_1(x)$ (Eq. (28)). Thus, for a variable U_{LED} , the objective function value will necessarily be lowest if U_{LED} is sufficiently high such that this upper bound will not be reached for any x_i . Put simply, if PPFD is increased or decreased by the same amount from any initial value, the magnitude of decrease in ETR at the lower PPFD will be greater than the magnitude of increase in ETR at the higher PPFD due to the asymptotic nature of the ETR response (Eq. (28)).

Table 3.1- Plant physiological terminology, with abbreviations (if applicable), units, and definitions.

Photosynthetic photon flux density (PPED)	μ mol m ⁻² s ⁻¹	Micromoles of incident photons within the
defisity (111D)		square meter, per second.
Daily light integral (DLI)	mol m ⁻² d ⁻¹	Daily (24-hour) integral of incident photons within the photosynthetically-active range, per square meter.
Electron transport rate (ETR)	µmol m ⁻² s ⁻¹	Micromoles of electrons transported through photosystem II, per square meter leaf area, per second.
Daily photochemical integral (DPI)	mol m ⁻² d ⁻¹	Daily (24-hour) integral of electrons transported through photosystem II, per square meter leaf area.
Photoperiod	S	Continuous interval within a 24-hour period during which plants are exposed to light; photoperiod \leq 24 h (\leq 86,400 s).

Table 3.2- Parameter values used for the example problem (sections 4.1 – 4.2)		
DPIT	$3 \times 10^6 \mu mol m^{-2}$	
п	900 s	
τ	64	
а	121 µmol m ⁻² s ⁻¹	
k	0.00277	
Uled	200	

Table 3.3- Electricity cost for 365 days of supplemental lighting based on the Kalamazoo, MI typical meteorological year for the optimal control strategy and an on/off strategy, for a one ha area.

Photoperiod (h)	optimal control electricity cost (U.S. \$)	on/off control electricity cost (U.S. \$)	
16	160,263	172,854	
20	147,017	162,547	
Table 3.4- Nomenclature		\overline{S}	vector of ETRs <i>x</i> from sunlight
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<i>Symbols with meaning and units (if applicable)</i>		$ar{s}_i$	scalar value for i^{th} entry of vector \bar{s} (µmol m ⁻² s ⁻¹); represents the average ETR over the i^{th} discrete time interval
а	asymptote of ETR as a function of PPFD (μ mol m ⁻² s ⁻¹)	U_{LED}	upper bound for all x_i ; maximum PPFD output of the LED lights (µmol m ⁻² s ⁻¹)
b	a feasible solution	$\overline{U}_{LED,i}$	upper bound for each \bar{x}_i ; maximum possible ETR with PPFD of sunlight plus the maximum PPFD of the LED lights (µmol m ⁻² s ⁻¹)
C	constraint matrix	x	vector of PPFDs from supplemental LED lights
DPIT	target, or required, daily photochemical integral (μmol m ⁻²); integrated over a photoperiod	Xi	scalar value for i^{th} entry of vector x (µmol m ⁻² s ⁻¹); represents the average PPFD over the i^{th} discrete time interval
g()	constraint function	\bar{x}	vector of ETRs from supplemental LED lights
$h(\bar{x})$	sum of ETRs from the LED lights, summed over a photoperiod, divided by $n \ (\mu mol m^{-2} s^{-1})$	\bar{x}_i	scalar value for i^{th} entry of vector \bar{x} (µmol m ⁻² s ⁻¹); represents the average ETR over the i^{th} discrete time interval
Ĥ	submatrix of active constraints; consists of the τ rows corresponding to lower bounds of all \bar{x}_i	У	vector of threshold PPFDs, all entries are equal
k	exponential decay constant for ETR as a function of PPFD	<i>Yi</i>	scalar value of threshold PPFD $(\mu mol m^{-2} s^{-1})$
£()	Lagrangian function	\overline{y}	vector of threshold ETRs, all entries are equal
п	length of discrete time intervals (s)	$ar{y}_i$	scalar value of threshold ETR (μ mol m ⁻² s ⁻¹)
р	a null space vector for Ĥ	Z +	null space basis matrix for the Jacobian of nondegenerate constraints

p̂	a null space vector for \widehat{H} for which the inner product of \widehat{p} and \overline{x} is equal to $h(\overline{x})$	λ	vector of Lagrange multipliers; with subscript, indicates a single entry of λ
S	vector of PPFDs from sunlight	τ	number of discrete time intervals per photoperiod
Si	scalar value for i^{th} entry of vector <i>s</i> (µmol m ⁻² s ⁻¹); represents the average PPFD over the i^{th} discrete time interval	*	in superscript, indicates the value of a variable at the global minimum



Fig. 3.1 - The regression model of electron transport rate (ETR) of 'Green Towers' lettuce as a function of PPFD for a greenhouse under natural lighting conditions. Solid line represents the best-fit regression equation ETR = $121(1-\exp(-0.00277*PPFD))$, with $R^2 = 0.95$ and p < 0.0001. Reprinted from Weaver and van Iersel, 2019. These values resulted from sunlight alone, no supplemental lighting was used.



Fig. 3.2 - Daily photochemical integral (DPI) of 'Green Towers' lettuce evaluated as a function of DLI in a greenhouse under natural lighting conditions. Solid line represents the best-fit regression equation DPI = $3.30(1-\exp(-0.122*DLI))$, with $R^2 = 0.82$ and p < 0.0001. Reprinted from Weaver and van Iersel, 2019. These values resulted from sunlight alone, no supplemental lighting was used.



Fig. 3.3 - Convergence of the described algorithm for the example problem (sections 4.1 and 4.2). The vector of ETRs from sunlight (\bar{s}) is shown with closed symbols. The initial guess of \bar{y}_i^* (long dashes), second guess of \bar{y}_i^* (short dashes), and final optimal \bar{y}_i^* (solid line) are shown.



Fig. 3.4 - Optimal solution x^* for the example problem (section 4.1). Where *x* represents the vector of PPFDs from the supplemental LED lights (open symbols), with values of *s* (the vector of PPFDs from sunlight, closed symbols) for reference.



Fig. 3.5 - Optimal solutions for three days of greenhouse PPFD data collected in Athens, GA. Optimal PPFDs of the supplemental LED lights (open symbols), PPFDs from sunlight (closed symbols), and the optimal threshold PPFD (dashed line) are shown.

CHAPTER 4

LONGER PHOTOPERIODS WITH ADAPTIVE LIGHTING CONTROL CAN IMPROVE GROWTH OF GREENHOUSE-GROWN 'LITTLE GEM' LETTUCE (LATUCA SATIVA)³

³ Weaver, G. M. and van Iersel, M. W. 2019. To be submitted to *HortScience*.

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 utilize 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), will improve growth because light is used more efficiently to drive photosynthesis at lower PPFDs. 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 h photoperiod using adaptive lighting control of LED lights. As the photoperiod for supplemental lighting was increased and supplemental light was provided at lower average PPFDs, 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 h. 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 PPFDs.

Introduction

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 grown under supplemental light would be beneficial to greenhouse vegetable growers. Lighting control approaches which ensure that supplemental light is used efficiently to drive photosynthesis and growth of greenhouse vegetable crops can improve the economic return on supplemental lighting and the profitability of greenhouse vegetable production.

Light-emitting diode (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 (van Iersel et al., 2016). 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 photosynthetic photon flux density (*PPFD*) of sunlight and supplemental light combined reaches some 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 *PPFDs* (Aikman, 1989; Weaver and van Iersel, 2018). The decrease in photosynthetic light-use efficiency at higher *PPFDs* is due in part to photoprotective processes which 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. However, similar results have not yet been reported for plants grown in a greenhouse, where lighting conditions are highly variable and 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 daily light integral (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 February 11 to March 5, 2018 (22 d), and the second experiment was conducted from March 26 to April 16, 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 \times 30 cm width) sections separated by aluminum sheets (90 cm length \times 30 cm height), and each tray was a complete block. Light-emitting diode light bars with a mixture of cool and warm white and a few red LEDs and 112 cm length \times 5.1 cm width (SPYDR Physiospec Greenhouse; 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 BioSciences, Lincoln, NE) were positioned on the south-facing side of each section of the middle tray, approximately 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 0-10,000 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 (\pm standard deviation) temperature, relative humidity and vapor pressure deficit were: 23.8 ± 3.1 °C, $56 \pm 17\%$, and 1.37 ± 0.82 kPa during the first experiment, and 24.2 ± 3.4 °C, $49 \pm 17\%$, and $1.67 \pm$ 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 non-zero PPFDs, 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 how much. 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 4.1 shows the spectrum within the photosynthetically-active region (\approx 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.

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/m²). 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 one week after germination. In each supplemental lighting treatment, a minimum DLI of $17 \text{ mol} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ was provided by the LED lights and sunlight combined. This DLI 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 hours and the plants were exposed to sunlight before 0730 EST. In the case where the DLI from sunlight alone exceeded the required 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-hour 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".

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 two seconds. 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 4.3). 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. 4.2) were created by applying the control algorithm presented in table 4.3 and the adaptive lighting control rule given above to two days of sunlight data collected during our experiments in the control (sunlight only) treatment for a 12 and 21 h photoperiod 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. The maximum output of the LED light bars at the quantum sensor position used in the experiments was $400 \pm 5 \ \mu mol \cdot m^{-2} \cdot s^{-1}$, and hence, a DLI of 17 mol $\cdot m^{-2} \cdot d^{-1}$ could be reached in the absence of sunlight for all photoperiods used.

Crop growth measurements. The experiments were ended when the plants had reached a marketable size in all supplemental lighting treatments. At the conclusion of each experiment, chlorophyll content index (CCI) was measured on 8 mature leaves for each tray (i.e. each treatment × block combination) using a handheld CCI meter (CCM-200 plus; Apogee Instruments, Inc., Logan, UT). 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). Sixteen fully-expanded, non-senescent, leaves were randomly selected from each tray and digitally photographed against a white background with a black 10 cm² reference disk. These images were analyzed (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 5-7 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 and power consumption of the

fixture, 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 expended on 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 \times experiment combination was calculated according to: [(dry weight) - (mean dry weight of 5 control replications)] \times 32/ [total driver energy use / 5]. The supplemental light covered a space substantially larger than the space occupied by the plants. Since 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, Agawam, MA), and fertigated daily with a 100 mg·L⁻¹ N liquid fertilizer (15N:2.2P:12.45K; 15-5-15 Cal-Mag; Everris, Marysville, OH) using ebb-and-flow benches in the greenhouse. Chlorophyll fluorescence measurements were taken on these

plants over a 20-d period (March 16 – April 4, 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} . Photosynthetic photon flux density was measured using the built-in quantum sensor on the leaf clip, and the rate of linear electron transport through 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 \times 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 mixedmodel analysis of variance, where experiment and block were treated as random effects. In SAS, 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 (version 9.2: SAS

Institute, Cary, NC). 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

Supplemental lighting and energy use. During the first experiment, the DLI from sunlight alone was less than 17 mol·m⁻²·d⁻¹ on all 22 days (Table 4.1). In the four supplemental lighting treatments, the target 17 mol·m⁻²·d⁻¹ DLI was met and not exceeded on all days (standard deviation of 0.0 mol·m⁻²·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 4.1) because the supplemental light was provided at lower *PPFD*s due to lower threshold values for adaptive lighting control with longer photoperiods. Figure 4.2 (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 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. 4.2, top). Energy use varied between the four supplemental lighting treatments, ranging from 1.02 to 1.13 MJ (Table 4.1). 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 which 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 days. Thus, on many days, the plants received DLIs greater than 17 mol·m⁻²·d⁻¹ even without the application of supplemental lighting, and on these days, excess light was generally provided by the LED lights due to the nature of the control algorithm used (Table 4.3). Figure 4.2 (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 Figure 4.2.

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 4.1 and 4.2). As with the first experiment, energy use also varied between treatments (Table 4.2), due to different daily amounts of sunlight being perceived by each of the five quantum sensors. Photoperiod *PPFD* generally decreased as photoperiod was extended in the supplemental lighting treatments. On days for which the DLI from sunlight alone exceeded the required minimum DLI, the amount of excess light provided at the beginning of the photoperiod was greater with shorter photoperiods, because the initial threshold *PPFD* was higher. Hence, energy use also tended to be higher in the shorter photoperiod treatments on these days.

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 (Fig. 4.4). 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 4.1 and 4.2), dry weight was 0.075 g (14.3%) greater than in the first experiment, averaged over all treatments (Table 4.4). 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 4.4). 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. 4.3).

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. 4.4). 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 cm² (12.3%) greater in the 21 h photoperiod treatment than in the 12 h photoperiod treatment. Leaf size was 18.2 cm² (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 cm² (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 m²·kg⁻¹ (33.1%) greater in the second experiment than in the first (p = 0.0003) and was affected by the treatment × experiment interaction (p = 0.028). Leaf size was positively correlated with dry weight (Fig. 4.5; $R^2 = 0.77$ 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 increasing similarly with allowed photoperiod in both experiments. Chlorophyll content index was positively correlated with dry weight (Fig. 4.6; $R^2 = 0.75$ 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 tip burn 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 4.5). The incidence of tipburn was higher (16.5 plants, 426%) in the second experiment (p < 0.0001) (Table 4.5), during which DLIs were generally greater (Tables 4.1 and 4.2), and there was an effect of treatment × experiment (p = 0.0097).

Quantum yield and electron transport rate. As expected, Φ_{PSII} decreased in an exponential (convex) manner with increasing *PPFD*, and ETR could be described as a negative exponential function of *PPFD* (Fig. 4.7). Electron transport rate increased in an

asymptotic (concave) manner with *PPFD* to an asymptote of 287 μ mol·m⁻²·s⁻¹ with an initial slope of 0.35 mol electrons transported per mol of absorbed photons.

Discussion

Quantum yield and electron transport rate. The asymptotic pattern of increase in ETR with *PPFD*, and attendant decrease in Φ_{PSII} (Fig. 4.7) is common for many 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 *PPFDs*. 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 *PPFDs*. Because light is used more efficiently to drive the light reactions of photosynthesis at lower *PPFDs*, 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 paper (Weaver and van Iersel, 2019), we hypothesized that lettuce growth should 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 observed in this study (Fig. 4.7). 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).

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 PPFDs (Tables 4.1 and 4.2). Similar results have been reported from growth chamber experiments. Koontz and Prince (1986) showed that providing a DLI of 22.4 mol \cdot 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 30-50% compared to 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, in growth chambers, that 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, 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 species (Langton and Adams, 2005). Thus, there is likely some effect of photoperiod extension on crop growth that cannot be explained by increased photosynthetic 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.

In our first experiment, dry weight (Fig. 4.3) and conversion efficiency (Fig. 4.4) both increased as the allowed photoperiod for supplemental lighting was extended (Table 4.1). In our second experiment, the photoperiod was not extended on 14 of the 21 days. 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. 4.4; Table 4.1). These results lend support to the idea that the increases in growth under longer photoperiods with the same DLI are due to an increase in photosynthetic light use efficiency when supplemental lighting is provided at lower *PPFD*s (photoperiod *PPFD* is decreased), but for a longer period of time, because the photoperiod was not consistently extended beyond the natural daylength in any treatment. Although relatively little light was provided at lower *PPFD*s in the longer photoperiod treatments (Fig. 4.2), and a large increase in conversion efficiency was observed as the allowed photoperiod was increased from 12 to 21 h (Fig. 4.4).

For lettuce, increased growth leads to an increase in leaf size. Thus, as the allowed photoperiod was extended and the plants grew more, leaf size also increased (see below). Increased leaf size leads to more light interception, which further contributes to an increase in photosynthesis and growth because more of the light reaching the growing area is absorbed by the plants.

Leaf size and specific leaf area. In both experiments, leaf size and dry weight both increased as the allowed photoperiod for supplemental lighting was increased. Leaf size correlated positively with dry weight (Fig. 4.5). Larger leaf size leads to increased light interception, 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 4.4). However, SLA was higher in the second experiment as compared to the first. The thicker leaves with reduced area characteristic of plants from the first experiment (Fig. 4.5) may be due to a higher fraction of blue light those plants received. The LED lights used in these experiments have a relatively low ratio of red to blue light (Fig. 4.1), as compared to sunlight. 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, while 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 4.1 and 4.2). Leaf chlorophyll content has been reported to increase with photoperiod extension using weak light sources for several species (Langton et al., 2003), and 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 *PPFDs* (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 *PPFDs* (Ruban, 2015). However, Kleinhenz et al. (2003) showed that applying 50% shade had little effect on leaf chlorophyll concentration in four lettuce cultivars, compared to plants grown in full sunlight.

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, because tipburn is linked to localized calcium deficiency caused by inadequate calcium transport to growing tissue (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 still 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, 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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Table 4.1. Greenhouse lighting conditions for experiment 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 (h) 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·m⁻²·d⁻¹ in the photoperiod treatments using adaptive lighting control (see Table 4.3). Mean \pm standard deviation of realized photoperiod, daily light integral (DLI), and average non-zero *PPFD* during the photoperiod (photoperiod *PPFD*). Total supplemental lighting hours (number of hours during which the LED lights are on at any non-zero *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	Realized	DLI	Photoperiod	Total	Energy
photoperiod	photoperiod		PPFD	lighting time	use
(h)	(h)	$(\text{mol·m}^2 \cdot d^2)$	$(\mu mol \cdot m^{-2} \cdot s^{-1})$	(h)	(MJ)
				(11)	
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 4.2. Greenhouse lighting conditions for experiment 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 (h) 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·m⁻²·d⁻¹ in the photoperiod treatments using adaptive lighting control (see Table 4.3). Mean \pm standard deviation of realized photoperiod, daily light integral (DLI), and average non-zero *PPFD* during the photoperiod (photoperiod *PPFD*). Total supplemental lighting hours (number of hours during which the LED lights are on at any non-zero *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	Realized	DLI	Photoperiod	Total	Energy
photoperiod	photoperiod		PPFD		use
(h)	(h)	$(\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1})$	$(\mu mol \cdot m^{-2} \cdot s^{-1})$	ngnung ume	(MJ)
				(h)	
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 4.3. Control algorithm with description (left) and equations (right). Target *PPFD* (*PPFD_T*) for adaptive lighting control of the LED lights is calculated by dividing the difference of the target DLI (*DLI_T*) and the current sum of daily *PPFD*, assuming units of mol·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_{θ} is the initial time step, the first second of the photoperiod.

DescriptionEquationIf 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 $PPFD_T = \frac{(DLI_T - \sum_{t=0}^{t} PPFD)}{t_f - t}$ DLI and the current sum of PPFD, divided by
the time remaining in the photoperiod: $PPFD_T = \frac{(DLI_T - \sum_{t=0}^{t} PPFD)}{t_f - t}$

If there is no time remaining in the photoperiod, or the target DLI has been met or exceeded:

The target *PPFD* for adaptive lighting control is zero, the lights are powered off:

If
$$DLI_T \leq \sum_{t=0}^{t} PPFD$$
 , or $t \geq t_f$

$$PPFD_T = 0$$

Table 4.4. Lettuce crop growth measurements. Mean \pm standard deviation 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 (h) 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 non-zero *PPFD* from sunlight and the LED lights combined (photoperiod *PPFD*, see Tables 4.1 and 4.2) 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 experiments 1 (upper rows) and 2 (lower rows).

Allowed		Dry Weight		Leaf size	Specific leaf area
photoperiod	Experiment	(g/plant)	CCI	(cm^2)	$(m^2 \cdot kg^{-1})$
(h)					
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	$68.2\pm\!\!2.8$	79.7 ± 26.8

Table 4.5. Percentage of lettuce plants showing symptoms of tipburn in response to different photoperiods at the conclusion of experiments 1 (upper rows) and 2. (lower rows). Allowed photoperiod indicates the photoperiod (h) 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 *PPFD* from sunlight and the LED lights combined (photoperiod *PPFD*, see Tables 4.1 and 4.2) 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.

Allowed photoperiod (h)	Experiment	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



Figure 4.1. 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.



Figure 4.2. Simulated operation of the control algorithm for photoperiods of 12 and 21 h (see Table 4.3). 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 experiment 1. Bottom: a representative day for which the daily light integral (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 photosynthetic photon flux densities (*PPFD*s) at which supplemental light is provided are higher in the 12 h photoperiod (dotted dashed line) than in 21 h photoperiod (dashed line). This pattern of supplemental lighting control was typical during experiment 2.



Figure 4.3. Dry weight of lettuce as a function of mean realized photoperiod for the supplemental lighting treatments in experiment 1 (closed symbols) and experiment 2 (open symbols). At longer photoperiods within each experiment, the average non-zero *PPFD* from sunlight and the LED lights combined (photoperiod *PPFD*, see Tables 4.1 and 4.2) 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 versus mean photoperiod for both experiments combined ($R^2 = 0.35$, p < 0.0001). Bars represent ± one standard deviation.



Figure 4.4. Conversion efficiency of lettuce, 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 non-zero *PPFD* from sunlight and the LED lights combined (photoperiod *PPFD*, see Tables 4.1 and 4.2) 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 versus mean photoperiod for both experiments combined ($R^2 = 0.44$, p < 0.0001). Bars represent ± one standard deviation.



Figure 4.5. Leaf size as a function of dry weight for experiment 1 (closed symbols) and experiment 2 (open symbols). Lines represent the regression equation of leaf size versus dry weight for each experiment. Experiment 1: $R^2 = 0.77$, p < 0.0001. Experiment 2: $R^2 = 0.31$, p = 0.0038.



Figure 4.6. Chlorophyll content index as a function of lettuce dry weight for experiment 1 (closed symbols) and experiment 2 (open symbols). Lines represent the regression equation of CCI versus dry weight for each experiment. Experiment 1: $R^2 = 0.75$, p < 0.0001. Experiment 2: $R^2 = 0.37$, p = 0.0012.



Figure 4.7. Electron transport rate (ETR, top) and the quantum yield of photosystem II (Φ_{PSII} , bottom) as functions of *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)] versus *PPFD*. For ETR, R^2 = 0.98, p < 0.0001, and for Φ_{PSII} , R^2 = 0.90, p < 0.0001. Data was collected using diurnal chlorophyll fluorescence monitoring; plants were measured once every 15 minutes under ambient greenhouse lighting conditions for 20 days.

CHAPTER 5

AN EFFECTIVE TWO-POINT APPROXIMATION FOR THE RESPONSE OF ELECTRON TRANSPORT RATE TO PHOTOSYNTHETIC PHOTON FLUX DENSITY⁴

⁴ Weaver, G. M. and van Iersel, M. W. 2019. To be submitted to *HortScience*.

Abstract

Developing efficient lighting control strategies for greenhouse supplemental lighting requires a quantitative understanding of plant responses to photosynthetic photon flux density (PPFD). Electron transport rate (ETR) is a measure of the rate of the light reactions of photosynthesis which can be expressed as a function of *PPFD* by the equation: ETR = $a^*(1 - \exp(-(\alpha/a)^*PPFD))$, where a is the asymptote and α is the initial slope of the ETR response to *PPFD*. Because this equation has only two parameters, we hypothesized that the ETR response to *PPFD* can be accurately described by a two-point approximation obtained by measuring ETR at a low *PPFD* to estimate α and at a high PPFD to estimate a. Electron transport rate of six annual bedding plant species was measured at a *PPFD* of $\approx 3 \,\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and $\approx 2100 \,\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in a growth chamber to estimate the parameters. The resulting curve was compared to ETR data collected in a greenhouse using diurnal chlorophyll fluorescence measurements, and ETRs measured at eight *PPFD*s in a growth chamber for the six species. In most cases, the two-point approximation slightly over-approximated ETR as compared to the greenhouse and growth chamber data, but the approximation was still reasonably accurate. In the greenhouse, the observed ETRs for impatiens (Impatiens walleriana) and petunia (*Petunia* \times *hybrida*) were much lower than those predicted by the two-point approximation, and this may have occurred due to mechanical damage to the leaves incurred during the measurement process in the greenhouse. For impatiens, the ETRs observed in the growth chamber were much higher than those predicted by the two-point approximation, and this may be because the $\approx 2100 \ \mu mol \cdot m^{-2} \cdot s^{-1} PPFD$ used for the approximation caused light-induced damage to the photosynthetic apparatus for this

species, lowering the measured value of *a*. For the remaining species, begonia (*Begonia* semperflorens), geranium (*Pelargonium* x hortorum), salvia (*Salvia splendens*), and vinca (*Catharanthus roseus*), the predicted ETRs were within 10% of the observed values from the greenhouse and growth chamber.

Introduction

In greenhouses, supplemental lighting can be used to improve the growth and quality of floricultural crops. Annual bedding plants are typically grown during late winter and early spring, when photosynthetic photon flux densities (*PPFDs*) and daily light integrals (DLIs) from sunlight are relatively low and may be insufficient to for growing high quality plants (Currey et al., 2012; Hutchinson et al., 2012). However, the electricity required for providing supplemental light can be expensive (van Iersel and Gianino, 2017; Watson et al., 2018). Thus, supplemental lighting control strategies which reduce the amount of supplemental light required for greenhouse crop production would be beneficial to greenhouse growers.

Currently, lighting recommendations for greenhouse crops are made based on providing an ideal DLI (*e.g.* Torres and Lopez, undated). However, such recommendations do not account for crop photosynthetic responses to *PPFD*. Because photosynthetic rate increases in a concave manner with *PPFD*, supplemental light will always be used more efficiently to drive photosynthesis and growth when it is provided at relatively low *PPFD*s (Aikman, 1989; Weaver and van Iersel, 2018; Weaver et al., 2019). The decrease in photosynthetic efficiency with increasing *PPFD* is clearly evidenced by a decrease in the quantum yield of photosystem II (Φ_{PSII}), a unitless measure of the efficiency with which absorbed photons are used to drive the light reactions of photosynthesis. The quantum yield can be directly quantified using chlorophyll fluorometry (Baker, 2008; Genty, 1989; Rasher et al., 2000; Weaver and van Iersel, 2019). Lighting control strategies which account for photosynthetic responses to *PPFD* have been developed. For example, Kjaer et al. (2011) controlled high-pressure sodium (HPS) lamps to reach a daily sum of net carbon fixation, as approximated by a nonlinear model, and accounted for variable electricity prices. They demonstrated that providing supplemental light when *PPFD*s from sunlight alone are low and electricity is cheap, can reduce electricity costs by 25% without compromising the overall quality of two ornamental *Campanula* species. Weaver and van Iersel (2018) estimated that the total amount of electricity used over a 4-week growing cycle could be reduced by 24% for petunias (*Petunia* × *hybrida*) and 37% for impatiens (*Impatiens walleriana*) using a similar method with dimmable light-emitting diode (LED) lights. Likewise, Weaver et al. (2019) estimated that energy use of supplemental lighting for lettuce (*Lactuca sativa*) production could be reduced by about 10% by using dimmable LEDs and accounting for the nonlinear light response.

Developing and applying lighting control strategies which account for photosynthetic responses to *PPFD* requires a reasonably accurate approximation of a crop's light response. Chlorophyll fluorometry is a powerful method for assessing the photosynthetic responses to *PPFD*. When *PPFD* is also measured, chlorophyll fluorometry can be used to estimate the rate of linear electron transport through PSII (electron transport rate; ETR), a measure of the rate of the light reactions of photosynthesis. In addition to their usefulness for directly probing the light reactions of photosynthesis, chlorophyll fluorometers are small and portable, have simple operation, and require no re-calibration. Thus, chlorophyll fluorometry is an ideal tool for studying

crop light responses in the field (Baker and Rosenqvist, 2004; Genty et al, 1989; Maxwell and Johnson, 2000).

Estimates of the ETR response to *PPFD* can be obtained using instant light response curves which are a pre-programmed feature of many commercially available chlorophyll fluorometers. Light is provided by the fluorometer at a at a range of increasing *PPFD*s, with *PPFD* held constant between steps, and Φ_{PSII} and ETR are recorded at each *PPFD*. However, these are typically performed over a relatively brief period (often just a few minutes) with a highly-focused light source and may not accurately represent the ETR response to *PPFD* under greenhouse lighting conditions. Inaccuracies may arise because the *PPFD* received by a measured leaf is not known with certainty due to variations in the position of the fluorometer fiber optics (Rascher et al., 2000). Additionally, if ETR is measured at several *PPFD*s during a brief period, the interval between measurements may not sufficiently long for photoprotective processes to reach a steady state, as this occurs over a scale of several minutes (Demmig-Adams et al., 2012; Kaiser et al., 2018; Ruban, 2015). Furthermore, repeated application of saturating pulses at short intervals may cause light-induced damage to the photosynthetic apparatus (photoinhibition), which decreases Φ_{PSII} and ETR (van Iersel et al., 2016).

Weaver and van Iersel (2019) used diurnal chlorophyll fluorescence monitoring to evaluate the ETR response of lettuce in a greenhouse. Plants were measured once every 15 min under ambient greenhouse lighting conditions for five weeks in order to obtain an accurate description of the response of ETR to *PPFD* for this crop. While diurnal chlorophyll fluorescence monitoring is a sound method for evaluating crop light responses, it is also time-consuming, and may not be practical for gauging responses for a

wide variety of crops. This would be especially true in a production greenhouse, where many species and cultivars may be grown at once. Thus, there is a need to develop an accurate, yet rapid, method for screening crop ETR responses to allow for the implementation of energy-efficient supplemental lighting control strategies in commercial greenhouses.

Electron transport rate can be expressed as an asymptotically increasing function of *PPFD* using an equation of the form: $ETR = a \times (1 - \exp(PPFD \times (\alpha/a)))$, where *a* is the asymptote of the ETR response curve and α is the initial slope, with units of moles of electrons transported through photosystem II per mole of photons incident on the leaf (Rascher et al., 2000; Stanghellini et al., 2019). Because this equation has only two parameters, *a* and *a*, the ETR response to *PPFD*s could, in theory, be accurately described if only these two parameters are known. Thus, we tested the hypothesis that ETR responses to *PPFD* obtained in a greenhouse using diurnal chlorophyll fluorescence monitoring, and in a growth chamber using dimmable LED lights, can be accurately replicated using only two measurements. The accuracy of two-point approximation of the ETR response to *PPFD* was evaluated for six annual bedding plant species.

Materials and Methods

Plant material and growing conditions. Species studied were *Begonia semperflorens* 'Ambassador Scarlet' (begonia), *Catharanthus roseus* 'Jams N Jellies Blackberry' (vinca), 'Daddy blue' petunia, *Pelargonium* x *hortorum* 'Maverick Violet'(geranium), *Salvia splendens* 'Mojave' (salvia), and 'Super Elfin Violet' impatiens. These species are commercially-important crops with a range of light requirements. Seeds were sewn in 15cm round pots filled with a peat:perlite substrate (Fafard 1P; Sun Gro Horticulture,

Agawam, MA) in May 2017. Five plants of each species were grown in a glass-covered greenhouse on ebb-and-flow benches of 1.5 m length \times 0.9 m width \times 4 cm height (MidWest GroMaster, St. Charles, IL) covered with commercial-grade weed cloth (Weed Free Pro Fabric; DuPont, Wilmington, DE) and fertigated daily with a 100 mg·L⁻¹ N liquid fertilizer (15N:2.2P:12.45K; 15-5-15 Cal-Mag; Everris, Marysville, OH). Begonias and impatiens were grown under 50% shade using a shade cloth. Greenhouse temperature, vapor pressure deficit, and DLI were (mean ± standard deviation) 25.3 ± 2.8 °C, 1.00 ± 0.41 kPa, and 9.69 ± 1.74 mol·m⁻²·d⁻¹ for the plants used to obtain the greenhouse light response curves, and 23.5 ± 1.6 °C, 1.08 ± 0.44 kPa, and 9.09 ± 3.88 mol·m⁻²·d⁻¹ for the plants used with the growth chamber light response curves and two-point approximations.

Chlorophyll fluorometry. Measurements were taken using a chlorophyll fluorometer with an attached leaf clip with built-in quantum sensor (JUNIOR-PAM Heinz Walz, Effeltrich, Germany). The quantum yield of PSII was measured using the fluorometer, and *PPFD* was measured using the quantum sensor. Electron transport rate was calculated 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). The dark-adapted value of Φ_{PSII} (F_v/F_m) was measured after plants had been in the dark (*PPFD* = 0 µmol·m⁻²·s⁻¹) for at least 30 min. This value is a good indicator of the maximum potential quantum efficiency of PSII.

The fluorometer sensor head and quantum sensor were not located in the same position, being about 1.5 cm apart, and thus may have been exposed to different *PPFD*s

due to uneven shading. If the *PPFD* received at the part of the leaf where Φ_{PSII} is measured differs from that measured by the quantum sensor, the ETR calculation will become unreliable.

Greenhouse light response curves. Diurnal chlorophyll fluorescence monitoring in the greenhouse was performed eight to 16 weeks after germination (August to October 2016). The outermost leaf of one plant was placed in the leaf clip and positioned such that the quantum sensor was fully exposed to the south side of the greenhouse and not shaded by other leaves. Begonias and impatiens were measured under 50% shade. Chlorophyll fluorescence measurements were taken once every 15 minutes during the day and once an hour at night; Φ_{PSII} and *PPFD* were measured and ETR was calculated. After 24 h, a new plant was selected for measurement. Measurements commenced at least one hour after sunset to verify that F_v/F_m was within an acceptable range (at least 0.79, with a theoretical maximum of around 0.85). This was done five times for each species using a different plant for each measurement day, for a total of five complete 24-h periods per species.

Growth chamber light response curves. The following year, plants were again grown as described above. Measurements were taken in a growth chamber (E15, Conviron, Winnipeg, Manitoba, Canada) 12 to 14 weeks after germination (July to August 2017) with temperature set to 25 °C, using a fluorometer and attached leaf clip (JUNIOR-PAM, Walz). Light was provided using four red and white LED light bars (SPYDRx Physiospec Indoor; Fluence Bioengineering, Inc., Austin, TX) powered by a 0-100 V, 15 A adjustable direct current power supply (CSI10015; Circuit Specialists, Tempe, AZ). A reference quantum sensor (LI-190, LI-COR BioSciences, Lincoln, NE)

was positioned in the center underneath the four LED light bars used to calibrate the quantum sensor attached to the fluorometer leaf clip. Plants were transferred to the growth chamber and allowed to dark-adapt for 30 min. After a dark-adapted measurement was taken and F_v/F_m was determined to be within an acceptable range (0.79 to 0.85), light was provided at a series of eight *PPFD*s (0, 50, 150, 300, 500, 750, 1050, 1400 µmol·m⁻²·s⁻¹; as measured by the reference quantum sensor), with *PPFD* controlled by adjusting the voltage provided to the LED light bars. Plants were allowed to adjust to each *PPFD* for 20 min before *ETR* was determined, and *PPFD* was held constant during these 20-min periods. This procedure was repeated five times for each species.

Two-point approximations. The two-point approximation method was studied using the same plants as the growth chamber light response curves during December 2017 and January 2018. Light was provided using the four LED light bars and DC power supply as described above, and leaf clip quantum sensor calibration was verified using the reference quantum sensor. Plants were transferred to the growth chamber and allowed to dark-adapt for 30 minutes, and F_v/F_m was measured to determine that it was within an acceptable range (0.79 to 0.85). The lights were turned on and the voltage of the power supply was adjusted to provide a *PPFD* of approximately 3 µmol·m⁻²·s⁻¹. After 5 min, Φ_{PSII} was measured using the fluorometer and ETR was calculated. The lights were then set to provide a *PPFD* of approximately 2100 µmol·m⁻²·s⁻¹, and Φ_{PSII} and ETR were again determined. The 5-min waiting period between measurements was determined to be sufficiently long for the fluorescence signal to reach a steady value based on observations made during a previous study (van Iersel et al., 2016). This procedure was repeated five times for each species.

The initial slope of the ETR response to *PPFD* was estimated as Φ_{PSII} observed under the low (3 µmol·m⁻²·s⁻¹) *PPFD* times 0.42. This calculation results from dividing the ETR equation by *PPFD*, which gives a linear approximation of the slope from zero to the low *PPFD*, using an estimated 84% leaf absorptance and assuming that 50% of the excitation energy is used by PSII. The asymptote of the ETR response to *PPFD* was estimated as the ETR observed at 2100 µmol·m⁻²·s⁻¹. These values were averaged over the five replications for each species. After the average values of *a* and *a* were determined, an approximation of the ETR response to *PPFD* was generated for each species using the equation ETR = $a^*(1-\exp(PPFD^*(\alpha/a))$.

Statistical analyses. Regression analyses were performed using SigmaPlot (version 13; Systat Software, Inc., San Jose, CA). For the greenhouse and growth chamber light response curves, Φ_{PSII} and ETR were evaluated as functions of *PPFD* using nonlinear regression. Observed values of ETR from the greenhouse and growth chamber were evaluated as functions of the values of ETR predicted by the two-point approximation method for the corresponding observed *PPFD*s using linear regression. For the two-point approximations, analysis of variance was used to test for significant differences in *a* and *a* among species at a significance level of $\alpha = 0.05$ using the general linear model in SAS (version 9.2: SAS Institute, Cary, NC). Means of *a* and *a* for each species were compared using Tukey's multiple comparison test with $\alpha = 0.05$.

Results and Discussion

Quantum yield of PSII and electron transport rate. Quantum yield of PSII decreased in an exponential manner for all species in the greenhouse and growth chamber (Fig. 5.1.). This occurs because, as *PPFD* increases, a greater proportion of absorbed light energy is

dissipated as heat due to the up-regulation of photoprotective processes, leaving a smaller fraction of the light to drive photochemistry (Demmig-Adams et al., 2012; Horton, 2012; Rochaix, 2014; Ruban, 2015).

Electron transport rate increased in an asymptotic manner with *PPFD*, and the negative exponential equation (ETR = $a^*(1-\exp(PPFD^*(\alpha/a)))$) fit the ETR response of all species in the greenhouse and growth chamber with $R^2 > 0.87$ and p < 0.0001 (Fig. 5.2). Equations of this form have been shown to fit the ETR response to *PPFD* well for many species (Rascher et al., 2000; Weaver and van Iersel, 2019). While ETR increases with increasing *PPFD*, the slope of the ETR response continuously decreases, and this occurs because Φ_{PSII} decreases exponentially as *PPFD* increases linearly.

The variability in the ETR response to *PPFD* was greater in the greenhouse than in the growth chamber, as evidenced by the lower R^2 values for the fitted curves with the greenhouse data (Fig. 5.2). This variability may be caused, in part, by spatially heterogeneous shading in the greenhouse, which may have led to different *PPFD*s being received at the measured leaf section and quantum sensor. In the greenhouse, *PPFD*s are also temporally variable, and the *PPFD* received by the measured leaf section prior to the measurement of Φ_{PSII} may affect the readings because transient exposure to high light levels can reduce light use efficiency for several minutes after *PPFD* decreases (Kaiser et al., 2018; Slattery et al., 2018). Similarly, if the leaf was exposed to a lower *PPFD* shortly before a measurement, Φ_{PSII} may not have adequate time to reach a new steady state because the up-regulation of photoprotective processes in response to increased *PPFD* occurs over several minutes (Demmig-Adams et al., 2012; Kaiser et al., 2018; Ruban, 2015). In the growth chamber, spatial and temporal variations in *PPFD* between

measurements were not a factor, and hence there was less variability in the ETR response. Similar differences in variability were observed for Φ_{PSII} . In the greenhouse, the regression equations for Φ_{PSII} fit the observed data with R^2 values of 0.79 to 0.89, while in the growth chamber R^2 values ranged from 0.95 to 0.98 (Fig. 5.1).

Two-point approximations. Generally, the ETR response estimated using the twopoint approximation fit the observed data well, for the greenhouse and growth chamber. The predicted values of ETR from the two-point approximation fit the observed values from the greenhouse with $R^2 > 0.87$ and p < 0.0001 (Fig. 5.3), and those from the growth chamber with $R^2 > 0.90$ and p < 0.0001 for all species (Fig. 5.4). The approximation was somewhat less accurate for the greenhouse data, as evidenced by the lower R^2 values, and this is primarily due to the greater amount of variability in the greenhouse data.

The R^2 value for the linear regression observed versus predicted ETR (Figs. 5.3 and 5.4) gives an indication of the fraction of the variability in the observed data that can be explained by the predictor. However, this R^2 value alone is insufficient for gauging the accuracy of the approximation, and the slope and intercept of the fitted curve must also be considered. If the intercept is zero, slopes greater than one indicate that that the twopoint approximation under-estimates the ETR response to *PPFD*, while slopes less than one indicate that the approximation is too low.

Among species, there were significant differences in the values of a (p < 0.0001) and α (p < 0.033) obtained using the two-point approximation method (Table 5.1). The asymptotes of salvia, vinca, geranium, and begonia did not differ statistically, and the mean value of a for these four species combined was 198 µmol·m⁻²·s⁻¹. Petunia had a significantly higher a than all other species (331 µmol·m⁻²·s⁻¹), and impatiens had a

significantly lower *a* than all other species (100 μ mol·m⁻²·s⁻¹). The initial slope of the ETR response was lower for begonia ($\alpha = 0.317 \text{ mol·mol}^{-1}$) than for impatiens ($\alpha = 0.327 \text{ mol·mol}^{-1}$) or petunia ($\alpha = 0.328 \text{ mol·mol}^{-1}$), and there were no other significant differences among species.

In general, the ETRs predicted by the two-point approximation were somewhat higher than the ETRs observed in the greenhouse, and the fitted slope was less than 0.97 mol·mol⁻¹ for all species (Fig. 5.3). For petunia (slope = $0.74 \text{ mol·mol}^{-1}$), and impatiens (slope = $0.81 \text{ mol} \cdot \text{mol}^{-1}$), the predicted ETRs were much higher than those observed using diurnal chlorophyll fluorescence monitoring in the greenhouse (Figs. 5.2 and 5.3). This may have been due to mechanical stress or damage of the measured leaves due to the prolonged application of pressure from the fluorometer leaf clip over the 24-h measuring period. Physical damage to the measured leaves of these two species was frequently observed in the greenhouse. This was not an issue in the growth chamber because the light response curves were collected in less than 2.5 hours. For these two species, the intercepts of the observed greenhouse ETRs versus the values predicted by the two-point approximation were also significantly higher than zero, being 1.6 for impatiens and 5.38 for petunia. For the remaining four species, the fitted slope ranged from 0.92 to 0.96 mol·mol⁻¹ (Fig. 5.3), and the intercepts did not differ significantly from zero.

Compared to data from the growth chamber light response curves, the predicted ETRs also tended to be too high. The intercepts did not differ significantly from zero for any species, and the fitted *m* was less than 1 mol·mol⁻¹ for all species except for impatiens (slope = $1.45 \text{ mol·mol}^{-1}$). In the case of impatiens, the predicted ETRs were much lower

than those observed in the growth chamber (Figs. 5.2 and 5.4). This likely occurred due to photoinhibition. At the high *PPFD* (2100 μ mol·m⁻²·s⁻¹) used to approximate *a*, damage to the photosynthetic apparatus may have occurred for this shade-obligate species, and this would cause a decline in ETR at the high PPFD used for the two-point approximation. The rapid decline in Φ_{PSII} with increasing *PPFD* observed for this species (Fig. 5.2) indicates that impatiens is likely a shade-obligate species which uses light inefficiently at high *PPFD*s, and thus may be prone to photoinhibition. In the case where photoinhibition occurs, the two-parameter negative exponential equation is not useful for approximating ETR, and additional parameters must be included to account for the decline in ETR at high PPFDs (Ralph and Gademann, 2005). Thus, the two-point approximation may be unsuitable for use with shade-obligate species. For the remaining five species, the fitted slope ranged from 0.90 to 0.99 mol·mol⁻¹ (Fig. 5.4). The two-point approximation method generally somewhat over-estimated ETR, as compared to the greenhouse and growth chamber data. This may be because the five-minute waiting period used in the two-point approximation procedure may not have been long enough for the plants to acclimate to the *PPFD* of approximately 2100 μ mol·m⁻²·s⁻¹. Using a longer acclimation time may improve the accuracy of the prediction, and further research is needed to determine the ideal acclimation time and refine this two-point approximation method. However, the estimates obtained with the two-point approximation may still be sufficiently accurate within the relevant *PPFD* range for supplemental lighting control. Typical commercial supplemental LED lighting installations used for ornamental plant production can provide a *PPFD* of around 50 - 100 μ mol·m⁻²·s⁻¹. For impatiens, the species for which the approximation was poorest, the two-point approximation gives an

ETR of 15.1 μ mol·m⁻²·s⁻¹ at a *PPFD* of 50 μ mol·m⁻²·s⁻¹. This is 1.6 μ mol·m⁻²·s⁻¹ greater than the ETR observed in the greenhouse at a *PPFD* of 200 μ mol·m⁻²·s⁻¹, according to the fitted curve. At a *PPFD* of 100 μ mol·m⁻²·s⁻¹, the two-point approximation predicted an ETR of 27.9 μ mol·m⁻²·s⁻¹ for impatiens, which is 3.2 μ mol·m⁻²·s⁻¹ greater than the ETR observed in the greenhouse.

Conclusions

The two-point approximation method is a useful and reasonably accurate method of describing the response of ETR to *PPFD* for specific crops. Generally, the predicted ETRs were somewhat higher than those observed in the greenhouse or growth chamber, but the approximation was accurate for four of six species based on the greenhouse data, and for five of six species based on the growth chamber data. The approximation was likely poor for impatiens and petunia in the greenhouse due to mechanical damage to the leaves from the fluorometer leaf clip. Further work is needed to refine this method, especially by determining the ideal period for exposure to high *PPFD* for approximating the asymptote of the ETR response.

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Weaver, G.W., M.W. van Iersel, and J. Mohammadpour Velni. 2019. A photochemistrybased method for optimising greenhouse supplemental light intensity. Biosystems Eng. 182:123-137. Table 5.1. Asymptote (*a*) and initial slope (*a*) of the electron transport rate (ETR) response to photosynthetic photon flux density (*PPFD*) for begonia, geranium, impatiens, petunia, salvia, and vinca. Parameters (mean \pm standard error) are derived from curves fitted to data from five measurement days of diurnal chlorophyll fluorescence monitoring in a greenhouse (greenhouse), curves fitted to data from five light response curves conducted using eight *PPFD*s in a growth chamber (growth chamber), or the mean of five values derived from a two-point approximation where the quantum yield of photosystem II and ETR were measured at approximately 3 and 2100 µmol·m⁻²·s⁻¹ (two-point).

		a	
Species	Greenhouse	Growth Chamber	Two-point
Begonia	126 ± 4	152 ± 6	163 ± 9
Geranium	219 ± 8	172 ± 6	206 ± 9
Impatiens	74.9 ± 2.8	146 ± 6	100 ± 7
Petunia	183 ± 5	266 ± 19	331 ± 24
Salvia	211 ± 10	177 ± 6	213 ± 7
Vinca	209 ± 6	207 ± 9	210 ± 5
		α	
Species	Greenhouse	Growth Chamber	Two-point
Begonia	0.329 ± 0.013	0.379 ± 0.046	0.317 ± 0.003
Geranium	0.284 ± 0.016	0.379 ± 0.034	0.323 ± 0.002

Impatiens	0.299 ± 0.023	0.380 ± 0.044	0.327 ± 0.001
Petunia	0.329 ± 0.015	0.372 ± 0.053	0.328 ± 0.003
Salvia	0.295 ± 0.021	0.372 ± 0.035	0.324 ± 0.002
Vinca	0.313 ± 0.013	0.311 ± 0.021	0.323 ± 0.002





Figure 5.1. Quantum yield of photosystem II (Φ_{PSII}) as a function of photosynthetic photon flux density (*PPFD*) for begonia, impatiens, geranium, petunia, salvia, and vinca. Data was collected in a greenhouse (left) and growth chamber (right). Solid line represents the regression equation of Φ_{PSII} vs *PPFD* using the equation: $\Phi_{PSII} = b + c^* \exp(-d^*PPFD)$, where *b*, *c*, and *d* are regression parameters. The regression fit all species with p < 0.01.


Figure 5.2. Electron transport rate (ETR) as a function of photosynthetic photon flux density (*PPFD*) for begonia, geranium, impatiens, petunia, salvia, and vinca. Data was collected in a greenhouse (left) and growth chamber (right). Solid line represents the regression equation of ETR vs *PPFD* using the equation: ETR = 1 - a*exp(- $(\alpha/a)*PPFD$), where α is the initial slope and a is the asymptote. The regression fit all species with p < 0.0001. The dashed line represents the estimated ETR obtained with the two-point approximation method.



Figure 5.3. Greenhouse electron transport rates (ETRs) versus predicted ETRs obtained with the two-point approximation method for begonia, geranium, impatiens, petunia, salvia, and vinca. Solid lines represent linear regression equations. Dashed line represents a slope (*m*) of one. The regression fit all species with p < 0.0001.



Figure 5.4. Growth chamber electron transport rates (ETRs) versus predicted ETRs obtained with the two-point approximation method for begonia, geranium, impatiens, petunia, salvia, and vinca. Solid lines represent linear regression equations. Dashed line represents a slope (*m*) of one. The regression fit all species with p < 0.0001.

CHAPTER 6

CONCLUSIONS

The response of electron transport rate (ETR) to photosynthetic photon flux density (PPFD) provides a useful means for assessing crop light use and developing effective control strategies for greenhouse supplemental lighting control. Simulations presented in chapter two suggested that extending the amount of time during which plants are exposed to light during a 24-hour period (photoperiod), and providing the same total daily amount of light, but at lower instantaneous *PPFD*s will improve lettuce growth. The results presented in chapter four demonstrate this effect for 'Green Towers' lettuce (*Lactuca sativa*) and show that the simulated improvements in crop light use efficiency (chapter two) do indeed lead to improved crop growth. Additional simulations presented in chapter two, as well as the numerical optimization and simulations of chapter three, suggest that for a fixed photoperiod, the most efficient way to apply greenhouse supplemental light is to use the most uniform possible PPFD, equivalent to providing light to a single threshold *PPFD* over the course of each day using adaptive lighting control. These simulated results have yet to be tested in a greenhouse, and plant growth trials are needed to confirm the model-predicted benefits of providing supplemental light in a uniform manner. While these simulations were based on an ETR response curve obtained over a five-week period in a greenhouse, the results of chapter five suggest that crop-specific ETR responses to PPFD can be evaluated much more quickly and with reasonable accuracy using a simple two-point approximation. This method can be

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expanded upon by including additional measurements, which may yield a more accurate approximation, especially for shade-obligate species.