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Light-emitting diodes as an alternative supplemental lighting source for greenhouse tomato propagation and production

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LIGHT-EMITTING DIODES AS AN ALTERNATIVE SUPPLEMENTAL LIGHTING SOURCE FOR GREENHOUSE TOMATO PROPAGATION AND PRODUCTION

A Dissertation
Submitted to the Faculty
of
Purdue University
by
Celina Gómez Vargas

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of
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For my family

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ABSTRACT

Gómez Vargas, Celina. Ph.D., Purdue University, December 2014. Light-Emitting Diodes as an Alternative Supplemental Lighting Source for Greenhouse Tomato Propagation and Production. Major Professor: Cary A. Mitchell.

Intensive year-round local production of greenhouse-grown tomatoes (*Solanum lycopersicum* L.) requires the use of supplemental lighting (SL) to complement solar radiation in light-limited seasonal climates. However, SL represents a large expense to greenhouse-vegetable production. Currently, energy is second only to labor as the most expensive indirect cost of production. Thus, the greenhouse industry is interested in cost-effective, energy-efficient sources of supplemental photosynthetic light to sustain steady supplies of high-quality produce during the off-season. Overhead (OH) high-pressure sodium (HPS) lamps are considered the industry standard in greenhouse SL because of their capability to deliver adequate photosynthetically active radiation (*PAR*) to crops. However, HPS lamps are inefficient consumers of electrical energy with a high life-cycle cost, an intense environmental impact, and an orange-biased, blue-deficient emission spectrum. Light-emitting diodes (LEDs) offer an exciting opportunity to improve energy efficiency in greenhouse lighting because their relatively low surface temperature allows them to operate in close proximity to plant tissue without overheating or scorching plants, thereby increasing available *PAR* at leaf level using less input power than HPS lamps. In

addition, unlike traditional light sources used in commercial greenhouses today, LEDs are solid state, robust, long-lasting, and can be designed to emit narrow-band wavelengths that can be selected to maximize photosynthesis and growth for specific crops.

The goal of our research is to enable U.S. greenhouse growers to transition from HPS lighting to LED technologies for supplemental photosynthetic lighting. The specific objective of this research was to evaluate LEDs as alternative SL sources for greenhouse tomato propagation and production. Three research goals were established to support my objective: 1) to compare seasonal growth responses to three red:blue ratios of LED SL vs. HPS SL vs. ambient light for the propagation of six tomato cultivars; 2) quantify plant growth, yield, and energy consumption using intracanopy lighting (ICL) with LEDs (ICL-LED) or OH-HPS lamps as different SL sources and positions for high-wire greenhouse tomato production; 3) compare crop physiological responses to different SL sources and positions [ICL-LED vs. OH-HPS vs. hybrid lighting (ICL-LED + OH-HPS)] within an indeterminate high-wire tomato canopy.

Supplemental lighting increased hypocotyl diameter, epicotyl length, shoot dry weight, leaf number, and leaf expansion relative to control, whereas hypocotyl elongation decreased when SL was applied. For all cultivars tested, the combination of red and blue in SL typically increased growth of tomato seedlings. Our results indicate that blue light in SL has potential to increase overall seedling growth compared to blue-deficient LED SL treatments in overcast, variable-DLI climates. Further production studies showed that the ICL-LED technology supports similar growth and yield compared to OH-HPS but at lower electrical costs (from SL only). Additionally, we found that CO_2 assimilation measured under ambient environmental conditions (*A*), photosynthetic quantum yield (θ), maximum gross CO_2 assimilation (A_{max}) and the light-saturation point of photosynthesis were good indicators of how ICL diminishes the top-to-bottom decline in photosynthetic activity that typically occurs with OH SL. However, we did not find any yield differences among SL treatments, indicating that higher source activity from ICL does not necessarily lead to yield increases. Based on the lower energy consumption measured for ICL-LED, and, to a lesser extent, for hybrid SL, compared to OH-HPS, we concluded that replacing OH-HPS lamps with ICL-LED or hybrid SL has great potential for energy savings during high-wire greenhouse tomato production. However, our results showed that higher total canopy photosynthesis did not lead to higher yields, most likely due to a redistribution of photoassimilate partitioning to non-harvested, vegetative plant parts.

CHAPTER 1: INTRODUCTION AND LITERATURE REVIEW

Summary

Intensive, year-round, local production of greenhouse-grown vegetables requires the use of supplemental lighting (SL) to offset seasonally limited solar radiation in northern climates. The recent surge in popularity of light-emitting diodes (LEDs) has prompted research to evaluate LEDs as SL sources for greenhouse plant propagation and production. The review herein explains the need for SL in greenhouse crop production and provides an introduction to the importance of light for plant growth and development, followed by a review of research reporting plant growth with LEDs as sole-source or SL.

Introduction

When greenhouses were first introduced by the French in the seventeenth century, they essentially served as sheltered structures for the cultivation of orange trees in temperate climates (Raviv and Lieth, 2008). Over time, greenhouses became a semi-controlled type of protected cultivation aiming to provide and maintain favorable growth environments to maximize yield and extend the growing season of high-value crops (Jensen and Malter, 1995). Gradually, these structures became important for commercial plant production and their use was split into four main areas: floriculture, bedding plants, nursery plants, and vegetable crops (Campbell et al., 1969). Common practices for greenhouse vegetable production, especially those related to light management within greenhouses, will be discussed in detail in this review.

Greenhouse vegetable production

Since the mid-1990s, the greenhouse vegetable industry has expanded in both Europe and North America as the preferred production system for high-quality crops (Jones, 2008). Today, greenhouses have different configurations that range from simple film-covered tunnels, to tall glass-glazed structures with advanced, computer-controlled environments (Hanafi, 2003). In general, production costs for greenhouse vegetables are higher than those for field production because of the required capital inputs (infrastructure) and ongoing expenses (labor, heating, and electricity). However, there are many advantages of growing plants in greenhouses including but not limited to the following: off-season production, higher yields, better input management and control, extension of the growing season, improved produce quality, and high market value.

Worldwide, the most important greenhouse-grown vegetables are tomato (*Solanum lycopersicum* L.), cucumber (*Cucumis sativus* L.), lettuce (*Lactuca sativa* L.), sweet pepper (*Capsicum annuum* L.), eggplant (*Solanum melongena L.*), and strawberry (*Fragaria* × *ananassa* L.) (Hickman, 2014). In 2014, an estimate of the world's total greenhouse vegetable production area was 411,262 hectares (Hickman, 2014). According to the 2007 Census of Horticulture Specialties, the total number of commercial greenhouse farms producing vegetables and fresh-cut herbs in the United States (U.S.) was 4,075; this accounted for ≈574 hectares (USDA, 2009).

Today, the U.S. greenhouse vegetable industry consists of many small, family-run operations and a few large facilities (Greer and Diver, 2000). Large greenhouses typically are located in the southwestern and western U.S., where climate enables profitable production during winter, when vegetable prices are highest (Cook and Calvin, 2005). Nevertheless, several greenhouse facilities are also located in light-limited temperate climates, where optimal yield and quality of vegetables can be achieved only by using supplemental lighting (SL) (Dorais et al., 1991; McAvoy and Janes, 1984; Rodriguez and Lambeth, 1975; Tibbitts et al., 1987). However, the use of SL represents an additional expense to greenhouse vegetable production. Currently, energy is second only to labor as the most expensive indirect cost of production (Frantz et al., 2010). Thus, the greenhouse industry is interested in cost-effective, energy-efficient sources of supplemental photosynthetic light to sustain steady supplies of high-quality produce during the off-season. To understand the importance of SL for greenhouse vegetable production, one must consider several factors affecting plant responses to light.

Understanding Plant Growth in Response to Light

Plant growth and development is affected by three interacting light parameters: 1) quantity, which refers to the number of photons incident per unit time on a unit surface; 2) quality, referring to the distribution of photons at specific wavelengths; and 3) duration or photoperiod, which is the relative length of the light period. Light measurements for instantaneous photosynthetic activity are normally expressed as photosynthetic photon flux (*PPF*), which is the number of photons within the photosynthetically active radiation (*PAR*) spectrum (400 to700 nm) incident per unit time on a unit surface ($\mu mol \cdot m^{-2} \cdot s^{-1}$). Yet, a more useful method to measure light quantity is the daily light integral (DLI) described as the cumulative *PPF* or dose that plants receive during a 24-h day ($\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$).

While it is widely accepted that any wavelength of light within *PAR* contributes to photosynthesis and crop productivity (McCree, 1972), the relative quantum efficiency curve, which weights the quantum yield (moles of carbon fixed per moles of photons absorbed) for each wavelength of light, indicates that broadband blue (400 to 500 nm) and red (600 to 700 nm) light are among the most efficient wavelengths for driving photosynthesis and potentially promoting plant growth (Inada, 1976; McCree, 1972). Moreover, while *PAR* is the primary driver of photosynthesis, spectra within and outside the 400 to 700 nm spectrum also influence photomorphogenic and photochemical plant responses (Fisher and Runkle, 2004).

Depending on their physiological effects, light-mediated responses in plants can be classified into two groups: 1) plant photosynthesis, generally associated with plant growth and productivity (Blankenship, 2010), and 2) photomorphogenic responses, which reflect changes in plant development and morphology (Brutnell, 2006). Both groups of responses are largely controlled by plant pigments and photoreceptors.

Protein pigments

Chlorophylls are the most important photoreceptor pigments for photosynthesis in higher plants. Although all photosynthetic organisms contain chlorophyll *a*, only higher plants contain chlorophyll *b*, which serve as accessory pigments for light absorption (Blankenship, 2010). Both chlorophylls absorb light most effectively in the blue and red regions of the *PAR* spectrum. Conversely, chlorophyll molecules are poor absorbers of green (400-600 nm) and near-green light, hence the green color of chlorophyll-containing tissues. Moreover, although chlorophyll *a* and *b* are both involved in the light-harvesting reactions centers, only some forms of chlorophyll *a* are linked to the energy-processing centers of photosynthesis (Kriedemann, 2010). Carotenoids, a kind of accessory pigment, mainly absorbs light in the blue and green regions of the *PAR* spectrum. Carotenoids also contribute in the photochemical events of photosynthesis but are primarily in charge of protecting chlorophyll molecules against photodamage; their abundance in mature leaves of higher plants is only one third that of chlorophyll (*a* + *b*) (Kriedemann, 2010). Although some green light is reflected or transmitted, chlorophyll and carotenoids together absorb light throughout most of the *PAR* spectrum, and thus, are considered the two major photosynthetic pigments of higher plants (Franklin, 2005).

Photoreceptors

Plant photomorphogenic and physiological responses are generally regulated by plant photoreceptors such as ultra-violet (UV), phototropins, cryptochrome, or phytochrome, respectively, which are mainly stimulated by UV (100 to 380 nm), blue, and the ratio of red and far-red (700 to 770 nm) light, respectively. Phytochromes are a family of proteins that have two interconvertible forms, the physiologically inactive, red-light-absorbing form (Pr) and the active, far-red-absorbing form (Pfr). The Pr form, which has peak absorption (λ_{max}) at 660 nm, undergoes a conformational shift to the Pfr form when it absorbs red light. The Pfr form, which has λ_{max} at 730 nm, undergoes a conformational shift to the Pr form when it absorbs far-red light (Brutnell, 2006). Additionally, the Pfr form slowly converts back to the Pr form in darkness. Because of the relative differences in absorption and the subsequent conformational changes, both forms of phytochrome are always present in plants. The ratio of Pfr to total phytochrome (Pfr + Pr) creates a phytochrome photoequilibrium that mediates phytochrome-related plant responses, which include but are not limited to activation of seed germination, hypocotyl elongation in dark-grown seedlings, initiation of leaf expansion, flowering regulation, gravitropism, phototropism, and the shade-avoidance response (Briggs and Olney, 2001; Brutnell, 2006).

Phototropins are UV-A- (315 to 380 nm), blue-, and green-light-absorbing photoreceptors that mediate several plant responses including phototropism, chloroplast movement, light-induced stomatal opening, leaf expansion, nuclear positioning, leaf flattening, leaf positioning, sun tracking, and growth inhibition (Folta and Spalding, 2001; Kagawa et al., 2001; Kinoshita et al., 2001; Zeiger, 2010). Cryptochromes are UV-A- and blue-light photoreceptors responsible for several photomorphogenic responses like inhibition of hypocotyl elongation or increased anthocyanin production (Jao et al., 2005; Kim et al., 2004; Moe, 1990; Shinkle and Jones, 1988). Cryptochromes sometimes work in conjunction with phytochromes to regulate cell elongation and photoperiodic flower induction and are also known to interact with phototropins to mediate stomatal opening (Zeiger, 2010). Ultra-violet photoreceptors are known to initiate stress responses in plants that ultimately affect plant morphology and protein pigment synthesis (Lercari et al., 1992; Paul et al., 2005). Interactions between photoreceptor responses can be synergistic or antagonistic, depending on the light signals received and/or the plant's developmental stage (Casal, 2000). Because photoreceptors allow plants to alter their growth in response to light spectra, they pose the potential for manipulating light in the growing environment to control several plant developmental parameters.

Light Sources for Greenhouse Plant Production

Sunlight is the primary light and energy source for all living organisms on earth. However, its intensity, duration, and quality are affected by a location's latitude, sun's relative position (seasonal and daily), cloud density and composition, atmospheric dust, moisture, elevation, and the plane of exposure, among others (Bickford and Dunn, 1972). It is said that the most stable characteristic of solar radiation is its variability. Thus, little reliance can be placed upon sunlight as the only light source with which to grow plants in greenhouses on a year-round basis, especially with increasing distance away from the equator in either direction. On the other hand, because no electric light source used for SL has a spectral distribution identical to sunlight, it is difficult to directly compare plant-growth responses to variables such as daylength and irradiance under greenhouse and field conditions (Withrow and Withrow, 1947).

Electric light sources

The use of electric lighting for commercial plant production began with the introduction of carbon arc lamps (Siemens, 1880; Parker and Borthwick, 1949). Further research in lighting for plant growth led to the search for new lamps with acceptable electrical efficiencies, long life spans, and relatively broad light spectra (Wheeler, 2008). Withrow and Withrow (1947) suggested that the most important factors to consider when using electric lighting for plant growth are the spectral energy distribution, the proportion of energy dissipated as radiated infrared (>770 nm), and the efficiency of producing radiant energy within the *PAR* spectrum. Other factors that must be considered when selecting lamps for greenhouse SL include commercial availability, installation costs, and ease of lamp operation and replacement.

Incandescent (INC) lamps irradiate blue-deficient, yellow (550 to585 nm)- and red-biased light with high proportions of far-red and infrared radiation, which can cause stem elongation in plants (Arthur and Stewart, 1935). For that reason, INC lamps often are used for enriching far-red light in plant-growth chambers, for photoperiod control (night breaks) in the floriculture industry, and less frequently for supplemental photosynthetic lighting (Chia and Kubota, 2010). Although INC lamps have a relatively low initial cost, they provide low electrical efficiencies that generally range from 2% to 13% (Agrawal et al., 1996); most of the electricity they consume is converted into heat rather than light. Estimates place lighting as requiring 20% of the world's electricity consumption, with 70% of this energy being consumed by inefficient lamps (International Energy Agency, 2006). Thus, INC lamps are gradually being replaced by more energy-efficient lamps, with improved ratios of light-to-heat generation. In the U.S., federal law has scheduled the most common INC light bulbs to be phased out by 2014.

Different types of gas-discharge lamps have been used in the horticulture industry; however, they tend to be inefficient sources of red light (Withrow and Withrow, 1947). Arthur and Stewart (1935) compared growth of buckwheat (*Fagopyrum esculentum* Moench.) using INC lamps vs. three types of low-pressure gas discharge lamps: neon, mercury, and sodium in a controlled environment. Their results demonstrated that sodium lamps were more energy efficient for plant lighting compared to the other lamps. Further research showed that SL with sodium vapor lamps in combination with 2 h per d from mercury arc lamps improved plant growth for geranium (*Pelargonium* × *hortorum* Bailey), cotton (*Gossypium* spp.), and buckwheat (Arthur and Harvill, 1937). Later, Johnston (1938) compared the development of tomato grown under different combinations of water-filtered INC lamps in conjunction with mercury arc lamps. He concluded that INC lamps combined with up to 51% light from mercury arc lamps produced more dry mass due to the additional blue light. Eventually, it was discovered that low-pressure mercury arc lamps provided large percentages of UV light, a finding that led to development of fluorescent lamps.

Fluorescent lamps are a type of low-pressure gas discharge lamp that have a phosphor coating (fluorescent chemical) on the inside wall of the lamp. Electricity is passed between two filament cathodes and transforms the UV energy of excited mercury-vapor into radiant energy of visible (380 to 770 nm) and UV wavelengths (Bickford and Dunn, 1972). The chemical composition of the phosphor coating is what ultimately determines the wavelengths of generated light (Sersen, 1990). The light intensity from these lamps decreases with the increasing number of operational hours and generally lasts until the emissive material has been depleted from the cathode (Bickford and Dunn, 1972).

Numerous studies have evaluated different types of fluorescent lamps in plant-growth chambers and greenhouses. Due to their high energy efficiency (compared to INC lamps) and wide spectral distribution (series of spikes of different wavelengths used to approximate white light), cool-white fluorescent (CWF) lamps, used alone or in combination with INC, were long the standard light source in plant-growth chambers for seedling propagation of both herbaceous and woody plants (Brown et al., 1979; Cathey and Cambell, 1977; Downs, 1975). Nonetheless, when working in large production areas like greenhouses, CWF lamps provide limited irradiance levels and require close placement to plant tissue (≤ 1 m) to provide desirable *PPF* levels. Furthermore, CWFs often cause excessive shading of solar light in greenhouses due to their fixtures, are prone to failure when exposed to dripping water or water sprays, their light output is temperature sensitive, and because they contain mercury, are considered hazardous for human health and require proper handling for disposal. For these reasons, CWF lamps are a less suitable option for greenhouse vegetable production (Langhans, 1994).

Current standard for greenhouse SL

Overhead (OH) high-intensity discharge (HID) lamps are the preferred type of greenhouse SL because their high-intensity capability allows them to deliver adequate supplemental *PAR*. However, HID lamps, which include mercury-vapor, metal-halide (MH), and high-pressure sodium (HPS) lamps, among others, have a relatively high life-cycle cost (cost of buying, installing, operating, and maintaining a lamp during its lifetime), and have a significant environmental impact compared to other lamps that do not contain mercury or other hazardous materials.

High-pressure sodium lamps are powered by an AC voltage source in series with an inductive ballast. At low pressure, xenon gas is used as a "starter gas" in HPS lamps. An amalgam of metallic sodium and mercury lies at the coolest part of the lamp and provides the vapor required to create an arc. However, the temperature of the amalgam is determined to an extent by the lamp power. Higher power results in higher amalgam temperature, which increases the mercury and sodium vapor pressure within the lamp (Bickford and Dunn, 1972); HPS lamps tend to have high surface temperatures of up to 450 °C (Spaargaren, 2001).

High-pressure sodium lamps are considered the most suitable light source for large-scale SL in greenhouses. Furthermore, HPS lamps are up to 30% efficient in terms of converting electricity into useful light, and the remaining ‘waste’ thermal energy can be used to increase ambient greenhouse and plant temperature and offset winter heating costs (Tiwari, 2003). Brault et al. (1989) estimated that, in temperate climates, the heat emitted from HPS lamps can provide between 25% and 41% of the heating requirement for a greenhouse operation. Thus, heat generation is sometimes considered a useful by-product of HPS lamps. Also, HPS lamps typically require reflectors to direct the light from the bulbs onto crops, thereby providing satisfactory light distribution and efficiency, but as a result blocking some sunlight from reaching the crop. Additionally, their significant thermal output often requires a considerable separation distance between plants and lamps to avoid tissue scorching, which contributes to a higher lamp-power requirement to provide adequate *PPF* at increasing distances (Cathey and Campbell, 1977).

Like most available light sources, HPS lamps were originally designed for human use. These lamps emit a yellow-orange (550 to 630 nm)-biased, low-blue spectrum that does not correspond with the absorption peaks of chlorophyll pigments. Nonetheless, as mentioned previously, any wavelength of light within the *PAR* spectrum contributes to photosynthesis and crop productivity (McCree, 1972). Thus, with their high-intensity capabilities, HPS lamps have been widely adopted for greenhouse SL and currently are the most economically viable mass-produced light source available to provide adequate *PAR* irradiances for plant growth.

Markham (1969) conducted one of the first greenhouse experiments with HPS SL and reported that a number of different plants could grow under these lamps (plant species were not described). Further greenhouse research by Meijer (1971) reported more fresh and dry mass of tomato and cucumber seedlings grown under HPS compared to MH lamps. Austin and Edrich (1974) compared six lamp types (warm white fluorescent, mercury fluorescent, mercury halide, HPS, mercury fluorescent with an internal reflector, or low-pressure sodium) as SL sources for growing cereals in glasshouses during winter. They concluded that based on plant growth and lamp + energy costs, HPS lamps were more suitable for growing plants to seed. Elgin and McMurtrey (1977) reported similar results when comparing flowering and seed production of greenhouse-grown alfalfa (*Medicago sativa* L.) using HPS, MH, mercury vapor, incandescent, or no SL. They concluded that HPS was most effective for increasing seed yields. Later, McAvoy and Janes (1984) reported an increase in greenhouse tomato production when plants were grown under HPS lamps compared to unsupplemented controls, especially during winter months. Clark and Devine (1984) reported enhanced plant growth of 'Altex' rapeseed (*Brassica napus* L.), 'Neepawa' spring wheat (*Triticum aestivum* L.), 'Kay' orchard grass (*Dactylis glomerata* L.), Canada thistle (*Cirslum arvense* (L.) Scop.), ‘Gaertn.’ Tartary buckwheat, and 'Buttercrunch' lettuce when using HPS lamps compared to MH and fluorescent lamps in a greenhouse experiment. Over the years, HPS lamps have served as an adequate light source for greenhouse SL. However, recent interest has focused on alternative SL sources that can reduce production costs by decreasing electrical energy consumption while maintaining crop yield and quality.

Light-emitting diodes (LEDs) for Plant Growth

Light-emitting diodes are a promising SL technology for the greenhouse industry as they surpass in many aspects capabilities of commercially available lamps commonly used in horticulture (Morrow, 2008). As described by Bourget (2008), LEDs are robust, solid-state semiconductor devices that can be designed to produce narrow-spectrum light to maximize photosynthetic quantum efficiency for specific crop species. In 2008, LEDs were as electrically efficient as fluorescent lamps and slightly less efficient than HPS lamps at converting electrical energy to light (Bourget, 2008). As of 2014, red and blue LEDs are up to 38% and 49% efficient, respectively (Nelson and Bugbee, 2014; Philips, 2012).

The estimated lifetime of LEDs is generally rated for ≈50,000 h of operation before their output falls below 70% of its initial intensity (M. Bourget, personal communication, 2012). Also, unlike traditional HID light sources used in commercial greenhouses today, the relative coolness to the touch of LED photon-emitting surfaces allows them to operate in close proximity to plant tissue without overheating or scorching plants, thereby increasing available *PAR* at leaf level using less energy. In addition, LEDs can tolerate frequent on/off switching and dimming without negative impacts on longevity, unlike conventional light sources that fail faster when cycled often (e.g., fluorescent and HPS lamps), and/or require some time before restarting (HID) (Avago Technologies, 2008). Other benefits of using LEDs include reduced maintenance labor, precise intensity control, and high resolution zonal control to ensure that only areas populated by plants are irradiated. With ongoing improvements in terms of energy efficiency and availability of photosynthesis-driving wavebands, LEDs provide a potential solution to part of the profitability issues that greenhouse growers face.

Testing of LEDs for plant growth in the U.S. began with early models of LED arrays in the late 1980s and early 1990s and continues today (Barta et al., 1990; Bula et al., 1991; Ignatius et al., 1988; Morrow et al., 1989). The need to develop better light sources for space-based plant-growth research gave rise to initial developments of LED lamps for plant research. Bula et al. (1991) were the first to test LEDs for plant lighting. They reported that growth of lettuce grown under red LEDs (660-nm peak wavelength) supplemented with blue fluorescent (BF) lamps was equivalent to that reported in the literature using CWF and INC lamps.

Sole-source lighting with LEDs for space missions

In a description concerning the characteristics of LEDs for space-based plant lighting, Barta et al. (1992) stated that because of their long lifespan, minimal mass and volume, and high-quality spectral output for photosynthesis, LEDs were a promising alternative for plant irradiation in space-based research or bio-regenerative life-support systems. Following this, several research groups examined effects of LED-based lighting systems on yield and physiological responses of numerous crops to be included in space missions. Morrow et al. (1995) reported that growth and development of dwarf wheat and *Brassica rapa* L. seedlings grown in a spaceflight experiment using red and blue LEDs (no spectrum defined) appeared normal and similar to that of plants grown under terrestrial conditions.

Goins et al. (1997) compared photomorphogenesis, photosynthesis, and seed yield of wheat plants produced in a growth chamber using 350 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ from either daylight fluorescent (white) lamps, red LEDs (660-nm peak wavelength, 25-nm bandwidth at half-peak height), or a combination of red LEDs + either 1% or 10% blue light provided by BF lamps. They reported that plants grown under red LEDs alone produced fewer shoots and less seed yield compared to plants grown under white light. However, results showed that wheat grown under red LEDs + 10% BF light had comparable shoot dry-matter accumulation and seed yield relative to wheat plants grown under white light. They concluded that wheat plants could complete their life cycle under red LEDs alone, but larger plants with higher yields are obtained under red LEDs supplemented with blue light. Further research by Yorio et al. (2001) compared growth of radish (*Raphanus sativus* L.), spinach (*Spinacia oleracea* L.), and lettuce using CWF lamps and red LEDs (660-nm peak wavelength) with and without additional blue light (10%) from BF lamps at equal *PPF*. They observed higher leaf photosynthetic rates, more stomatal conductance, and additional dry mass in plants grown under CWF lamps than those grown under red LEDs, with or without supplemental blue light. However, radish and spinach grown under red LEDs +10% BF had more dry mass than when no blue light was added. They concluded that the addition of blue light improved plant growth but was still insufficient to achieve maximal plant growth.

Furthermore, Massa et al. (2005) developed a reconfigurable red (640-nm peak wavelength) and blue (440-nm peak wavelength) LED plant-growth-lighting array designed to reduce electrical energy requirements in a life-support system. The reconfigurable array had several independent LED "lightsicles" that hung vertically within a plant canopy, and each strip contained numerous light engines that were switched on/off incrementally as plants grew. The authors grew cowpea (*Vigna unguiculata* (L.) Walp.) and reported that the reconfigurable system illuminated a larger percentage of leaves within the canopy than OH lighting and reduced power consumption by only irradiating where leaves were present. Other crops that have been evaluated for space-related missions using LEDs as sole-source lighting include but are not limited to: potato (*Solanum tuberosum* L.)

leaf cuttings (Croxdale et al.,1997), lettuce (Massa et al., 2005; Tang et al., 2009;), spinach (Johnson et al.,1999), Swiss chard (*Beta vulgaris* L. 'Ruby Red Rhubarb') (Goins, 2002), pepper (Brown et al., 1995), and soybeans (*Glycine max* L.) (Zhou, 2005).

LEDs for plant propagation in controlled environments

The potential of LEDs as the primary light source for plant lighting in controlled environments has been vastly explored. Plant-growth chambers and tissue-culture laboratories have long adopted the use of LEDs in their search for more efficient light sources. Morrow (2008) reported that per watt of input power, LEDs provided three times more photosynthetic light than did HID lamps in controlled environments.

Nhut et al. (2000) grew strawberry leaf explants using red (70%) and blue (30%) LEDs (no spectrum defined) vs. fluorescent lamps in a growth room. Their results showed that LEDs improved growth of strawberry plantlets grown *in vitro* compared to fluorescent lamps. Other studies have reported successful *in vitro* production of various plants using LEDs, including but not limited to: chrysanthemum (*Chrysanthemum indicum* L.) (Kurilcik et al., 2008), banana (*Musa acuminata* Colla) (Nhut et al., 2002), Cymbidium orchids (Tanaka et al., 1998), Doritaenopsis orchids (Shin et al., 2008), potato (Jao and Fang, 2004), grapes (*Vitis vinifera*) (Poudel et al., 2008), and calla lilies (*Zantedeschia jucunda* ‘Black Magic’) (Jao et al., 2005).

Hoenecke et al. (1992) evaluated growth of ‘Grand Rapids’ lettuce seedlings using high-intensity red LEDs (660-nm peak wavelength) with or without supplemental blue light from BF lamps vs. CWF lamps in a growth chamber. Their objective was to determine the optimal percentage of blue light to obtain ‘normal’ development of lettuce seedlings grown under red LEDs. They reported that seedlings grown under blue-photon flux levels between 15 or 30 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for 12 h per day (total *PPF* of 150 or 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$, respectively) showed the most 'normal' growth. Later, Schuerguer et al. (1997) evaluated the effects of light quality on various anatomical features of pepper leaves and stems using MH lamps vs. different spectral combinations of red LEDs (660-nm peak wavelength, 25-nm bandwidth at half-peak height), far-red LEDs (735-nm peak wavelength, 25-nm bandwidth at half-peak height), or blue light from a blue fluorescent lamp. They showed that the effects of spectral quality on pepper stem and leaf tissue anatomy (cross-sectional area of pepper stems, thickness of secondary xylem, number of intraxylary phloem bundles in the periphery of stem pith tissues, leaf thickness, number of chloroplasts per palisade mesophyll cell, and thickness of palisade and spongy mesophyll tissue) were generally correlated to the percentage of blue light present in the light source, with MH resulting in leaves better adapted to maximize light absorption, compared to any of the LED treatments.

Heo et al. (2002) evaluated effects of LEDs (blue, red, or far-red; 440-, 650-, and 720-nm peak wavelengths, respectively) and fluorescent lamps on growth and morphology of Marigold (*Tagetes erecta* L. 'Orange Boy') and salvia (*Salvia splendens* F. Sello ex Ruem & Schult. 'Red Vista') seedlings. Their results showed that dry weight of marigold seedlings was reduced when monochromic blue light was used, whereas stem length was greatest under 100% blue light compared to a combination of fluorescent lamps + red, blue, or far-red LEDs. In contrast, they showed that salvia dry weights were greater under a combination of fluorescent lamps with additional blue, red, or far-red light compared to monochromatic red or blue and noted that fluorescent + far-red LEDs increased stem elongation for salvia. Also, their study suggested that blooming period for bedding plant production in controlled environments could be reduced when using monochromic blue or red LEDs in salvia or fluorescent + far-red LEDs in marigold. More recently, Chia and Kubota (2010) evaluated the effect of end-of-day far-red (EOD-FR) light quality [red to far-red ratio (R/FR)] and dose on hypocotyl elongation of tomato rootstocks using LEDs (red and far-red; 660- and 735-nm peak wavelength, respectively) and INC lamps in a growth chamber. They reported that EOD-FR treatments can effectively serve as non-chemical treatments to produce rootstock-elongated seedlings (for grafting vegetables) without reducing plant dry mass, stem diameter, or leaf developmental stage.

Crops grown under LEDs in controlled environments

Ménard et al. (2006) conducted a growth-chamber study comparing yield and developmental changes of tomato and cucumber grown under different DLIs using HPS (providing 510 $\mu mol \cdot m^{-2} \cdot s^{-1}$) or HPS + supplemental blue LEDs (455-nm peak wavelength). They evaluated different *PPF*s of blue light from LEDs (6.7, 7.5, or 16 $\mu mol \cdot m^{-2} \cdot s^{-1}$) and concluded that adding 6.7 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of blue light for 20 h or 16 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of blue light for 12 h, promoted fruit yield of cucumber but had no significant effect on tomato yield. They also reported a reduction in internode elongation with the addition of blue for both vegetable species. Previous research by Okamoto et al. (1997) compared growth of lettuce seedlings using different percentages of red and blue light from LEDs at a constant *PPF* in a growth chamber. The percentages of red light used in the experiment were 60%, 70%, 80%, and 90%, with the remainder being blue light. They observed a decrease in stem elongation with the increase of blue light and reported greater dry mass for plants grown under 80% red and 20% blue light compared to other treatments.

Other studies have evaluated the after-effects of sole-source LED lighting on growth, development, and yield of plants subsequently transplanted into greenhouses, with or without SL. Brazaitytė et al. (2009a) evaluated various wavelength combinations of LEDs on the subsequent growth of tomato. They compared HPS lamps vs. five LED modules with blue, red, and far-red LEDs (447, 638, 669, and 731-nm peak wavelength, respectively), which provided different light intensities that ranged from 178 to 220 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Each module was additionally supplemented with LEDs of different peak wavelengths that included at least one of the following: 380 nm, 520 nm, 595 nm, 622 nm, 660 nm, or 669 nm. Initial lighting effects on plant growth and development lasted 4 weeks in the greenhouse after sole-source LED lighting treatments had ceased, after which effects from the different lighting treatments were no longer noticeable. No treatment effect was observed for time of harvest. However, a decrease in total yield was reported for plants grown under the LED module supplemented with 595 + 669 nm. A similar study evaluated the after-effects of different LED treatments on cucumber growth and yield (Brazaitytė et al., 2009b). Results indicated that even though no differences in fruit yield occurred, adding green or orange light from LEDs (520 or 622-nm peak wavelength, respectively) accelerated plant maturity and thus, could potentially reduce overall energy consumption for greenhouse cucumber production. Samuoliene et al. (2010) evaluated the after-effects of sole-source LED lighting on strawberries grown in a greenhouse. They reported improved carbohydrate accumulation and overall better plant growth when a combination of red and blue LEDs (640 and 455-nm peak wavelength, respectively) was used during early crop establishment. Johkan et al. (2010) grew red leaf lettuce in a growth chamber using different combinations of light spectra to provide a total *PPF* of 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$.

The treatments evaluated were white fluorescent lamps, red (660-nm peak wavelength, 22-nm bandwidth at half-peak height), blue (468-nm peak wavelength, 22-nm bandwidth at half-peak height), or 1:1 red (655-nm peak wavelength, 20-nm bandwidth at half-peak height) + blue (467-nm peak wavelength, 21-nm bandwidth at half-peak height) LEDs. After 1 week of treatment, all plants were transplanted into a greenhouse supplemented with fluorescent lamps and grown for 28 days. They evaluated the after-effects of light quality on subsequent growth and yield and reported that, at harvest, leaf area and shoot fresh mass were highest for lettuce plants initially treated with blue alone or red + blue LEDs.

LEDs as SL for greenhouse vegetable production

Research growing plants under sole-source LEDs indicates that red light generally promotes fresh and dry weight, stem elongation, and leaf expansion (Heo et al., 2002; Johkan et al., 2010; Wu et al., 2007), and blue light affects morphological development and biomass production (Johkan et al., 2010; Kigel and Cosgrove, 1991; Savvides et al., 2012; Wang et al., 2009). Thus, most studies using LEDs for sole-source lighting demonstrate the need for supplementing monochromatic red LEDs with blue to obtain acceptable growth and development (Cope and Bugbee, 2013; Goins et al., 1998; Hoenecke et al., 1992; Tripathy and Brown, 1995; Yorio et al., 1998). However, plants that develop in growth chambers typically are exposed to a limited light spectrum that depends on the electric-lamp type used. In contrast, greenhouse-grown plants receive a broad spectrum of light from solar radiation in addition to that provided by any SL source. Thus, if LEDs are used to supplement sunlight, additional blue light may not be necessary because sunlight's broad light spectrum contains significant amounts of blue light at midday, which may be sufficient for normal plant growth and development. Then again, it is difficult to determine photomorphogenic and physiological effects of SL on greenhouse crops because a distinction cannot easily be made between light sources. Because SL typically constitutes only a fraction of total irradiance received by plants during light-limited seasons, photomorphogenic and physiological disorders that have been reported for plants grown under narrowband lighting in growth chambers (Morrow, 2008; Morrow and Tibbitts, 1988; Hogewoning, 2010) are potentially less likely to occur in greenhouse production using narrowband SL.

A small number of published studies have evaluated LEDs as SL for greenhouse vegetable production. However, with ongoing improvements in light-output levels, expanded wavelength availability and control, higher energy efficiencies, and relatively low operating temperatures, efforts continue to be made to test different LED technologies for growing greenhouse crops. Hogewoning et al. (2007) were the first to describe the use of LEDs for greenhouse tomato production. Their concern with introducing LED lighting in greenhouses was related to the capacity of daylight-adapted leaves to re-acclimate their photosynthetic apparatus to narrow-band lighting (NBL). They tested the re-acclimation capability of leaves to NBL by illuminating older leaves (approx. 70 d old; positioned low in the canopy) of a high-wire tomato crop with 70 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ provided by arrays of a single LED type with peak wavelengths of 470 nm (blue), 537 nm (green), or 642 nm (red). They reported that the maximum photosynthetic capacity of lower, older leaves increased over time after being irradiated with NBL, suggesting that leaves can re-acclimate their photosynthetic capacity to higher light intensities delivered by supplemental NBL.

Additionally, in order to distinguish the effects of leaf age and light intensity on photosynthesis, they compared the maximum photosynthetic capacity of tomato leaves at different developmental stages. For this purpose, plants were grown horizontally (accomplished by constantly binding the growing tip to a horizontal wooden frame) to avoid shading of older leaves by newer leaves and thus, ensuring an equal light distribution throughout the canopy. Their results showed that older tomato leaves that were never exposed to shading kept a similar photosynthetic capacity compared to younger leaves, suggesting that losses in photosynthetic capacity commonly observed in lower, older leaves of high-wire crops are not attributable to leaf age, but rather to mutual shading inside the plant canopy. They suggested that maintaining a continuously high light level within the canopy would be an effective way to keep lower leaves, otherwise in a shaded position, productive. No effects on fruit yield were mentioned for that study.

Interlighting and intracanopy lighting (ICL)

Traditionally, greenhouse crop production has relied on the use of OH lamps for SL. However, OH lighting tends to favor upper leaf layers by maximizing light interception incident at the top of the foliar canopy. This results in unequal light distribution where the middle and lower leaf canopies are shaded and, thus, *PAR* limited. Additionally, foliar canopy architecture differs among species and should be considered as an important factor for greenhouse SL. With low-growing rosette crops such as lettuce and cabbage, OH lighting seems to be appropriate for delivering adequate *PAR* to plants positioned underneath the lamps. However, mutual shading occurs for planophile crops, where upper leaf layers shade the lower leaf canopy and overhead photons are excluded from the inner canopy, thereby inducing premature senescence and leaf abscission (Frantz et al., 2000).

Some of the first attempts to evaluate LEDs as SL sources for greenhouse-vegetable production focused on their relative coolness (i.e., low radiant heat output), which allows for greater flexibility in lamp placement and resulting light distribution. This is especially beneficial for high-wire cropping systems (i.e., tomato, cucumber, sweet pepper, and eggplant) where plants are trained vertically along support wires, thereby creating conditions conducive to shading of middle and lower leaves by upper leaves, and potentially row-to-row shading, depending on lamp-mounting pattern and row direction. Intracanopy lighting (ICL) or interlighting, which refers to the strategy of lighting along the side or within the foliar canopy, could help prevent mutual shading for such high-wire crops. For this review, we use the terms 'ICL' and 'interlighting' interchangeably.

It has been reported that ICL in a sole-source mode can delay leaf senescence for cowpea (Frantz et al., 2000; Massa et al., 2005) and soybean (Stasiak et al., 1998) by maintaining high irradiances in the understory of the foliar canopy. Other studies have shown that partial interlighting (hybrid = OH + ICL) can increase fruit yield (size, weight, and/or number), increase percentage of first-class fruit, and extend the post-harvest shelf life of produce (Gunnlaugsson and Adalsteinsson, 2006; Hovi et al., 2004; Hovi-Pekkanen et al., 2006; Hovi-Pekkanen and Tahvonen, 2008; Pettersen et al., 2010). Moreover, research has shown that hybrid lighting can increase crop photosynthesis in high-wire greenhouse production of tomatoes (Trouwborst et al., 2010), cucumber (Pettersen et al., 2010), and for field-grown soybean (Johnston et al., 1969). However, all of these studies were conducted using either fluorescent, microwave-powered, or HPS lamps.

To our knowledge, Trouwborst et al. (2010) were the first to measure the effects of partial LED interlighting on yield of a high-wire greenhouse-grown cucumber crop. Additionally, they quantified light interception and photosynthetic capabilities of different vertical leaf levels within the crop. The experiment was conducted for 13 weeks during a winter production cycle using either a combination of LED-interlighting + OH-HPS or OH-HPS only to provide an average *PPF* of 221 $\mu mol \cdot m^{-2} \cdot s^{-1}$. For the hybrid treatment, they used LED arrays that provided 80% red (667-nm peak wavelength) + 20% blue (465-nm peak wavelength) light and 400 W HPS lamps. The LED and HPS portions of the hybrid treatment contributed to a *PPF* of 139 and 82 $\mu mol \cdot m^{-2} \cdot s^{-1}$, respectively. For the OH-HPS treatment, 600 W HPS lamp were used. They reported that hybrid SL improved photosynthetic properties in lower leaf layers and increased dry mass allocation to the leaves. However, fruit production was not increased when using LEDs + OH-HPS compared to OH-HPS only. The authors attributed their results to overall limiting light intensities in the experimental greenhouse and reduced light interception resulting from leaf curling caused by the LEDs. Dueck et al. (2012) compared the effects of different SL systems on growth and production of greenhouse-grown tomatoes in The Netherlands. They provided 170 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of SL from OH-HPS lamps, OH-LED arrays, or hybrid lighting with OH-HPS + OH-LEDs or OH-HPS + LED-interlighting. The LED lighting was composed of 12% blue (450-nm peak wavelength) and 88% red (660-nm peak wavelength) light. They concluded that a combination of OH-HPS + LED-interlighting is the most promising alternative for their climate, when taking into consideration production parameters and energy costs (lighting + heating) of using the different systems. Another experiment compared hybrid lighting using red (660-nm peak wavelength), blue (460-nm peak wavelength), or white (broad spectrum from 400 to 700 nm) LED-interlighting + OH-HPS vs. OH-HPS lamps (400 W) for the production of greenhouse mini-cucumber (Hao et al., 2012). The LED-interlighting treatments provided an additional *PPF* of 14.5 $\mu mol \cdot m^{-2} \cdot s^{-1}$ to that received by plants under the OH-HPS treatment (145 $\mu mol \cdot m^{-2} \cdot s^{-1}$). The study revealed that all hybrid SL treatments improved fruit visual quality (based on a color rating scale and fruit curvature ratings) compared to the OH-HPS treatment. However, fruit yield increased with LED-interlighting only during early stages of production but gradually decreased in effectiveness toward the mid and late stages of production, becoming even less effective than the OH-HPS treatment. Jokinen et al. (2012) reported an increase of 16% in total marketable yield of sweet pepper using LED-interlighting (light spectrum not reported) compared to plants grown with no SL. They concluded their results were due to an increase in fruit number and earlier fruit maturity induced by LED-interlighting. The recorded *PPF* levels inside the canopy showed less than 10 $\mu mol \cdot m^{-2} \cdot s^{-1}$ measured close to leaves with no SL and up to 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$ close to leaves with the LED-interlighting treatment.

Research by Lu et al. (2012) compared effects of interlighting on yield and quality of greenhouse tomatoes grown at high-planting densities using a single-truss tomato-production system. They provided different *PPF*s (ranging from 143 to 70 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at a distance of 5 cm) from lamps with either white (broad spectrum from 400 to 700 nm), red (660-nm peak wavelength), or blue (442-nm peak wavelength) LEDs. Results indicated that white and red LEDs increased fruit fresh mass by 12% and 14%, respectively, compared to plants grown under no SL. However, plants receiving blue LEDs showed no increase in fruit fresh mass. After calculating the effects of light quality on fruit fresh mass per unit of photons emitted, the authors concluded that white LEDs were the most efficient in promoting fruit fresh mass gain. They suggested that this was due to higher light penetration into the foliar canopy by green wavelengths emitted from the white LEDs.

Deram et al. (2014) compared three light levels (135, 115, or 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$) and three red (661-nm peak wavelength)-to-blue (449-nm peak wavelength) ratios (5:1, 10:1, or 19:1) of LED-interlighting for high-wire greenhouse tomato production. The light intensities were measured using a spectroradiometer and a spherical quantum sensor (for comparison). The LED-interlighting arrays were placed no more than 10 cm below the top of the plant canopy, and lamp height was adjusted depending on crop growth. Additionally, the author compared several LED treatments [different light intensities from interlighting, OH-lighting with red light only, bottom lighting with red light only, or hybrid lighting with LED-interlighting + OH-HPS (1:1)] vs. OH-HPS lighting. The study showed greater vegetative biomass production when a 19:1 red:blue ratio was used, with increasing total irradiance resulting in greater growth. However, fruit yield was enhanced only when using 135 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at the 5:1 red:blue ratio. Results also showed that marketable fruit production was highest when plants were grown under hybrid lighting with LED-interlighting + OH-HPS (1:1).

Overhead SL with LEDs

Martineau et al. (2012) compared OH-HPS (wattage not reported) vs. OH-LED lamps [with 400-, 450-, 640-, and 735-nm peak wavelengths + cool white (no spectrum defined) LEDs] as SL sources for greenhouse lettuce production. They reported similar yield for both treatments even though plants grown under the OH-LEDs received about half of the average irradiance from SL that plants under the OH-HPS lamps received (35.8 vs. 71.3 mol m^{-2}, respectively, over 4 weeks). Energy savings of 34% were reported for the OH-LED SL treatment compared to OH-HPS. Later, Gajc-Wolska et al. (2013) compared several harvest and physiological parameters for greenhouse-grown tomatoes using 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of supplemental *PPF* from OH-LEDs (640-, 660-, and 450- nm-peak wavelengths) or OH-HPS (400 W) lamps vs. no SL. The authors reported that although both SL treatments improved production relative to unsupplemented controls, OH-HPS increased marketable yield and fruit number compared to OH-LED. Moreover, they found that most physiological responses were similar between plants grown under OH-LEDs or without SL. Another comparison of OH-HPS lamps vs. OH-LED lighting investigated the effects of dynamic lighting control (DLC) on energy consumption and yield of lettuce plants grown in a greenhouse (Pinho et al., 2013). The LED-DLC treatment consisted of warm-white (broad spectrum from 400 to 700 nm) LED lamps that automatically compensated for variations of daylight intensity below a defined threshold *PPF* at plant canopy level. The authors used an on-off switching algorithm in order to maintain a constant *PPF* of 150 $\mu mol \cdot m^{-2} \cdot s^{-1}$ during the lighting period when the available solar *PPF* was below that value. As a reference, two additional lighting treatments were used: OH-HPS (400 W) and OH-LED (broad spectrum from 400 to 700 nm) lamps. The latter were controlled using a conventional on-off regime based on outside solar irradiances. The use of LED-DLC reduced energy consumption by 20% and 52% compared to the OH-LED and OH-HPS treatments, respectively. However, plants grown under both LED treatments performed similarly in terms of average fresh mass accumulated per electrical energy unit consumed. Results indicated that further optimization of the DLC regimes are needed in order to reduce energy consumption without affecting plant yield.

Current status and challenges for LED-SL technologies

As indicated by studies evaluating effects of narrow-spectrum lighting on plant growth and development, as well as testing of LED technologies for greenhouse operations, LEDs seem to be a promising SL technology for greenhouse crop production. Nonetheless, significant opportunities remain to optimize spectral-quality effects on plant growth and development. Considerable genetic variability across species (and sometimes cultivars) exists for plant responses to different red:blue ratios, as well as to other wavelengths that may alter productivity and yield of greenhouse vegetables. In addition, studies of targeted lighting, changing spectral composition throughout crop life cycles, and photomorphogenic optimization of leaf-light interactions are areas for further inquiry to fully leverage the benefits of LEDs as SL sources.

With ongoing, anticipated energy-efficiency improvements, as well as ever-improving light-distribution architectures, LEDs could become the dominant future SL technology for greenhouse crop production, eventually replacing OH-HPS and hybrid lighting technologies. Nevertheless, extensive field trials are needed to establish economically viable ‘best practices’ for how to use LED lighting in greenhouse productions and in this way help encourage its wide-spread adoption for horticultural enterprises. This research aims to: 1) quantify growth responses during the propagation of different tomato cultivars across seasons under no SL vs. OH-HPS lighting vs. OH arrays of high-intensity LEDs (with different red and blue ratios); and to 2) quantify high-wire tomato production during different seasons with and without SL and to evaluate different lighting positions + sources (OH-HPS lamps vs. ICL-LEDs towers) for several production and energy-consumption parameters, as well as to differentiate physiological responses to the different light treatments. Results of these system comparisons, in addition to furthering scientific and practical understanding of the impact of LED lighting on plant growth and development for tomato, will facilitate the technology development that could allow the replacement of HPS lamps with LEDs.

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CHAPTER 2: GROWTH RESPONSES OF TOMATO SEEDLINGS TO DIFFERENT SPECTRA OF SUPPLEMENTAL LIGHTING

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Summary

Seedlings of six tomato (*Solanum lycopersicum*) cultivars (‘Maxifort’, ‘Komeett’, ‘Success’, ‘Felicity’, ‘Sheva Sheva’, and ‘Liberty’) were grown monthly for 2-week treatment periods to determine photomorphogenic and developmental responses to different light-quality treatments from supplemental lighting (SL) across changing solar daily light integrals (DLI). Seedlings were grown in a glass-glazed greenhouse at a mid-north latitude (lat. 40° N, long. 86° W) under one of five lighting treatments: natural solar light only (control), natural + SL from a 100-W high-pressure sodium (HPS) lamp, or natural + SL from arrays of red and blue light-emitting diodes (LEDs) using either 80% red + 20% blue, 95% red + 5% blue, or 100% red. Varying solar DLI occurred naturally for all treatments while constant DLI of 5.1 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ was provided for all SL treatments. Supplemental lighting increased hypocotyl diameter, epicotyl length, shoot dry weight, leaf number, and leaf expansion relative to control, whereas hypocotyl elongation decreased when SL was applied. For all cultivars tested, the combination of red and blue in SL typically increased growth of tomato seedlings. These results indicate that blue light in SL has potential to increase overall seedling growth compared to blue-deficient LED SL treatments in overcast, variable-DLI climates.

Introduction

Adequate growing conditions in greenhouses are crucial to ensure successful transplant production. A major limitation for tomato-seedling propagation is that peak demand can occur when mean solar DLI is lowest. Low DLI, which typically is due to a combination of short days and cloud cover, reduces the rate of seedling growth and thus extends the transplant-production period. The recommended DLI for tomato-seedling growth ranges from 13 to 16 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ (Fan et al., 2013; Moe et al., 2006). However, in a temperate, seasonally light-limited climate, sunlight rarely provides adequate DLI within greenhouses to produce high-quality seedlings when the propagation season begins (November, December, or April, depending on the cropping schedule). High-quality tomato seedlings should be uniform in size with well-developed leaves and roots; straight, short (12 to 13 cm in length), thick stems; and deep-green leaves (Jones, 2008; Lee et al., 2010). Nevertheless, quality requirements depend on the intended transplant use, as morphological preferences for scions, rootstocks, or non-grafted production seedlings are different (Chia and Kubota, 2010).

Supplemental lighting promotes growth of greenhouse-grown vegetable seedlings by increasing total DLI. High-pressure sodium lamps are the most widely used electric-light source for greenhouse SL during transplant production. In general, HPS lamps provide an orange-biased spectrum by primarily emitting light in the range of 565 to 700 nm. Nonetheless, it is widely accepted that any wavelength of light within the photosynthetically active radiation spectrum (*PAR*; 400-700 nm) contributes to photosynthesis and crop productivity (McCree, 1972). Thus, with their high-intensity capabilities, HPS lamps can deliver adequate supplemental DLI to support transplant production. However, over the past decade, interest has shifted toward alternative SL sources that can reduce production costs by decreasing electrical energy consumption while maintaining transplant quality. Because LED arrays typically have low power density ($kW \cdot m^{-2}$) and offer a diversity of narrow wavebands, LED lamps can be designed to provide specific light spectra to potentially optimize seedling growth and morphology while using less energy than conventional HPS lighting fixtures.

Several studies have evaluated LEDs for sole-source lighting of vegetable transplants including tomato (Fan et al., 2013; Liu et al., 2011; Nanya et al., 2012), pepper (*Capsicum annuum*) (Brown et al., 1995), cucumber (*Cucumis sativus*) (Hogewoning et al., 2010b; van Ieperen et al., 2012), eggplant (*Solanum melongena*) (Hirai et al., 2006), pea (*Pisum sativum*) (Wu et al., 2007), spinach (*Spinacea oleracea*) (Yorio et al., 2001), radish (*Raphanus sativus*) (Yorio et al., 2001), and lettuce (*Latuca sativa*) (Hoenecke et al., 1992; Kim et al., 2005; Massa et al., 2008). Findings from sole-source LED lighting research indicate that red light (600-700 nm) generally promotes fresh and dry weight gain, stem elongation, and leaf expansion (Heo et al., 2012; Johkan et al., 2010; Wu et al., 2007), whereas blue light (400-500 nm) affects morphological development and biomass production in species-specific and growth-environment-specific ways (Johkan et al., 2010; Kigel and Cosgrove, 1991; Savvides et al., 2012; Wang et al., 2009). Most studies using LEDs for sole-source lighting demonstrate the need to supplement monochromatic red LEDs with blue light to obtain acceptable growth and development (Cope and Bugbee, 2013; Goins et al., 1998; Hoenecke et al., 1992; Tripathy and Brown, 1995; Yorio et al., 1998). However, if LEDs are used to supplement sunlight, additional blue light may not be necessary because the broad solar spectrum contains significant amounts of blue light at midday, which may be sufficient for normal plant growth and development.

Other studies have evaluated LEDs as SL for greenhouse vegetable propagation (Gislerød et al., 2012; Hernández and Kubota, 2012; Hernández and Kubota, 2014a; Hernández and Kubota, 2014b; Hogewoning et al., 2012). Although general crop responses have not been broadly determined, one conclusion from those studies is that growth and morphological responses to LED SL are species-specific. Yet, potential cultivar-specific responses to light quality remain to be defined. The objective of the present study was to quantify growth responses of six tomato cultivars to different light-quality treatments from SL. We compared photomorphogenic and developmental responses to SL across changing solar DLIs at a mid-north latitude to reveal cultivar and/or spectral effects. Results are expected to provide baseline information to assist in designing SL protocols for propagating tomato seedlings intended for grafting or for direct transplanting into greenhouses or field production.

Materials and Methods

Plant material and growing conditions. Cultivars with different functional roles (i.e., rootstock or production seedlings intended for grafting or grow-out on own roots) and differing fruit size/shape were selected. Seeds of rootstock 'Maxifort' (*S. lycopersicum* × *S. habrochaites*, De Ruiter Seeds, Bergshenhoek, The Netherlands) and production cultivars 'Komeett' (De Ruiter Seeds; truss-type), 'Success' (De Ruiter Seeds; truss-type), 'Felicity' (Hazera Seeds, Haifa, Israel; cherry-type), 'Sheva Sheva' (Hazera Seeds; roma-type), and 'Liberty' (Hazera Seeds; beefsteak-type) were grown for 3 weeks from germination in a glass-glazed greenhouse in West Lafayette, IN (lat. 40° N, long. 86° W).

Seeds were sown into 17-cell seedling trays of Agrifoam soil-less plugs (5 × 2.5 cm; SteadyGROWpro; Syndicate Sales, Kokomo, IN) during the first week of each month in 2012. Once cotyledons had expanded fully (≈7 days from sowing), eight seedlings of each cultivar were selected for uniformity and placed randomly in each of five lighting treatments. Within each treatment, seedlings were randomly rotated daily to minimize location effects within the experimental area. Seedlings were irrigated as necessary with acidified water supplemented with a combination of two water-soluble fertilizers (3:1 mixture of 15N-2.2P-12.5K and 21N-2.2P-16.6K, respectively; The Scotts Co., Marysville, OH) to provide the following (in $mg \cdot L^{-1}$): 200 $N\text{-}NO_3$, 26 P, 163 K, 50 Ca, 20 Mg, and micronutrients. Average ambient day (from 0500 to 2100 HR) and night (from 2100 to 0500 HR) air temperature of the greenhouse were set at 27 and 15 °C, respectively. Air temperature and solar DLI were monitored using fine wire thermocouples (Type K, 0.1-mm diameter) and a quantum sensor (190 SB; LI-COR Biosciences, Lincoln, NE), respectively, interfaced to a datalogger (CR1000; Campbell Scientific, Logan, UT). Three thermocouples were used (one for each light source) and placed directly under a leaf (near-canopy air temperature) at the center of a given treatment. DLI data were collected at mid-plant height in the center of a treatment without SL. Measurements were made every 10 s and data were recorded at 10-min intervals.

Lighting treatments. Five lighting treatments were evaluated in the greenhouse: natural solar light only (control); natural + SL from a 100-W HPS lamp (Ceramalux, Philips Lighting Company, Somerset, NJ) emitting 13%, 49%, and 38% broadband blue, green (500-600 nm), and red light, respectively; or natural + SL from LEDs using either 80% red

+ 20% blue (80R-20B); 95% red + 5% blue (95R-5B); or 100% red (100R-0B). The red and blue LEDs used in the arrays had 627-nm and 450-nm peak wavelengths, respectively (as specified by the manufacturer). The spectral distribution of sunlight (at solar noon), for HPS lamps, and for the LED arrays are shown in Fig. 1. All SL treatments provided an average DLI of 5.1 $\mathrm{mol \cdot m^{-2} \cdot d^{-1}}$ (23-h photoperiod from 0000 to 2300 HR; 61 ± 2 $\mathrm{\mu mol \cdot m^{-2} \cdot s^{-1}}$) at mid-plant height [measured with a spectroradiometer (EPP-2000; StellarNet Inc., Tampa, FL)]. Light pollution from one treatment to another along the bench was minimized by allowing sufficient separation distance between treatments, delimited by $\leq 2\ \mathrm{\mu mol \cdot m^{-2} \cdot s^{-1}}$ from adjacent arrays. Scans of direct sunlight were recorded monthly at solar noon inside the greenhouse (not under SL) with a spectroradiometer. These measurements were collected on clear-sky and overcast days to calculate the average percentage of solar blue, green, and red light representative of each month.

LED source. Overhead LED arrays (Orbital Technologies Corporation, Madison, WI) were designed specifically for greenhouse transplant propagation. Each 1.2 m × 1.3 m array consisted of eight aluminum bars with alternating red and blue LEDs. Each red and blue bar had 28 or 24 LEDs, respectively, along their 1.2-m length. Arrays were air-cooled via hollow aluminum mounts and fans that drew greenhouse air into the center of each bar and exhausted waste heat from both ends. The 1.2-cm-wide bars were spaced 16-cm apart and oriented east to west. The sunlight-shading factor from the LED arrays and the HPS lamps was <10% at the bench surface.

Plant measurements. Growth parameters were measured 14 d after SL treatment initiation. Hypocotyl diameter was measured immediately below the cotyledons using an electronic digital caliper (DigiMax; Wiha, Schonach, Germany). Hypocotyl length and epicotyl length were measured using a ruler. Seedling shoots were then cut at the plug surface and leaf number (for leaves >1 cm in length) and total leaf area were recorded. Leaf area was measured using a leaf area meter (LI-3000A; LI-COR Biosciences). Shoot dry weight was measured after drying samples in a forced-air oven at 77 °C for 72 h.

Data analysis. The relationship between each response variable and the monthly average solar DLI (DLI_{ave}) was modeled with the GLIMMIX procedure of SAS (version 9.2; SAS Institute, Cary, NC) using a generalized linear mixed model with a Gaussian distribution and an identity link function. Analysis of the data was conducted using DLI_{ave}, treatment, cultivar, DLI_{ave} × cultivar, and treatment × cultivar as fixed factors, and DLI_{ave} × treatment and DLI_{ave} × treatment × cultivar as random factors to account for the split-plot structure of our experimental design (treatment was the whole plot factor and cultivar was the subplot factor). The treatment and cultivar main effect estimates describe the intercepts associated with the regression lines. The interaction effect estimates describe differences in slopes. All pairwise comparisons were completed using Tukey's honestly significant difference (HSD) test with a significance level of $\alpha = 0.05$. The appropriateness of these models were checked by examining the normality and constant variance of the residuals. Data collected in Feb. and May were excluded from this analysis because of lack of replication for some cultivars. The data from June were also not included in the analysis. An explanation for June's exclusion can be found in the "Results and Discussion" section.

Results and Discussion

Environmental conditions. Solar DLI and near-canopy air temperature measured inside the greenhouse during the experimental period are shown in Fig. 2. DLI_{ave} in Jun. was more than double the DLI_{ave} measured in Jul. (month within the analysis with the second highest DLI_{ave}; 29.3 vs. 13.3 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$, respectively) (Fig. 2A). Thus, data in Jun. were excluded from the statistical model as we chose not to draw inference in the large range of DLI_{ave} between Jun. and Jul. Nonetheless, the general growth responses recorded in Jun. indicate that somewhere between the range of DLI_{ave} from Jun. and Jul., seedling growth was saturated (data not shown). From the data used in the analysis, the average contribution of SL to total DLI ranged from 28% in Jul. to 79% in Dec. Similarly, the highest and lowest 24-h average near-canopy air temperatures were recorded in Jul. (26.5 °C) and Dec. (21.4 °C), respectively (Fig. 2B). The lack of differences among near-canopy air temperatures recorded under our three light sources (sunlight, HPS, and LEDs) suggests that temperature effects from SL were most likely negligible. However, the large month-to-month variability in air temperature (falling outside of set points) implies that any changes in plant growth measured during the different months were partly due to the effect of sunlight's short-wave radiation on greenhouse air temperature. Fig. 3 shows the average percentage of midday solar blue, green, and red light representative of each month and indicates that the relative percentages of broadband light quality from sunlight were relatively uniform across months ranging from 25% to 33% blue, 35% to 38% green, and 30% to 39% red light. Interestingly, although light intensity was lower in overcast compared clear-sky days, the relative percentages of broadband light quality at midday were nearly constant within months (data not shown).

Light quality effects on plant growth and morphology. We found a linear relationship between seedling growth and DLI_{ave} for all treatments measured in our study (Fig. 4). Test of fixed effects in statistical models indicated significant treatment differences (Table 1). Based on the mean associated with a regression line at the midpoint DLI_{ave}, we found that except for hypocotyl length, all SL treatments increased growth and development in tomato seedlings compared to control (Table 2). Seedlings grown under HPS, 95R-5B, or 80R-20B had similar growth but resulted in 18% thicker hypocotyls, up to 55% larger leaves, and up to 50% more shoot dry weight than to those grown under 100R-0B SL. Leaf number per seedling was instead greatest for those grown under 95R-5B (4.7 leaves) but was not different among HPS, 95R-5B, or 80R-20B SL.

To date, limited research has evaluated LEDs as SL sources for vegetable transplant production. Studies conducted in desert climates (i.e., Tucson, AZ) have shown that SL with red light only is sufficient to increase tomato or cucumber seedling growth (shoot dry weight, leaf count, or leaf area) relative to seedlings grown without SL (Hernández and Kubota, 2012; Hernández and Kubota, 2014a; Hernández and Kubota, 2014b). Our study indicated that, in general, 100R-0B was the least beneficial of the SL treatments for increasing seedling growth relative to unsupplemented controls (Table 2). The underlying cause of differences between our findings and those of Hernández and Kubota (2012; 2014a; 2014b) may be associated with differences in solar DLI during the experimental periods. Cope and Bugbee (2013) suggested that constant-high *PPF*s can partially substitute for low percentages of blue in the light spectrum. Therefore, different red:blue photon flux ratios from SL may not strongly affect vegetable-seedling growth in non-cloudy, high-insolation-rate environments that allow for relatively constant DLI backgrounds. However, in the present study, solar DLI fluctuated by up to 13.1 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ within an experimental period (Fig. 2). With high day-to-day fluctuations of solar DLI (leading to both high- and low-DLI environments), plant responses to spectral differences from SL were observed.

Our findings support studies showing enhanced morphological development of vegetable seedlings grown under sole-source lighting using a combination of red and blue light compared to monochromatic red light alone (Brown et al., 1995; Hogewoning et al., 2010b; Kim et al., 2005; Nanya et al., 2012; van Ieperen et al., 2012). A possible explanation for the similarities between our results and those of others using LEDs as sole-source lighting may be associated with the 23-h photoperiod used in the present study. When SL was extended past the natural photoperiod from sunlight, it was perceived by seedlings as sole-source lighting. Therefore, the growth responses measured in our study are most likely the result of an interaction between supplemental and sole-source light-quality plant responses.

It has been shown that during early vegetative growth, tomato seedlings respond positively to increases in total DLI by either increasing the *PPF* at leaf level (Bleasdale, 1973; Bruggink, 1987; McAvoy and Janes, 1990) or by extending the photoperiod (up to 24-h of light) (Calvert, 1959; Demers et al. 1998; Omura et al., 2001; Sysoeva et al., 2012). Because the average intensity of SL was a limiting factor in our study, we used a 23-h photoperiod to maximize the DLI delivered from SL aiming to approach a target total DLI of 16 mol·m^{-2}·d^{-1}. Although physiological injuries (chlorosis or necrosis) caused by long photoperiods (≥16 h) have been reported for vegetative, mature, and reproductive tomato plants (Arthur et al., 1936; Cushman and Tibbitts, 1998; Demers et al., 1998; Dorais et al., 1996; Globig et al., 1997; Withrow and Withrow, 1949), fewer studies have shown such effects on juvenile tomato seedlings (Hillman, 1956). Moreover, it has been proposed that, when long photoperiods have no negative effect on plant growth, then prolonged lighting at lower intensities is a better approach to supplement sunlight than are higher light intensities of shorter duration (Hurd and Thornly, 1974; Moe, 1997). Furthermore, diurnal temperature fluctuations ≥8 °C between day and night air temperatures prevent chlorosis in species otherwise adversely affected by long photoperiods *per se* (Cao and Tibbitts, 1992; Demers and Gosselin, 2002; Hillman, 1956; Matsuda et al., 2012; Matsuda et al., 2014; Murage and Masuda, 1997; Ohyama et al., 2005a; Ohyama et al., 2005b; Omura et al., 2001; Tibbitts et al., 1990). In our study, damage to early vegetative growth was further prevented (no visual damage was observed) by combining a long SL photoperiod (used to maximize DLI) with a 16/8-h day/night thermoperiod of pronounced temperature differential (>10 °C).

Hypocotyls of seedlings grown without SL elongated up to 1 cm more than those grown under SL (Table 2). Further, the 100R-0B SL treatment produced the second longest hypocotyls (2.3 cm). In contrast, epicotyl length was unaffected by SL treatment, but epicotyls of seedlings grown without SL were at least 1.8 cm shorter than those of seedlings grown under SL. Hypocotyl elongation of tomato seedlings is known to respond to photomorphogenic cues (Ballaré et al., 1995; Blom et al., 1995; Kasperbauer and Peaslee, 1973; Volmaro et al., 1998) and reflects the sub-terranean growth of seedlings in nature before they break crust during the germination process, whereas epicotyls, which support active photosynthetic leaves, are affected by both photomorphogenic and photosynthetic cues. Thus, the general decrease in hypocotyl elongation and increase in epicotyl length in response to SL could be attributed to the perception of antagonistic signals received by different photoreceptors present in hypocotyl and epicotyl tissues.

Some variability in hypocotyl length between seedlings grown under SL treatments and those without SL could have been the result of different end-of-day (EOD) light quality sensed by phytochrome photoreceptors, which are known to affect hypocotyl elongation (Blom et al., 1995; Kasperbauer and Peaslee, 1973). Seedlings grown under SL received a significant percentage of EOD-red light caused by LED or HPS emission spectra at and beyond sunset (Fig. 1). Although SL-grown plants experienced natural day length, it was overlaid with low-level supplemental DLI and, thus, SL reduced the natural EOD-far-red light effect from sunlight. In contrast, controls received only sunlight and, consequently, far-red-enriched EOD light. A high red:far-red EOD spectrum is known to produce short, compact transplants (Chia and Kubota, 2010; Decoteau and Friend, 1991; Lund et al., 2007) and, thus, may explain the general trend for the shorter hypocotyls of SL-grown seedlings.

Our study also showed that 80R-20B SL produced more compact hypocotyls compared to those of seedlings grown under 100R-0B (2.0 vs. 2.3 cm, respectively) (Table 2). Several growth-chamber studies using sole-source LED lighting have reported blue-light-mediated inhibition of hypocotyl elongation for tomato (Nanya et al., 2012), pepper, (Brown et al., 1995), cucumber (Shinkle and Jones, 1988), sunflower (*Helianthus annuus*) (Cosgrove and Green, 1981), pea (Kigel and Cosgrove, 1991), and lettuce (Dougher and Bugbee, 2001; Hoenecke et al., 1992), which likely are mediated by the blue-light photoreceptors cryptochrome and/or phototropin (Ballaré et al., 1995; Volmaro et al., 1998). In contrast, it has been noted that 100% red or 100% blue SL in the greenhouse caused similar hypocotyl elongation of tomato seedlings, but 100% blue SL caused taller, thinner hypocotyls for cucumber seedlings compared to 100% red (Hernández, 2013). Our findings suggest that increasing proportions of blue in SL can reduce hypocotyl elongation in tomato. Longer hypocotyls typically are desired for rootstock cultivars because they allow for ease of grafting and decrease the risk of scion exposure to soil/substrate surfaces. However, hypocotyl elongation is not a desired characteristic for non-grafted production seedlings, as it may lead to weak transplants (Jones, 2008).

Although not statistically significant, for five of the six growth parameters measured in our study, 95R-5B tended to promote more growth than did 80R-20B SL (Fig. 4; Table 2). This indicates that there likely is a threshold above which blue light increases tomato seedling development before it starts acting antagonistically towards growth. Numerous studies have shown that increasing blue light can reduce stem length and leaf area and increase leaf mass area for different crop species (Cope and Bugbee, 2013; Hogewoning et al., 2010a; Hogewoning et al., 2010b; Li and Kubota, 2009; Trowborst et al., 2010). However, the extent to which blue-light affects plant growth and development is not yet fully understood. Research by Dougher and Bugbee (2001) and Cope and Bugbee (2013) has sought to determine whether certain growth parameters are better predicted by either absolute ($\mu mol \cdot m^{-2} \cdot s^{-1}$ of blue photons) or relative (percentage of total *PPF*) blue light. From their findings, it is apparent that blue light responses are species-dependent, and that growth inhibition by blue light could depend on the total intensity of light and/or the relative distribution of light quality. Further research evaluating different red:blue photon flux ratios to identify specific thresholds to optimize growth for different cultivars and species of greenhouse-grown vegetable seedlings would be of interest.

Cultivar main effects. Of particular interest to growers are the species- and cultivar-specific responses to LED SL. Studies have shown that some plant responses to greenhouse SL are species- and cultivar-specific (Gunnlaugsson and Adalsteinsson, 2006; Hernández, 2013; Hernández and Kubota, 2014a; Hogewoning et al., 2012). Yet, the lack of treatment × cultivar interaction found in our study suggests that, although genetic variation was apparent among cultivars, their response to a given SL treatment was similar (Table 1).

All cultivars showed a linear relationship between seedling growth and DLI_{ave} (data not shown). Based on the mean associated with a regression line at the midpoint DLI_{ave}, we found that hypocotyl diameter for ‘Komeett’ and ‘Success’ was 12% thicker than for ‘Felicity’ and ‘Sheva Sheva’ but similar to ‘Liberty’ and ‘Maxifort’ (Table 3). ‘Komeett’ produced the longest hypocotyls whereas hypocotyl length for ‘Felicity’ was 0.4 cm shorter than that for ‘Liberty’ or ‘Sheva Sheva’. Epicotyls of ‘Success’ and ‘Felicity’ were 15% and 20% shorter than those of ‘Maxifort’, respectively. ‘Maxifort’ also produced more and larger leaves than any other cultivar, and its shoot dry weight was 25% higher than that of ‘Felicity’. However, occurrence of intumescence was observed in ‘Maxifort’ leaves throughout the experiment, most likely due to a lack of ultraviolet-B radiation in the greenhouse (Craver et al., 2014).

The greater growth (epicotyl length, leaf count, leaf area, and shoot dry weight) measured for ‘Maxifort’ relative to the other production cultivars can be attributed to its vigorous growth pattern (De Ruiter Seeds, unpublished data). Nonetheless, because ‘Maxifort’ is a rootstock cultivar strictly used for grafting, leaf-growth responses are considered less important than those for stem morphology, especially hypocotyl length and diameter. In contrast, leaf growth and development are critical growth responses for production cultivars, as they set precedence for the development of active photosynthetic leaves. We found that all production cultivars had similar leaf-growth responses.

Conclusion

For all tomato cultivars evaluated, a combination of red and blue wavebands in SL has potential to increase seedling growth compared to blue-deficient SL treatments in overcast, variable-DLI climates. As indicated by studies evaluating effects of narrow-spectrum lighting on plant growth and development, as well as testing of LED technologies for greenhouse operations, LEDs are a promising SL technology for propagating greenhouse crops. Nonetheless, significant opportunities remain to optimize spectral-quality effects on plant growth and development. Considerable genetic variability across species (and sometimes cultivars) exists for plant responses to different red:blue photon flux ratios, as well as to other wavelengths that may alter seedling morphology. In addition, studies of targeted lighting, changing spectral composition throughout crop life cycles, and photomorphogenic optimization of leaf-light interactions are areas for further inquiry to fully leverage the benefits of LEDs as SL sources.

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Table 1. Significance level for the test of fixed effects in linear mixed models evaluating several growth parameters measured for tomato seedlings propagated in a glass-glazed greenhouse in West Lafayette, IN under different lighting treatments. [z,y]

Fixed effect	Hypocotyl diameter	Hypocotyl length	Epicotyl length	Leaf No.	Leaf area	Shoot dry weight
	Probability > F[x]					
DLI[w]	NS	***	***	*	***	**
Treatment	***	***	***	***	***	***
Cultivar[v]	***	**	***	***	***	**
DLI × Cultivar	NS	NS	NS	NS	NS	NS
Treatment × Cultivar	NS	NS	NS	NS	NS	NS

[z] The treatments evaluated were natural solar light only (control); natural + supplemental lighting (SL) from a high-pressure sodium lamp; or natural + SL from light-emitting diodes using either 80% red + 20% blue; 95% red + 5% blue; or 100% red light.

[y] The experiment was conducted every month in 2012. Data from Feb., May, and Jun. was not included in the model.

[x] *P* values from *F* tests.

[w] DLI = daily light integral.

[v] The cultivars evaluated were 'Maxifort', 'Komeett', 'Success', 'Felicity', 'Sheva Sheva', and 'Liberty'.

***, **, *, NS indicate statistical significance at the 0.001, 0.01, and 0.05 $P \leq$ level and not significant, respectively

Table 2. Least squares means for several growth parameters measured for tomato seedlings propagated in a glass-glazed greenhouse in West Lafayette, IN under different lighting treatments.^{z,y,x}

Treatment	Hypocotyl diameter (mm)	Hypocotyl length (cm)	Epicotyl length (cm)	Leaf No.	Leaf area (cm^2)	Shoot dry weight (g)
Control	1.6 c^w	3.0 a	3.1 b	2.7 c	21.4 c	0.06 c
HPS	2.8 a	2.1 bc	5.4 a	4.3 b	59.4 a	0.18 a
100% R - 0% B	2.3 b	2.3 b	4.9 a	4.2 b	41.0 b	0.12 b
95% R - 5% B	2.8 a	2.1 bc	5.6 a	4.7 a	63.4 a	0.17 a
80% R - 20% B	2.8 a	2.0 c	5.0 a	4.3 b	58.1 a	0.16 a

[z] The treatments evaluated were natural solar light only (control); natural + supplemental light [SL; 5.1 $mol \cdot m^{-2} \cdot d^{-1}$ (23-h photoperiod from 0000 to 2300 HR; 61 ± 2 $\mu mol \cdot m^{-2} \cdot s^{-1}$)] from a high-pressure sodium (HPS) lamp, or natural + SL from light-emitting diodes using different red (R) and blue (B) percentages.

[y] The experiment was conducted once every month in 2012. Data from Feb., May, and Jun. were not included in the statistical model.

[x] Data represent a pooled average for cultivars ‘Maxifort’, ‘Komeett’, ‘Success’, ‘Felicity’, ‘Sheva Sheva’, and ‘Liberty’.

[w] Means within columns followed by the same letter are not different based Tukey’s honestly significant difference test at $P \leq 0.05$.

Table 3. Least squares means for several growth parameters measured on different cultivars of tomato seedlings propagated in a glass-glazed greenhouse in West Lafayette, IN.[z,y]

Cultivar	Hypocotyl diameter (mm)	Hypocotyl length (cm)	Epicotyl length (cm)	Leaf No.	Leaf area (cm^2)	Shoot dry weight (g)
‘Maxifort’	2.5 ab[x]	2.2 bc	5.4 a	4.7 a	62.5 a	0.15 a
‘Felicity’	2.3 b	2.0 c	4.6 b	4.1 b	43.1 b	0.12 b
‘Komeett’	2.6 a	2.7 a	4.9 ab	3.7 c	43.3 b	0.14 ab
‘Liberty’	2.5 ab	2.4 b	4.9 ab	3.9 bc	48.4 b	0.13 ab
‘Sheva Sheva’	2.3 b	2.4 b	4.8 ab	3.9 bc	45.2 b	0.13 ab
‘Success’	2.6 a	2.2 bc	4.3 b	3.7 c	49.5 b	0.14 ab

[z] The experiment was conducted once every month in 2012. Data represent a pooled average for all months except Feb., May, and Jun.

[y] Data represent a pooled average for seedlings grown under natural solar light only (control); natural + supplemental light (SL) from a high-pressure sodium lamp, and natural + SL from light-emitting diodes using different red and blue percentages.

[x] Means within columns followed by the same letter are not different based Tukey’s honestly significant difference test at $P \leq 0.05$.

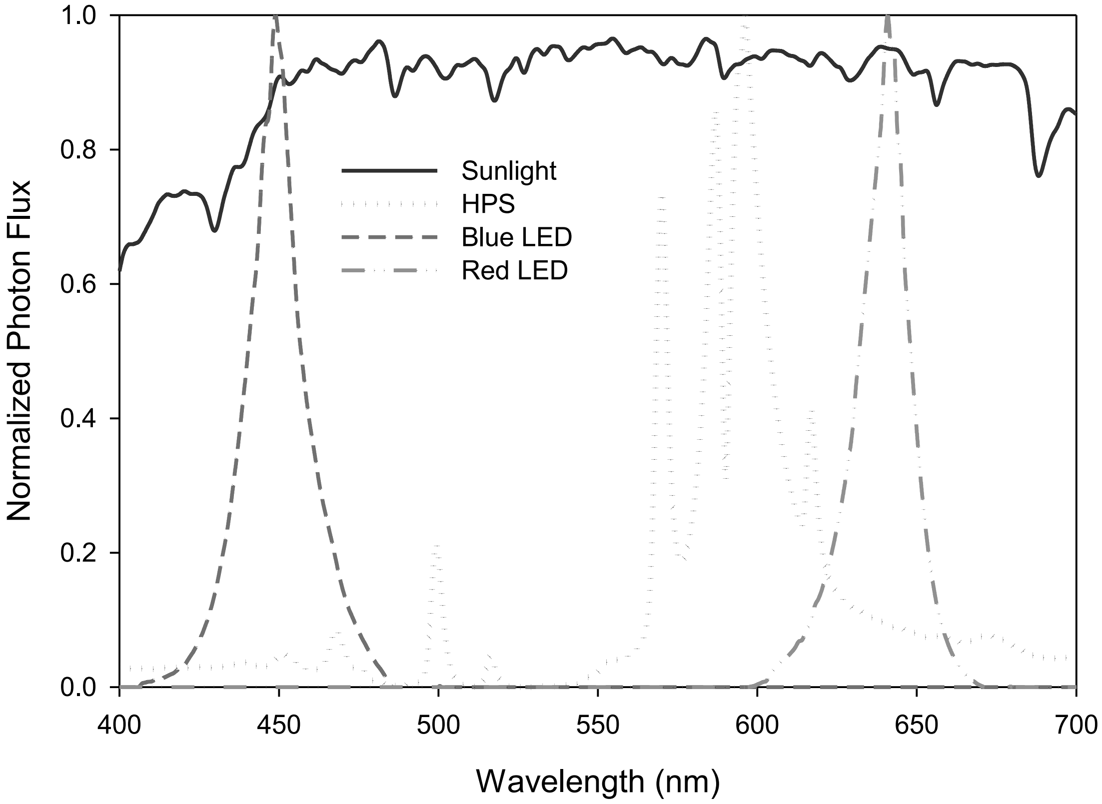

Figure 1. Spectral distribution of sunlight (at solar noon), high-pressure sodium (HPS) lamps, or arrays with blue and red-light-emitting diodes (LED).

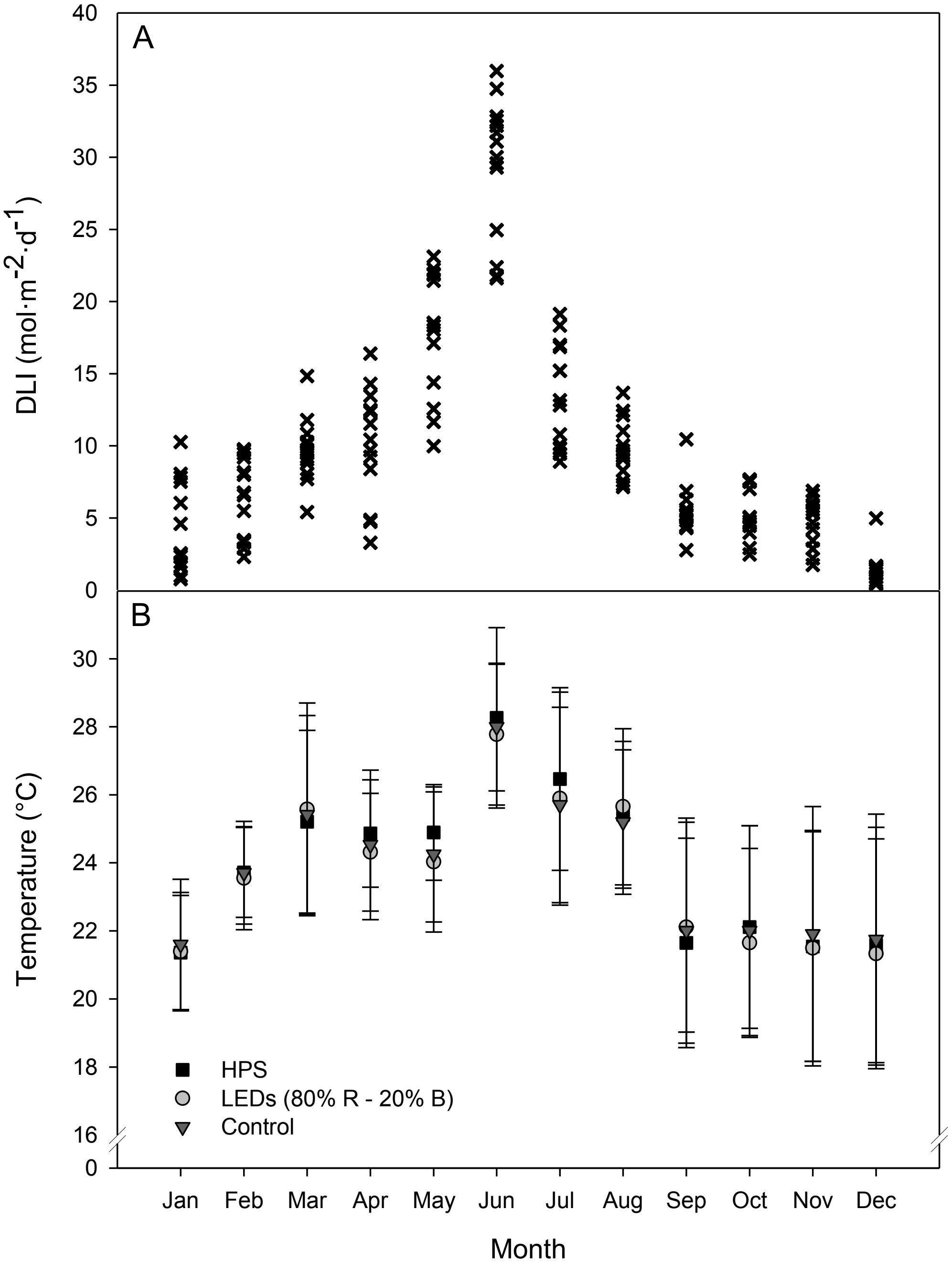

Figure 2. Daily light integral (DLI) (A) and near-canopy air temperature (± SD) (B) measured inside a glass-glazed greenhouse in West Lafayette, IN during the experimental dates in 2012. DLI data were collected at mid-plant height under no supplemental lighting. Temperature data represent the average 24-h near-canopy air temperature measured under each light source: HPS = High-pressure sodium lamps; LEDs = arrays of light-emitting diodes (R = red light; B = blue light); control = sunlight.

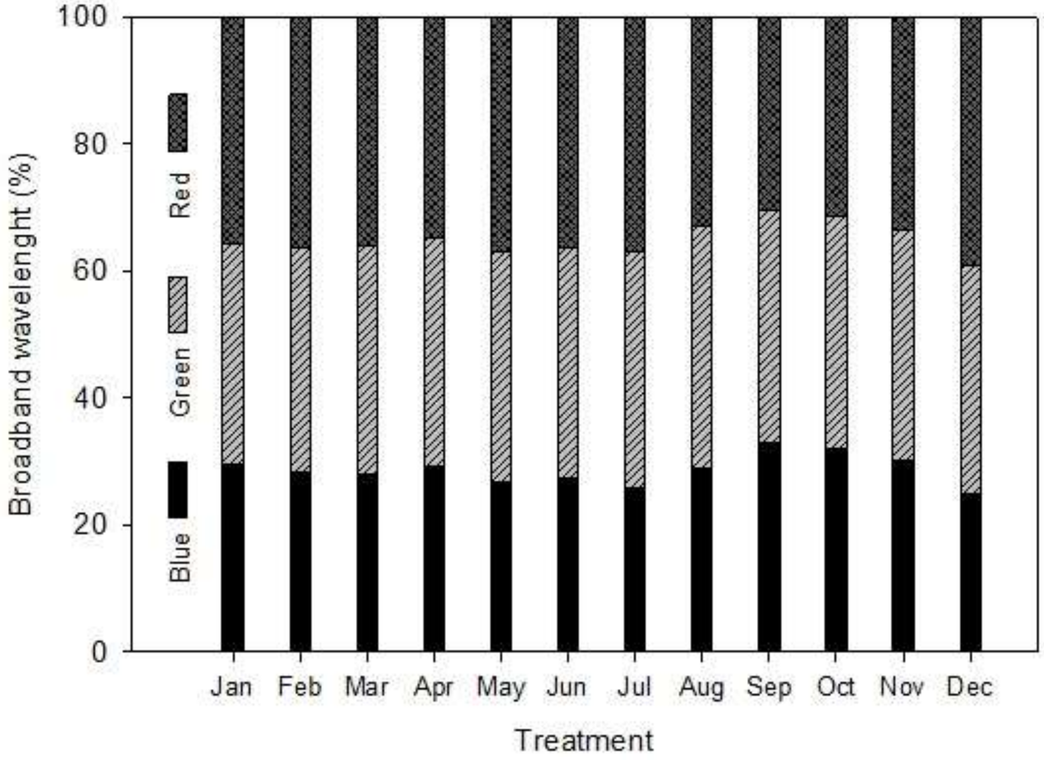

Figure 3. Percentage of broadband blue (400-500 nm), green (500-600 nm), and red (600-700 nm) light calculated from the photosynthetic photon flux measured at solar noon inside a glass-glazed greenhouse in West Lafayette, IN in 2012. Spectral scans were collected during the experimental period at bench height. Data represent an average of at least two scans per month on clear-sky and overcast days.

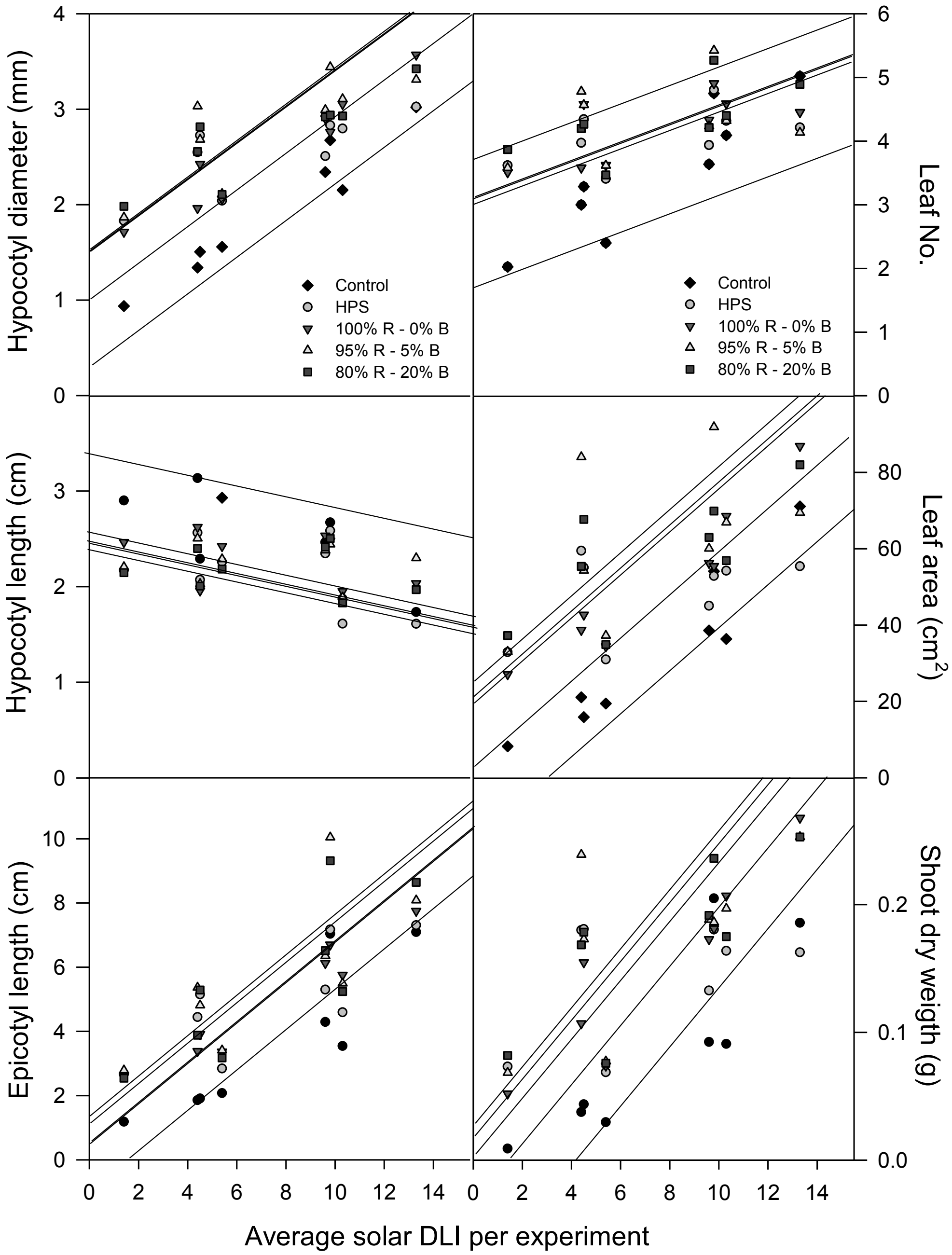

Figure 4. Effect solar daily light integral (DLI) on several growth parameters measured for tomato seedlings propagated in a glass-glazed greenhouse in West Lafayette, IN under different lighting treatments. The treatments evaluated were natural solar light only (control); natural + supplemental light [SL; 5.1 mol·m–2·d–1 (23-h photoperiod from 0000 to 2300 HR; 61 ± 2 µmol·m–2·s–1)] from a high-pressure sodium (HPS) lamp, or natural + SL from light-emitting diodes using different red (R) and blue (B) percentages. Each data point represents the average of 48 seedlings with all measurements taken 14 days after treatment initiation.

CHAPTER 3. GREENHOUSE-GROWN TOMATOES AS AFFECTED BY DIFFERENT SUPPLEMENTAL LIGHTING SOURCES AND POSITIONS WITHIN THE CANOPY: PLANT GROWTH, FRUIT YIELD, AND ENERGY CONSUMPTION

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HortTechnology 23:93–98.

Summary

Overhead (OH) high-pressure sodium (HPS) lamps are the present preferred type of supplemental lighting (SL) for greenhouse vegetable production because their high-intensity capability allows them to deliver significant supplemental photosynthetically active radiation (*PAR*). Furthermore, OH-HPS lamps currently are the most economically viable mass-produced light source available for greenhouse SL that provide adequate *PAR*. Light-emitting diodes (LEDs) are a promising SL technology for greenhouse crop production because they offer an opportunity to improve energy efficiency for greenhouse lighting. We conducted four experiments in a glass-glazed greenhouse during 2012 and 2013. The objective was to quantify growth and yield of winter-to-summer [increasing natural daily light integral (DLI)] and summer-to-winter (decreasing natural DLI) high-wire tomato (*Solanum lycopersicum* L.) production in a temperate climate (lat. 40° N, long. 86° W) with and without (control) SL. We evaluated two different SL positions + sources

[OH-HPS vs. intracanopy (ICL; lighting from within the canopy)-LED] and compared those to a control for several production and energy-consumption parameters. Even though minor improvements were made between experiments, general productivity and yield trends remained consistent. Neither the number nor total mass of fruit were different between OH-HPS and ICL-LED treatments, and generally, both SL treatments yielded more fruit and had more fruit mass than did controls. The electrical conversion efficiency of ICL-LED energy into fruit biomass was higher than that of OH-HPS, and energy savings ranged from 28% to 50% for ICL-LED relative to OH-HPS SL. These results suggest that, with ongoing, anticipated energy-efficiency improvements, as well as ever-improving light-distribution architectures, LEDs could become the dominant future SL technology for greenhouse crop production, eventually replacing OH-HPS. Significant opportunities remain to optimize spectral-quality effects on plant growth and development. Extensive trials are needed to establish economically viable 'best practices' for how to use LED lighting in greenhouse production and to further promote its wide-spread adoption.

Introduction

Tomato is considered a high-light-requiring crop, and an average daily light integral (DLI) of 20-35 $mol \cdot m^{-2} \cdot d^{-1}$ is generally recommended for optimal growth and production (Dorais, 2003; Faust, 2001; Jones, 2008; Moe et al., 2006; Spaargaren, 2001). However, in a temperate, seasonally light-limited climate, sunlight rarely provides adequate DLI within greenhouses to sustain year-round tomato production. Traditionally, greenhouse crop production has relied on the use of overhead (OH) high-pressure sodium (HPS) lamps for supplemental lighting (SL) because they are the most widely used and currently the most economically viable mass-produced electric-light source available for SL. Furthermore, HPS lamps are up to 30% efficient at converting electricity into useful light, and the remaining 'waste' thermal energy can be used to increase ambient greenhouse and plant temperature to offset winter heating costs (Tiwari, 2003). However, alternative SL sources are being evaluated to reduce production costs by decreasing electrical energy consumption while maintaining yield and quality. Light-emitting diodes (LEDs) can be used to improve energy efficiency in greenhouse SL because their relative coolness (low radiant heat output) allows them to be operated in close proximity to plant tissue, thereby increasing available irradiance at leaf level while using less input power than HPS lamps.

Overhead vs. Interlighting/intracanopy lighting (ICL)

Overhead lighting tends to favor upper leaf layers by maximizing light interception incident at the top of the foliar canopy. This results in unequal light distribution where the middle and lower leaf canopies are shaded and, thus, light limited (Frantz et al., 2000). Some of the first attempts to evaluate LEDs as SL sources for greenhouse-vegetable production focused on their relative coolness, which allows for greater flexibility in lamp placement and resulting light distribution. This is especially beneficial for high-wire-cropping systems such as greenhouse tomato, cucumber (*Cucumis sativus* L.), sweet pepper (*Capsicum annuum* L.), and eggplant (*Solanum melongena* L.), where plants are trained vertically along support wires, thereby creating conditions conducive to shading of middle and lower leaves by upper leaves, and potentially row-to-row shading, depending on lamp-mounting pattern and row direction. For such high-wire crops, shaded leaves within a canopy could potentially benefit from ICL or interlighting. For the purpose of this chapter, we will use the terms ‘ICL’ and ‘interlighting’ interchangeably, referring to the strategy of lighting along the side or within the foliar canopy.

Intracanopy lighting helps increase the efficiency of irradiation by allowing direct light into the inner canopy of crop stands. It has been reported that ICL can serve as a sole source of irradiation in growth chambers for crops like cowpea (Vigna unguiculata (L.) Walp.) (Frantz et al., 2000; Massa et al., 2005) and soybean (Glycine max L.) (Stasiak et al., 1998) and as SL for field-grown soybean (Johnston et al., 1969). Several studies have evaluated interlighting for greenhouse production of cut-back roses (*Rosa* spp.) (Carpenter and Rodrigues, 1971), tomatoes, (Grimstad, 1987; Gunnlaugsson and Adalsteinsson, 2006; Lu et al., 2012a; Rodriguez and Lambeth, 1975), sweet pepper (Grodzinski et al., 1999; Hovi-Pekkanen et al., 2006), and cucumber (Heuvelink et al., 2006; Hovi et al., 2004; Hovi-Pekkanen and Tahvonen, 2008). However, all of these greenhouse studies used either fluorescent, microwave-powered, or HPS lamps. More recently, studies have evaluated partial (hybrid = OH + ICL) or total LED interlighting on yield of high-wire greenhouse-grown cucumber (Hao et al., 2012; Trouwborst et al., 2010), tomato (Deram et al., 2014; Dueck et al., 2012; Lu et al., 2012b), and sweet pepper (Jokinen et al., 2012).

Our research approach to promote profitable, quality, local greenhouse-tomato production in temperate climates considers reducing production costs by decreasing energy consumption for SL. Replacing HPS lamps with high-intensity LEDs could potentially reduce electrical costs by providing photosynthetic photon flux (*PPF*) at lower canopy level using less input power and energy. Nevertheless, being an emergent lighting technology, extensive trials evaluating LEDs are required to determine economic feasibility, lamp placement within foliar canopies, and appropriate spectral quality for optimum crop productivity. In order to address crucial aspects to further develop LED technology for greenhouse-tomato production, four consecutive experiments evaluating growth, yield, and energy consumption from winter-to-summer (increasing natural DLI; Expt. 1 and 3) or summer-to-winter (decreasing natural DLI; Expt. 2 and 4) were conducted in a temperate, seasonal climate. The experiments aimed to evaluate crop responses to SL using two different lighting positions + light sources (OH-HPS vs. ICL-LED).

Materials and Methods

Expt.1

Plant materials and growing conditions. Tomato rootstock 'Maxifort' (*Solanum lycopersicum* × *S. habrochaites*; De Ruiter Seeds, Columbus, OH) and scions 'Komeett' (De Ruiter Seeds) and 'Success' (De Ruiter Seeds) were sown into 17-cell seedling trays of Agrifoam soil-less plugs (5 × 2.5 cm; SteadyGROWpro; Syndicate Sales, Kokomo, IN) on 27 Dec. 2011 and placed in a glass-glazed greenhouse in West Lafayette, IN (lat. 40° N, long. 86° W; USDA hardiness zone 5b) oriented east-to-west, with 3.7-m gutter height and 6.7-m peak height. The greenhouse has a floor area of 111 m^2, is equipped with pad-and-fan evaporative cooling system and radiant hot water pipe heating.

Once the cotyledons had expanded fully, SL of an average of 60 $\mu mol \cdot m^{-2} \cdot s^{-1}$ from a 100-W HPS lamp (Ceramalux, Philips Lighting Company, Somerset, NJ) was provided daily for 18 h. All seedlings were irrigated as necessary with acidified water supplemented with a combination of two water-soluble fertilizers (3:1 mixture of 15N-2.2P-12.5K and 21N-2.2P-16.6K, respectively; The Scotts Co., Marysville, OH) to provide the following (in $mg \cdot L^{-1}$): 200 N-NO_3, 26 P, 163 K, 50 Ca, 20 Mg, and micronutrients. Scions cut from seedlings were grafted onto rootstocks on 11 Jan. 2012 and allowed to heal. On 25 Jan. 2012, grafted seedlings were randomly selected for each lighting treatment and transplanted into rooting blocks (4 × 4 × 2.5 cm; SteadyGROWpro; Syndicate Sales), which were then placed into wetted coir slabs (90 × 15 × 8 cm; Coco Agro Ltd., Veyangoda, Sri Lanka). Slabs were placed on top of custom-made steel gutters (9.8 m × 25 cm; FormFlex Horticultural Systems, Ontario, Canada). Following transplant, plants were pinched at the axillary bud to induce double-heading at a density of 2.3 stems/m^2 in the production system. Plants were irrigated daily throughout the 5-month experiment with a commercial complete fertilizer mix (4.5N-14P-34K; CropKing, Lodi, OH) providing a 30% leaching fraction (LF). Irrigation frequency was adjusted as necessary depending on the LF. Water was treated with 93% sulfuric acid (Brenntag, Reading, PA) at 0.08 mL·L^{-1} to reduce alkalinity to 100 mL·L^{-1} and a pH range of 6.0 to 6.2. Electrical conductivity (EC) and pH of the influx and efflux were measured daily with a hand-held EC and pH meter (Hanna Instruments, Woonsocket, RI) to ensure values were maintained within recommended ranges (2.5-3.5 dS·m^{-1} and 5.8-6.3 for EC and pH, respectively) (Jones, 2008). Average ambient day and night temperatures of the greenhouse were set at 27 °C and 18 °C, respectively.

Lighting treatments. The greenhouse floor area was divided into six half-row sections (3.7 × 4.9 m) of different treatments running in an east-to-west direction (Figure 5). Each section was separated by one layer of 6-mil (0.15 mm)-thick black polyethylene plastic between two layers of white plastic (curtains) hanging from the upper frame of the greenhouse structure (≈3.6 m from the top to the floor). The plastic curtains were used to prevent light pollution between treatments and hung parallel to the rows. Short sections of plastic curtain hung perpendicular at the halfway point of each row separating different lighting treatments. Each half-row section was one replicate of a treatment lighting eight double-headed, grafted treatment plants (four ‘Komeett'/‘Maxifort’ and four ‘Success’/‘Maxifort’) and one non-grafted, double-headed non-treatment plant at each section border (guard plant).

The SL treatments were started on 28 Jan. 2012. Supplemental lighting was kept at an average DLI of 9 $mol \cdot m^{-2} \cdot d^{-1}$ from either 1000-W OH-HPS lamps (Lumalux/ECO; Osram Sylvania Ltd., Danvers, MA) or ICL-LED towers (Orbital Technologies Corporation, Madison, WI) programmed to mix 95% red (627 nm peak wavelength) and 5% blue (450 nm peak wavelength) light (Figure 6). Each 2.5-m-tall LED tower supported three rectangular, vertically movable 0.60 × 0.12 m LED zones that were separately controlled (Figure 7). Each rectangular LED zone has opposite lighting panels for irradiation in both directions within a row, each containing four red and one blue, dimmable LED strips with 12 LEDs mounted vertically within each strip. Towers were air-cooled via hollow internal tubes and fans that drew greenhouse air into the center of each tower and exhausted heat either above the canopy (during the cooling season) or below the canopy (during the heating season). A control treatment also was included for which no SL was provided.

Before starting the experiment, a light map was developed (after sunset) at three heights in the greenhouse to determine the maximum *PPF* for each lamp type. The measured heights corresponded to the center of each vertical LED panel in a tower. Measurements were taken in the space where a plant would be. Because of differences in light distribution and direction from the lamps, a global *PPF* was used to represent the *PPF* around a given point. Global *PPF*s were determined by calculating the sum of four measurements taken from rotating the sensor four times at 90° (the base point directly facing the lamp) and dividing by two (Frantz et al., 1998). The output of supplemental *PPF* was calibrated to be equivalent for both SL-treatments using a line quantum meter (MQ-303; Apogee Instruments, Inc., Logan, UT) calibrated against a spectroradiometer (EPP-2000; StellarNet Inc., Tampa, FL).

Kilowatt-hours (kWh) of energy consumed were monitored using a built-in datalogger in every LED tower, and an energy monitor (e2 classic 2.0; Efergy U.S.A., Miami, FL) was used for groups of four HPS lamps. Removal of lower leaves and plant leaning and lowering was conducted as needed. Fruits were pruned to four per cluster (to maintain fruit grade/size uniformity) and were harvested weekly when the last fruit within a cluster was at maturation stage 6, based on the USDA Visual Aid TM-L-1 tomato color standards. Fruit fresh weight (FW) and fruit number were recorded immediately following harvest. Number of flowers (at anthesis) and fruit number per plant were recorded weekly (from week 9 through 13) for all plants. Upon experiment termination (28 Jun. 2012), number of nodes per plant was recorded.

Expt. 2

Seeds of ‘Komeett’ and ‘Success’ were sown on 20 Jun. 2012. Plants were grown under conditions identical to Expt. 1 with the following exceptions: (1) Ambient day and night greenhouse temperature set points were kept at 25 °C and 15 °C, respectively. (2) Plants were grown as side-by-side non-grafted, single-headed seedlings rather than as grafted, double-headed plants. (3) 1000 W-HPS lamps were replaced with 600-W HPS

(HS2000; P.L. Lights, Beamsville, Ontario, Canada) lamps. (4) SL photoperiod was modified monthly to complement seasonal changes in solar DLI aiming for a target total DLI of 25 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$. Average DLI values (at plant height) from SL were 8.8, 10.0, 13.8, 16.5, and 16.5 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ for Aug., Sept., Oct., Nov., and Dec., respectively (after Korczynski et al., 2002; assuming 50% solar light transmission into the greenhouse). (5) Movable rather than stationary curtains were used to minimize solar blockage during the daytime (withdrawn when lamps were off). (6) Due to high solar DLI and ambient temperature at the beginning of the experiment, SL treatments were initiated on 16 Aug. and, thus, used only during the last 4 months of the experiment. The experiment was terminated 15 Dec, 2012.

Expt. 3

Seeds of ‘Komeett’ and ‘Rebelski’ (De Ruiter Seeds) were sown on 27 Dec. 2013. Plants were grown under conditions identical to Expt. 2 with the following exceptions: (1) Rockwool slabs (100 × 15 × 7.5 cm; Grodan Vital, Roermond, The Netherlands) were used instead of coconut coir. (2) Eight 100 W incandescent (INC) bulbs (Ace Soft White; Ace Hardware Corp., Oak Brook, IL) were used in the control treatment during the first 90 days of the experiment. This was done to support photoperiodic control within the treatment, not as a means to provide SL. (3) SL treatments were initiated on 28 Jan. and provided an average DLI (at plant height) of 10.8, 13.0, 8.8, 3.8, and 3.8 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ for Feb., Mar., Apr., May, and Jun., respectively. (4) No record was kept for weekly plant growth. The experiment was terminated 24 Jun., 2013.

Expt. 4

Seeds of ‘Komeett’ were sown on 19 Jun. 2013. Plants were grown under conditions identical to Expt. 3 with the following exceptions: (1) Rockwool slabs were replaced with coconut coir slabs (100 × 15 × 10 cm; Riococo 200, Ceyhinz Link International Inc., Dallas/Fort Worth Metroplex of Texas, TX). (2) No INC bulbs were used in control treatments. (3) SL treatments were initiated on 14 Aug. and provided an average DLI (at plant height) of 8.8, 10.0, 13.8, 18.8, and 18.8 $mol \cdot m^{-2} \cdot d^{-1}$ for Aug., Sept., Oct., Nov., and Dec., respectively. The experiment was terminated 16 Dec., 2013.

Experimental design and statistical analysis. For each experiment, data were analyzed as a randomized complete block design and were subject to analysis of variance (ANOVA) and the general lineal model procedure of SAS (version 9.2; SAS Institute, Cary, NC). For Expt. 1-3, the tomato cultivars responded similarly to the lighting treatments, so data were pooled and averaged across cultivars.

Results

Solar DLI measured inside our greenhouse in 2012 indicated that at 40° N latitude and 86° W longitude, SL was required for most of the year to achieve a target DLI of 25 $mol \cdot m^{-2} \cdot d^{-1}$, with low-solar DLI months requiring more SL than high-solar DLI months (Figure 8). The complete record of solar DLI measured inside the experimental greenhouse in 2013 was partly compromised due to a short circuit in the datalogger. However, from records of a plastic polyhouse in close proximity, as well as periodic measurements recorded in our specific greenhouse zone, we know that solar DLI in 2013 was higher than that in 2012, suggesting a lower SL requirement for optimal plant growth in 2013 compared to 2012.

Crop responses. Supplemental lighting induced early fruit production compared to unsupplemented controls during Expt. 1 (24 d earlier for OH-HPS and 22 d earlier for ICL-LED) (Table 4), allowing for a longer harvest period. However, no treatment differences were observed for harvest duration during Expt. 2, 3, and 4. Fruit number and total fruit FW increased in response to SL during Expt. 1, 2, and 4. Moreover, except for cluster weight in Expt. 2 and node number in Expt. 3, there were no differences between the two SL treatments for any of the harvest parameters measured across experiments. Interestingly, there were no significant differences in fruit yield (fruit number or fruit FW) between controls and either SL treatments in Expt. 3.

Seasonal variations also were apparent for weekly plant growth. In Expt. 1, both SL treatments promoted flower and fruit formation equally relative to the control (Figure 9). However, except for week 12, Expt. 2 indicated no differences in flower or fruit number among treatments. Nonetheless, the trend observed for fruit number in Expt. 2, as well as the significant differences in overall yield, suggest that as solar DLI declined seasonally, SL supported normal fruit set relative to unsupplemented controls. Also, in Expt. 1, leaves of plants grown under no SL were significantly longer than those grown under ICL-LED and OH-HPS (Figure 10). However, differences among treatments for leaf length were only apparent after week 11 during Expt. 2, corresponding with the seasonal decline of solar DLI.

Energy consumption. Figure 11 illustrates the energy used by both SL treatments during each experimental period; the different trends among Expt. 1 and Expt. 2-4 reflect the different approaches to provide SL: Expt. 1 had a constant SL DLI of 9 mol·m^{-2}·d^{-1}, whereas Expt. 2-4 had variable month-to-month SL DLI. The high energy consumed by the OH-HPS treatment during the first ≈50 days of treatment during Expt. 1 and Expt. 2 was due to longer photoperiods required to achieve target DLI at the top of the short crop stand. Once plants grew and reached the top height of our measured light map (≈2.2 m above the floor), the average photoperiod was kept constant to achieve target DLI. In general for Expt. 2 and Expt. 4, kWh per day of energy consumed from OH-HPS lamps increased as solar DLI decreased. Nonetheless, kWh per day for the ICL-LED treatment declined close to the experiment termination, even if solar DLI was low. This is explained by the ability to turn off the bottom panels of the ICL-LED towers as plants were defoliated and fruit clusters harvested from the bottom up, thereby saving additional energy by not lighting where photosynthetic tissue was no longer present. For all experiments, average energy consumption by the OH-HPS treatment was significantly higher than that by the ICL-LED treatment. The differences in energy consumption between Expt. 1 vs. Expt. 2-4 from OH-HPS were due, in part, to the different lamp wattage used to conduct the experiments (1000 W vs. 600 W OH-HPS lamps, respectively).

The ICL-LED SL technology resulted in energy savings relative to OH-HPS lighting across seasons (Table 5). Average daily energy consumption for the OH-HPS treatment (2 reps × 4 lamps) during Expt. 1-4 were 129, 86, 70, and 95 kWh per day, respectively; which were significantly higher than the average 31, 39, 19, and 25 kWh per day consumed by the ICL-LED treatment (2 reps × 4 towers). The electrical conversion efficiency of ICL-LED energy into fruit biomass was higher than that of OH-HPS, and energy savings ranged from 55% to 76% for ICL-LED relative to OH-HPS SL. An alternative approach to compare energy efficiency between the two SL treatments was based on calculating the theoretical energy consumption for the OH-HPS treatment. Following guidelines from a greenhouse engineering manual (Aldrich and Bartok, 1994), we calculated the electric energy usage for commercial greenhouse-tomato production using OH-HPS lighting; we then downscaled the results to correspond to our experimental area (Table 6). According to this comparison, electric savings from ICL-LED SL technology ranged from 9% to 45% in Expt. 1-4.

Discussion

A photon is a photon. While it is widely accepted that any wavelength of light within the photosynthetically active radiation spectrum (*PAR*; 400-700 nm) contributes to photosynthesis and crop productivity (McCree, 1972), the relative quantum efficiency curve, which weights the quantum yield (moles of carbon fixed per moles of photons absorbed) for each wavelength of light, indicates that broadband blue (400 to 500 nm) and red (600 to 700 nm) light are the most efficient wavelengths for driving photosynthesis and potentially promoting plant growth (Inada, 1976; McCree, 1972). Thus, as an approach to capitalize from their high relative quantum efficiency, most research using LEDs for SL have used blue and red LEDs. However, other studies have shown that for SL, light intensity (*PPF*) has a much larger effect on plant growth and productivity than light quality (Cope et al., 2014; Johkan et al., 2012). Therefore, optimal plant growth can be achieved with any wavelength of light within *PAR* if an adequate *PPF* is provided or optimal DLI is achieved (Dueck et al., 2007; McAvoy and Janes, 1990).

In our study, the similarities in overall plant growth and yield between the two SL treatments found within experiments could be the result of plants growing under the same *PPF* across the vertical plane of the high-wire crop stand. Plants under SL grew under an average *PPF* of 240, 229, 179, and 144 $\mu mol \cdot m^{-2} \cdot s^{-1}$ during Expt. 1, 2, 3, and 4, respectively, in addition to the natural DLI received from sunlight. These average SL intensities were dictated by the *PPF* measured (after sunset) from the OH-HPS treatment at three heights (bottom, middle, and top) within the vertical plane of the experimental area; the ICL-LED treatment was set to correspond to the *PPF* delivered from OH-HPS SL. Potentially, by increasing SL *PPF* at the middle- and bottom-height of a high-wire crop stand, or by maintaining a constant *PPF* along the vertical plane, crop productivity would increase by not having that dramatic decrease in *PPF* from the top to the bottom of the canopy. Future experiments should compare different light intensities along the vertical plane of a high-wire crop to determine if selectively lighting different portions of the vertical crop stand affects plant growth and productivity.

Can high-solar DLI trump SL for greenhouse tomato production? Due to high solar DLI and ambient temperature at the beginning of both summer-to-winter experiments, SL treatments were used only during the last 4 months of each experiment. The similarities among treatments for harvest duration in Expt. 2 and 4 are likely due to flowering being already induced by the time SL started and thus, fruit harvest was not delayed from the lack of SL (Table 4).

The unexpected outcome for Expt. 3, where control treatments resulted in similar yields to supplemented treatments, could be attributed to one or a combination of the following:

1) An atypical high solar DLI during late winter in 2013 compared to 2012: In Expt. 3, more days were recorded when solar DLI was above our target *PPF* (25 $mol\cdot m^{-2}\cdot d^{-1}$) than in Expt. 1 (Figure 8). Thus, the similarities among all treatments in Expt. 3 could be explained by the high solar DLI, which most likely contributed to most of the light energy required for optimal plant production. Additionally, because it is widely accepted that growth benefits from SL in greenhouse tomato production are greatest during low-ambient DLI (Dorais and Gosselin, 2002), the highest increase in fruit yield from SL during Expt. 1 compared to Expt. 3 could be the result of the lower solar DLI during the late winter in 2012.

2) Addition of far-red (700 to 770 nm) light: Although the contribution to total DLI from INC photoperiodic lighting was minor (<0.5 $mol\cdot m^{-2}\cdot d^{-1}$), there was a noticeable increase in stem elongation (visual observation) for control treatments compared to previous-year controls. This observation is most likely a response to the far-red component of INC supplementation, which affects the phytochrome photoreceptor, known to mediate morphological and physiological plant responses (Briggs and Olney, 2001). The ratio of phytochrome in the physiologically active far-red-absorbing state (Pfr) to total phytochrome [Pfr + phytochrome in the inactive red-absorbing state (Pr)] influences the magnitude of the shade-avoidance response in sun-plants, like tomato, and has been shown to affect stem elongation (Kasperbauer, 1987; Thomas and Vince-Prue, 1997). Longer stems could potentially minimize mutual shading within high-wire crop stands as they would allow for light to penetrate deeper into the foliar canopy and prevent shading of lower leaves by upper leaves.

Because of this outcome, INC supplementation was not provided to control treatments during the subsequent summer-to-winter experiment of 2013 (Expt. 4). However, further research should explore the effects of photomorphogenic responses to far-red light in high-wire tomato production, as well as interactions between photomorphogenic- and photosynthetic-dependent reactions affecting plant growth. This is especially important because photoreceptors and physiological plant responses are greatly responsive to both light intensity and quality (Blom et al., 1995; Franklin, 2005).

3) Control plants behaving as shade-adapted plants during the early phase of the winter-to-summer experiments: Figure 9 showed that for Expt. 1, leaves developing under no SL expanded more than those under either SL treatment. Moreover, although not measured for Expt. 3, there was a noticeable increase in leaf expansion for control treatments compared to previous-year controls (visual observation). Shade- and light-adapted plants have morphological and biochemical differences associated with specific functions, among which thinner, larger leaves are characteristic of shade-adapted plants, as it allows for better light capture and absorption (Ehleringer and Sandquist, 2010). Control plants grown during our winter-to-summer experiments most likely adapted to the sub-optimal light intensities and developed as shade plants.

If the combination of supplemental far-red light and a shade-plant-type of adaptation (due to the lack of SL) can induce plant photomorphogenic responses that positively affect fruit yield (i.e., increased stem length to prevent mutual shading of lower leaves by upper leaves or increased leaf area to capture more light), far-red supplementation using LEDs could potentially be an effective way to promote plant growth and fruit yield using less input power than supplemental photosynthetic lighting. Then again, it might be that results from Expt. 3 are just a response to the unusually high solar DLI measured in the late winter of 2013.

Think of ICL as precision lighting. Improvements in production efficiency using ICL as sole-source lighting are supported by Frantz et al. (1998), who reported that cowpea grown with ICL yielded 50% of the edible biomass of plants grown under OH lighting while consuming only 10% as much electrical energy. Massa et al. (2005) also reported higher electrical-use efficiency and inner-canopy leaf retention for intracanopy-grown cowpea compared to OH-lighted plants grown in a growth chamber. Although we found no increase in yield using ICL SL, our results showed significant energy savings without compromising fruit yield. The energy savings in our study can be accounted for by the ICL-LED towers consuming less input power than OH-HPS lamps. Furthermore, the ability to provide focused lighting with LEDs allowed for additional energy savings when we selectively switched the panels on/off, depending on presence of photosynthetic leaf tissue. With OH lighting, lamps are traditionally mounted at a fixed height that maximizes light distribution and uniformity at a given height within the greenhouse. However, when plants are young and widely spaced, energy is wasted when OH photons fall on empty space; when foliar canopies close, then photons coming from above are excluded from the inner canopy and mutual shading can occur. Using OH-HPS lighting, upper-canopy photon capture efficiency can be maximized for mature crops grown in large greenhouses with narrow aisles, yet focused lighting with ICL can increase canopy capture rates to near 100% (Nelson and Bugbee, 2014). Nonetheless, focused radiation also makes it challenging for ICL to create uniform light distribution in large open areas. In greenhouses, SL selection should primarily be based on the cost to deliver photons to the plant canopy surface and on potential benefits from increasing productivity or affecting plant growth and/or morphology.

Do we need hybrid lighting? Most research using ICL as SL has evaluated ICL as hybrid lighting. Fewer studies have used ICL lighting alone *per se* (Deram et al., 2014; Grimstad, 1987; Jokinen et al., 2012; Lu et al., 2012a; Lu et al., 2012b). Hybrid lighting has been shown to positively affect plant growth when compared to OH SL by improving light-use efficiency within greenhouse crops (yield per electric energy consumption of lighting), increasing fruit yield (size, weight, and/or number) and percentage of first-class fruit, and extending post-harvest shelf life, among others (Gunnlaugsson and Adalsteinsson; 2006; Hovi et al., 2004; Hovi-Pekkanen et al., 2006; Hovi-Pekkanen and Tahvonen, 2008; Pettersen et al., 2010). However, most studies reporting increases in crop yield with hybrid lighting have used HPS lamps mounted OH and within the canopy (as with ICL). In contrast, other studies comparing hybrid SL with OH-HPS lamps + ICL-fluorescent or -LED lamps to OH-HPS lighting have shown either negative (Heuvelink et al., 2006), minimal (Hao et al., 2012) or no significant increase in fruit yield from hybrid lighting (Deram et al., 2014; Dueck et al., 2012; Trouwborst et al., 2010). It is likely that the increase in fruit yield when using 100% HPS-hybrid lighting is, in part, the result of the additional thermal energy irradiated by ICL-HPS, which could have accelerated fruit maturation and, thus, reduced time to harvest. Nonetheless, using high-wattage HPS lamps for ICL is not feasible for commercial applications because the separation distance required to prevent tissue scorching from the heat load of HPS lamps would reduce plant density and, consequently, decrease total yield. Conversely, if ICL does not irradiate much heat, as in the case of LED lamps, or, to a lesser extent, fluorescent tubes, hybrid lighting may not increase yield for greenhouse-grown crops.

Our study showed that when using ICL-LED SL with high-output, actively heat sinked LEDs, hybrid lighting is not required to maintain yields similar to those obtained with OH-HPS lighting. This conclusion is in agreement with Deram et al. (2014), who compared different light intensities and red-to-blue ratios from ICL-LED vs. hybrid lighting [ICL-LED:OH-HPS (1:1)] vs. OH-HPS lighting for greenhouse tomato production. They reported a significant increase in fruit yield and vegetative biomass production with ICL-LED compared to OH-HPS or hybrid lighting but found that marketable fruit production (fruits ≥ 90 g) was only increased when plants were grown under hybrid lighting.

Comparing energy savings. We used two approaches to compare energy savings between the two SL treatments: 1) calculating the electric cost per plant using data recorded in our experiments (Table 5); and 2) comparing the theoretical energy consumption by OH-HPS to data recorded for the ICL-LED treatments (Table 6). Both comparisons showed energy savings from ICL-LED SL technology compared to OH-HPS SL. Nonetheless, the second approach is considered a more legitimate comparison because it takes into account the lamp density required to achieve desired light intensities for optimal greenhouse production. It also considers an ideal fixture spacing to optimize uniform light distribution within the production area. Moreover, calculations are based on the specific photon emission rate ($\mu mol \cdot m^{-2} \cdot s^{-1} \cdot lamp^{-1}$) for the OH-HPS lamps that were used in our experiments. However, some consideration regarding the different lamp types is needed when comparing both systems: the ICL-LED towers are research-grade prototypes specifically designed for ‘proof of concept’ studies, not for commercial applications, and were built with relatively inefficient fans, controllers, and power supplies (M. Bourget, personal communication, 2013). Additionally, features like dimming capability and self-monitoring of energy consumption may not be required for commercial prototypes. In contrast, the OH-HPS lamps used in our study are commercially available and their fixtures (lamp, luminaire, and ballast) are designed to be energy efficient and cost-effective. Based on our second approach to compare energy savings between the two SL treatments (after Aldrich and Bartok, 1994), between 9% and 45% of the energy consumed by OH-HPS was saved with ICL-LED SL in Expt. 1-4 (Table 6). However, if the inefficiencies inherent with the ICL-LED towers are not considered, and results are based solely on the kWh of electricity consumed by the LEDs for the duration of the experiments, electric savings from the ICL-LEDs relative to the theoretical energy consumed by OH-HPS lighting ranged from 31% up to 67% in Expt. 1-4.

A bright future for greenhouse SL. Electric savings from LED SL technologies are expected to increase in the near future, as improvements in power supplies and luminous efficiencies in conjunction with decreasing operating costs of LEDs are occurring rapidly. Haitz and Tsao (2011) projected that the luminous flux per lamps for LEDs would increase 20x in a decade. Thus, LED SL remains to be a promising technology for which advances in innovative designs to improve light distribution and energy efficiency will occur. Nonetheless, improvements in other lighting technologies for plant growth are also occurring rapidly. As of 2014, HPS fixtures with electronic ballasts and double-ended lamps are 1.7x more efficient than commonly used mogul-base HPS fixtures, like the ones used in our study (Nelson and Bugbee, 2014). Furthermore, efficiency improvements for OH lighting are being made by optimizing luminaire architectures to maximize light distribution under a specific growing area. For high-wire crops, OH lighting with additional green light also could be of particular interest, as green light penetrates deeper into the foliar canopy than other wavelengths and thus, overhead lighting could potentially support the photosynthetic activity of lower leaves (Kim et al., 2004; Lu et al., 2012b). Other SL alternatives that promise to increase yields or reduce production costs in commercial greenhouses include, but are not limited to, induction lighting, sulfur lamps, and plasma lamps, among others. However, as with LEDs, research evaluating these technologies is needed to help discover any opportunities and/or limitations associated with them.

Of particular interest to growers is the species- and cultivar-specific response of plants to LED SL. Although the tomato cultivars evaluated in our study responded similarly to the lighting treatments, other studies have shown that some plant responses to greenhouse SL are species- and cultivar-specific (Gunnlaugsson and Adalsteinsson; 2006; Hernández, 2013). Thus, it is likely that not all plants will respond the same to LED SL. Further research evaluating growth and productivity for several commercially-relevant greenhouse-vegetable cultivars grown under LED SL is needed. Furthermore, research should evaluate different hues and color ratios to determine if supplemental light quality can optimize production or promote improvements in fruit quality and/or plant morphology. This is especially important for LED SL because there seem to be seasonally changing plant sensitivities to SL spectrum in the presence of a changing solar background (see Chapter 2 for more information). Moreover, the optimal light spectrum for plant growth and development likely changes with plant age and could result in the need for specific crop life-cycle spectral requirements within a species or cultivar (Cope and Bugbee, 2013).

Today. Currently, the most efficient HPS and LED fixtures have equal efficiencies, but the initial capital cost per photon delivered from LED fixtures is five to ten times higher than that for HPS (Nelson and Bugbee, 2014). Moreover, most commercially available LED fixtures tend to have limited spectral choices, fixed-color ratios, low output intensities, and are not specifically designed to maximize light-distribution within greenhouses. Additionally, commercial LED fixtures tend to be passively heat sinked (no active heat dissipation; conductive and convective heat is exchanged with the surrounding air), which limits the density of LEDs that can be used per fixture and thus, reduce the maximum light intensity from a given fixture. Manufacturers need to improve existing LED SL technologies to offer products with improved reliability and lower capital costs.

Conclusions

Although our results suggest that the ICL-LED technology supports similar yields compared to conventional OH-HPS lighting but at lower electrical costs, the use of ICL-LED technology needs further development. Our experiments establish proof of concept that LEDs can be used successfully for SL in greenhouse tomato production. However, further research needs to be conducted evaluating different light-distribution architectures, lamp densities, and spectral composition. Further research will determine wavelength efficacies at different stages of crop development to achieve optimal productivity. Results of this technology comparison and experiment, in addition to furthering scientific and practical understanding of the impact of LED lighting on plant growth and development for tomato, also demonstrate that ICL-LED SL is a viable alternative to OH-HPS. Additional research is needed to demonstrate the applicability of this technology to produce other greenhouse crops.

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Table 4. Harvest and growth parameters per plant for tomatoes grown in a greenhouse under one of three lighting treatments during two winter-to-summer (Expt. 1 and 3) and two summer-to-winter (Expt. 2 and 4) production cycles in 2012 and 2013.z

Treatments[y]	Harvest period (d)	Nodes (No.)	Fruit harvested (No.)	Cluster weight (g)	Total fruit FW (g)[x]
Expt. 1					
OH-HPS	68 a[w]	46 a	97 a	537 a	14159 a
ICL-LED	66 a	45 a	94 a	542 a	13406 a
Control	44 b	35 b	67 b	496 b	9067 b
Exp. 2					
OH-HPS	76 a	49 ab	125 a	523 b	14281 a
ICL-LED	75 a	51 a	136 a	556 a	15236 a
Control	77 a	48 b	96 b	366 c	9361 b
Expt. 3					
OH-HPS	57 a	53 a	105 a	691 a	17182 a
ICL-LED	57 a	50 b	106 a	663 a	16593 a
Control	52 a	49 b	97 a	629 b	14965 a
Exp. 4					
OH-HPS	84 a	-	133 a	572 a	15855 a
ICL-LED	83 a	-	132 a	573 a	15835 a
Control	81 a	-	106 b	472 b	11723 b

[z] Plants were two-headed in Expt. 1. For all other experiments, values represent results for two side-by-side plants. Data were pooled and averaged across two cultivars in Expts. 1-3.

[y] OH-HPS= overhead high-pressure sodium; ICL-LED = intracanopy light-emitting diodes.

[x] FW = fresh weight.

[w] Means within Expt. and within columns followed by the same letter are not significantly different based on the least significant difference test ($P \leq 0.05$).

Table 5. Electrical energy consumption, operating cost (in US dollars), and yield parameters for tomatoes grown for 5 months in a greenhouse under one of three lighting treatments.[z]

Crop parameters	Winter-to-summer			Summer-to-winter		
	Control	OH-HPS	ICL-LED	Control	OH-HPS	ICL-LED
2012						
Total energy consumption (kWh)	-	19578	4697	-	10062	4542
Energy consumption per plant (kWh)	-	1224	294	-	629	284
Total fruit FW per plant (g)[y]	9067.10	14159.30	13406.00	9361	142801	152356
Energy consumption per fruit FW (kWh/g)	-	0.09	0.02	-	0.004	0.002
Cost of electricity ($/kWh)	-	0.05	0.05	-	0.05	0.05
Cost of electricity ($/g of fruit)	-	0.004	0.001	-	0.0002	0.0001
Average fruit weight (g)	136.00	144.90	142.04	102	121	121
Lighting cost ($/fruit)	-	0.63	0.16	-	0.03	0.01
Lighting cost ($/plant)		61.18	14.68		31.44	14.19
2013						
Total energy consumption (kWh)	-	10307	2832	-	11553	4179
Energy consumption per plant (kWh)	-	644	177	-	722	261
Total fruit FW per plant (g)	14965	17182	16593	11723	15855	15835
Energy consumption per fruit FW (kWh/g)	-	0.04	0.01	-	0.05	0.02
Cost of electricity ($/kWh)	-	0.05	0.05	-	0.05	0.05
Cost of electricity ($/g of fruit)	-	0.002	0.001	-	0.002	0.001
Average fruit weight (g)	154	163	157	120	131	133
Lighting cost ($/fruit)	-	0.31	0.08	-	0.30	0.11
Lighting cost ($/plant)		32.2	8.9		36.1	13.1

[z] OH-HPS= overhead high-pressure sodium; ICL-LED = intracanopy light-emitting diodes; [y] FW = fresh weight. 1g = 0.0353 oz.

[v] Average electrical energy cost for the state of Indiana during 2012.

[t] Means within columns followed by the same letter are not significantly different based on the least significant difference test (*P* ≤ 0.05).

Table 6. Comparison of electrical energy consumption between overhead high-pressure sodium (OH-HPS) lamps and intracanopy light-emitting diode (ICL-LED) towers for the production of high-wire tomatoes grown in a greenhouse during two winter-to-summer (Expt. 1 and 3) and two summer-to-winter (Expt. 2 and 4) growing seasons in 2012 and 2013.

Code	Parameters affecting energy consumption	Experiment			
		1	2	3	4
	Energy consumed by OH-HPS				
A	Fixture power draw (W)^{z}	1100	660	660	660
B	Target photosynthetic photon flux at crop height (µmol·m^{-2}·s^{-1})	309	279	266	255
C	Commercial surface area (bay area; m2)	1125	1125	1125	1125
D	Photon emission rate (µmol·m^{-2}·s^{-1}·lamp^{-1})^{y}	1925	1045	1045	1045
	Fixture efficiency (A/D; µmol·m^{-2}·s^{-1}·W)	1.8	1.6	1.6	1.6
E	Fixtures needed per bay area (B×C/D; no.)	181	300	286	275
	Fixture density (E/C; no. fixtures·m^{-2})	0.16	0.27	0.25	0.24
F	Input power density (E×A/C; W·m^{-2})	177	176	168	161
G	Experimental growing area (m^{2})	18	18	18	18
H	Input power density for experimental area (F×G; W·m^{-2} of experimental area)	3178	3172	3024	2899
I	Hours of fixture operation (no.)	1628	2013	1711	1799
J	Theoretical energy use (H×I/1000; kWh·experimental area·experiment duration)^{x}	5173	6385	5174	5215
	Energy consumed by ICL-LEDs^{w}				
	Hours of fixture operation (no.)	1628	2013	1711	1799
K	Total energy consumed (throughout experiment)	4685	4574	2835	4179
L	Energy consumed by fans and controller (kWh)^{v}	1095	1354	1151	1210
M	Energy consumed by LEDs (K-L; kWh)	3591	3220	1684	2969
N	ICL-LED electric savings compared to OH-HPS ([100-(K×100)/J]; %)	9	28	45	20
O	ICL-LED electric savings compared to OH-HPS w/o fans and controllers ([100-(M×100)/J]; %)	31	50	67	43

[z] Includes power draw by the light bulb wattage + additional 10% from the ballast.
[y] Obtained from the manufacturer.
[x] Calculated after Aldrich and Bartok (1994), Greenhouse Engineering, NRAES-33.
[w] Total power draw by one ICL-LED at full power = 1240 W, out of which 567 W are drawn by the LEDs and 673 W by the power supply, controller, and fans required to run the system.
[v] Power drawn by power supply, controller, and fans (673 W) × hours of fixture operation/1000.

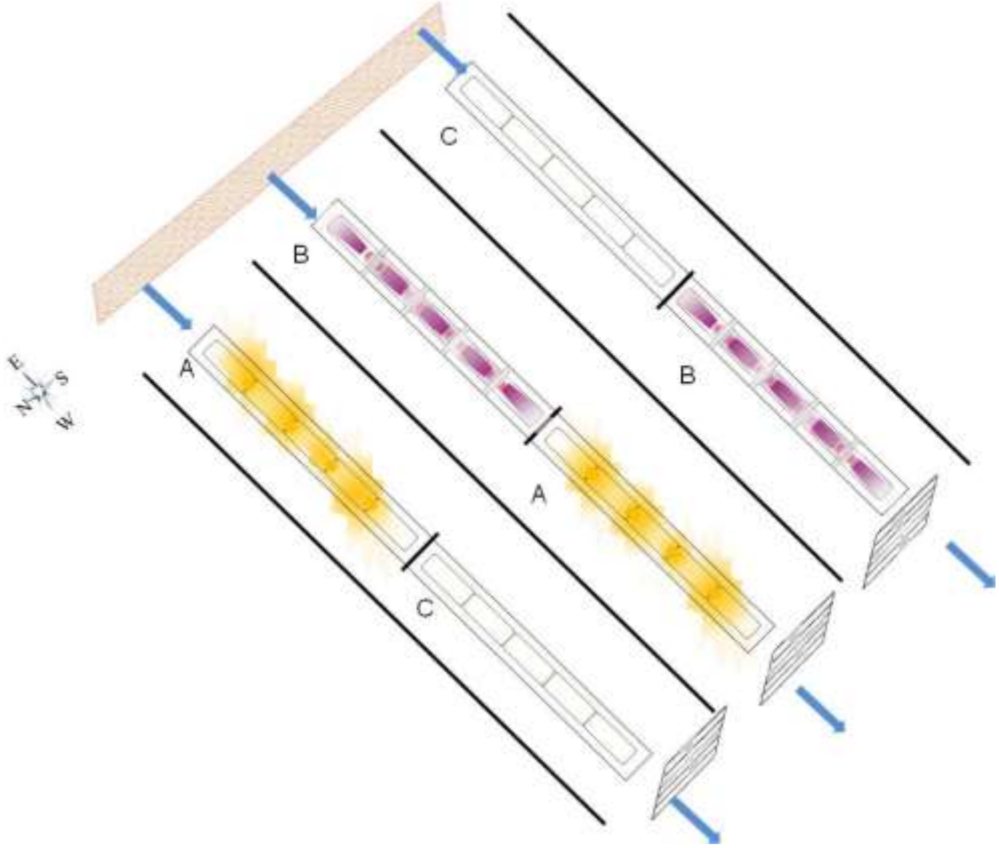

Figure 5. Schematic representation of the experimental greenhouse showing six half-row sections of different lighting treatments running in an east-to-west direction. Each section was separated by a white plastic curtain (bold black lines) hanging from the upper frame of the greenhouse structure and running the entire length of the rows. Short sections of plastic curtain hung perpendicular at the halfway point of each row separating different lighting treatments. Each half-row section represents one replicate of a treatment lighting eight double-headed, grafted treatment plants (four 'Komeett'/'Maxifort' and four 'Success'/'Maxifort') and one non-grafted, double-headed non-treatment plant at each section border (guard plant). The lighting treatments included A) four 1000-W high-pressure sodium lamps emitting yellow light from above, B) four Intracanopy LED towers emitting purple light in both directions along the row, and C) control treatments receiving no supplemental lighting.

Figure 6. Schematic representation of an intracanopy light-emitting diode (LED) tower indicating row-straddling supports, three vertically movable LED panels on each side within a row, and room at the top of the mount to move all three LED panels up by one panel equivalent. Power supply, individual panel switches, and dimming controls for each color of LED are located on the lower right.

Figure 7. (A) Two intracanopy light-emitting diode (LED) towers providing two-way SL with two tomato plants growing between towers. Note that the upper panel was switched off because most of the plants had not yet reached the height of the panel. (B) Side view of a half-row section with plants growing in the LED treatment.

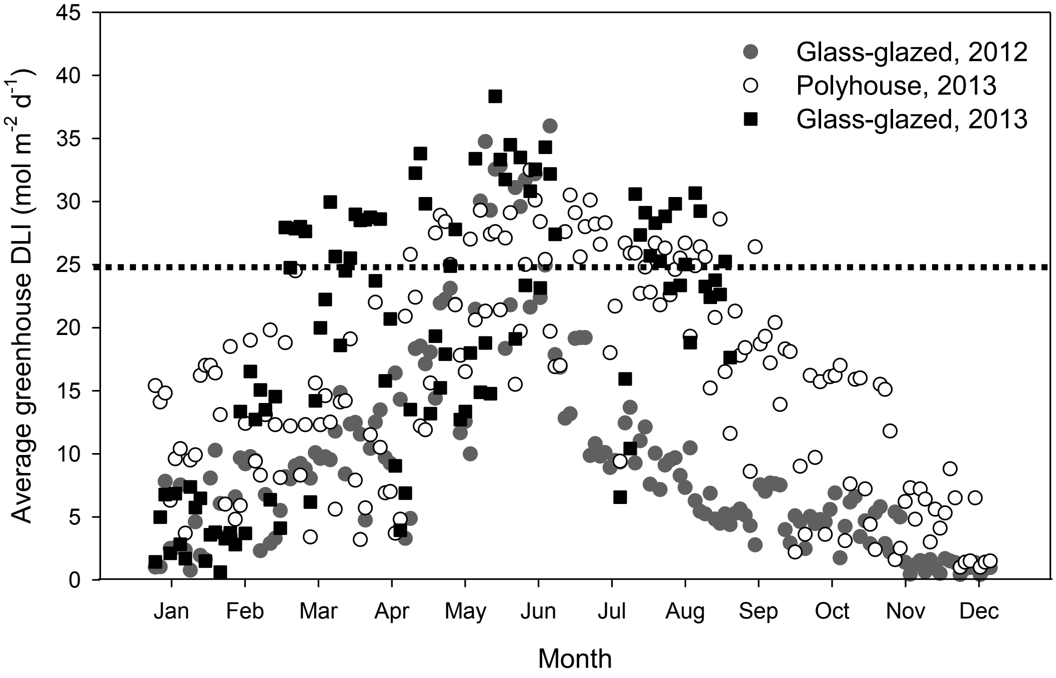

Figure 8. Daily light integral (DLI) inside a glass-glazed greenhouse or a polyhouse in West Lafayette, IN (40° N. latitude). The dotted line represents the threshold of solar DLI below which supplemental lighting is required for optimal tomato production.

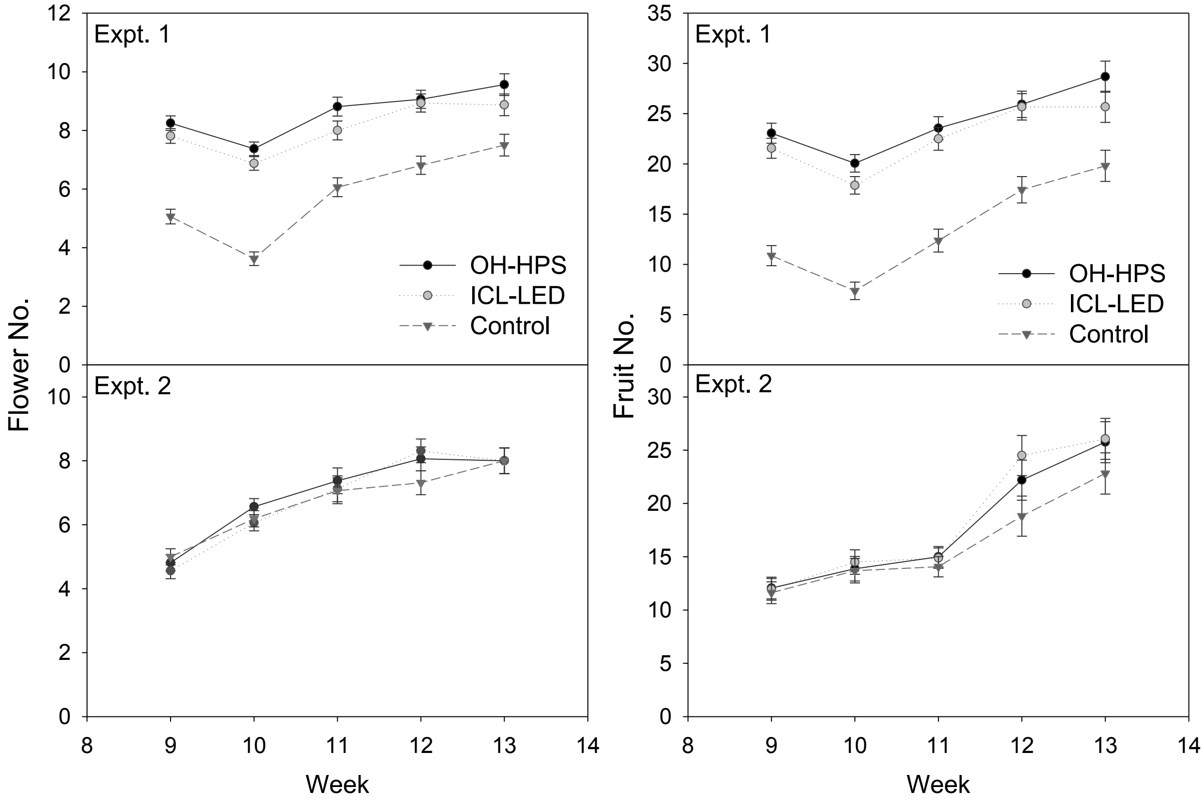

Figure 9. Seasonal variation (Expt. 1 = winter-to-summer; Expt. 2 = summer-to-winter) in weekly counts of flower and fruit number for tomato. Plants were grown in a greenhouse under one of three lighting treatments. The treatments were overhead-high-pressure sodium (OH-HPS) lamps vs. intracanopy LED (ICL-LED) towers vs. no supplemental lighting (control). Values represent the mean ± SE (n = 8) for one two-headed plant in Expt. 1 and two single-headed plants in Expt. 2.

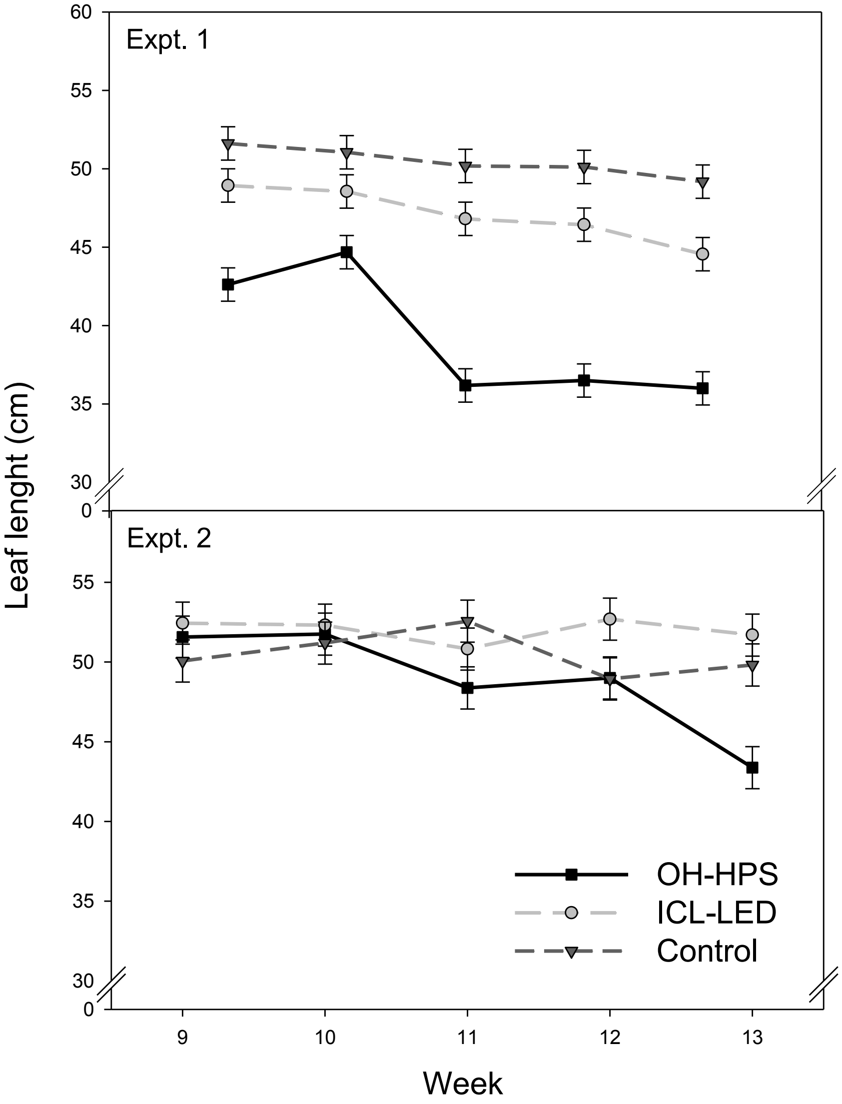

Figure 10. Seasonal variation (Expt. 1 = winter-to-summer; Expt. 2 = summer-to-winter) in leaf length of the last fully expanded leaf for tomato plants grown in a greenhouse under one of three lighting treatments. The treatments were overhead-high-pressure sodium (OH-HPS) lamps vs. intracanopy LED (ICL-LED) towers vs. no supplemental lighting (control). Values represent the mean ± SE (n = 8) for one two-headed plant in Expt. 1 and two single-headed plants in Expt. 2.

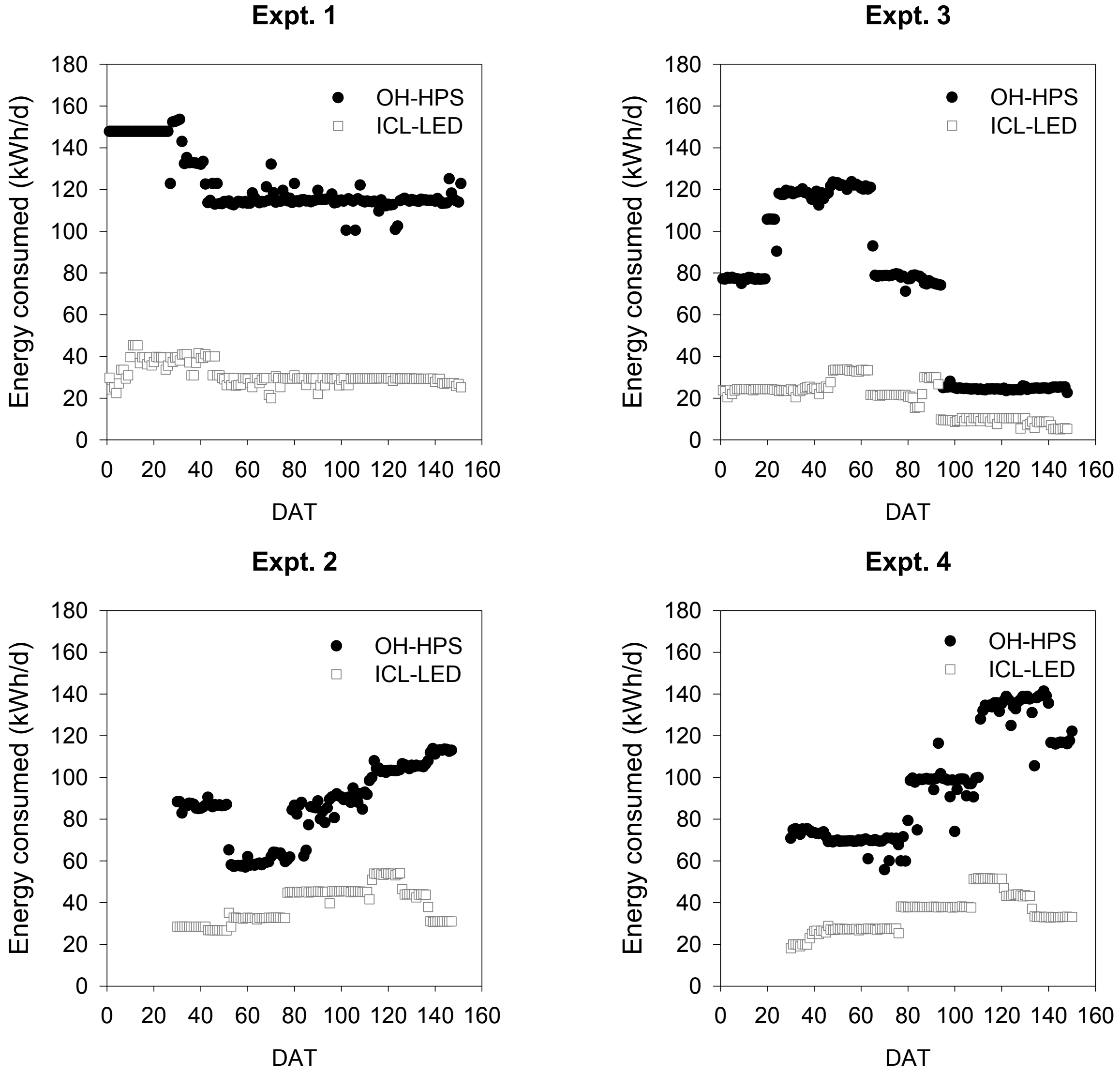

Figure 11. Daily energy consumed from overhead high-pressure sodium (OH-HPS) lamps or intracanopy light-emitting diode (ICL-LED) towers for the production of high-wire tomatoes grown in a greenhouse during two winter-to-summer (Expt. 1 and 3) and two summer-to-winter (Expt. 2 and 4) growing seasons in 2012 and 2013. DAT = days after transplanting.

CHAPTER 4. COMPARISON OF LIGHT-EMITTING DIODES AND HIGH-PRESSURE SODIUM LAMPS FOR GREENHOUSE SUPPLEMENTAL LIGHTING: PHYSIOLOGICAL RESPONSES OF AN INDETERMINATE HIGH-WIRE TOMATO CANOPY

Summary

Intensive year-round local production of greenhouse-grown vegetables requires the use of supplemental lighting (SL) to offset seasonally limited solar radiation. Intracanopy light-emitting diode (ICL-LED) towers were compared to overhead high-pressure sodium lamps (OH-HPS) or a hybrid treatment (ICL-LEDs + OH-HPS) as alternative SL sources for high-wire greenhouse tomato (*Solanum lycopersicum* L.) production. A control treatment also was included for which no SL was provided. Plants were grown from winter-to-summer in a glass-glazed greenhouse located in a mid-northern climate (40°N. latitude, West Lafayette, IN, USA). Several crop physiological responses were measured, and fruit production and energy consumption were quantified for plants grown under the different treatments. Among the physiological parameters evaluated, CO_2 assimilation measured under ambient environmental conditions (A), photosynthetic quantum yield (θ), maximum gross CO_2 assimilation (A_{max}) and the light-saturation point of photosynthesis proved to be good indicators of how ICL improves light absorption within a high-wire tomato canopy

by diminishing the top-to-bottom decline in photosynthetic activity typically measured with OH lighting only (SL or solar). Although SL generally increased yield relative to control, no yield differences were recorded among SL treatments, indicating that higher source activity does not necessarily always lead to yield increases. Based on the lower energy consumption measured for ICL-LED, and, to a lesser extent, for hybrid SL, compared to OH-HPS, replacing OH-HPS lamps with ICL-LED or hybrid SL has great potential for energy savings during high-wire greenhouse tomato production.

Introduction

Year-round production of greenhouse-grown tomatoes in temperate climates typically requires supplemental lighting (SL) for optimal fruit yield and quality. High-pressure sodium (HPS) lamps are the preferred type of greenhouse SL because their high-intensity capability allows them to deliver adequate supplemental photosynthetically active radiation (*PAR*; 400 to 700 nm) to crops. Traditionally, HPS lamps are mounted overhead (OH) at a fixed height that minimizes excess heat load on crops but maximizes light distribution and uniformity at a given height within the greenhouse. Although the wide-angle beam distribution of OH lighting can maximize upper-canopy photon capture efficiency for mature crops (Nelson and Bugbee, 2014), when plants are young and widely spaced, energy is wasted when OH photons fall on empty spaces within the production area. Then, when foliar canopies close, photons coming from above are excluded from the inner canopy and mutual shading occurs, leading to a decline in leaf photosynthesis, premature senescence, and leaf abscission (Frantz et al., 2000).

Unlike HPS lamps, the relative coolness to the touch of the photon-emitting surface from light-emitting diodes (LEDs) allows them to operate in close proximity to plant tissue, thereby increasing available *PAR* at leaf level without overheating or scorching plants. Flexibility of lamp placement and resulting light distribution within crop stands could benefit high-wire cropping systems (i.e., tomato, cucumber, sweet pepper, and eggplant) within which plants are trained vertically below horizontal support wires, thereby creating conditions conducive to shading of middle and lower-canopy leaves by upper leaves, and potentially row-to-row shading. Intracanopy lighting (ICL) or interlighting, which refers to the strategy of lighting along the side or within the foliar canopy, could help prevent mutual shading for such high-wire crops. For this chapter, we use the terms 'ICL' and 'interlighting' interchangeably.

It has been reported that ICL in a sole-source-lighting mode can delay leaf senescence for cowpea (*Vigna unguiculata* (L.) Walp.) (Frantz et al., 2000; Massa et al., 2005) and soybean (*Glycine max* L.) (Stasiak et al., 1998) by maintaining irradiance in the understory of the foliar canopy. Other studies have shown that hybrid SL (OH + ICL) increased crop photosynthesis in high-wire greenhouse production of tomatoes (Dueck et al., 2012; Trouwborst et al., 2010), cucumber (*Cucumis sativus*) (Pettersen et al., 2010; Trouwborst et al., 2011), and for field-grown soybean (Johnston et al., 1969) by increasing the photosynthetic activity of middle- and lower-canopy leaves. Moreover, hybrid SL has been shown to increase the light-use efficiency (LUE) within high-wire greenhouse-grown crops by increasing light absorption (ICL reduces losses associated with SL reflection and transmission) within the canopy and by delivering a more homogenous vertical light distribution to plants (Trouwborst, 2011).

Most research using ICL as SL has evaluated ICL as part of hybrid lighting (Dueck et al., 2012; Gunnlaugsson and Adalsteinsson; 2006; Hao et al., 2012; Heuvelink et al., 2006; Hovi et al., 2004; Hovi-Pekkanen et al., 2006; Hovi-Pekkanen and Tahvonen, 2008; Pettersen et al., 2010; Trouwborst et al., 2010). Fewer studies have used ICL alone *per se* (Deram et al., 2014; Grimstad, 1987; Jokinen et al., 2012; Lu et al., 2012a; Lu et al., 2012b). Moreover, a direct comparison of physiological responses to ICL from LEDs vs. OH-HPS SL has not been reported for high-wire tomato. Our objective was to compare crop physiological responses to different SL sources and positions [ICL-LED vs. OH-HPS vs. hybrid lighting (ICL-LED + OH-HPS)] within an indeterminate high-wire tomato canopy and to quantify fruit production and energy consumption for plants grown under the different lighting treatments.

Materials and Methods

Plant materials and growing conditions. Seeds of tomato ‘Komeett’ (De Ruiter Seeds, Columbus, OH) were sown into 17-cell seedling trays of Agrifoam soil-less plugs (5 × 2.5 cm; SteadyGROWpro; Syndicate Sales, Kokomo, IN) on 16 Dec. 2013 and placed in a glass-glazed greenhouse in West Lafayette, IN (lat. 40°N, long. 86°W; USDA hardiness zone 5b) oriented east-to-west, with 3.7-m gutter height and 6.7-m peak height. The greenhouse has a floor area of 111 m^2, is equipped with pad-and-fan evaporative cooling system and radiant hot water pipe heating. Once the cotyledons had expanded fully, SL of 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ from an OH-HPS lamp was provided for 14 h daily. All seedlings were fertigated as necessary with acidified water supplemented with a combination of two water-soluble fertilizers (3:1 mixture of 15N-2.2P-12.5K and 21N-2.2P-16.6K, respectively; The Scotts Co., Marysville, OH) to provide the following (in mg·L^{-1}): 200 N-NO3, 26 P, 163 K, 50 Ca, 20 Mg, and micronutrients. On 9 Jan. 2014, seedlings were randomly selected for each lighting treatment and transplanted into rooting blocks (4 × 4 × 2.5 cm; SteadyGROWpro; Syndicate Sales), which were then placed into wetted coconut coir slabs (100 × 15 × 10 cm; Riococo 200, Ceyhinz Link International Inc., Dallas/Fort Worth Metroplex of Texas, TX). Slabs were placed on top of custom-made steel gutters (9.8 m × 25 cm; FormFlex Horticultural Systems, Ontario, Canada). The stem density was initially 3.3 stems/m^2 but reduced to 2.2 stems/m^2 at 5 weeks after transplanting. Plants were irrigated with a commercial complete fertilizer mix (4.5N-14P-34K; CropKing, Lodi, OH) providing a daily leaching fraction (LF) of 30%. Irrigation frequency was adjusted as necessary depending on the LF. Electrical conductivity (EC) and pH of the influx and efflux were measured daily with a hand-held EC and pH meter (Hanna Instruments, Woonsocket, RI) to ensure that values were maintained within recommended ranges (2.5-3.5 dS·m^{-1} and 5.8-6.3 for EC and pH, respectively) (Jones, Jr., 2008). Average ambient day and night temperatures of the greenhouse were set at 25 °C and 15 °C, respectively.

Lighting treatments. The greenhouse floor area was divided into three rows separated by movable double layers of 6-mil (0.15 mm)-thick white polyethylene plastic (curtains) parallel to the rows from the upper frame of the greenhouse structure (≈3.6 m from the top to the floor). The plastic curtains were used to prevent light pollution between treatments and were withdrawn when lamps were off. Each row was comprised of four sections (1.8 × 2.4 m) of different treatments running in an east-to-west direction separated by short sections of plastic curtains hung perpendicular within each row. Each section was one replicate of a treatment lighting eight single-headed plants (two side-by-side plants per block).

The SL lighting treatments were started on 31 Jan. 2014 and provided an average DLI (at plant height) of 9.5, 13.0, 8.8, 3.8, and 3.8 $mol{\cdot}m^{-2}{\cdot}d^{-1}$ for Feb., Mar., Apr., May, and Jun., respectively. Three SL treatments were evaluated: 600-W OH-HPS lamps (HS2000; P.L. Lights, Beamsville, Ontario, Canada), ICL-LED towers [2.5-m-tall, with three 0.60 × 0.12 m LED zones irradiating both directions within a row; each panel had four red and one blue (627 and 450-nm peak wavelength, respectively), dimmable LED strips with 12 LEDs mounted vertically within each strip; actively air-cooled; Orbital Technologies Corporation, Madison, WI], or hybrid lighting using two LED interlighting modules [2.5-m long, with one horizontal strip of 160 red and 40 blue LEDs (alternating; 660 and 450-nm peak wavelength, respectively) irradiating both directions within two side-by-side plants; passively air-cooled; GreenPower LED interlighting module dr/b, Philips, Eindhoven, The Netherlands] (60 cm between interlights) + 400 W OH-HPS lamps (LU400ECO; Sylvania, Toronto, Ontario, Canada). Both LED lamp types provided a mix of 93% red and 7% blue. A control treatment also was included for which no SL was provided.

Before starting the experiment, a light map was developed (after sunset) at three heights in the greenhouse to determine the maximum photosynthetic photon flux (*PPF*) for each SL treatment (no plants present). Light intensity was measured using a spherical quantum sensor (LI-250A; LI-COR Biosciences) calibrated against a spectroradiometer (EPP-2000; StellarNet Inc., Tampa, FL). The output of supplemental DLI was set to be equivalent for all SL treatments. Nonetheless, although ICL-LED was set to provide the same light intensity along the vertical plane of the crop stand as OH-HPS (282, 180, and 118 μmol·m^{-2}·s^{-1} for the top, middle, and lower canopy), hybrid SL delivered more light to the mid-portion of the canopy (188 μmol·m^{-2}·s^{-1}; 154 + 34 μmol·m^{-2}·s^{-1} from the interlights + OH-HPS, respectively), than the bottom (24 μmol·m^{-2}·s^{-1}), and to a lesser extent, the upper canopy (71 μmol·m^{-2}·s^{-1}). In addition, the average *PPF* from hybrid SL (197 μmol·m^{-2}·s^{-1}; 154 + 43 μmol·m^{-2}·s^{-1} from the interlights + OH-HPS, respectively) was higher than that from the two other SL treatments (193 μmol·m^{-2}·s^{-1}) and thus, a different photoperiod had to be used in order to achieve the same supplemental DLI.

Air temperature and solar DLI were monitored using shielded temperature probes (107-L) and quantum sensors (190 SB; LI-COR Biosciences, Lincoln, NE), respectively, interfaced to a datalogger (CR1000; Campbell Scientific, Logan, UT). Shielded temperature probes were placed at mid-canopy height in the center of each treatment replication. Quantum sensors monitored solar DLI at three heights within the greenhouse: 1) mid-canopy height in control treatments; 2) directly above top-canopy height in control treatments; and 3) top of the greenhouse rafters. Measurements were made every 10 s and data were recorded at 10-min intervals. Average day and night air temperature and average solar DLI for the experimental period are reported in Figures 1 and 2, respectively.

Data collection. Kilowatt-hours (kWh) of energy consumed were monitored using a built-in datalogger and energy monitors (e2 classic 2.0; Efergy U.S.A., Miami, FL) for each ICL-LED tower and the OH-HPS/hybrid lighting treatments, respectively. Removal of lower leaves and plant leaning and lowering were conducted as needed. Fruits were pruned to five per cluster (to maintain fruit grade/size uniformity), and clusters were harvested weekly when the last fruit within a cluster was at maturation stage 6, based on the USDA Visual Aid TM-L-1 tomato-color standards. Fruit fresh weight (FW) and fruit number (FN) were recorded immediately following harvest. Upon experiment termination (16 Jun. 2014), node number per plant was recorded.

The maximum photosystem II (PSII) efficiency (F_v/F_m) was estimated by measuring chlorophyll fluorescence using a portable pulse-modulated chlorophyll fluorometer (OS-30p; Opti-Sciences, Inc. Hudson, NH). Four plants per treatment replication were selected, and leaves to be measured were tagged, aiming to reduce leaf-to-leaf variability among measurements recorded from leaf initiation (newest leaf ≥ 16 cm; L_1) to pruning. Data were collected for the adaxial epidermis of the largest leaflet (typically the middle leaflet) within an inner-canopy and an outer-canopy leaf. Fluorescence measurements were collected once weekly for 6 weeks. Data were recorded at night (>30 min SL was turned off) to ensure dark adaptation. Tissue temperature was recorded with a hand-held infrared thermometer (Agry-Therm II; Everest Interscience, Tucson, AZ) (emissivity = 0.97); measurements were recorded on four random dates (forecasted for clear-skies) between 8:00 AM and 10:00 AM. Temperature data were recorded for the apical meristem (shoot tip), newest fully expanded leaf (8th leaf below L_1), and oldest leaf (approx. 18th leaf below L_1).

Gas exchange measurements were performed using a portable infra-red gas analyzer system (CIRAS-3, PP Systems, Amesbury, MA) fitted to a 4.5-cm^2 leaf chamber with built-in LED light sources (475, 528, 625, and 425-650-nm peak wavelengths for the blue, green, red, and white LEDs, respectively). Three leaf layers (LL) were selected for measurements: newest fully expanded leaf (LL1) (approx. 8th leaf below L_l), 13th leaf below L_l (LL2), and the oldest leaf (LL3) (approx. 18th leaf below L_l). Net photosynthesis (NP) was measured using *PPFs* of 1000 and 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ in order to determine light-saturated (A_{sat}) and light-limited (A_{lim}) rates of photosynthesis, respectively. Two weeks prior to collecting NP measurements, spectral scans for each treatment at each LL were collected on two clear-sky days (SL + sunlight) (Figure 14). Spectral percentages for broad-band (BB) blue (400 to 500 nm), green (500 to 600 nm), and red (600 to 700 nm) light (BGR) were determined and averaged across LLs for each lighting treatment. The light unit in the cuvette was programed to correspond to a treatment-specific spectrum: OH-HPS = 24%, 39%, and 37% BGR, respectively; ICL-LED = 28%, 24%, and 48% BGR, respectively; hybrid = 31%, 32%, and 37% BGR, respectively; solar (control) = 33%, 34%, and 33% BGR, respectively. In order to reveal differences when taking photosynthesis measurements under a treatment-specific vs. a common spectrum across samples, A_{sat} and A_{lim} were measured first, using a treatment-specific spectrum followed by measurements under solar spectrum. The reference CO_2 concentration, leaf temperature, relative humidity (RH), and flow rate inside the chamber were 400 $\mu mol \cdot mol^{-1}$, 25 °C, approx. 60%, and 400 $mL \cdot min^{-1}$, respectively. For each LL within a given treatment, six leaves from different plants were randomly selected; NP was measured on the largest leaflet within a leaf. Measurements were conducted between 0800 and 1500 HR from 5 to 9 Apr. 2014; during this period, average solar DLI directly above plant canopy was 10.3 $mol \cdot m^{-2} \cdot d^{-1}$.

Survey photosynthesis (A), stomatal conductance (g_s), transpiration (E), and leaf temperature were measured on overcast and clear-sky days to compare physiological responses under contrasting solar light intensities. As for NP, six leaves at each LL from different plants within a treatment were randomly selected and measured on the largest leaflet within a leaf. Measurements were conducted under ambient greenhouse temperature and RH; reference CO_2 concentration and flow rate inside the chamber were 400 $\mu mol \cdot mol^{-1}$ and 400 $mL \cdot min^{-1}$, respectively. Data were collected between 0800 and 1200 HR (while SL was in use) on 15-17 (overcast) and 19-22 (clear-sky) Apr. 2014; during this period, average solar DLI directly above plant canopy was 6.5 and 17.8 $mol \cdot m^{-2} \cdot d^{-1}$ for overcast and clear-sky days, respectively.

Following NP and survey measurements, photosynthetic light-response curves (LRC) were measured under seven different *PPF* levels (1000, 800, 500, 350, 200, 75, and 0 $\mu mol \cdot m^{-2} \cdot s^{-1}$). The light unit in the cuvette was programed to provide 33%, 34%, and 33% BGR. The reference CO_2 concentration, leaf temperature, RH, and flow rate inside the chamber were 400±5 $\mu mol \cdot mol^{-1}$, 26 °C, 60%, and 400 $mL \cdot min^{-1}$, respectively. Data were fitted to the following model equation:

$$Anet = -Rd + \frac{\theta \times PPF + A\mathrm{max} - \sqrt{(\theta \times PPF + A\mathrm{max})^2 - 4\theta \times PPF \times k \times A\mathrm{max}}}{2k}$$

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

Experimental design and statistical analysis. Harvest and growth parameters were analyzed according to a randomized complete block (RCB) design. For all physiological responses [gas exchange (except data for LRCs), fluorescence, and tissue temperature], data were analyzed as an RCB design with four lighting treatments × three LLs as factorial levels. A non-rectangular hyperbola was used to fit the LRC data using the non-linear fitting procedure of SAS (version 9.2; SAS Institute, Cary, NC). All results were subjected to analysis of variance and the general lineal model procedure of SAS.

Results

Fruit yield, plant growth, and energy consumption. Supplemental lighting increased total fruit production regardless of the light source or lighting position within the canopy by at least 33% compared to unsupplemented controls (Table 7). However, plants under ICL-LED produced clusters similar in FW to those of plants grown without SL (570 vs. 490 g, respectively). Conversely, clusters of plants grown under OH-HPS or hybrid SL were 27% or 29% larger than those developed under control, respectively. Although the increase in fruit number from SL ranged from 16% up to 23%, the number of fruits per plant produced under hybrid SL was not statistically different from that of plants grown without SL (108 vs. 93 fruits). A significantly higher number of nodes was recorded for plants grown under OH-HPS compared to those with ICL-LED or without SL. Harvest duration was not different among treatments and ranged from 50 to 58 days.

Daily electrical energy consumption is shown in Figure 15. The average energy consumed during the experiment was 33, 22, and 13 kWh/d for the OH-HPS, hybrid, and ICL-LED SL treatments, respectively, and they were all significantly different from one another. Only 38% of the total energy consumed by the hybrid SL treatment was used by the LED interlights; the remaining 62% of energy was consumed by the OH-HPS lamps.

Tissue temperature and chlorophyll fluorescence. On 26 Feb. 2014, the tissue temperature was significantly lower for the shoot tip and the newest fully expanded leaf of plants grown without SL compared to those grown with SL (Table 8). Nevertheless, for the rest of the measured dates, although tissue temperature differed up to 1.5 °C among treatments, data were not significantly different for any of the plant parts measured. There was no effect of lighting treatment on the efficiency of PSII as estimated by F_v/F_m (Figure 16), indicating no stress symptoms from initial leaf development until leaf-pruning.

Net photosynthesis. No significant differences occurred when NP was measured using a treatment-specific- or under-solar spectrum (data not shown). Thus, data for A_{sat} and A_{lim} under different spectra were pooled within treatments. In general, the light-saturated and light-limited rates of photosynthesis were higher for plants grown under SL compared to those grown without SL, regardless of the treatment used (Table 9). However, for LL3, A_{sat} was not significantly different for leaves of plants grown under OH-HPS or those grown without SL (11.0 vs. 8.6 $\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$). For all treatments, A_{sat} and A_{lim} generally declined from the top (LL1) to the bottom (LL3) of the canopy.

Survey gas exchange measurements. Overall, A, g_s, and leaf temperature were higher in clear-sky than in overcast days, regardless of the treatment or leaf layer, indicating higher photosynthetic activity under high solar irradiance (Table 10).

<u>Clear-sky days</u>: *A* was 80% or 58% higher for plants grown with hybrid or ICL-LED SL, respectively, compared to those grown under control. While OH-HPS resulted in the same *A* as that of either LED-containing treatments, it was also statistically similar to that of plants grown without SL (14.3 vs. 9.9 µmol $CO_2 \cdot m^{-2} \cdot s^{-1}$, respectively). Across treatments, *A* decreased from the top (21.0 µmol $CO_2 \cdot m^{-2} \cdot s^{-1}$) to the bottom of the canopy by 31% and 62% for LL2 and LL3, respectively.

Stomatal conductance was 40% higher for leaves of plants grown under OH-HPS compared to those grown without SL (Table 10). Also, g_s decreased by 24% and 50% from that of LL1 (749 $mmol \cdot m^{-2} \cdot s^{-1}$) to LL2 and LL3, respectively. There were no significant differences in *E* or leaf temperature among treatments or LLs. However, the average leaf temperature across LLs was 1.2 °C warmer under OH-HPS than for the control, which, although not statistically significant, may be of biological relevance.

<u>Overcast days</u>: With few exceptions, *A* was highest for leaves in LL1 measured under OH-HPS SL (Table 10). However, only for OH-HPS did *A* significantly decrease from the top (LL1) to the bottom (LL3) of the canopy. Moreover, *A* measured across treatments was generally similar within LLs. Stomatal conductance and leaf temperature did not differ significantly among treatments or LLs. For all treatments, *E* decreased in proportion to canopy depth.

Photosynthetic LRCs. Based on the shape of the LRCs, upper leaves had a similar photosynthetic capacity regardless of treatment (Figure 17). However, for LL2, leaves grown without SL had the lowest maximum A_{net} level. A clear treatment differentiation of the LRCs is shown for LL3. The estimated parameters from photosynthetic LRCs are shown in Table 11. Across treatments, R_d was higher in LL2 than LL3, but equal to that measured for LL1. The photosynthetic θ was similar across LLs for plants grown under ICL-LED or hybrid SL, demonstrating that the proportion of absorbed light used in photosynthesis remains constant along the vertical plane of the high-wire crop with ICL SL. In contrast, θ was lower in LL3 compared to the upper canopy for plants grown under OH-HPS or without SL. Across LLs, the k of the LRC was slightly but significantly higher for leaves grown without SL compared to those developed under hybrid SL, indicating a more abrupt transition from light limitation to light saturation when plants are grown without SL. With ICL-LED or hybrid SL, A_{max} was not different among LLs and ranged from 28 to 24 or 32 to 24 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$, respectively, suggesting that the photosynthetic capacity of leaves was similar across LLs. Similarly, A_{max} for LL1 and LL2 were not different within treatments, but were 48% or 60% lower in LL3 compared to LL1 for leaves grown under OH-HPS or without SL, respectively.

The calculated LCP of photosynthesis was not different across treatments or LLs (Table 12). In contrast, the LSP for plants grown under OH-HPS or without SL decreased significantly in the lower canopy (LL3) compared to LL1, whereas plants grown with hybrid or ICL-LED SL maintained equivalent LSP across LLs that ranged from 1338 to 943 μmol$\cdot m^{-2} \cdot s^{-1}$.

Discussion

SL increases fruit production. Results from this study reinforce the findings presented in Chapter 3, which indicate that SL generally increases fruit yield (size, weight, and/or number) under light-limiting conditions, compared to unsupplemented controls, regardless of the treatment used. It is well stablished that SL is needed to maintain or increase fruit production in light-limited environments, especially for high-light-requiring crops, such as tomato (Blacquiere and Spaargen, 2003; Dueck et al., 2007; Gajc-Wolska et al., 2013). Moreover, if no other factors are limiting, optimal plant growth can be achieved with adequate *PPF* or optimal DLI. In our study, supplemental DLI was kept constant across treatments, which probably accounts for some of the similarities in plant growth and yield measured among SL treatments. It is likely that the ICL-LED or hybrid treatments did not increase fruit yield relative to OH-HPS because they did not provide more light.

Although hybrid lighting has been shown to improve light-use efficiency within greenhouse crops (yield per unit of electric energy consumption of lighting), increase fruit yield and percentage of first-class fruit, and extend the post-harvest shelf life of produce compared to OH SL (Gunnlaugsson and Adalsteinsson; 2006; Hovi et al., 2004; Hovi-Pekkanen et al., 2006; Hovi-Pekkanen and Tahvonen, 2008; Pettersen et al., 2010), most studies reporting increases in crop yield with hybrid lighting have used HPS lamps mounted OH and within the canopy (as with ICL). In contrast, studies comparing hybrid SL using OH-HPS lamps + ICL-fluorescent or -LED lamps to OH-HPS lighting alone have shown either negative (Heuvelink et al., 2006), minimal (Hao et al., 2012), or no significant increase in fruit yield from hybrid lighting (Deram et al., 2014; Dueck et al., 2012; Trouwborst et al., 2010). It is likely that increases in fruit yield when using 100% HPS-hybrid lighting are, in part, the result of the additional thermal energy irradiated by ICL-HPS, which could accelerate fruit-maturation rate and, thus, reduce time to harvest. Conversely, if ICL does not irradiate much heat, as in the case of the LED lamps used in our study, hybrid lighting may not increase yield of greenhouse-grown crops.

Tissue temperature. Although continuous measurements of tissue temperature allow for a better understanding of radiant-energy effects on plant growth and development, surface-temperature measurements of specific plant parts served as a baseline to quantify changes in tissue temperature caused by SL. In general, tissue temperature was not significantly different among treatments, but did show slight variances of up to 1.5 °C. These variations in tissue temperature, although not statistically significant, may still have an effect on plant growth, as higher temperatures increase sink strength of the fruits and are known to accelerate developmental processes.

Some studies have suggested that temperature, light, and their interaction are among the most critical environmental parameters affecting tomato growth and development (Adams et al., 2001; Uzun, 2006). Thus, sub- or supra-optimal temperatures have great potential to affect several developmental processes in tomato. Bonan (2008) stated that at 90% RH, leaf temperature can be up to 2 °C higher than ambient air temperature, whereas at 55% RH, leaf temperature is similar to ambient. During our study, the average daytime RH was 52% and the maximum ambient daytime temperature measured at mid-canopy height ranged from 27.9 to 29.3°C across treatments. The moderate RH during the experiment, in addition to the maximum ambient temperatures being <30-32 °C [upper threshold temperature for optimal tomato growth and quality (Dumas et al., 2003; Jones 2008)], indicate that tissue temperature was not a limiting factor for plant growth. Moreover, the minor changes in tissue temperature among treatments suggest that growth and physiological responses could not be attributed entirely to tissue-temperature differences resulting from SL.

The resulting thermal energy created from absorption of direct sunlight also may play a significant role in canopy-tissue temperature. Others have shown that with OH sole-source lighting, air and tissue temperature can be cooler in the understory of a plant canopy compared to the top (Frantz et al., 2000; Kitaya et al., 1998). Although in our study, OH SL did not affect tissue temperature, the shoot tip was generally warmer than leaves lower in the canopy. The similarities in tissue temperature among treatments, coupled with differences in temperature between the top and bottom of the canopy, suggest that direct radiation from OH solar light to the upper canopy rather than SL was responsible for changes in tissue temperature within the canopy.

Chlorophyll fluorescence. Chlorophyll fluorescence was used to determine whether onset of leaf senescence was associated with plant responses to changing light conditions in the growth environment (i.e. self or mutual shading) (Barreiro et al., 1992; Brouwer et al., 2012). Researchers have shown that a negative carbon balance occurs when high-light-acclimated leaves are exposed to low-light conditions, turning leaves from photosynthethic sources to sinks and triggering premature leaf senescence (Boonman et al. 2006; Veierskov, 1987). Frantz et al. (2000) reported a premature decline in single-leaf fluorescence measurements from OH-lighted- compared to ICL-lighted-cowpea in a growth chamber. The authors attributed their results to changes over time in: 1) spectral energy distribution caused by preferential absorption of specific wavelengths in the upper canopy (and subsequent filtered irradiance in the understory); and 2) decline in light intensity when additional leaf layers form on top of the upper canopy (acclimated to direct light). It is likely that in our study, plants gown under OH-HPS lamps or without SL experienced similar changes over time in the radiation environment as those previously described. However, our findings showed no evidence of premature leaf senescence for any of the treatments evaluated. It is possible that even with SL, greenhouse-grown plants are acclimated to changes in irradiance due to the ever-changing distribution of solar light, from which plant canopies are irradiated from all angles, depending on the time of day and leaf positions within the canopy. In addition, the spectra, intensity, and directionality of solar light changes constantly in the greenhouse. Conversely, plants grown in controlled environments tend not to experience such sudden environmental changes. Therefore, it is likely that some physiological responses (i.e., leaf senescence) of greenhouse crops are not affected by different SL sources or positions within the canopy to the same extent as they are in controlled environments with sole-source lighting because greenhouse-grown plants have grown adapted to changes in irradiances.

Moreover, weekly removal of lower leaves is a common practice for commercial tomato production in greenhouses, especially after harvest begins (Hogewoning et al., 2007). Thus, it is likely that leaf senescence does not occur during the life cycle of a tomato leaf as grown in commercial greenhouses (approx. 8-10 weeks). However, if leaves were to be kept on the plant longer, visual and measurable signs of leaf senescence caused by changes in the radiation environment from OH lighting (supplemental or solar) would likely occur in lower, older leaves.

Net Photosynthesis. Wang et al. (2014) described light intensity and distribution as a fundamental factor affecting photoassimilate translocation in greenhouse-grown crops. Nishizawa et al. (2009) reported that for tomato, the percentage of carbon exported from source leaves is not affected by light intensity. However, the amount of carbon translocated per unit leaf area depends on the carbon pool, which is contingent on light intensity, leaf photosynthetic capacity, and/or leaf anatomy (Grodzinski et al., 1999). In our study, hybrid lighting allowed lower leaves to maintain a higher photosynthetic capacity than that measured for plants grown with OH lighting (solar or HPS-SL), presumably by increasing light absorption and distribution within the mid- and lower-canopy. More leaves with positive net photosynthetic rates result in higher net canopy assimilation, which has been widely correlated with the light-intensity profile within the canopy, and can sometimes improve crop productivity (Frantz et al., 2000; Gonzalez-Real et al., 2007; Ninemets, 2007; Stasiak et al., 1998). Li et al. (2014) saw similar effects on tomatoes grown in a greenhouse covered with diffuse glass. They reported that a more uniform vertical-light distribution from solar light dispersion increased calculated crop photosynthesis by up to 7%. Moreover, the top-to-bottom decline in NP measured for plants grown under OH-HPS or without SL is in agreement with studies reporting lower photosynthetic rates in the lower canopy of tobacco (*Nicotiana tabacum* L.) (Boonman et al., 2006) or high-wire tomato (Xu et al., 1997) grown under OH-HPS SL.

The underlying cause for the higher $A_{\mathrm{sat;LL3}}$ in hybrid SL compared to ICL-LED, and the similarities in $A_{\mathrm{sat;LL3}}$ between ICL-LED and OH-HPS (Table 9) may be associated with one or a combination of the following:

1) Long-term developmental effects caused by different *PPF*s along the vertical plane of the crop stand: Although ICL-LED or hybrid SL increased light absorption within the canopy relative to OH lighting (SL or solar), the vertical light distribution between ICL-LED and hybrid SL were different. Hybrid SL delivered more light to the mid portion of

the canopy than the upper or lower canopy. Conversely, for comparative analysis, the ICL-LED treatment provided the same supplemental *PPF* along the vertical plane as did OH-HPS SL (without plant tissue present). Any long-term effects caused by differences in vertical light distribution between hybrid vs. ICL-LED could account for differences in A_{sat} in the lower canopy.

2) Spectral differences among treatments: As described by others, green light can penetrate deeper into the canopy than red and blue, and thus, can drive photosynthesis more efficiently when used to supplement the broad solar spectrum (Kim et al., 2004; Lu et al., 2012; Terashima et al., 2009). Moreover, depending on species, the relative quantum efficiency (RQE) of absorbed BB green light can be comparable with that of red (RQE of red is 5%-30% more efficient than green), and higher than that of blue (RQE of green can be up to 20% higher than blue) (Inada, 1976; McCree, 1972). McCree (1972) found that for chamber-grown tomato, the RQE of BB green light was 18% more efficient than that of BB blue light. Therefore, a higher percentage of green relative to blue light could potentially enhance net carbon assimilation in tomato, especially when applied from above. In our study, plants grown under OH-HPS lamps received more BB green (39%) than BB blue light (24%) within the *PAR* spectrum, whereas plants grown with ICL-LED light received similar percentages of BB green and blue light (24% and 28% from *PAR*, respectively). Although plants grown with ICL-LED had higher light absorption (and potentially, an improved light distribution) compared to OH-HPS SL, the higher percentage of BB green light in OH-HPS could have promoted plant photosynthesis by penetrating deeper in the canopy and therefore, may explain the similarities in A_{sat} and A_{lim} found between the two SL treatments.

3) Solar blocking from SL infrastructure: Although ICL aims to reduce mutual shading by increasing the total amount of light delivered to the lower portion of the canopy, depending on time of day and size of the fixture, ICL fixtures can potentially block solar light from reaching the crop. It is likely that the shading factor from ICL-LED vertical towers (<10% measured at solar noon) reduced the total light intensity received by the plants during mornings and afternoons and further affected their A_{sat} and A_{lim} responses.

Survey gas exchange. Gas exchange at the single-leaf level can be measured using imposed environmental conditions typically selected to correspond with set-point environmental parameters for plant growth. However, response measurements at imposed conditions do not provide enough information to understand the *in-situ* physiological performance of plants, especially when grown in semi-controlled environments like greenhouses, with frequent fluctuations of light, temperature, and RH. On the other hand, survey measurements at ambient conditions portray real-time physiological activity and can further explain plant responses to lighting treatments.

Similar to NP under light-saturating and light-limited irradiances, A, g_s, and leaf temperature were higher during clear-sky than overcast days. Hao and Papadopoulos (1999) saw similar effects for cucumber plants grown under different greenhouse-covering materials (glass vs. acrylic vs. double inflated polyethylene film) with or without SL. Nonetheless, we found that the magnitude of the response for E was not different under contrasting solar light intensities. The rate of E can be a function of temperature, RH, CO_2 concentration, light intensity, and water availability, among others. Therefore, the fact that E was not different under contrasting solar light intensities suggests that other environmental parameters may have contrasting effects on *E*. Because changes in leaf *E* can affect nutrient uptake, leaf water potential, and tissue-temperature regulation, the fact that higher irradiances did not increase leaf *E* could be of particular interest for nutrient and water-conservation strategies (Holbrook, 2010). None of the parameters measured for survey gas exchange showed a SL treatment response. It is likely that the similar responses of survey gas exchange measured across SL treatments are due to some of the long-term physiological effects previously described in the NP discussion.

Depending on prevailing environmental conditions, stomates are one factor that regulate gas exchange in and out of leaves by responding to signals that control water loss and CO_2 uptake. Several environmental parameters are known to affect stomatal conductance, including but not limited to light quality and intensity, RH, CO_2 levels, and ambient temperature (Ehleringer and Sandquist, 2010). Studies indicate that light signaling plays a key role in controlling stomatal movement by coordinating light-energy conversion, membrane ion transport, and metabolic activity in guard cells (O'Carrigan et al., 2014). Furthermore, blue light is known to stimulate stomatal opening (Lee et al., 2007; Voskresenskaya and Polyakov, 1975; Zeiger, 2010), whereas short exposure to green light can reverse blue- light-induced stomatal responses (Farquhar and Sharkey, 1982; Frechilla et al., 2000). In our study, each SL treatment affected light quality within the foliar canopy differently, either by providing a lamp-specific emission spectrum or by possibly modifying canopy architecture and/or the degree of canopy closure and, thus, changing the spectral energy distribution in the lower canopy. However, because some days solar light contributed a large percentage of the total DLI received by plants (from 47% up to 81% during the course of the experiment; as calculated from the monthly average of solar DLI measured above canopy height), the lack of differences in g_s among SL treatments could suggest that spectral responses for g_s may be saturated at high irradiances from broad spectrum (such as in the case of sunlight).

Higher g_s promotes CO_2 diffusion into the leaf and in some cases correlates well with net photosynthesis. Although A and g_s were affected by lighting treatment during clear-sky days, the different trends in response to the treatments, in addition to the lack of g_s response during overcast conditions, may indicate that CO_2 diffusion through stomata was not responsible for the changes in A measured in our study. Instead, given that supplemental DLI was constant when survey gas exchange data were collected, the distinct reduction for most responses from clear-sky days compared to overcast conditions suggests that gas exchange measurements were largely affected by solar radiation (and most likely by the inherent changes in ambient temperature), and, to a lesser extent, by SL. Because g_s is known to increase at higher ambient temperatures (Ehleringer and Sandquist; 2010), the significant LL effect occurring on clear-sky days may indicate a correlation of g_s with changes in ambient air temperature within the canopy. In our study, daytime ambient greenhouse air temperature measured at mid-canopy height (LL2) was ~1 °C warmer under OH-HPS or hybrid SL compared to ICL-LED or no SL (Figure 12). However, no significant SL treatment differences were found for any of the survey gas exchange parameters evaluated. The similarities of survey gas exchange responses among SL treatments may suggest that thermal radiation from direct sunlight, rather than from the long-wave thermal radiation commonly given off by OH-HPS lamps, affected the LL treatment differences recorded under ambient environmental conditions.

Light-response curves. LRCs and their estimated parameters further explain how properties of the photosynthetic apparatus change as a function of available light. The negative portion of a LRC, known as R_d, is often referred to as 'negative CO_2 assimilation' because rather than being fixed, CO_2 is given off by the plant. Typically, OH SL results in a gradual top-to-bottom canopy decline in R_d, most likely as an acclimation response to light-limited conditions, reducing metabolic activity in the lower canopy and ultimately leading to the reallocation of photoassimilates from lower leaves to growing organs (Pettersen et al., 2010). In contrast, hybrid lighting has been reported to increase respiration rates in lower leaves of greenhouse-grown cucumber (Trouwborst et al., 2010; Pettersen et al., 2010). Trouwborst et al. (2011) proposed that higher R_d of lower leaves grown under hybrid SL using LEDs can be correlated to higher $A_{\max}$ due to either a photosynthetic 'overcapacity' that most likely increases the photosynthate availability for R_d, leading to a higher leaf mass per area (LMA), or in response to the percentage of blue light, as more blue increases LMA and $A_{\max}$ (Hogewoning et al., 2010). Similarly, McDonald (2003) stated that leaves acclimated to high-light environments have greater R_d in order to sustain the metabolic requirements associated with increased organelle activity from higher photosynthetic capacity (i.e. $A_{\max}$ and LSP). Nevertheless, higher R_d could lead to a decrease in net canopy assimilation, and potentially affect plant productivity. In our study, R_d was unaffected by lighting treatment but did show that, across treatments, LL2 had higher respiration rates than LL3. Similarly, Li et al. (2014) evaluated hazing as an approach to increase light-absorption uniformity within a tomato canopy, and found that diffusion had a significant effect on R_d across canopy layers, but did not affect any of the estimated parameters from the LRCs, including R_d.

The photosynthetic θ represents the slope of the linear portion of a LRC and is typically defined as the increase in photosynthesis per unit increase of light absorbed. Researchers have shown that θ does not differ between leaves from sun- or shade-adapted plants having the same photosynthetic pathway (Björkman and Demmig, 1987; Boardman, 1977). Because plants grown under SL vs. without SL can be expected to behave similarly as sun vs. shade-adapted plants, we anticipated similar θ across treatments and LLs. However, we found that θ was lowest in LL3 when plants were grown under OH-HPS or without SL. Hogewoning et al. (2012) reported that, depending on the acclimation to light-limited or light-saturated environments, light quality has different effects on leaf θ. Thus, we attribute much of the variation in θ to the differences in spectral distribution among treatments and to the light-limited conditions in the lower canopy of the OH-HPS and control treatments.

The convexity of the LRC (*k*) is a qualitative measurement of the photochemical efficiency of leaves. Ögren (1993) reported that *k* is determined by the position of the inflection point between the light-limited electron transport rate and the CO_2-limited carboxylation capacity of Rubisco. We found that across LLs, *k* was higher for leaves grown without SL compared to that with hybrid SL. Higher *k* indicates a more abrupt transition from light limitation to light saturation and tends to be representative of low-light- adapted leaves (Leverenz; 1987; Ögren, 1993).

In our study, the LRCs show that $A_{\max}$ remained constant along the vertical plane of the crop stand when plants were grown with ICL-LED or hybrid SL. Others have shown that hybrid SL can maintain higher $A_{\max}$ in lower leaves of high-wire crops (Dueck et al., 2012; Pettersen et al., 2010; Trouwborst et al., 2010; Trouwborst et al., 2011). Pettersen et al. (2010) reported that plants grown with hybrid SL experience fewer changes in light intensity and quality over time compared to plants grown with OH SL, therefore, hybrid SL can reduce the top-to-bottom decline in A_{max}. Moreover, Trouwborst (2011) concluded that ICL can increase crop photosynthesis either by increasing light absorption within the canopy or by providing a more homogenous vertical light distribution to plants. Our results further support the conclusion that ICL can improve the radiation environment for high-wire crop production compared to OH SL by increasing the overall light absorption from interior leaves and improving light distribution within the canopy.

Light compensation is the light level at which CO_2 uptake balances CO_2 release, and indicates the point at which further increases in irradiance promote net photosynthesis. Light saturation is the point where irradiance no longer increases photosynthesis, indicating that factors other than light (e.g., rubisco activity, CO_2 concentration, or the metabolism of triose phosphates) have become limiting (Ehleringer and Sandquist, 2010). With traditional OH lighting, middle and lower leaves within a crop foliar canopy may at times be below the LCP of photosynthesis due to mutual shading, while the upper canopy may approach light saturation from incident direct light. It is well known that both LCP and LSP for high-light-adapted leaves are higher than those for plants acclimated to low light, indicative of their capacity to convert more absorbed light energy into photosynthetic products (Ehleringer and Sandquist, 2010; Gu et al., 2008). Therefore, a higher LSP in the lower leaves of plants grown with ICL-LED or hybrid SL compared to those grown under OH lighting (SL or solar) is not surprising, considering that ICL increases light absorption and improves the vertical light distribution within the canopy.

Conclusions

Based on our results, A, θ, $A_{\max}$, and LSP are good indicators of how ICL improves light absorption within a high-wire tomato canopy by diminishing the top-to-bottom decline in photosynthetic activity generally found with OH lighting (SL or solar). Although we found a general increase in lower-leaf photosynthetic capacity from using ICL-LED or hybrid SL, compared to OH-HPS or no SL, no yield differences were recorded among the SL treatments. A possible limitation to yield increases with ICL is the preferential partitioning of photoassimilates to non-harvested, vegetative plant parts (i.e., stems, leaves, roots). Trouwborst et al. (2010) compared total plant production of greenhouse-grown cucumber using hybrid SL (ICL-LED + OH-HPS) vs. OH-HPS lamps and found that LMA and dry mass allocation to leaves were significantly higher under hybrid SL. Furthermore, the authors concluded that, although most photosynthetic parameters were significantly increased in the lower canopy, hybrid SL did not increase total biomass or fruit production relative to OH-HPS SL. Another alternative that may explain the similarities in overall plant growth, yield, and physiological responses measured in our study is that all SL treatments provided the same supplemental DLI. Therefore, similar yield increases relative to control are not necessarily surprising.

Our results further support the conclusion that higher source activity does not always lead to yield increases. However, as shown in this study, replacing OH-HPS lamps with ICL or hybrid SL using LEDs has great potential for energy savings. Given that OH-LED SL has not yet been proven to increase or maintain similar yields relative to OH-HPS (Deram et al., 2014; Dueck et al., 2012; Gajc-Wolska et al., 2013), ICL or hybrid SL with

LEDs can be considered a promising SL alternative for high-wire greenhouse vegetable production. Further research needs to evaluate different light-distribution architectures, lamp densities, spectral composition, and wavelength efficacies at different stages of crop development to achieve optimal productivity and ultimately enable the use of ICL with LEDs for greenhouse vegetable production.

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Table 7. Yield and growth parameters for tomatoes grown in a greenhouse under one of four lighting treatments during a winter-to-summer production cycle in 2014.[z]

Treatments[y]	Total fruit FW (g)[x]	Cluster weight (g)	Fruit harvested (No.)	Nodes (No.)	Harvest period (d)
OH-HPS	15521 a[w]	622 a	114 a	58 a	58 a
ICL-LED	14268 a	570 ab	114 a	54 bc	55 a
Hybrid	14864 a	633 a	108 ab	56 ab	52 a
Control	10753 b	490 b	93 b	51 c	50 a

[z] Values represent results for two side-by-side plants.

[y] Solar + supplemental lighting from overhead high-pressure sodium (OH-HPS) lamps; intracanopy light-emitting diodes (ICL-LED); hybrid lighting (OH-HPS + ICL-LED); or unsupplemented controls.

[x] FW = fresh weight.

[w] Means within columns followed by the same letter are not different based on the least significant difference test ($P \leq 0.05$).

Table 8. Surface tissue temperature of tomatoes grown in a greenhouse under one of four lighting treatments during a winter-to-summer production cycle in 2014.[z]

Treatment[y]	Temperature (°C)[x]			
	2/26[w]	4/1	4/30	5/21
Apex (shoot tip)				
OH-HPS	19.1 a[v]	23.9 ab	27.4 a	26.4 a
ICL-LED	19.3 a	23.2 ab	26.5 a	26.4 a
Hybrid	18.8 a	24.1 a	26.7 a	26.5 a
Control	17.4 b	24.0 ab	26.3 a	26.1 a
FEL				
OH-HPS	16.9 a	23.3 a	24.3 a	25.4 a
ICL-LED	16.6 a	23.4 a	24.5 a	26.0 a
Hybrid	16.6 a	23.2 a	23.2 a	24.5 a
Control	15.6 b	23.4 a	23.5 a	24.8 a
Oldest leaf				
OH-HPS	-	22.7 ab	22.1 a	23.3 a
ICL-LED	-	23.3 a	23.0 a	23.7 a
Hybrid	-	22.6 ab	22.2 a	23.4 a
Control	-	22.2 a	22.9 a	23.4 a

[z] Data were recorded for the apical meristem, newest fully expanded leaf (FEL); 8th leaf below newest leaf $\geq$ 16 cm;(L_1), and/or oldest leaf (approx. 18th leaf below L_1) using a hand-held infrared thermometer.

[y] Solar + supplemental lighting from overhead high-pressure sodium (OH-HPS) lamps; intracanopy light-emitting diodes (ICL-LED); hybrid lighting (OH-HPS + ICL-LED); or unsupplemented controls.

[x] All temperature measurements had a standard error of ± 0.1 °C.

[w] Measurements were recorded on four random dates (forecasted for clear-skies) between 8:00 AM and 10:00 AM.

[v] For each plant part, means within columns followed by the same letter are not different based on the least significant difference test ($P \leq 0.05$).

Table 9. Light-saturated (A_{sat}) and light-limited (A_{lim}) photosynthesis for individual tomato leaves from plants grown in a greenhouse under one of four lighting treatments.[z]

Treatment[y]	A_{sat} (μmol·m^{-2}·s^{-1})			A_{lim} (μmol·m^{-2}·s^{-1})			
	LL1	LL2	LL3		LL1	LL2	LL3
OH-HPS	26.6 a[w]	17.3 b	11.0 de	7.0 a[v]	7.7 a[u]	6.9 b	6.2 c
ICL-LED	24.4 a	18.4 b	12.9 d	7.0 a			
Hybrid	26.2 a	20.0 b	16.6 bc	7.5 a			
Control	18.9 b	12.3 cde	8.6 e	6.2 b			
Treatment		***			***		
Leaf layer (LL)[x]		***			***		
Treatment × LL		***			NS		

[z] A_{sat} and A_{lim} were measured using a photosynthetic photon flux of 1000 or 200 μmol·m^{-2}·s^{-1}, respectively.

[y] Solar + supplemental lighting from overhead high-pressure sodium (OH-HPS) lamps; intracanopy light-emitting diodes (ICL-LED); hybrid lighting (OH-HPS + ICL-LED); or unsupplemented controls.

[x] Top (LL1), middle (LL2), and bottom (LL3) leaves.

[w] Means followed by the same letter are not different based on the least significant difference test ($P \leq 0.05$).

[v] Means within columns followed by the same letter are not different based on the least significant difference test ($P \leq 0.05$).

[u] Means within rows followed by the same letter are not different based on the least significant difference test ($P \leq 0.05$).

Table 10. Photosynthesis (A), stomatal conductance (g_S), transpiration (E), and leaf temperature (LT) measured at ambient environmental conditions for individual tomato leaves from plants grown in a greenhouse under one of four lighting treatments.[z]

Treatment[y]	A (μmol·m^{-2}·s^{-1})				g_s (mmol· m^{-2}·s^{-1})				E (mmol·m^{-2}·s^{-1})				LT (°C)
		LL1	LL2	LL3		LL1	LL2	LL3		LL1	LL2	LL3	
Clear-sky													
OH-HPS	14.3 ab[w]	21.0 a[u]	14.4 b	7.9 c	768.4 a	748.5 a	571.3 ab	375.8 b	5.3				28.0
ICL-LED	15.6 a				493.8 ab				4.2				27.3
Hybrid	17.9 a				558.8 ab				4.5				27.5
Control	9.9 b				469.7 b				3.9				26.8
Treatment	***				**				NS				NS
Leaf layer (LL)[x]	***				***				NS				NS
Treatment × LL	NS				NS				NS				NS
Overcast													
OH-HPS		8.0 a[v]	4.2 abcd	0.5 de	294.3					4.6 a	3.5 ab	3.1 b	26.4
ICL-LED		5.3 abc	3.7 bcde	1.9 cde	269.9								26.4
Hybrid		5.2 abc	2.9 bcde	2.2 cde	354.8								26.5
Control		1.5 cde	1.8 cde	0.2 e	232.4								26.1
Treatment	***				NS				NS				NS
LL	***				NS				*				NS
Treatment × LL	*				NS				NS				NS

[z] Data were collected between 0800 and 1200 HR on Apr. 15-17 and Apr. 19-22, 2014; during this period, the average solar daily light integral directly above plant canopy was 6.5 and 17.8 mol·m^{-2}·d^{-1} for overcast and clear-sky days, respectively.

[y] Solar + supplemental lighting from overhead high-pressure sodium (OH-HPS) lamps; intracanopy light-emitting diodes (ICL-LED); hybrid lighting (OH-HPS + ICL-LED); or unsupplemented controls.

[x] Top (LL1), middle (LL2), or bottom (LL3) leaves.

[w] Means within column followed by the same letter are not different based on the least significant difference test ($P \leq 0.05$).

[v] Means followed by the same letter are not different based on the least significant difference test ($P \leq 0.05$).

[u] Means within row followed by the same letter are not different based on the least significant difference test ($P \leq 0.05$).

Table 11. Photosynthetic parameters estimated from light-response curves measured in three leaf layers (LL) from tomato plants grown in a greenhouse under one of four lighting treatments.[z]

Treatment (T)[y]	Dark respiration ($\mu mol \cdot m^{-2} \cdot s^{-1}$)			Quantum use efficiency (mol CO_2 ·mol photon^{-1})			Convexity (*k*)	A_{max} ($\mu mol \cdot m^{-2} \cdot s^{-1}$)[x]		
	LL1	LL2	LL3	LL1	LL2	LL3		LL1	LL2	LL3
OH-HPS	0.7 ab[w]	1.2 a	0.6 b	0.048 a[v]	0.048 a	0.039 c	0.935 ab[u]	30.0 ab	27.4 abc	15.6 de
ICL-LED				0.046 ab	0.050 a	0.045 ab	0.928 ab	26.5 abc	28.3 abc	23.7 abcd
Hybrid				0.049 a	0.048 a	0.043 ab	0.915 b	31.7 a	29.8 ab	23.5 abcd
Control				0.045 ab	0.043 ab	0.032 c	0.950 a	27.4 abc	19.9 cde	10.9 e
T		NS			***		*		***	
LL		*			***		NS		***	
T × LL		NS			*		NS		*	

[z] Top (LL1), middle (LL2), or bottom (LL3) leaves.

[y] Solar + supplemental lighting from overhead high-pressure sodium (OH-HPS) lamps; intracanopy light-emitting diodes (ICL-LED); hybrid lighting (OH-HPS + ICL-LED); or unsupplemented controls.

[x] A_{max} = maximum gross CO_2 assimilation.

[w] Means within row followed by the same letter are not different based on the least significant difference test ($P \leq 0.05$).

[v] Means followed by the same letter are not different based on the least significant difference test ($P \leq 0.05$).

[u] Means within column followed by the same letter are not different based on the least significant difference test ($P \leq 0.05$).

Table 12. Light compensation point (LCP) and light saturation point (LSP) calculated from light-response curves measured for individual tomato leaves from plants grown in a greenhouse under one of four lighting treatments.[z]

Treatment[y]	LCP ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	LSP ($\mu mol \cdot m^{-2} \cdot s^{-1}$)		
		LL1	LL2	LL3
OH-HPS	25.9	1185.4 ab[w]	974.1 abcd	641.3 de
ICL-LED	23.7	1001.5 abc	1337.7 a	1131.2 ab
Hybrid	26.2	1260.3 ab	1273.8 ab	943.4 bcd
Control	18.0	952.7 bcd	722.5 cde	517.8 e
Treatment	NS		***	
Leaf layer (LL)[x]	NS		**	
Treatment × LL	NS		*	

[z] LCP and LSP were calculated as the photosynthetic photon flux associated when CO_2 assimilation = 0 and CO_2 assimilation = maximum gross CO_2 assimilation × 0.90, respectively.

[y] Solar + supplemental lighting from overhead high-pressure sodium (OH-HPS) lamps; intracanopy light-emitting diodes (ICL-LED); hybrid lighting (OH-HPS + ICL-LED); or unsupplemented controls.

[x] Top (LL1), middle (LL2), and bottom (LL3) leaves.

[w] Means followed by the same letter are not different based on the least significant difference test ($P \leq 0.05$).

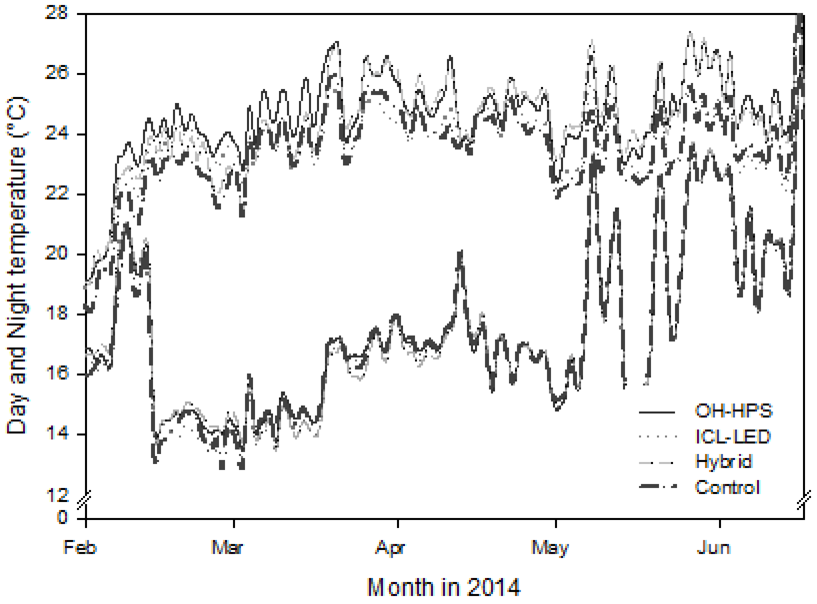

Figure 12. Ambient day and night greenhouse-air temperatures under one of four lighting treatments: solar + supplemental lighting from overhead high-pressure sodium (OH-HPS) lamps; intracanopy light-emitting diodes (ICL-LED); hybrid lighting (OH-HPS + ICL-LED); or unsupplemented controls. Measurements were made every 10 s and a datalogger recorded means at 10-min intervals throughout the duration of the experiment.

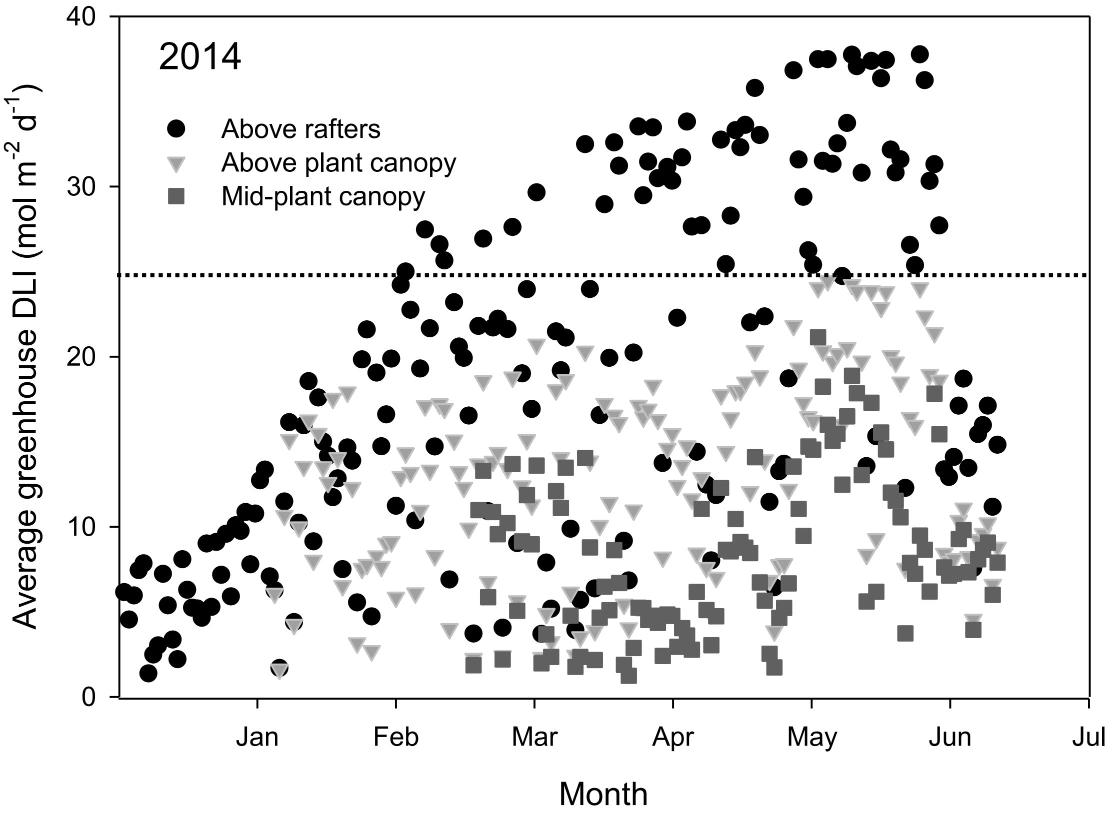

Figure 13. Solar daily light integral (DLI) inside a glass-glazed greenhouse in West Lafayette, IN (40° N. latitude). The dotted line represents the threshold of solar DLI below which supplemental lighting was required for optimal tomato production.

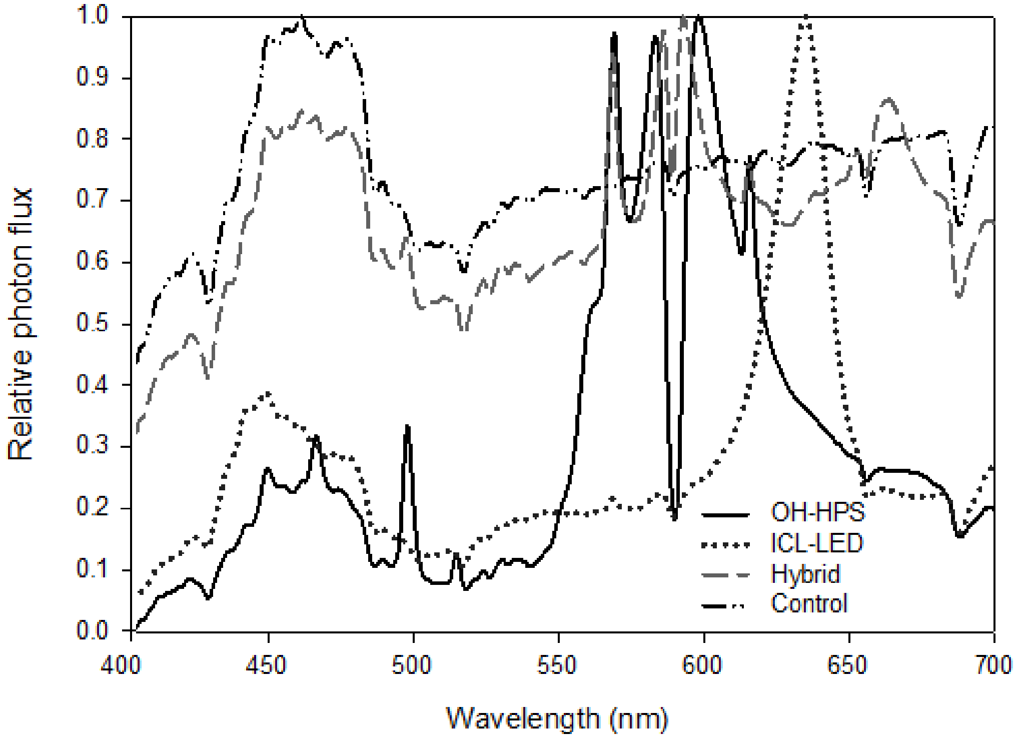

Figure 14. Treatment-specific spectra [solar + supplemental lighting (SL)] averaged across three leaf layer within a high-wire tomato canopy. The treatments evaluated were: overhead high-pressure sodium (OH-HPS) lamps; intracanopy light-emitting diodes (ICL-LED); hybrid SL (OH-HPS + ICL-LED); or unsupplemented controls. Measurements were collected inside a glass-glazed greenhouse on two clear-sky days using a spectroradiometer.

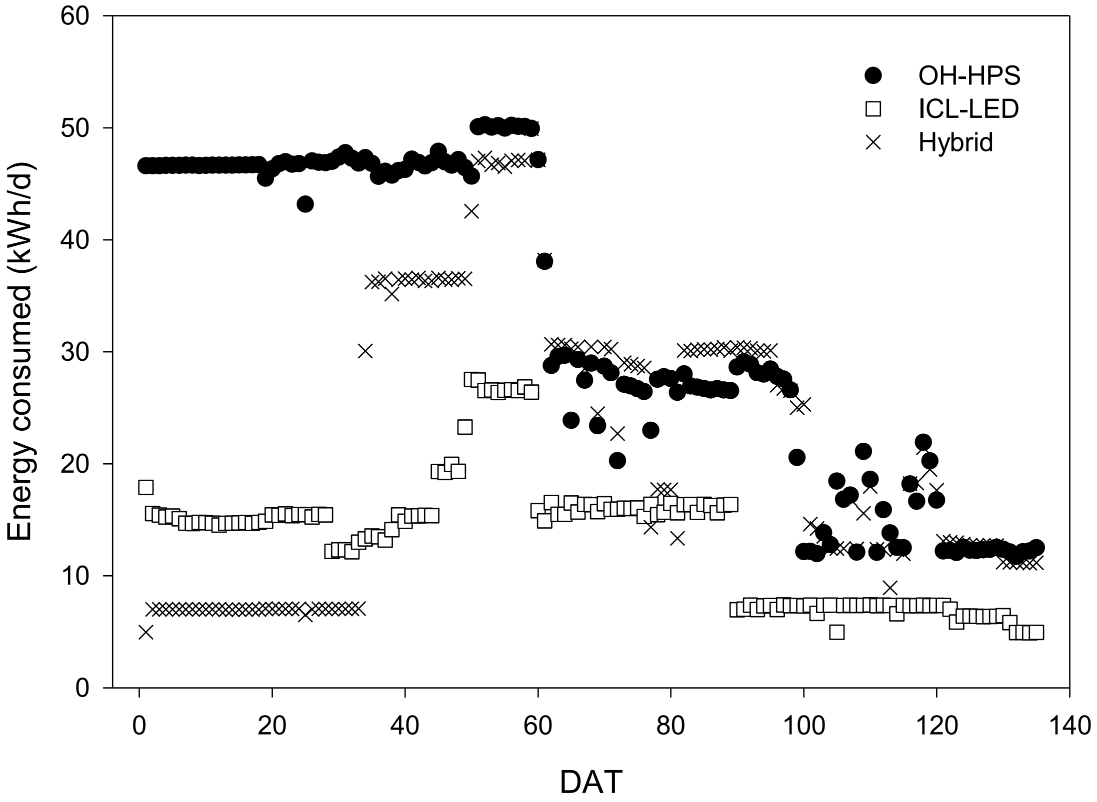

Figure 15. Daily energy consumption from three supplemental lighting treatments [overhead high-pressure sodium (OH-HPS; 600 W) lamps, intracanopy light-emitting diode (ICL-LED) towers, or hybrid (400 W OH-HPS + 2 tier- LED interlights)] used for the production of greenhouse-grown tomatoes during a winter-to-summer production cycle in 2014. Values represent the total energy consumed from 3 reps × 2 lamps/towers. DAT = days after transplanting.

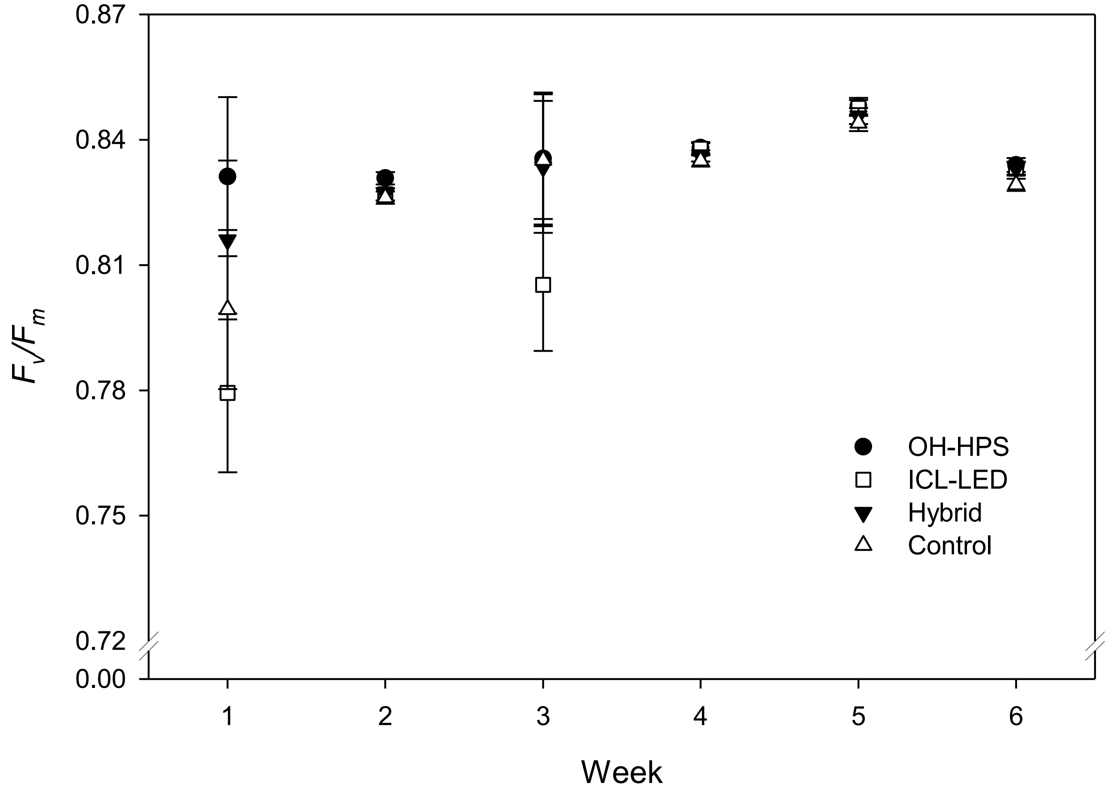

Figure 16. Maximum photosystem II efficiency (F_v/F_m) of tomato leaves from plants grown in a greenhouse under one of four lighting treatments: solar + supplemental lighting from overhead high-pressure sodium (OH-HPS) lamps; intracanopy light-emitting diodes (ICL-LED); hybrid lighting (OH-HPS + ICL-LED); or unsupplemented controls. Data represents means ± SE (n = 24).

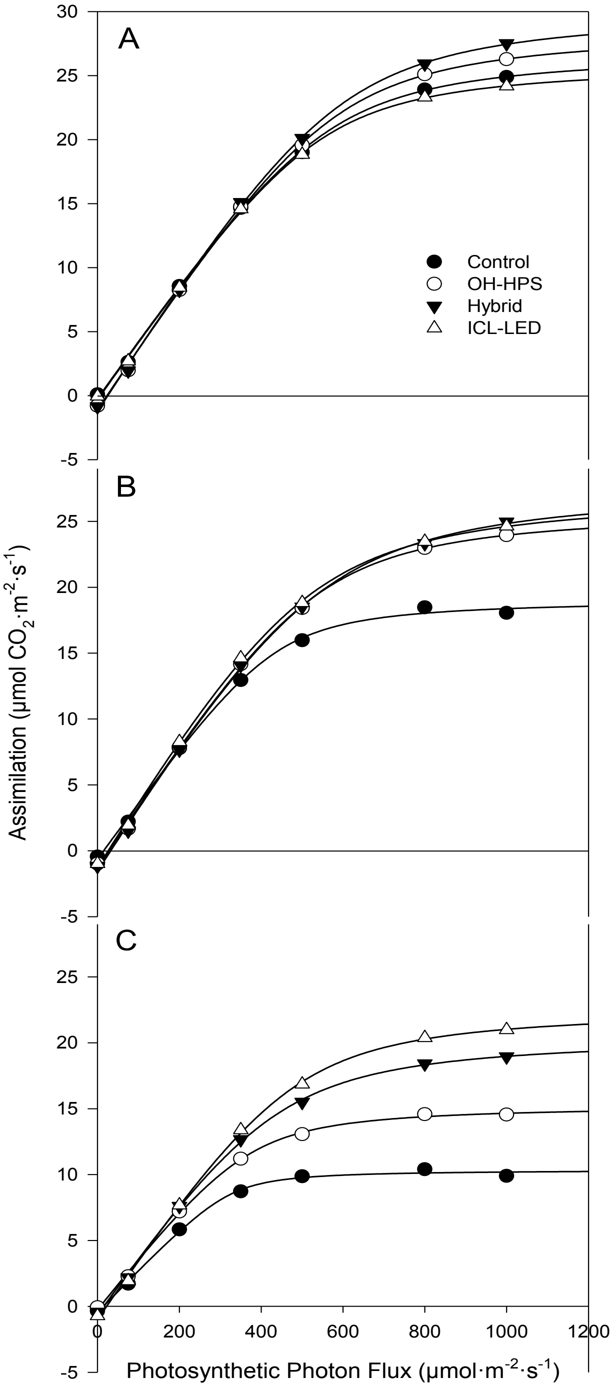

Figure 17. Photosynthetic light-response curves for top (A), middle (B) and bottom (C) leaves from tomato plants grown in a greenhouse under one of four lighting treatments: unsupplemented controls; solar + supplemental lighting from overhead high-pressure sodium (OH-HPS) lamps; intracanopy light-emitting diodes (ICL-LED); or hybrid lighting (OH-HPS + ICL-LED).

CHAPTER 5: SUMMARIZING CONCLUSIONS AND SUGGESTIONS FOR FUTURE WORK

Introduction

The objective of this research was to evaluate light-emitting diodes (LEDs) as alternative supplemental lighting (SL) sources for greenhouse tomato (*Solanum lycopersicum* L.) propagation and production. Tomato was selected as a model crop based on its high-light requirement: an average daily light integral (DLI) $\geq$16 $\mathrm{mol \cdot m^{-2} \cdot d^{-1}}$ is considered optimal for tomato-seedling production (Fan et al., 2013; Moe et al., 2006), whereas 20-35 $\mathrm{mol \cdot m^{-2} \cdot d^{-1}}$ are generally recommended for maximizing yields (Dorais, 2003; Faust, 2001; Jones, 2008; Moe et al., 2006; Spaargaren, 2001). The studies herein compared overhead (OH) high-pressure sodium (HPS) lamps (industry standard) to LED SL, and establish proof of concept that LEDs can be used effectively for greenhouse SL. This chapter summarizes how results from these system comparisons contribute to furthering scientific and practical understanding of the impact of LED lighting on plant growth and development. The chapter concludes with some questions raised from our work and comments on what I consider are important matters that could be further explored with LED SL.

Seasonal Growth-Responses to Different Spectra of SL (Chapter 2)

In Chapter 2 we compared seasonal growth responses to three red:blue ratios of LED SL vs. HPS lamps vs. unsupplemented controls for the propagation of six tomato cultivars. Our general findings suggests that spectral effects on tomato-seedling growth from different SL treatments are season-specific and most likely depend on ambient solar DLI and seasonal fluctuations in greenhouse air temperature. In general, we found that for all cultivars evaluated, a combination of red and blue wavebands in SL increased growth and productivity of tomato seedlings during winter and summer (lowest- and highest-solar DLI, respectively), whereas fewer SL treatment effects were observed during the transitional-solar DLI spring and fall periods. Therefore, adding blue light to SL has the potential to increase overall seedling growth compared to blue-deficient SL treatments in overcast, variable-DLI climates. Based on the results from chapter 2, we recommend that LED systems for commercial applications include variable wavelength and dimming capabilities that can offer propagators the ability to select light spectra for maximizing transplant growth during different seasons.

Intracanopy Lighting with LEDs (Chapter 3)

Intracanopy lighting (ICL) refers to the strategy of lighting along the side or within the foliar canopy. In Chapter 3 we compared SL from OH-HPS lamps vs. ICL using LEDs (ICL-LED) for high-wire greenhouse tomato production. The objective of the study was to quantify plant growth, yield, and energy consumption using different SL sources and positions within the canopy. We found that the ICL-LED technology supports similar growth and yield compared to OH-HPS but at lower electrical costs (from SL only).

Therefore, we concluded that ICL-LED is a viable alternative to OH-HPS SL. With ongoing, anticipated energy-efficiency improvements, as well as ever-improving light-distribution architectures, LEDs have the potential to become a dominant SL technology for greenhouse crop production.

Physiological Responses of High-Wire Greenhouse-Grown Tomato to ICL (Chapter 4)

Chapter 4 was, to some extent, a continuation of the studies reported in Chapter 3. The objective of the study was to compare crop physiological responses to different SL sources and positions [ICL-LED vs. OH-HPS vs. hybrid lighting (ICL-LED + OH-HPS)] within an indeterminate high-wire tomato canopy. We also quantified fruit production and energy consumption for plants grown under the different lighting treatments. Our results provide some insight into how ICL modifies the vertical light distribution and light absorption within a high-wire tomato canopy relative to OH SL. We found that CO_2 assimilation measured under ambient environmental conditions (A), photosynthetic quantum yield (θ), maximum gross CO_2 assimilation (A_{max}) and the light-saturation point of photosynthesis were good indicators of how ICL diminishes the top-to-bottom decline in photosynthetic activity typically observed with OH SL. However, we did not find any yield differences among SL treatments, indicating that higher source activity does not necessarily lead to yield increases. Based on the lower energy consumption measured for ICL-LED, and, to a lesser extent, for hybrid SL, compared to OH-HPS, we concluded that replacing OH-HPS lamps with ICL-LED or hybrid SL has great potential for energy savings during high-wire greenhouse tomato production. However, our results showed that higher canopy photosynthesis does not lead to higher yields, most likely due to a redistribution of photoassimilate partitioning to non-harvested, vegetative plant parts.

Questions Raised and Suggestions for Future Studies

- Would homogeneous light distribution from SL increase fruit production and/or affect plant physiological responses?

For comparative analysis, our studies were conducted in such a way that ICL-LED SL provided similar vertical light intensities as OH-HPS, that is, plants growing in both treatments experienced a decline in photosynthetic photon flux (*PPF*) with increasing vertical distance from to top to the bottom of the canopy (in the absence of plants). However, in some aspects, this approach defeats the purpose of delivering more homogeneous light distribution within the canopy, which is one of the main advantages of ICL (another being increasing light absorption within the canopy). An experiment could be conducted comparing a treatment with a decline in top-to-bottom *PPF* vs. a constant vertical *PPF* (keeping the average of total SL DLI the same). It is possible that by maintaining a homogenous light intensity along the canopy, yield increases may occur and/or physiological metrics would respond differently.

- Would changing the light spectrum according to a plant’s physiological age affect plant growth and productivity?

As suggested by Cope and Bugbee (2013), it is likely that the optimal light spectrum for plant growth and development changes with plant age. An experiment could evaluate spectral effects of LED SL [by comparing different red:blue ratios (or additional wavelengths)] during different plant-growth stages (vegetative vs. reproductive). If possible, tomato plants would be propagated under a set of different light-quality treatments and grown into a reproductive phase (harvest 1-3 clusters per plant) with either the same or additional light-quality treatments. Alternatively, an experiment could be conducted using the ICL-LED towers where the different panels within a tower (upper, middle, and bottom) would provide different spectra in such a way that the new growth (upper canopy) would receive a different red:blue ratio than older leaves (from the mid- and/or lower canopy). Evaluating physiological, developmental, and production metrics could help determine if plant growth can be further optimized with changes in light quality from SL.

- Can start-of-day selective lighting serve as an energy-savings strategy?

Daily photosynthetic induction occurs gradually after leaves have been in darkness for a certain period of time and then transferred to a saturating light level (Lambers et al., 2008). At this point, the photosynthetic rate increases progressively over a period of up to one hour to a new steady-state rate, with stomatal conductance increasing more or less in parallel. Additionally, there is evidence that blue light has a major role in stimulating stomatal opening in plants (Zeiger, 2010). Thus, we hypothesize that plants could start their photosynthetic induction process using less light than that required for photosynthetic purposes. An experiment could test different levels of blue light only vs. red + blue during the first hour of the targeted photoperiod. Survey leaf gas exchange measurements would help find the light level/spectra that induces early photosynthetic induction in plants. Also, photosynthetic measurements could indicate when plants coming out of darkness are ready to resume a significant level of photosynthesis. This experiment could potentially show whether start-of-day selective lighting can lead to extra energy savings (by not ‘wasting’ SL when plants are not ready for it) or not.

- Where should we focus the SL when growing high-wire greenhouse-grown tomatoes? Will only lighting the mature leaves be enough to support clusters with developing fruits?

To address this question in terms of long-term fruit yield, an experiment could compare treatments that provide different light distribution within the canopy: using only the middle panel of an ICL-LED tower (see Chapter 3 for full description) vs. all three panels energized vs. only top two panels vs. only bottom two. The output of supplemental light intensity should be equivalent for all treatments.

- What are the best criteria for leaf pruning?

This question can be addressed through leaf gas exchange measurements, which will help determine when leaves can or should be defoliated. Different photosynthetic metrics might indicate which leaves are photosynthetically competent and when. Also, net photosynthesis could help determine when young leaves are no longer sinks and when mature leaves become sinks again as they become older. To do this, the same leaf should be measured during different stages of development. However, this raises the question, even if lower leaves are photosynthetically competent, are they still needed (especially if fruit clusters near them already have been harvested)? This could be done as a side-study in an experiment comparing OH-HPS vs. ICL-LED.

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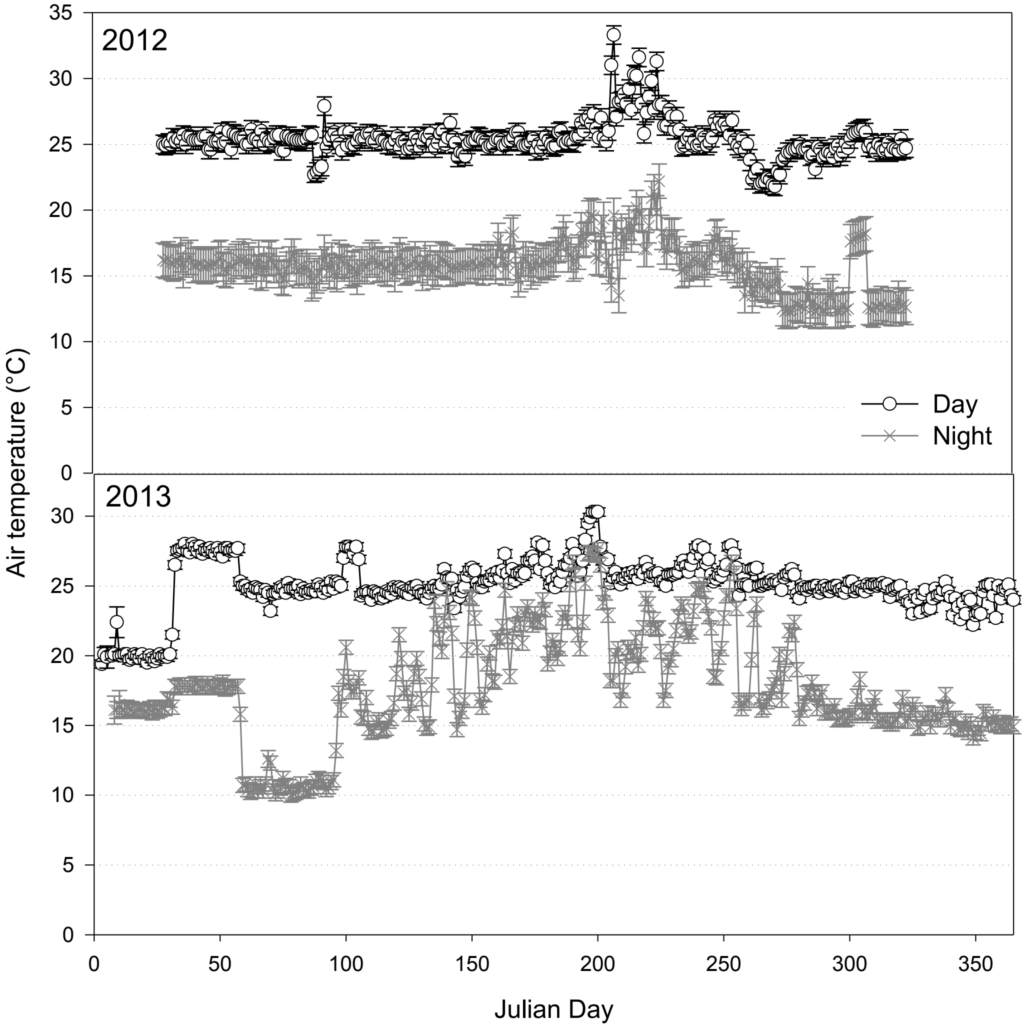
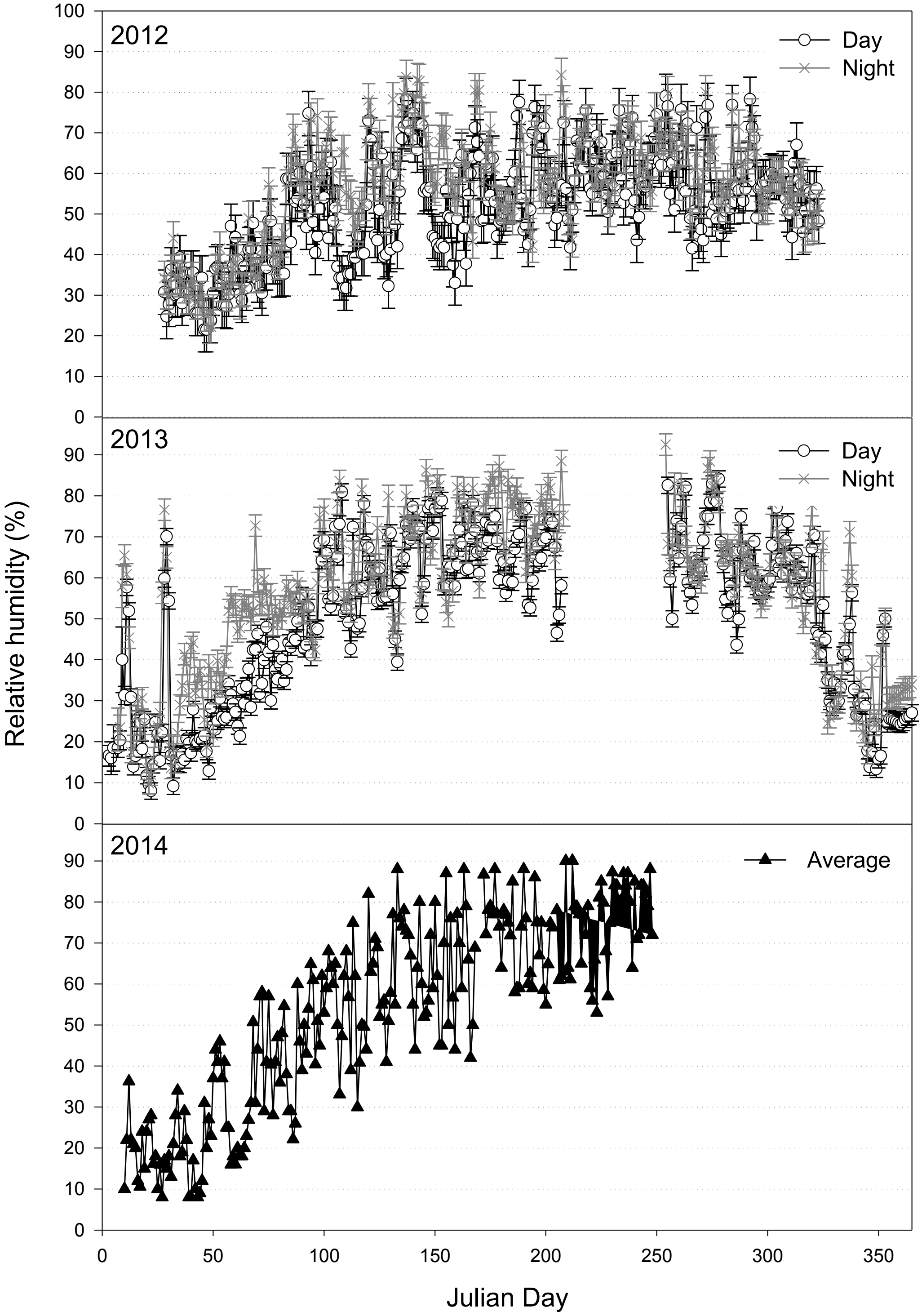
APPENDICES



Appendix A. Average day and night greenhouse-air temperature. Measurements were at the mid-point of the greenhouse every 10 s and a datalogger recorded means at 3-hour intervals.



Appendix B. Average greenhouse-relative humidity. Measurements were at the mid-point of the greenhouse every 10 s and a datalogger recorded means at 3-hour intervals.

VITA

VITA

Celina Gómez Vargas was born January 4th, 1986 to José María Gómez Lugo and Lilliana Vargas Rojas. She briefly grew up, along with her three siblings, José María, Renée Alejandra, and Luis Fernando in San José, Costa Rica. At the age of 7, Celina and her family moved to Guatemala City, Guatemala, where they lived for the next 16 years. Before turning 17, Celina moved to Reggio nell'Emilia, Italy, to start a one-year study-abroad program where she lived with Cecilia and Luigi Borettini. During that year (2002-2003), she learned about the Italian culture and got to share her intercultural experience with students from all over the world. After returning home and finishing high school, Celina moved to Valle del Yeguare, Honduras and attended college at Zamorano University. In 2008 she earned a Bachelor's of Science degree in Plant and Animal Production (Agriculture) with an emphasis in Horticulture advised by Gloria Arévalo de Gauggel. Upon graduation, Celina moved to Fayetteville, Arkansas and entered the Masters of Agriculture program in Horticulture at the University of Arkansas. In 2010, Celina completed her Masters with Dr. James Robbins working on soil-less container substrates for nursery production. In 2011, Celina started her Ph.D. program in the Horticulture and Landscape Architecture Department at Purdue University, working under the advice of Dr. Cary A. Mitchell. Upon graduation, Celina would like to get a job with the industry to continue her research path in controlled environment agriculture.

CURRICULUM VITAE- CELINA GÓMEZ VARGAS

EDUCATION

Ph.D. candidate in Horticulture January 2011-present
Departments of Horticulture and Landscape Architecture (HLA)
Purdue University, West Lafayette, IN
Focus: Environmental plant physiology, controlled environments, and greenhouse crop production
Major Professor: Cary A. Mitchell

M.Sc. in Horticulture, University of Arkansas, Fayetteville, AR December 2010
Focus: Nursery production and substrate evaluation
Major Professor: James A. Robbins

B.Sc. in Agronomy, Zamorano University, Honduras December 2008
Focus: Hydroponics and protected crop production
Major Professor: Gloria Arévalo de Gauggel

PROFESSIONAL AND RESEARCH EXPERIENCE

Graduate Research and Teaching Assistant January 2011-present
HLA Department, Purdue University

- Conducted research aiming to optimize the light environment for greenhouse crop production
- Mentored undergraduate students interested in applied research
- Assisted in teaching Plant Physiology to undergraduate students in the College of Agriculture

Graduate Research Assistant 2010-2011
Horticulture Department, University of Arkansas

- Evaluated different substrates for propagating and producing nursery crops

Professional Internship 2008
Entomology and Nematology Department, University of Florida

- Assisted in the development of prediction models to anticipate spring emergence of insect pests
- Facilitated the design of several web pages describing insect pests

Professional Internship 2004
Biology Department, Del Valle University, Guatemala
Two-week internship assisting researchers in the tissue culture laboratory

REFEREED PUBLICATIONS/RESEARCH PROCEEDINGS

Gómez, C. and C.A. Mitchell. 2015. Growth responses of tomato seedlings to different spectra of supplemental lighting. HortScience *In press*.

Gómez, C. and C.A. Mitchell. 2014. Supplemental lighting for greenhouse-grown tomatoes: intracanopy LED towers vs. overhead HPS lamps. Acta Hort. 1037:855-862.

Gómez, C., R.C. Morrow, C.M. Bourget, G.D. Massa, and C.A. Mitchell. 2013. Comparison of intracanopy light-emitting diode towers and overhead high-pressure sodium lamps for supplemental lighting of greenhouse-grown tomatoes. HortTechnology 23:93-98.

Gómez, C. and Robbins, J. 2011. Pine bark substrates amended with parboiled rice hulls: physical properties and growth of container-grown spirea during long-term nursery production. HortScience 46:784-790.

Gómez, C. and Robbins, J. 2011. Parboiled rice hulls effect on physical properties of amended pine bark substrates during long-term nursery crop production. Proc. Southern Nursery Assoc. Research Conf. 56:254-259.

J. Robbins and **C. Gómez**. 2011. Evaluation of eight slow-release fertilizers on the growth of container grown Spiraea × bumalda L. ‘Anthony Waterer’. Proc. Southern Nursery Assoc. Research Conf. 56:288-291.

Gómez, C. and J. Robbins. 2011. Rooting of two woody ornamental plants in eight propagation substrates. Proc. Southern Nursery Assoc. Research Conf. 56:393-396.

Gómez, C. and J. Robbins. 2010. Parboiled rice hull effects on plant growth and water requirements of container-grown shrubs. Proc. Southern Nursery Assoc. Research Conf. 55:55-63.

Gómez, C. and J. Robbins. 2009. Rooting of three ornamental plants in eight propagation substrates. Comb. Proc. Intl. Plant Prop. Soc. 59:534-538.

REFEREED PUBLICATIONS- IN PREPARATION

C. Mitchell, J.F. Burr, M.J. Dzakovich, **C. Gómez**, R. Lopez, R. Hernández, C. Kubota, C.J. Currey, Q. Meng, E.S. Runkle, C.M. Bourget, R. C. Morrow, and A.J. Both. 2015. Light-Emitting Diodes in horticulture. Under revision in Hort. Reviews

Gómez, C., M. Clark, and C.A. Mitchell. Tomato growth, productivity, and physiological responses as affected by root-zone temperature and/or LED-supplemental lighting at supraoptimal air temperature. To be submitted in Acta Hort.

EXTENSION PUBLICATIONS

Gómez, C. and R. Mizell. 2008. *Euschistus servus*. Featured Creature article UFL Dept. of Entomol. and Nematol.

Gómez, C. and R. Mizell. 2008. *Proxys punctalatus*. Featured Creature article UFL Dept. of Entomol. and Nematol.

Gómez, C. and R. Mizell. 2008. Cypress twig gall midge. Featured Creature article UFL Dept. of Entomol. and Nematol.

Gómez, C. and R. Mizell. 2008. *Acrosternum hilare*. Featured Creature article UFL Dept. of Entomol. and Nematol.

Gómez, C. and R. Mizell. 2008. *Br*yobia praetiosa. Featured Creature article UFL Dept. of Entomol. and Nematol.

SCIENTIFIC ORAL PRESENTATIONS

American Society of Horticultural Sciences (ASHS) conference, Orlando, FL. 2014- Can we increase the production efficiency of an indeterminate high-wire tomato crop with LED intracanopy supplemental lighting?

North Central Extension & Research Activity–101 (NCERA-101) meeting, Fairbanks, AK. 2014- Use of light-emitting diodes for greenhouse-grown tomato propagation and production.

International Society of Horticultural Sciences, GreenSys Conference, Jeju, S. Korea. 2013- Supplemental lighting for greenhouse-grown tomatoes: Intracanopy LED towers vs. overhead HPS lamps.

ASHS conference, Palm Desert, CA. 2013- Supplemental Lighting for Greenhouse-grown Tomatoes: Intracanopy LED Towers vs. Overhead HPS Lamps.

Departmental research retreat, HLA Department, Purdue University. 2013- Year-round production of high-wire greenhouse-grown tomatoes: Intracanopy LED towers vs. overhead HPS lamps.

NCERA-101 meeting, West Lafayette, IN. 2013 Light-emitting diodes as an alternative for supplemental lighting of high-wire greenhouse grown tomatoes.

ASHS conference, Miami, FL. 2012- Evaluation of LEDs for supplemental lighting of greenhouse-grown tomatoes for a northern climate.

NCERA-101 meeting, Ames, IA. 2011- Light-emitting diodes: a lighting option for greenhouse-grown tomatoes.

Southern Nursery Association (SNA) meeting, Mobile, AL. 2010- Parboiled rice hulls effect on plant growth and irrigation requirements of container-grown shrubs.

Southern Region International Plant Producers Society (IPPS) meeting, Biloxi, MS, 2009- Rooting of three ornamental plants in eight propagation substrates.

Georgia Entomological Society Meeting, Codele, GA. 2008- A day-degree model for plum curculio.

ACADEMIC AWARDS/ RECOGNITIONS

• 1st place, Controlled Environment Working Group (CEWG) student oral competition, ASHS Conference, Orlando, FL	2014
• 3rd place, graduate student poster competition, ASHS Conference, Orlando, FL	2014
• 3rd place, PhD student poster competition, HLA Department, West Lafayette, IN	2014
• 3rd place, student poster competition, NCERA-101 meeting, Fairbanks, AK	2014
• 2nd place, CEWG oral student competition, ASHS Conference, Palm Desert, CA	2013
• 3rd place, CEWG oral student competition, ASHS Conference, Miami, FL	2012
• 2nd place, student poster competition, NCERA-101 meeting, Ames, IA	2011

- Outstanding M.Sc. Student, Horticulture Department, University of Arkansas 2010
- 1st place, student oral competition, Southern IPPS meeting, Biloxi, MS 2010
- The Nippon Foundation Scholarship, Zamorano University 2005-2008

LEADERSHIP EXPERIENCE

- Vice-president, Association of Zamorano Alumni at Purdue University 2013-2014
- Graduate student representative, HLA Safety Committee 2013-2014
- President- HLA Department, Grad. Student Committee, Purdue University 2012-2013
- HLA Departmental graduate student rep., College of Agriculture, Graduate Student Advisory Council, Purdue University 2012-2013
- Secretary, Association of Zamorano Alumni at Purdue University 2011-2012

LANGUAGE AND TECHNICAL SKILLS

Fluent in Spanish (native), English (high proficiency) and Italian (high proficiency).

Broad awareness of experimental approaches for data acquisition, analysis, and interpretation. Wide range managing computer software: Windows, Office, SAS Programming, JMP, Sigmaplot graphing.