SEEDLING GROWTH IS GENERALLY SIMILAR UNDER SUPPLEMENTAL
GREENHOUSE LIGHTING FROM LIGHT-EMITTING DIODES OR HIGH-PRESSURE
SODIUM LAMPS

By

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ABSTRACT

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Light-emitting diodes (LEDs) have the potential to replace high-pressure sodium (HPS) lamps to provide supplemental lighting (SL) in greenhouses and consume less energy. Different wavebands of light can be delivered by LEDs to potentially regulate plant morphology by stimulating photoreceptors. However, we postulated that differences in the light quality of SL would be diminished given the broad spectral distribution of sunlight plants receive in greenhouses. Two series of experiments were performed with seedlings of tomato, pepper, geranium, petunia, and snapdragon. Plants were grown at 20 °C under five SL treatments (four from LEDs and one from HPS lamps) at a *PPFD* of 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$ or at 10 $\mu mol \cdot m^{-2} \cdot s^{-1}$ from HPS lamps, all for 16 $h \cdot d^{-1}$. Regardless of light quality, growth was greater under the higher SL intensity. There was little or no effect of the percentage of blue (400-500 nm) light (from 10 to 45%) on leaf area, leaf number, plant height, and dry shoot and root weight when seedlings were grown under the same SL intensity. When SL was applied during the seedling phase alone, there was no effect of SL quality on subsequent flowering, but when SL treatments were continued after transplant, geranium under 45% blue + 55% red (600-700 nm) was shorter at flowering than those grown under HPS lamps. Including far-red (700-800 nm) radiation in SL showed some promotion of flowering but also extension growth. The LEDs used in this study were more energy efficient than HPS lamps while seedling and flowering plants were of similar quality. Thus, while LED SL did not elicit specific morphological effects, the LEDs used in these experiments are suitable and more energy-efficient replacements for HPS lamps.

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Supplemental Lighting in the Michigan Bedding Plant Industry

The commercial wholesale value of floriculture crops sold in 15 of the largest producing states in the U.S. is reported each year and in 2014, it was valued at $4.07 billion (USDA, 2015). Michigan is the third largest producing state with a reported wholesale value of $406 million for crops sold in 2014. Bedding plants are the largest contributor to total floriculture sales and Michigan leads the nation in production of annual bedding and garden plants and propagative floriculture material, valued at $204 million and $83 million, respectively (USDA, 2015). Bedding plants and many other floriculture crops are started from seeds or cuttings and grown in controlled greenhouse environments in high density plantings to optimize space usage. To coordinate production cycles and have finished plant material ready for spring markets, production of seedlings for transplant occurs in the winter when natural light levels are lowest. The daily light integral (DLI), which is the total amount of photosynthetically active radiation (PAR; 400-700 nm) accumulated in a day, depends on weather conditions, latitude, and the time of year. In Michigan and other northern latitudes, DLI outdoors can be as low as 5 to 10 $mol \cdot m^{-2} \cdot d^{-1}$ (Korczynski et al., 2002). Additionally, glazing material, structural components, and other obstructions such as hanging baskets can reduce ambient light inside the greenhouse by 50% or more (Fisher and Runkle, 2004).

During the seedling phase, DLI has a direct effect on transplant quality parameters such as increased dry mass per internode or compactness and reduced time to flower after transplant. Pramuk and Runkle (2005) measured the response of five species of bedding plant seedlings to DLI ranging from 4.1 to 14.2 $mol \cdot m^{-2} \cdot d^{-1}$ while maintaining similar temperatures among

treatments. In four of the five species tested, as DLI increased to 14.2 mol·m^{-2}·d^{-1}, average dry shoot weight per internode increased linearly. In salvia (*Salvia splendens* 'Vista Rose'), average dry shoot weight per internode reached a maximum at 12 mol·m^{-2}·d^{-1}, showing that different species attain saturation of DLI effects at higher and lower DLIs (Pramuk and Runkle, 2005). The study also showed that increasing DLI had a direct effect on reducing time to flower and number of nodes before flower initiation. For example, time to flower of celosia (*Celosia argentea* var. *plumosa* 'Gloria Mix') and salvia was reduced by 24% and 41% as DLI increased from 4.1 to 14.2 mol·m^{-2}·d^{-1}, and time to flower of marigold (*Tagetes patula* 'Bonanza Yellow'), viola (*Viola ×wittrockiana* 'Crystal Bowl Yellow'), and impatiens (*Impatiens walleriana* 'Accent Red') was reduced by 19%, 28%, and 33%, respectively, as DLI increased to 11 to 13 mol·m^{-2}·d^{-1}. In general, however there was a tradeoff; reduced time to flower coincided with reduced plant mass and total flower number at flowering, most likely because plants under low DLI conditions had a longer vegetative phase (Pramuk and Runkle, 2005).

Numerous methods have been used to increase the DLI in greenhouses. Greenhouse coverings or glazing materials vary in the amount of light transmitted. Typical maximum light transmittance of glazing materials ranges from 90% for single-layer glass to 80% for double-layered polyethylene (Both and Faust, 2004). These percentages are reported for new materials; as dust accumulates and glazing materials age and degrade, light transmission is further reduced. Choosing the most suitable glazing material and maintaining it, as well as minimizing overhead obstructions like heating pipes and electrical conduits, can reduce light losses, but to increase DLI, supplemental lighting (SL) is provided by electric light fixtures. The most common method for providing SL is through high-intensity discharge (HID) lamps, which includes both metal halide (MH) and high-pressure sodium (HPS) fixtures (Ciolkosz et al., 2001). High-pressure

sodium lamps are commonly used in favor of MH lamps for SL in greenhouse crop production because they have a higher energy conversion factor and longer bulb life (Fisher and Both, 2004). Fluorescent lamps are relatively energy efficient but the large number of tubes and their ballasts create too much shading for most commercial greenhouse applications. A relatively new lighting technology, light-emitting diodes (LEDs), has the prospect of being used for SL in greenhouse crop production.

Light-emitting Diode Technology

Light-emitting diodes are fundamentally different than other lighting systems used for SL. They feature solid-state construction and emit light as current passes across a diode junction (Pimputkar et al., 2009). The robustness and potential long lifespan of LEDs helped drive their early use in power-signaling operations such as indicator lights, traffic lights, and automotive lighting, where increased implementation costs were offset by their compactness and durability (Haitz et al., 2000). Depending on the materials used in the junction, LEDs can emit radiation with wavelengths from 250 nm to over 1,000 nm (Bourget, 2008). Because there are no bulbs or filaments involved in the emission of light, LEDs potentially have a longer life span. For conventional lamps, repeated on/off cycles reduce the lifetime of filaments, and electronic ballasts must be periodically replaced (Morrow, 2008). The current reported operating life of LED units ranges from 20,000 to 50,000 hours (Morrow, 2008). Rather than failing completely, the intensity of LED arrays decreases over time as individual diodes fail. Therefore, operating life is defined by the point when their output drops to some percentage of their initial irradiance, often 70 or 80% (Philips Lumileds, 2012). The closed (damp proof) construction of LEDs is an

important feature for greenhouse use to minimize exposure to high humidity, misting, sprays, and disinfectants.

The solid-state construction of LEDs also creates the potential for effective spatial distribution of fixtures to create a very uniform light intensity in greenhouse bays. High-pressure sodium and MH lights have extremely high operating temperatures that require sufficient distance between the fixture and crop canopy to avoid heat stress and excessive drying of the substrate (Fisher and Both, 2004). Thus, they must be placed at an appropriate height above the crop canopy and additional fixtures are needed around the greenhouse perimeter to achieve uniformity (Ciolkosz et al., 2001; Nelson and Bugbee, 2014). Compared to HID lamps, LEDs emit a relatively small amount of infra-red radiation and for passively cooled fixtures, the heat that is created can be dissipated through the mounting surface and transferred to the greenhouse structure (Bourget, 2008). Given their reduced operating temperature, LED fixtures can be placed close to or within the crop canopy and canopy photon capture can approach 100% (Nelson and Bugbee, 2014). LED arrays can also be placed directly above a growing crop and allow for multiple tiers of production in the same footprint (Watanabe, 2011).

Different materials used in the LED junction result in different spectral output (Bourget, 2008). Depending on the materials used for the emission of different colors, electrical conversion efficiencies differ (Haitz et al., 2000; Nelson and Bugbee, 2014). When LED technology was first being explored for plant lighting, red light (R, 600-700 nm) conversion efficiency was much greater than blue (B, 400-500 nm) and green (G, 500-600 nm) (Barta et al., 1992; Bula et al., 1991; Haitz et al., 2000). Early experiments showed sole-source R LEDs alone could drive photosynthesis and vegetative growth in lettuce (*Lactuca sativa*) (Bula et al., 1991; Mitchell, 2015). Initial materials used in B light emission had poor conversion efficiencies and made them

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impractical for use in plant lighting, but introduction of new materials in the early 1990s yielded more efficient B and G LEDs (Pimputkar et al., 2009). Current reported efficiencies for R and B LEDs are 32% and 49%, respectively, and these values will continue to increase as the technology develops (Nelson and Bugbee, 2014).

White light can be created from LEDs either by combining R-, B-, and G-emitting diodes or more commonly, by applying a phosphor coating to a B-emitting diode (Pimputkar et al., 2009). A phosphor coating absorbs the photons emitted from the diode and releases the excitation energy in the form of longer-wavelength photons in the G and R portions of the spectrum. The characteristics of the phosphor can be manipulated to influence the distribution of longer wavelengths. The electrical efficiency of white LEDs has increased concomitantly with B LED efficiency (Cope et al., 2013). The currently reported electrical efficiency for cool-white LEDs is ≥33% (Nelson and Bugbee, 2014).

Photons for Plant Growth and Development

Light and photosynthesis. Photosynthesis is the process by which plants and other phototrophic life forms convert radiation from the sun to chemical energy stored as carbohydrates. The sun emits a wide spectrum of electromagnetic radiation and contained within this, photons within the waveband of approximately 400 to 700 nm can provide the energy for photosynthesis. Light and other electromagnetic radiation exists as both waves and particles (photons) containing energies or quanta, the amount of which is inversely proportional to the wavelength. When a photon is absorbed by a molecule, the transfer of energy can excite it to a higher energy state. Depending on the quantum energy of the photon, the transition from the excitation state to the ground state can occur via the dissipation of heat, fluorescence, energy

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transfer to another molecule, or reversion to a triplet state where photochemistry can occur (Hopkins and Hüner, 2009). In green plants, pigments in the chloroplast, mainly chlorophyll, absorb light that can be used in photosynthesis. Chlorophyll molecules contain a phytol tail, which anchors them within their hydrophobic surroundings, and a porphyrin ring that acts as a chromophore, responsible for absorbing light. Two types of chlorophyll are present in plants (chlorophyll *a* and *b*) and an additional two types are limited to brown or red algae (chlorophyll *c* and *d*). All four species of chlorophyll differ structurally with respect to the moieties on the porphyrin rings or, in the case of chlorophyll *c*, the absence of a phytol tail. Both chlorophyll *a* and *b* primarily absorb radiation between 400 and 700 nm, with absorption maxima in the B and R portions of the spectrum, but exhibit slight differences in absorbance due to differences in porphyrin head structure. Both species absorb G light less than B or R light, and this greater reflectance of G light is why plants appear green to people. In addition to chlorophyll, carotenoid accessory pigments such as carotenes and xanthophylls absorb light and transfer excitation energy to the photosynthetic pathway. Absorption spectra of the carotenoids vary, but their maximum absorption is in the G portion of the spectrum. The number of photons (in micromoles) within PAR incident on a square meter per second is termed photosynthetic photon flux (*PPF*) or *PPF* density (*PPFD*).

Within the chloroplast, chlorophyll and carotenoid pigments aggregate to form antenna complexes that absorb light and transfer excitation energy to a reaction center complex. At the reaction center, this energy is conserved through transfer to electrons supplied by the oxidation of water. Excitation energy is passed through the electron transport chain, creating high energy adenosine triphosphate to provide energy and nicotinamide adenine dinucleotide phosphate to be reduced in the carbon fixation reactions (Nelson and Ben-Shem, 2004).

Photoreceptors and photomorphogenesis. Plants use light as a cue to sense their immediate environment. Light intensity, quality, and duration provide information that can regulate germination, growth, photomorphogenesis, and development (Devlin et al., 2007). The ability to respond to changes in light quality, such as shading from a neighboring plant, allows plants to maximize growth and ultimately survive by attempting to out-compete neighboring plants for the limiting resource of light. This can be achieved by elongated growth of leaves and stems, signaling the reorientation of chloroplasts in response to light intensity, or signaling the transition to flowering (Folta and Carvalho, 2015).

Plant photoreceptors are specialized complexes, usually chromoproteins, that absorb and respond to specific radiation wavelengths and intensities. These chromoprotein receptors consist of an apoprotein with catalytic properties and a chromophore light-absorbing antenna (Devlin et al., 2007; Franklin and Whitelam, 2005). The characteristics of the chromophore and apoprotein of the receptor influence the absorption spectra. Extensively studied chromoprotein photoreceptors include phytochromes, cryptochromes, phototropins, and zeitlupe/adagio (ZTL/ADO) family receptors (Devlin et al., 2007). Although it lacks a traditional chromophore, ultraviolet-B resistance 8 (UVR8) is a protein photoreceptor that responds to UV-B radiation (280-315 nm) and regulates transcription associated with UV-related photomorphogenesis (Jenkins, 2014). From the UV-B regulated UVR8 to the far-red-absorbing form of phytochrome, photoreceptors respond to radiation from 260 nm to 800 nm (Folta and Carvalho, 2015), therefore including wavelengths outside of PAR.

Red light, far-red light, and phytochrome. When a plant canopy receives radiation, photons can be absorbed, reflected or transmitted. Radiation transmitted through a plant canopy is relatively high in G and especially far-red (FR, 700-800 nm); most B and R photons have been

absorbed by plant pigments (Kami et al., 2010). The ratio of R to FR photons can be used as a signal by the phytochrome family of photoreceptors. Phytochrome is a homodimer protein bonded to photochromobilin, a tetrapyrrole chromophore that absorbs primarily R and FR radiation (Devlin et al., 2007; Franklin and Whitelam, 2005). The chromophore enables photo-conversion between two forms of phytochrome: Pr, which primarily absorbs R at a peak wavelength of 660 nm, and Pfr, which primarily absorbs FR at a peak wavelength of 730 nm and is often considered the active form (Franklin and Whitelam, 2005). Absorbed R light causes a *cis-trans* conformational change in the structure of the Pr chromophore to the Pfr form, thereby affecting absorption spectrum (Andel et al., 1997). Because solar and broad-band radiation generally contains R and FR, Pr and Pfr are in an equilibrium, which is known as the photoequilibrium of the phytochrome pool (Devlin et al., 2007; Holmes and Smith, 1977). Therefore, under conditions when the R:FR ratio is high, the phytochrome equilibrium will be converted primarily to the active Pfr form. In darkness, Pfr is converted back to Pr through the process of dark reversion (Folta and Childers, 2008; Rockwell et al., 2006). The active Pfr form is translocated to the cell nucleus and influences gene transcription to initiate shade-avoidance responses including extension of stems, hypocotyls, leaves, and petioles (Folta and Childers, 2008; Quail, 2002).

Phytochromes in angiosperms are encoded by a family of genes (*PHYA-PHYC*) with genes *PHYD* and *PHYE* additionally present in at least some dicotyledonous plants, such as the model plant species *Arabidopsis thaliana* (Franklin and Whitelam, 2005). In *Arabidopsis*, the functions of individual phytochromes overlap, but some forms mediate specific processes. For example, phyA is the most abundant form of phytochrome in dark-grown etiolated seedlings and light absorption and signaling via phyA leads to de-etiolation (Franklin and Quail, 2010). Shade

avoidance responses, such as hypocotyl and petiole extension, are largely transduced by phyB with redundant roles in phyD and phyE (Franklin and Quail, 2010). Under plant canopy-induced shading or when the light environment has a low R:FR, the decrease in the active phytochrome form, Pfr, results in the loss of inhibition of elongated growth (i.e., extension growth is stimulated) (Devlin et al., 2007, Franklin and Whitelam, 2005). Far-red signaling of phyA plays an important role in activation of the flowering gene *FT* by antagonizing degradation of the CO protein (Valverde et al., 2004).

Blue light, cryptochromes, and phototropins. The cryptochrome photoreceptors (cry1 and cry2) utilize pterin and flavin chromophores for the absorption of B light (Ahmad et al., 2002). By observing spectrum-dependent responses in *Arabidopsis cry1cry2* double mutants, Ahmad et al. (2002) determined that cryptochromes respond to wavelengths between 380 and 500 nm. Identification of the CRY1 protein was aided by the study of an *Arabidopsis* mutant (*hy4*), which lacks B-mediated inhibition of hypocotyl elongation (Folta and Childers, 2008). Overexpression of CRY1 results in a stronger inhibition of hypocotyl elongation. By studying antisense-*CRY1* transgenic rapeseed (*Brassica napus)*, Chatterjee et al. (2006) showed *in vivo* how cry1 is involved in regulating stem extension. Rapeseed plants lacking cry1 photoreceptors exhibited elongated growth in addition to decreased accumulation of anthocyanins, suggesting that cry1 mediates both responses (Chatterjee et al., 2006). Cry2 also plays a role in hypocotyl elongation, especially at low light intensities (Lin et al., 1998). In response to B, cry2 interacts with transcription factors that indirectly promote a transition to flowering by the same pathway described above for phyA (Galvao and Fankhauser, 2015; Valverde et al., 2004). Ahmad et al. (2002) observed in pulse lighting experiments that R treatment augmented cry2-dependent growth inhibition in *Arabidopsis* through a synergistic effect. Seedlings over-expressing either

CRY1 or CRY2 displayed further inhibition of hypocotyl extension when treated with a pulse of R+B compared to B alone. Since the response was not seen in wildtype or *cry1cry2* double mutants, interaction between B- and R-absorbing photoreceptors may be present (Ahmad et al., 2002).

The plant phototropins, phot1 and phot2, also elicit morphological responses that optimize photosynthesis from absorbed B. Light absorption is mediated by two light-oxygen-voltage-sensing (LOV) domains that each bind a flavin mononucleotide chromophore (Salomon et al., 2000). Through the study of an *Arabidopsis* mutant deficient in a phototropic hypocotyl B response, the gene encoding phot1 was isolated (Christie et al., 1998). Light absorption by phototropins mainly occurs between 425 and 470 nm (Briggs and Christie, 2002).

Phototropins have overlapping functions in plants to mediate phototropism (growth towards a light source), chloroplast migration and stomatal opening. Phot1 and phot2 are redundant in the responses they mediate, but are responsive to different light intensities. Under low-intensity B, *phot1* mutants lack phototropic growth towards a light source, but under high-intensity B, the response returns. In *phot1phot2* double mutants, phototropism is absent at both intensities, suggesting a functional redundancy with phot1 and phot2 responsive to low and high intensities, respectively (Briggs and Christie, 2002). Phototropins mediate the intracellular movement of chloroplasts in response to light intensity (Taiz and Zeiger, 2010). Under low-intensity light, chloroplasts are oriented within mesophyll cells to the upper and lower surfaces (accumulation) through signaling by phot1 and phot2 to maximize light absorption. To avoid photodamage under high light intensity, phot2 signals for the relocation of chloroplasts parallel to incident light (avoidance) (Sakai et al., 2001). Phot1 and phot2 have also been implicated in the regulation of stomatal opening (Kinoshita et al., 2001).

Stomatal responses to light quality. In controlled greenhouse environments under SL, the main factor limiting photosynthesis in well-watered plants is internal leaf CO_2 concentration. In addition to boundary layer and liquid phase resistance, stomatal resistance is the primary inhibitor of CO_2 diffusion from outside the leaf into the chloroplast. Generally under lighted conditions, stomata open in response to low internal CO_2 and close when CO_2 is sufficiently high. Light intensity has an indirect effect on the opening of stomata because photosynthesis and CO_2 assimilation can lower internal CO_2 concentration. After treating *Arabidopsis* guard cells with a compound that uncouples electron transport, there was still partial stomatal opening in response to incident light, indicating a stomatal response independent from photosynthetic reduction of internal CO_2 (Sharkey and Raschke, 1981). This was further evidenced by additional stomatal opening when B was added to a background of R light that saturated photosynthesis (Karlsson, 1986). It has been suggested that B stimulates H^+-ATPase in the guard cells, which causes an influx of ions and solutes. This decreases the osmotic potential within the cell, and the resulting intake of water increases the turgor pressure of the guard cells and therefore increases stomatal aperture (Briggs and Christie, 2002). Kinoshita et al. (2001) observed *Arabidopsis phot1phot2* double mutants lacked a specific stomatal opening response to B light added to an R background. Stomatal opening occurred when epidermal strips were irradiated with 50 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of R. When 10 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of B was added, stomatal aperture in the wild type increased, but this response was absent in double mutants. *Phot1* and *phot2* single mutants each displayed some stomatal opening, indicating the two phototropins have redundancy in signaling stomatal opening (Kinoshita, 2001).

The carotenoid zeaxanthin has also been suggested as a photoreceptor in B-mediated stomatal opening. Frechilla et al. (1999) added 20 $\mu mol \cdot m^{-2} \cdot s^{-1}$ B to three background R light

intensities (50, 100, 150 $\mu mol \cdot m^{-2} \cdot s^{-1}$) provided to epidermal strips of an *Arabidopsis* wild type and *npq1*, a mutant lacking zeaxanthin production. Stomata in mutants were unresponsive to the additive B, while stomata in wild type strips displayed normal opening enhancement from B and background R (Frechilla et al., 1999). Similarly, in experiments when zeaxanthin production was blocked by an inhibitor, B responses were absent from guard cells (Srivastava and Zeiger, 1995).

Green light has been shown to reverse B-mediated stomatal opening (Frechilla et al., 2000; Talbott et al., 2003, 2006). Frechilla et al. (2000) observed a reversal of stomatal opening in broad bean (*Vicia faba* 'Windsor Long Pod') when 20 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of G was added to 10 $\mu mol \cdot m^{-2} \cdot s^{-1}$ B with a background of 120 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of R. Green light alone, however, triggered stomatal opening, most likely via a photosynthesis-dependent response. In pulse experiments, when 120 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of R was continuously delivered, addition of 1,800 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of B for 30s triggered stomatal opening. When 3,600 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of G for 30s immediately followed the B pulse, the signal for stomatal opening was reversed and stomata closed. The action spectrum proposed for G reversal is 480 to 600 nm with a maximum at 540 nm (Frechilla et al., 2000). It has been proposed that zeaxanthin undergoes isomerization in response to B absorption, resulting in a G-absorbing form allowing G reversal of stomatal opening (Milanowska and Gruszecki, 2005).

Whole Plant Effects of Light Quality

Blue light effects. In many sole-source lighting studies using LEDs, R photons comprise the majority of the PPF (Brown et al., 1995; Bula et al., 1991; Kim et al., 2004a, 2004b; Yang et al., 2011). Many past experiments have focused on the fraction of B light needed to be included for normal growth and development of plants (Cope et al., 2013; Dougher and Bugbee, 2001;

Goins et al., 1997, 1998). Due to advances in output efficiency, B LEDs were used more in research in the early 2000s. Prior to their availability, B light was included through filtered or blue fluorescent (BF) lamps (Massa et al., 2008). An early experiment by Hoenecke et al. (1992) identified that as the intensity of B (peak wavelength of 435 nm filtered from fluorescent lamps) increased from 0 to 60 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and was supplemented with R from LEDs, hypocotyl length of lettuce decreased from 30 to 2 mm. Supplementing R with 15 to 30 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of B elicited hypocotyl extension similar to the morphology of seedlings grown in a field or greenhouse environment. A similar experiment by Goins et al. (1997) investigated the development and yield of wheat (*Triticum aestivum* 'USU-Super Dwarf') grown under a *PPFD* of 350 $\mu mol \cdot m^{-2} \cdot s^{-1}$ from R alone, R + 1% BF, R + 10% BF, or white fluorescent (WF) alone. At 15 to 40 d after planting, increasing B significantly increased dry matter and leaf net photosynthesis. At final harvest, R + 10% BF grown plants had greater seed number and total yield compared to wheat grown under R alone or R + 1% BF. The authors attributed greater photosynthetic rates partly to increased stomatal conductance in the R + 10% BF and WF grown plants (Goins et al., 1997). Yorio et al. (2001) also reported increased dry matter production with R + 10% BF or cool white fluorescent (CWF) compared to R alone in lettuce. However, for radish (*Raphanus sativus*) and spinach (*Spinacea oleracea*), CWF-grown plants had greater dry matter accumulation than R + 10% BF, suggesting there may be an effect outside of B and R wavelengths as well as species-specific B light responses (Yorio et al., 2001).

Hogewoning et al. (2010) investigated the role of B light by growing cucumber (*Cucumis sativus* 'Hoffman's Giganta') under a *PPFD* of 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ delivered with different ratios of B (peak wavelength of 450 nm) and R (peak wavelength of 638 nm) light. At 0% B, leaf photosynthetic capacity was lowest and increased to a maximum at 50% B. The largest increase

in photosynthetic capacity occurred between 0% and 7% B, suggesting a semi-qualitative response to B. Quantitative responses to increasing B light were reported for chlorophyll content, leaf mass area and stomatal conductance. These responses were analogous to leaf acclimation to increased irradiance, suggesting the increasing proportion of B light may be responsible for these changes as a result of an increase in absolute B rather than the full spectrum of PAR (Hogewoning et al., 2010).

Light quality delivered to seedlings can also have an effect on subsequent growth and development after transplant. Jokhan et al. (2010) investigated the effect of light quality on seedling quality and growth after transplant in a common greenhouse environment. Ten-day-old lettuce seedlings were grown under 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ delivered by WF, R LEDs (peak wavelength of 660 nm), B LEDs (peak wavelength of 468 nm) or 50% R + 50% B LEDs for 7 d, then they were transplanted and grown in a greenhouse supplemented with WF for an additional 28 d. At transplant, lettuce grown under R had the greatest leaf area and fresh weight, but 45 d after sowing, plants grown with only B light or 50% B + 50% R had the greatest leaf area and fresh weight. The authors partly attributed the increased performance of the B-light grown transplants to a low shoot to root ratio (Jokhan et al., 2010). Furthermore, a compact transplant with strong root structure improves transplant establishment (Jokhan et al., 2010; Pramuk and Runkle, 2005).

Green light effects. A portion of G light is reflected by or transmitted through green plants (Klein, 1992), which has led to a misconception that G plays an insignificant role in photosynthesis and morphogenesis (Jokhan et al., 2012). This fallacy partly stems from the low absorption of G when applied to dissolved chlorophyll in a spectrophotometer cuvette (Kim et al., 2004b). However, when an intact leaf or canopy is exposed to G, total absorption is significantly greater. G wavelengths not absorbed initially continue to be reflected within the leaf

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or transmitted through the canopy and typically over half of the G photons are absorbed (Kim et al., 2004b). Additionally, other pigments such as carotenoids can absorb G wavelengths and transfer excitation energies to reaction centers, but at a reduced efficiency compared to chlorophyll (Kim et al., 2004b, Hogewoning et al., 2012).

There is interest in including G light with R and B from LEDs to reduce the purplish appearance of plant tissue and thus, to make diagnosis of diseases and physiological disorders easier (Massa et al., 2008) and to make the working environment more comfortable (Kim et al., 2004b). Kim et al. (2004a) compared the growth of lettuce grown under 84% R (peak wavelength of 670 nm), 15% B (peak wavelength of 460 nm), and 1% G (peak wavelength not reported) LEDs to that under 78% R, 17% B, and 5% G. Both treatments delivered a total *PPFD* of 136 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for 18 $h \cdot d^{-1}$ over 26 d. Under these conditions, there were no significant differences in light and CO_2 photosynthetic response curves or physiological growth characteristics, suggesting that adding a minimal amount of G to R and B background does not have a negative effect on plant growth while providing an improved visual environment.

Building on their earlier work, Kim et al. (2004b) compared the effect of increasing G proportions on lettuce growth and development using 84% R and 16% B (as described above) LEDs, 61% R and 15% B with G fluorescent lamps (24% G), CWF (30% R, 19% B, and 51% G), and G fluorescent lamps alone (4% R, 10% B, and 86% G), all at 150 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for 18 $h \cdot d^{-1}$. After 28 d, lettuce grown under G fluorescent lamps alone had reduced photosynthetic capacity compared to other treatments and less total leaf area. Plants grown under R and B LEDs with G fluorescent lamps accumulated more dry weight compared to the other treatments. The authors concluded that a relatively small percentage of G stimulated plant growth, but increased

proportions of G, in this case greater than 50% of the PPF, was energetically wasteful and suppressed growth (Kim et al., 2004b).

Wollaeger and Runkle (2014) investigated the effect of different proportions of B (peak wavelength of 446 nm), G (peak wavelength of 516 nm) and R (two types, peak wavelengths of 634 and 664 nm) light delivered to bedding plant seedlings at 160 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for 18 $h \cdot d^{-1}$. All four species [(impatiens, petunia (*Petunia* ×*hybrida*), salvia, and tomato (*Solanum lycopersicum*)] tested showed decreased stem height under 50% G + 50% R compared to R alone and increased stem height compared to any treatment containing ≥25% B light. The authors attributed this to G light stimulating the cryptochrome-mediated suppression of stem elongation, but not to the extent of the B-containing treatments (Wollaeger and Runkle, 2014). Longer wavelengths of G (563 nm) light can reverse cryptochrome-mediated responses (Ahmad et al. 2002). In an additional experiment, Wollaeger and Runkle (2015) observed inhibition of stem elongation of tomato, salvia, and impatiens in their lowest tested B level of 10 $\mu mol \cdot m^{-2} \cdot s^{-1}$ added to background R and saturation of cryptochrome-mediated elongation inhibition with 40 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of B light.

The experiments performed by Kim et al. (2004a, 2004b) either did not specify the peak wavelength of G LED or provided broad-spectrum light from G fluorescent lamps. Jokhan et al. (2012) investigated the effects of multiple G peak wavelengths and intensities on the growth and development of lettuce. In a full factorial experiment, G from LEDs at peak wavelengths of 510, 524, and 532 nm and a WF control were delivered to 7-day-old lettuce plants at three different intensities: 100, 200, and 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for 24 $h \cdot d^{-1}$ for a 10-d period. Lettuce plants responded differently to the different G peak wavelengths and WF light treatments. Shoot growth of lettuce decreased under the G treatments at lower intensities, similar to Kim et al. (2004b), but

at the highest intensity (300 $\mu mol \cdot m^{-2} \cdot s^{-1}$), plants under the 510-nm G treatment accumulated the greatest dry weight, leaf number, and had a greater capacity for photosynthesis compared to the WF control.

Far-red light effects. Plants under FR-enriched environments display shade avoidance responses, such as increased stem, leaf, and petiole extension (Folta and Childers, 2008). Manipulation of the phytochrome equilibrium by the addition of FR has the potential to affect plant morphology and control of flowering (Folta and Carvalho, 2015). Brown et al. (1995) quantified the effects of additional FR on growth and dry matter partitioning of pepper (*Capsicum annuum* 'Hungarian Wax') grown under four lighting treatments. Twenty-one day old seedlings were grown under a *PPFD* of 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for 12 $h \cdot d^{-1}$ for 21 d from broad-spectrum MH, R LEDs (peak wavelength of 660 nm) alone, R + 59 $\mu mol \cdot m^{-2} \cdot s^{-1}$ from FR LEDs (peak wavelengths of 660 and 735 nm, respectively), or 99% R from LEDs + 1% from BF. Plants grown under the R+FR treatment had a lower leaf-to-stem dry mass ratio and longer stems than all other treatments, indicating that FR controlled the shade-avoidance response. Plants grown under treatments containing B (MH and R+BF) had shorter stems and was not correlated with the R:FR. Despite the MH treatment having an R:FR= 3.0, compared to a ratio of 5.0 under the R+FR treatment, plants under the R+FR treatment had longer stems, which was attributed to the lack of B in the R+FR treatment (Brown et al., 1995). The increased availability of FR and B LEDs should allow for a greater examination of their wavelength interactions on plant growth and development (Folta and Carvalho, 2015).

The interaction between solar radiation and applied light quality from SL can lead to different conclusions about ideal spectra for growth and development. For instance, rather than seeing an increase in net photosynthesis in cucumber seedlings with the inclusion of up to 16% B

from LEDs to R applied as SL at a *PPFD* of 54 μmol·m^{-2}·s^{-1}, at low (5.2 mol·m^{-2}·d^{-1}) and high

(16.2 mol·m^{-2}·d^{-1}) DLI, net photosynthetic rate and dry mass accumulation were similar under all

SL treatments (Hernandez and Kubota, 2014). Hernandez and Kubota (2012), using similar

experimental protocol, concluded growth and development of tomato seedlings was similar

under R+B SL compared to R SL alone. Tomato seedlings grown under SL at a *PPFD* of 61

μmol·m^{-2}·s^{-1} from LEDs providing 100% R had decreased leaf area and dry mass compared to

seedlings grown under HPS lamps or 95% R + 5% B and 80% R + 20% B from LEDs, but this

conflicting result could be associated with the 23-h photoperiod applied (Gómez and Mitchell,

2015). Growth and morphology responses can be dependent on solar DLI conditions and species-

specific, therefore further investigation into the effects of SL light quality is needed.

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LITERATURE CITED

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SECTION II

GREENHOUSE-GROWN SEEDLINGS UNDER SUPPLEMENTAL LIGHTING FROM
HIGH-PRESSURE SODIUM LAMPS OR LIGHT-EMITTING DIODES HAVE SIMILAR
GROWTH AND DEVELOPMENT

Greenhouse-grown Seedlings under Supplemental Lighting from High-pressure Sodium Lamps or Light-emitting Diodes Have Similar Growth and Development

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Abstract

Light-emitting diodes (LEDs) have the potential to replace high-pressure sodium (HPS) lamps as the main delivery method of supplemental lighting (SL) in greenhouses. However, few studies have compared growth under the different lamp types. We grew seedlings of geranium (*Pelargonium ×hortorum*), pepper (*Capsicum annuum*), petunia (*Petunia ×hybrida*), snapdragon (*Antirrhinum majus*) and tomato (*Solanum lycopersicum*) at 20 °C under six lighting treatments: five that delivered a photosynthetic photon flux density (*PPFD*) of 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$ from HPS lamps (HPS_{90}) or LEDs [four treatments composed of blue (B, 400-500 nm), red (R, 600-700 nm), and/or white LEDs] and one that delivered 10 $\mu mol \cdot m^{-2} \cdot s^{-1}$ from HPS lamps (HPS_{10}). Lamps operated for 16 $h \cdot d^{-1}$ for 14 to 40 d depending on cultivar and season. The LED treatments defined by their percentages of B, green (G, 500-600 nm), and R light were $B_{10}R_{90}$, $B_{20}R_{80}$, $B_{10}G_5R_{85}$, and $B_{15}G_5R_{80}$, while the HPS treatments emitted $B_6G_{61}R_{33}$. Seedlings of each cultivar grown under the 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$ SL treatments had similar dry shoot weights and all except pepper had a similar plant height, leaf area, and leaf number. After transplant to a common environment, geranium 'Ringo Deep Scarlet' and petunia 'Single Dreams White' grown under HPS_{90} flowered three days earlier than those grown under HPS_{10}, but flowering time was not different from LED treatments. There were no consistent differences in morphology or subsequent flowering among seedlings grown under HPS_{90} and LED SL treatments. The inclusion of white light in the LED treatments played an insignificant role in growth and development when applied as SL with the background ambient light. The LED fixtures in this study consumed substantially less electricity than the HPS lamps while providing the same photosynthetic photon flux density (*PPFD*), and seedlings produced were of similar quality, making LEDs a suitable technology option for greenhouse SL delivery.

Introduction

Michigan is the third largest floriculture producing state with a reported wholesale value of $406 million for crops sold in 2014, and bedding plants is the largest crop segment (USDA, 2015). To coordinate production cycles and have finished crops ready for spring markets, bedding plants and other floriculture crops are grown from seeds and cuttings in controlled-environment greenhouses at high densities during winter and spring. During this period, in Michigan and other northern climates, the mean daily light integral (DLI) received outdoors is as low as 5 to 10 mol·m^{-2}·d^{-1} (Korczynski et al., 2002). Inside a greenhouse, DLI can be reduced by 50% or more by glazing material, structural components, and other obstructions (Fisher and Runkle, 2004). During the propagation phase, increasing DLI when it is below a threshold of 10 to 12 mol·m^{-2}·d^{-1} can increase accumulated biomass, rate of development, rooting, and plant quality, while also reduce flowering time (Currey et al., 2012; Lopez and Runkle, 2008; Pramuk and Runkle, 2005; Torres and Lopez, 2011). Therefore, DLI can be increased during periods of low light using supplemental lighting (SL), usually provided by high-pressure sodium (HPS) lamps.

Light-emitting diodes (LEDs) have shown promise to be used as SL in horticultural applications (Hernandez and Kubota, 2014; Randall and Lopez, 2014, 2015). One advantage is that compared to traditional HPS lighting, LEDs potentially have a longer life span. For conventional lamps, on/off cycles reduce the lifetime of filaments and igniters, and electronic ballasts must be periodically replaced (Morrow, 2008). Additionally, by emitting specific wavebands of light, LEDs have the potential to provide a light spectrum that maximizes light absorption for growth and development by targeting the absorption peaks of chlorophyll and other important photobiological pigments (Mitchell et al., 2016).

The addition of ancillary wavebands of light to monochromatic LEDs have been shown to elicit photosynthetic and morphological responses in sole-source lighting (SSL) experiments. Cucumber (*Cucumis sativus* 'Hoffmann's Giganta') seedlings grown under red (R, 600-700 nm) light alone from LEDs developed leaves that had reduced (carbon dioxide) CO_2 assimilation mediated by decreased stomatal conductance and stomatal count compared to seedlings grown under 7% blue (B, 400-500 nm) + 93% R (Hogewoning, 2010). Similarly, Goins et al. (1997) reported wheat (*Triticum aestivum* 'USU-Super Dwarf') grown under R + 10% B (from B fluorescent lamps) had more than twice as much CO_2 uptake and dry weight was 153% greater than plants grown under R alone. Wollaeger and Runkle (2014) reported that partial substitution of R or green (G, 500-600 nm) light with B decreased seedling height and leaf expansion. Impatiens (*Impatiens walleriana* 'SuperElfin XP Red'), tomato (*Solanum lycopersicum* 'Early Girl'), and salvia (*Salvia splendens* 'Vista Red') seedlings were grown under LEDs at a photosynthetic photon flux density (*PPFD*) of 160 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and the light quality was 100% R or R with an increasing percentage of B. Those grown under at least 25% B were shorter and had decreased leaf area compared to seedlings grown under R alone (Wollaeger and Runkle, 2014).

Few studies have been published on how light quality of SL influences plant growth in greenhouses. Randall and Lopez (2014) reported decreased height of vinca (*Catharanthus roseus* 'Titan Punch'), celosia (*Celosia plumosa* 'Fresh Look Gold'), impatiens 'Dazzler Pearl Blue', petunia (*Petunia ×hybrida* 'Plush Blue'), marigold (*Tagetes patula* 'Bonanza Flame'), and viola (*Viola ×wittrockiana* 'Mammoth Big Red') seedlings grown under 15% B + 85% R light from LEDs compared to those grown under HPS SL at a *PPFD* of 160 $\mu mol \cdot m^{-2} \cdot s^{-1}$. However, there were no differences in height for the same species grown under 30% B + 70% R LED SL compared to those grown under 15% B + 85% R LED SL. In the production of vegetable

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transplants, the amount of B in SL for a desired growth habit remains unclear. Hernandez and

Kubota (2014) measured growth and development responses of cucumber seedlings grown under

increasing B:R ratios from LEDs under average DLIs of 5.2 and 16.2 mol·m^{-2}·d^{-1}. At the low

DLI, chlorophyll concentration increased as the B:R ratio increased, but dry mass, leaf area, and

leaf number decreased. In contrast, at the higher DLI, B:R treatments had no effect on the same

metrics.

It has been suggested that broad spectrum white (W) light as SL can increase yield in

greenhouse vegetable production because of increased penetration of G light into the canopy (Lu

et al., 2012). Single-truss tomato plants were provided with a *PPFD* of 70 to 143 μmol·m^{-2}·s^{-1} SL

from R, B or W LEDs for 28 d, and the authors concluded tomato plant yield under W LED SL

was greater per unit photon emitted compared to R or B alone due to increased light absorption

within the canopy (Lu et al., 2012). Increased biomass production has also been reported in

lettuce (*Lactuca sativa)* production from the addition of G light to R and B in (SSL) production

(Jokhan et al., 2012; Kim et al., 2004). Adding 24% G to 15% B + 61% R at a *PPFD* of 100

μmol·m^{-2}·s^{-1} increased shoot fresh and dry weight of lettuce 'Waldmann's Green' by

approximately 50% compared to a treatment of 16% B + 84% R (Kim et al., 2004). The addition

of G or broad spectrum W light also increased the color rendering index, reducing the purplish

appearance of plants grown under R + B alone, which allows for easier diagnosis of diseases and

disorders as well as creates a more comfortable working environment (Kim et al., 2004; Massa et

al., 2008). For LEDs to achieve their potential as a delivery method for SL, seedlings and

finished plants must be of equal or greater quality as those produced under HPS SL while be at

least as energy efficient. Our objective was to quantify the effects of SL from four different

commercial LED fixtures and HPS lamps on growth and subsequent development of seedlings of popular bedding plant crops.

Materials and Methods

Plant material. Seeds of geranium [*Pelargonium ×hortorum* 'Pinto Premium Salmon' ('PPS') and 'Ringo 2000 Deep Scarlet'('RDS')], pepper (*Capsicum annuum* 'Long Red Slim Cayenne'), petunia 'Single Dreams White' ('SDW') and 'Wave Misty Lilac' ('WML'), snapdragon (*Antirrhinum majus* 'Montego Yellow') and tomato 'Supersweet' were sown into 128-cell plug trays (2.7 × 2.7 cm; 12.0-mL volume) at a commercial greenhouse (C. Raker and Sons, Inc., Litchfield, MI). One (replication 1), nine (replication 2), or eight days (replication 3) after seed sow, plants were transported to the Plant Science Research Greenhouses at Michigan State University (MSU, East Lansing, MI). For each cultivar, six 128-cell trays were cut in half and the twelve half-trays were randomly assigned to six lighting treatments in adjacent greenhouse sections. Seedling trays of each cultivar were placed at approximately the same position in each section and rotated systematically every two days to minimize positional effects in the greenhouses. Seedlings were irrigated as necessary with water-soluble fertilizer providing (in mg·L^{-1}) 60 N, 23 P, 60 K, 27.7 Ca, 4.6 Mg, 1.3 Fe, 0.6 Mn, 0.6 Zn, 0.6 Cu, 0.4 B, and 0.1 Mo (MSU Plug Special; GreenCare Fertilizers, Inc., Kankakee, IL).

Environmental conditions. The six nearly identical greenhouse sections used for this research were oriented west to east and measured 4.0 m by 4.6 m, with a 2.2-m high gutter and 3.5-m peak. Whitewash (Kool Ray Classic; Continental Products Co., Euclid, OH) was applied on the glass-glazed greenhouse exterior to decrease the light intensity (by approximately 25%) and improve the uniformity of sunlight. In each section, light intensity at bench height was

recorded by a quantum sensor (LI-190SA, LI-COR, Lincoln, NE), air temperature by an aspirated thermocouple (Type E; Omega Engineering, Stamford, CT) near canopy height, and leaf canopy temperature by an infrared thermocouple (Type K, OS36-01; Omega Engineering, Stamford, CT) placed 15 cm above the canopy and oriented downward at a 45° angle. Environmental conditions in each section were monitored and logged using a data logger (CR-10; Campbell Scientific, Logan, UT) every 10 s and hourly averages were recorded. The target set point for air temperature was 20 °C during the day and night. Conditions were maintained by a greenhouse environmental control system (Integro 725, Priva North America, Vineland, Ontario, Canada) that controlled roof vents, exhaust fans, evaporative cooling pads, and steam heating. Environmental data are reported in Table 2.1.

Lighting treatments. The treatments delivered SL for 16 $h \cdot d^{-1}$ (0600 to 2200 HR) at a *PPFD* of 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (five sections) or 10 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (one section) as measured at plant height by a portable spectroradiometer (PS-200, Apogee Instruments Inc., Logan, UT) (Figure 2.1). In repetitions 1 and 2, supplemental lighting was delivered when ambient *PPFD* was <185 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and switched off when >370 $\mu mol \cdot m^{-2} \cdot s^{-1}$. In repetition 3, SL was delivered for the entire 16-h photoperiod, regardless of ambient *PPFD*. Two of the SL treatments were delivered by HPS lamps using either one 150-W fixture (LU150; Acuity Lithonia Lighting, Conyers, GA) or four 400-W fixtures (LR48877; P.L. Light Systems, Beamsville, Ontario, Canada) to deliver 10 or 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$, respectively. The four remaining SL treatments were delivered by LED fixtures that contained R (peak=660 nm), B, (peak=453 nm) and/or W LEDs (Philips GP-TOPlight DRB -LB2013; Koninklijke Philips N.V., Eindhoven, The Netherlands). The 100-nm waveband ratios of these four LED treatments, defined by their relative amounts of B, G, and R light, were $B_{10}R_{90}$, $B_{20}R_{80}$, $B_{10}G_5R_{85}$, and $B_{15}G_5R_{80}$. The 10 and 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$ HPS lamps both

emitted ratios of $B_6G_{61}R_{33}$. Each LED fixture (122 cm long, 5 cm wide, and 10 cm tall) contained 10 arrays each consisting of 9 diodes. To achieve the desired *PPFD*, the heights of the HPS lamps and benches were adjusted. In addition, a flexible, neutral-density mesh (General Purpose Aluminum; New York Wire, Grand Island, NY) was placed over all LED arrays to reduce light intensity by approximately 35%. Each LED fixture was mounted horizontally 1.9 m above the bench height and the 400-W and 150-W HPS fixtures were mounted 1.3 m and 2.5 m above the plants, respectively. Glass walls between sections were coated with a heavy layer of whitewash to prevent light treatment contamination. Using a digital clamp-on current meter (DL379; UEi Test Instruments, Beaverton, OR), power consumption of the SL treatments was obtained by multiplying voltage, current, and the manufacturer-rated power factor of 0.95. This value was multiplied by the number of hours SL was run per day to provide power usage in $kWh \cdot d^{-1}$.

Common environment. After 14 to 40 days of lighting treatments (depending on cultivar and seasonal conditions), 10 seedlings (five from each block) of each cultivar, except pepper and tomato, from each treatment were transplanted into 10-cm pots containing 70% peat moss, 21% perlite and 9% vermiculite (SUREMIX, Michigan Grower Products Inc., Galesburg, MI), placed randomly in a common greenhouse environment, and grown until flowering. Daily mean air temperature was set at 20 °C and HPS lamps provided SL at a *PPFD* of 60 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for 16 h (0600 to 2200 HR). Lamps were switched on when ambient *PPFD* was <185 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and switched off when >370 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Date of first open flower and total number of flowers or inflorescences (old and existing) approximately 7-10 d after flowering was recorded.

Plant measurements and experimental design. The experiment was performed three times with seed sowings in Jan., Mar., and May 2015. The experimental design was a randomized

complete block design with subsamples to account for seasonal changes in daily light integral (DLI) and temperature, among other factors. At transplant, eight seedlings from each block were sampled at random, excluding those in edge rows, and the following measurements were made: leaf area [using a leaf area meter (LI-3000; LI-COR, Lincoln, NE)], leaf number, and plant height (from substrate surface). Shoots were abscised at the media surface and roots, separated from the media in a washbasin, were placed in paper envelopes and into a drying oven (NAPCO 630, NAPCO Scientific Co., Tualatin, OR) at 80 °C for at least 48 h then measured for shoot and root dry weight. Data were analyzed using the mixed model procedure (PROC MIXED) in SAS (SAS 9.3, SAS Institute, Cary, NC) and pairwise comparisons between treatments were performed using Tukey's honest significant difference test ($P \leq 0.05$).

Results

Dry shoot and root weight. None of the seven cultivars showed significant differences in dry shoot weights among the LED SL treatments and the HPS_{90} treatment (Figure 2.2). Geranium 'PPS', petunia 'SDW', petunia 'WML', snapdragon, and tomato seedlings grown under HPS_{10} had 37%, 40%, 37%, 50%, and 27% less dry shoot weight than seedlings grown under HPS_{90}. Dry root weight followed the same trend; petunia 'WML', snapdragon, and tomato seedlings accumulated 42%, 51%, and 38% less dry root weight, respectively, under HPS_{10} than HPS_{90}. Among 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$ treatments, six of seven cultivars had similar dry root weights. Tomato seedlings grown under the $B_{20}R_{80}$ LED SL treatment had 23% greater dry root weight than those grown under the $B_{10}R_{90}$ LED SL treatment, while all others were statistically similar.

Plant height. There were no differences in plant height of seedlings grown under any of the SL lighting treatments for five of seven cultivars (Figure 2.3). Snapdragon seedlings grown

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under HPS_{10} were 33% shorter than those grown under HPS_{90}, but were not significantly shorter than those grown under any LED SL treatment. Pepper seedlings grown under the $B_{15}G_5R_{80}$ LED SL treatment were 24%, 32%, and 34% taller than seedlings grown under the $B_{10}R_{90}$, $B_{20}R_{80}$, and $B_{10}G_5R_{85}$ LED SL treatments, respectively, but were not different from those grown under either HPS SL treatment.

Leaf area. In the seven cultivars tested, only pepper showed a response to the SL treatments with respect to leaf area. Pepper plants grown under $B_{15}G_5R_{80}$ LED SL had greater leaf area than plants grown under the $B_{20}R_{80}$ and $B_{10}G_5R_{85}$ LED treatments. However, plants under these two LED treatments were similar to the remaining LED three treatments.

Leaf number. In general, seedlings grown under HPS_{10} had fewer leaves than those under the 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$ treatments at transplant, but there were few consistent differences among leaf number under 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$ treatments (Figure 2.4). In geranium 'PPS', seedlings under HPS_{10} had 4.0 leaves at transplant compared to 4.4 and 4.5 for seedlings grown under HPS_{90} and $B_{20}R_{80}$ LED SL, respectively. In petunia 'WML', seedlings grown under $B_{10}R_{90}$ and $B_{15}G_5R_{80}$ LED SL had more leaves on average (7.9 and 8.1, respectively) than seedlings grown under HPS_{10} (6.9). Tomato seedlings grown under HPS_{10} had fewer leaves than seedlings grown under $B_{20}R_{80}$, but there were no other differences between treatments. There were fewer leaves on pepper seedlings grown under $B_{10}G_5R_{85}$ LED SL than those under $B_{15}G_5R_{80}$ LED SL (4.1 to 5.3, respectively). Again, there were no other differences between treatments.

Days to flower and total flower number. In all cultivars tested, time to flower and total flower or inflorescence number were similar when seedlings were grown under 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$ SL from either HPS or LEDs (Figure 2.5). Transplants of geranium 'RDS' and petunia 'SDW' grown under 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$ HPS SL flowered 3 d earlier than those grown under HPS_{10} and

snapdragons had 30% more inflorescences when grown under 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$ HPS or $B_{15}G_5R_{80}$ LED SL compared to HPS_{10}.

Discussion

We included the 10 $\mu mol \cdot m^{-2} \cdot s^{-1}$ SL treatment to provide the same photoperiod as the higher intensity treatments. Depending on the season and ambient conditions, the 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$ SL treatments provided an additional 1.4 to 4.6 $mol \cdot m^{-2} \cdot d^{-1}$ (Table 2.1), which increased the total DLI by 16 to 40%. An increase in DLI through SL can have positive impacts on transplant growth and quality of floriculture crops (Pramuk and Runkle, 2005; Randall and Lopez, 2015; Torres and Lopez, 2011). Pramuk and Runkle (2005) reported a linear increase in shoot dry weight per internode as DLI increased from 4.1 to 14.2 $mol \cdot m^{-2} \cdot d^{-1}$ in celosia 'Gloria Mix', impatiens 'Accent Red', marigold 'Bonanza Yellow', and viola 'Crystal Bowl Yellow'. An increase in shoot dry weight per internode also occurred in salvia 'Vista Rose', but reached a maximum as DLI reached 12 $mol \cdot m^{-2} \cdot d^{-1}$. Similarly, in our experiment, the increased DLI from SL at 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$ increased shoot dry weight in petunia 'SDW', petunia 'WML' and tomato, regardless of delivery from HPS or LED fixtures, compared to 10 $\mu mol \cdot m^{-2} \cdot s^{-1}$ SL. The maximum recorded DLI was 11.0 $mol \cdot m^{-2} \cdot d^{-1}$ and we did not observe a negative effect of increased DLI on shoot dry weight in any cultivar or treatment.

Randall and Lopez (2015) observed an increase in shoot dry mass of seedlings grown under SL or SSL (providing a DLI of 10.4 to 10.9 $mol \cdot m^{-2} \cdot d^{-1}$) when compared to those grown under ambient light with a DLI of 6.3 to 6.7 $mol \cdot m^{-2} \cdot d^{-1}$. Seedlings of vinca 'Titan Red Dark', impatiens 'Super Elfin XP Blue Pearl', geranium 'Bullseye Red', petunia 'Dreams Purple', and marigold 'Durango Yellow' had 50-164% greater dry mass, when grown under SL or SSL when

compared to those grown under ambient light alone. Their consistent increase in shoot dry mass of all species tested, which was not as common in our experiment, could be species- or cultivar-specific or attributed to the greater difference in DLI between ambient and SL treatments in their study. Similar to Randall and Lopez (2015), Hernandez and Kubota (2014) reported tomato and cucumber seedlings grown under LED SL had 47% and 39% more shoot dry mass, respectively, compared to those grown under ambient light alone, which can be attributed to a 22% and 67% increase in DLI from SL.

Previous experiments also showed that an increase in DLI during seedling production can reduce subsequent time to flower after transplant. Pramuk and Runkle (2005) reported that time to flower of celosia and salvia was reduced by 24% and 41% as DLI increased from 4.1 to 14.2 mol·m^{-2}·d^{-1}, respectively, while time to flower of marigold, viola, and impatiens was reduced by 19 to 33% as DLI increased from 4.1 to 11 mol·m^{-2}·d^{-1}. Randall and Lopez (2015) reported reduced time to flower for vinca and geranium transplants grown under HPS SL during the seedling phase compared to those grown under ambient light alone. Their results were slightly different for seedlings grown under $B_{13}R_{87}$ LED SL, where time to flower was reduced for geranium and petunia seedlings compared to those under ambient light. Similar to Randall and Lopez (2015), we observed very few differences in time to flower in any plants grown under SL from HPS or LEDs during the seedling phase, compared to the HPS_{10} treatment.

The HPS lamp is the most common type used by commercial greenhouse growers in temperate climates. Our experimental objective was to quantify and compare growth and morphological characteristics of seedlings grown under HPS and LED SL. Few comparative studies focusing on the use of HPS and LED SL for seedling production have been published. Randall and Lopez (2014) compared growth and quality of nine bedding plant species grown

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under ambient light with 100 μmol·m^{-2}·s^{-1} of SL from either HPS or LEDs providing 100% R, 85% R and 15% B, or 70% R and 30% B for 16 h·d^{-1}. In four species, there were no differences in shoot dry mass between seedlings grown under HPS or LED SL, but seedlings of impatiens, petunia, salvia, and viola had 18%, 25%, 24%, and 40% less shoot dry mass, respectively, when grown under 70% R and 30% B LED SL compared to those grown under HPS SL. Additionally, celosia seedlings grown under any of the LED treatments had reduced shoot dry mass compared to those grown under HPS SL. Furthermore, Randall and Lopez (2015) reported that impatiens and marigold grown under LED SL providing 13% B and 87% R had less shoot dry mass compared to seedlings grown under HPS SL. We, however, did not observe any differences in shoot dry weight among seedlings grown under any 90 μmol·m^{-2}·s^{-1} SL treatment.

When comparing seedling height at transplant, eight of nine species were shorter when grown under LED SL containing B light, compared to those grown under HPS SL (Randall and Lopez, 2014). Randall and Lopez (2015) also reported shorter seedlings in five species tested when grown under B-containing LED SL treatments compared to seedlings grown under HPS SL. In the seven cultivars we tested, there were no differences in height at transplant between 90 μmol·m^{-2}·s^{-1} LED and HPS SL treatments. The percentage of DLI provided by SL could explain the difference in results between these studies. Supplemental light provided approximately 20-40% of the DLI in our study while those of Randall and Lopez (2014, 2015) provided approximately 40-70% or 40% of the total DLI. The smaller proportion of DLI coming from the SL treatments likely reduced any spectral effects in our study because solar radiation likely contains enough B photons to saturate any morphological effects (Hernandez and Kubota, 2014).

The inclusion of B with R LEDs in SSL can decrease seedling height. In a study by Wollaeger and Runkle (2014), delivering up to 50% B light with R LED treatments reduced

height in impatiens, tomato, and salvia seedlings compared to seedlings grown under 100% R light from LEDs. The authors attributed the reduction in height to B light-mediated cryptochrome stem extension inhibition. We did not observe any consistent SL treatment effects on seedling height; five of seven cultivars showed no difference in height under any SL treatment with B light percentages of 10 to 20, regardless of intensity. However, pepper plants grown under the $B_{15}G_5R_{80}$ LED treatment were significantly taller than seedlings grown under the other LED SL treatments. This is in contrast with other SL studies in which 15% B + 85% R decreased height (Randall and Lopez, 2014, 2015). As mentioned earlier, the proportion of the DLI provided by the SL treatments (approximately 16-40%) in our study was likely not sufficient to elicit morphological changes as reported in the other experiments. Therefore, we postulate that to elicit photomorphogenic responses in a greenhouse, B light from SL must be more pronounced (e.g., ≥50% B light), the proportion of the DLI from SL must be greater, or both.

An additional objective of our study was to investigate growth or morphological responses from the inclusion of W LEDs with R and B LEDs. The four LED SL treatments used in our experiment were commercial production modules that had a fixed irradiance output and spectrum. Broad-band (W) light was provided by B LEDs with a phosphor coating, which scatters light into longer wavelengths (G and R light). It has been suggested that additional photons in the G region of the spectrum can have a positive impact on plant growth because G light penetrates deeper into the canopy (Jokhan et al., 2012; Terashima et al., 2009). Lin et al. (2013) compared lettuce growth under R+B to those grown under R+B+W and found no significant difference in biomass accumulation between treatments. In our study, there were also no differences in biomass accumulation between our LED SL treatments regardless of inclusion

of W, however any benefit from increased photon penetration would be limited in the application of SL to seedlings because transplant usually occurs soon after canopy closure. However, the addition of W to R and B LED SL delivered a much better color rendering index and was a subjectively more comfortable working environment without measureable differences in plant growth.

It is a misconception that LEDs are universally more efficient than conventional broad-band SL systems. Nelson and Bugbee (2014) tested the electrical efficiencies (efficacy) of five lamp types and reported the two most effective HPS fixtures (double-ended, electronic ballast) were similar to the most effective LEDs available at that time ($1.7 \; \mu mol \cdot J^{-1}$). Of the 10 LED modules tested, two had lower photon efficiencies than the 400-W HPS fixture with a magnetic ballast rated at $0.9 \; \mu mol \cdot J^{-1}$. In our experiment, the daily usage of the HPS_{90}, $B_{10}R_{90}$, $B_{20}R_{80}$, $B_{10}G_5R_{85}$, and $B_{15}G_5R_{80}$ treatments were 24.3, 17.3, 17.0, 17.8, and $17.3 \; kWh \cdot d^{-1}$, respectively (data not shown). Therefore, the LED fixtures used approximately 30% less power to provide the same *PPFD*. When factoring in the decreased distance between the HPS fixtures and bench compared to the LED fixtures (1.3 m and 2.5 m, respectively), and that the LEDs were shaded to deliver the same *PPFD*, the LED modules used in this research were much more effective than the older magnetic ballast HPS fixtures. Using the manufacturer rating of output efficacy, 2.0-2.3 $\mu mol \cdot J^{-1}$ (Philips Horticulture LED Solutions, 2015), the LED modules used in our experiment were 2.4 times more efficient than the 400-W magnetic ballast HPS fixture tested by Nelson and Bugbee (2014). Additionally, the emission of radiant heat from HPS lamps can influence the heat load on a crop canopy. Faust and Heins (1997) reported increases of 1.2, 1.5, and 1.7 °C on vinca shoot-tip temperature relative to air temperature under *PPFD* treatments of 50, 75, and 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ provided by four 400-W HPS lamps. We observed a similar increase in leaf

temperature relative to air temperature under the HPS_{90} treatment (but not in the LED treatments) in two replications (Table 2.1). In the third replication, when the natural photoperiod was much longer and light intensity was greater, leaf temperature relative to air temperature was higher under all treatments except HPS_{10}.

Compact seedlings that have a high dry mass per internode or are otherwise compact are considered more desirable for shipping and successful transplant. Based on previous experiments raising seedlings under LED SSL, we expected more compact seedlings by delivering B and R light as observed by Wollaeger and Runkle (2014), however in our experiment there were no consistent differences in dry matter accumulation or height with different proportions of B light. Additionally, there were few differences between seedlings grown under HPS and LED SL and there were no measurable differences in time to flower after transplanting seedlings to a common environment. We conclude that the difference in spectra provided by the HPS and LED SL treatments was not enough to elicit large morphological changes in seedlings grown in our ambient greenhouse light conditions. Future research could focus on the ambient solar conditions or DLI that could enable the spectra evaluated to elicit significant effects on plant morphology, or on modifying the spectra of the treatments to include substantially more B light.

APPENDIX

Table 2.1. Means (±SD) of greenhouse air temperature, leaf temperature, and photosynthetic daily light integral (DLI) as measured by aspirated thermocouples, infrared sensors, and quantum sensors, respectively, under ambient solar radiation with supplemental lighting treatments delivered by high-pressure sodium (HPS) or light-emitting diodes (LEDs). For the LED treatments, subscript values that follow each waveband of blue (B, 400 to 500 nm), green (G, 500 to 600 nm), and red (R, 600 to 700 nm) radiation indicate their percentages. Numbers in subscript following HPS treatments denote their intensity ($\mu mol \cdot m^{-2} \cdot s^{-1}$). All LED treatments were delivered at a *PPFD* of 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$.

Treatment initiation	Supplemental light treatment	Daytime air temperature (°C)	Daytime leaf temperature (°C)	Air – leaf temperature (°C)	DLI ($mol \cdot m^{-2} \cdot d^{-1}$)
22 Jan.	HPS_{10}	19.8 ± 1.1	16.8 ± 1.5	3.0	4.9 ± 0.5
	HPS_{90}	18.3 ± 0.6	19.0 ± 1.5	-0.7	Not recorded
	$B_{10}R_{90}$	19.6 ± 0.7	18.6 ± 1.5	1.0	7.3 ± 0.6
	$B_{20}R_{80}$	19.8 ± 0.7	18.2 ± 1.6	1.6	8.5 ± 0.7
	$B_{10}G_5R_{85}$	20.4 ± 0.8	19.3 ± 1.2	1.1	7.8 ± 0.5
	$B_{15}G_5R_{80}$	21.3 ± 0.8	19.9 ± 1.4	1.4	7.5 ± 0.5
5 Mar.	HPS_{10}	21.1 ± 1.0	19.0 ± 1.9	2.1	7.7 ± 1.2
	HPS_{90}	20.5 ± 1.4	21.2 ± 1.7	-0.7	8.8 ± 0.7
	$B_{10}R_{90}$	21.2 ± 0.8	20.6 ± 1.5	0.6	8.8 ± 0.8
	$B_{20}R_{80}$	20.6 ± 1.7	20.3 ± 2.1	0.3	9.0 ± 1.0
	$B_{10}G_5R_{85}$	20.8 ± 2.1	19.9 ± 1.4	0.9	8.8 ± 0.8
	$B_{15}G_5R_{80}$	20.5 ± 1.1	19.7 ± 1.7	0.8	9.1 ± 0.9
15 Jun.	HPS_{10}	22.9 ± 2.7	20.7 ± 3.7	2.2	6.4 ± 1.9
	HPS_{90}	21.9 ± 3.4	24.5 ± 4.5	-2.6	10.5 ± 1.9
	$B_{10}R_{90}$	22.1 ± 2.4	24.8 ± 4.7	-2.7	10.1 ± 1.9
	$B_{20}R_{80}$	22.0 ± 3.5	24.5 ± 4.9	-2.5	11.0 ± 2.1
	$B_{10}G_5R_{85}$	22.1 ± 2.6	24.4 ± 5.4	-2.3	9.8 ± 2.1
	$B_{15}G_5R_{80}$	21.6 ± 2.8	24.7 ± 4.5	-3.1	9.8 ± 1.9
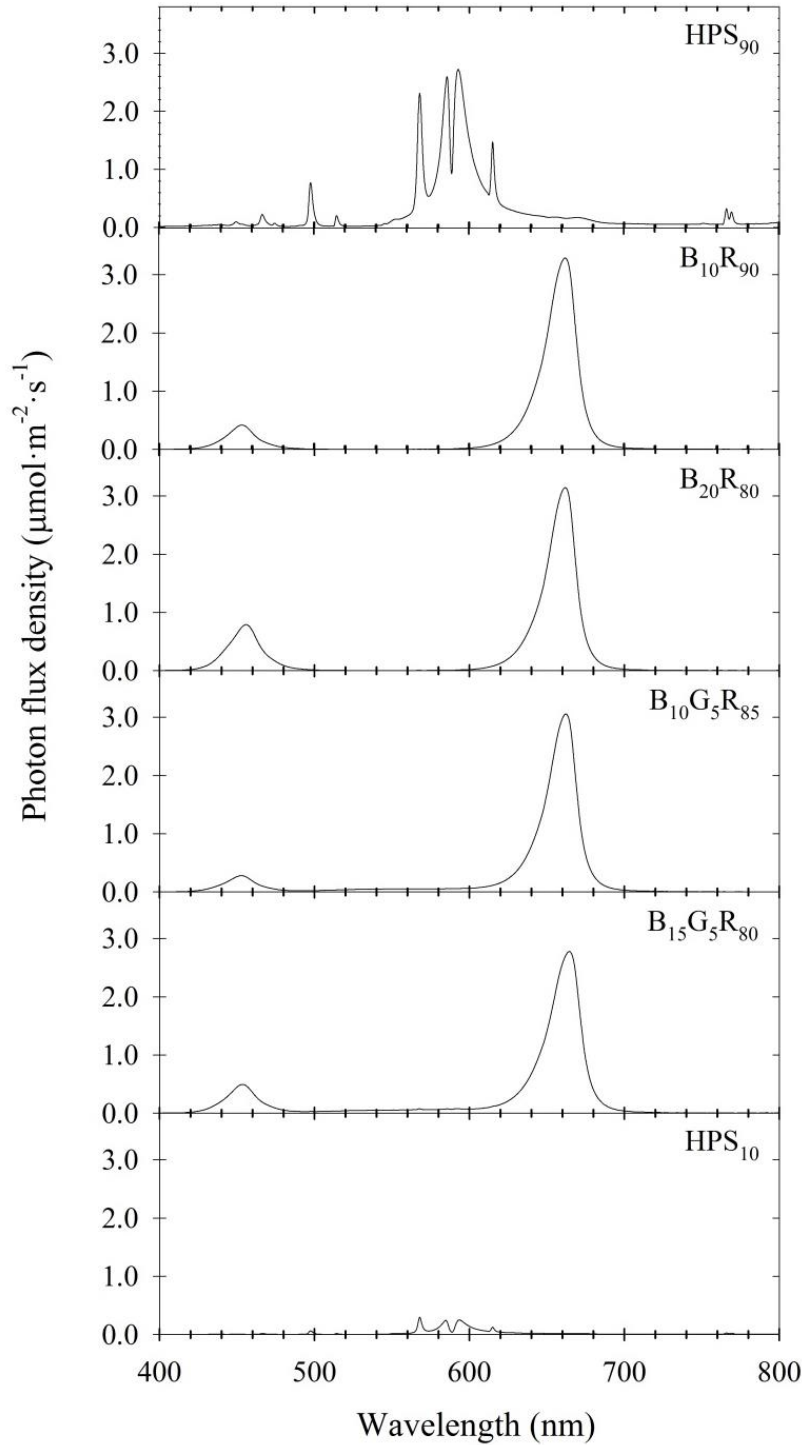
Figure 2.1. Spectral distribution of six supplemental lighting treatments between 400 and 800 nm from high-pressure sodium (HPS) and light-emitting diodes (LEDs) delivering different proportions of (B, 400 to 500 nm), green (G, 500 to 600 nm), and red (R, 600 to 700 nm). Numbers in subscript following HPS denote the intensity delivered, in $\mu mol \cdot m^{-2} \cdot s^{-1}$, and the numbers in subscript following the LED treatments denote the percent B, G, and R in each, which totaled 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$.

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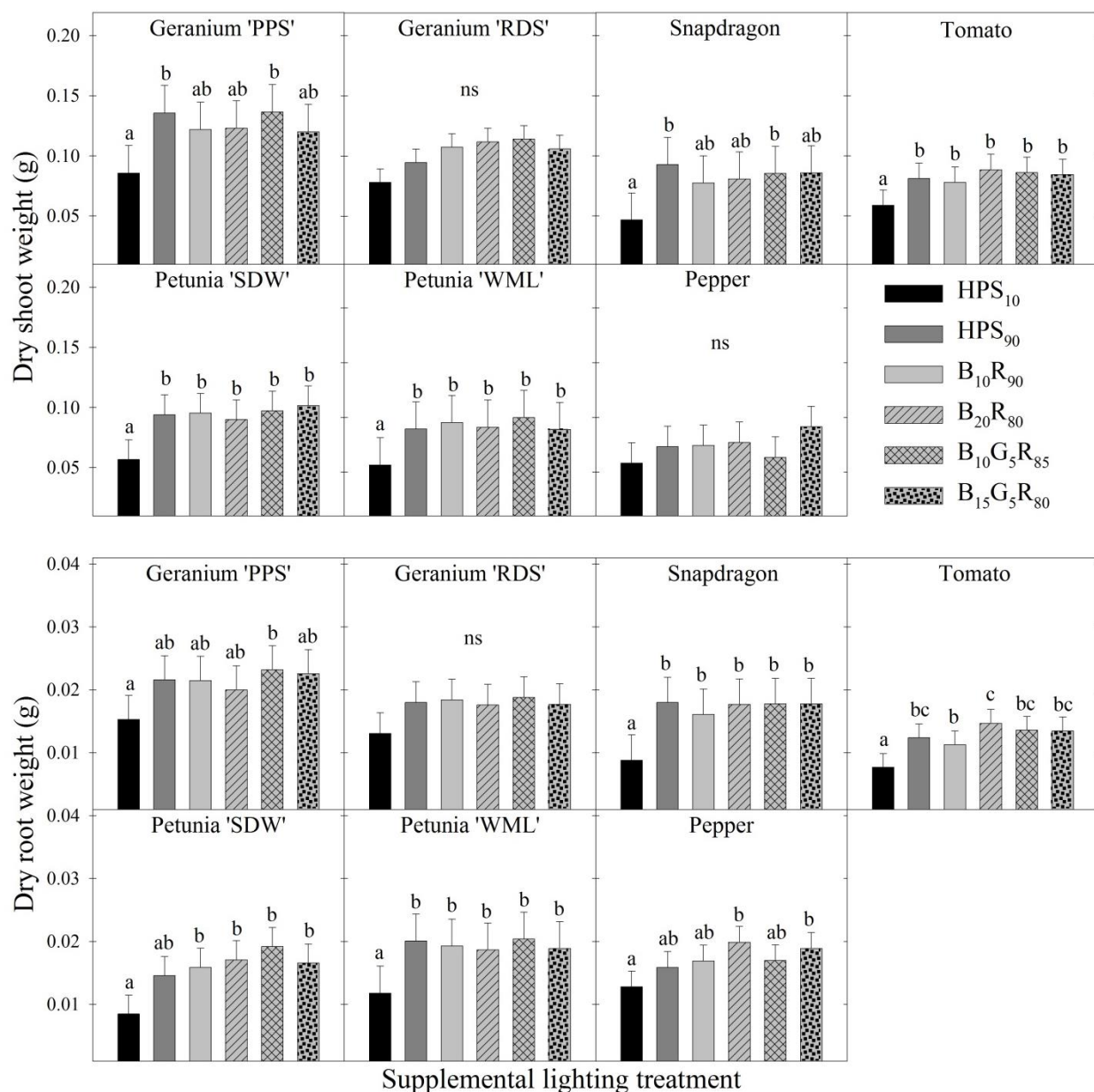
Figure 2.2. Dry shoot and root weights of seven seedling cultivars grown under ambient light and supplemental lighting from two high-pressure sodium (HPS) or four light-emitting diode (LED) treatments delivering different proportions of blue (B, 400 to 500 nm), green (G, 500 to 600 nm), and red (R, 600 to 700 nm). All treatments were delivered at a *PPFD* of 90 µmol·m^{-2}·s^{-1}, except HPS$_{10}$ delivered at 10 µmol·m^{-2}·s^{-1}. Numbers in subscript of LED treatments denote proportion of intensity in 100 nm wavebands. Means sharing a letter are not statistically different by Tukey's honest significant difference test at $P \leq 0.05$. Error bars indicate standard error. 'PPS', 'Pinto Premium Salmon'. 'RDS', 'Ringo 2000 Deep Scarlet'. 'SDW', 'Single Dreams White'. 'WML', 'Wave Misty Lilac'.

Figure 2.3. Plant height and leaf area of seven seedling cultivars grown under ambient light and supplemental lighting from two high-pressure sodium (HPS) or four light-emitting diode (LED) treatments delivering different proportions of blue (B, 400 to 500 nm), green (G, 500 to 600 nm), and red (R, 600 to 700 nm). All treatments were delivered at a *PPFD* of 90 μmol·m^{-2}·s^{-1}, except HPS$_{10}$ delivered at 10 μmol·m^{-2}·s^{-1}. Numbers in subscript of LED treatments denote proportion of intensity in 100 nm wavebands. Means sharing a letter are not statistically different by Tukey's honest significant difference test at $P \leq 0.05$. Error bars indicate standard error. 'PPS', 'Pinto Premium Salmon'. 'RDS', 'Ringo 2000 Deep Scarlet'. 'SDW', 'Single Dreams White'. 'WML', 'Wave Misty Lilac'.

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Figure 2.4. Leaf number at transplant of seven seedling cultivars grown under ambient light and supplemental lighting from two high-pressure sodium (HPS) or four light-emitting diode (LED) treatments delivering different proportions of blue (B, 400 to 500 nm), green (G, 500 to 600 nm), and red (R, 600 to 700 nm). All treatments were delivered at a *PPFD* of 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$, except HPS_{10} delivered at 10 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Numbers in subscript denote proportion of intensity in 100 nm wavebands. Means sharing a letter are not statistically different by Tukey's honest significant difference test at $P \le 0.05$. Error bars indicate standard error. 'PPS', 'Pinto Premium Salmon'. 'RDS', 'Ringo 2000 Deep Scarlet'. 'SDW', 'Single Dreams White'. 'WML', 'Wave Misty Lilac'.
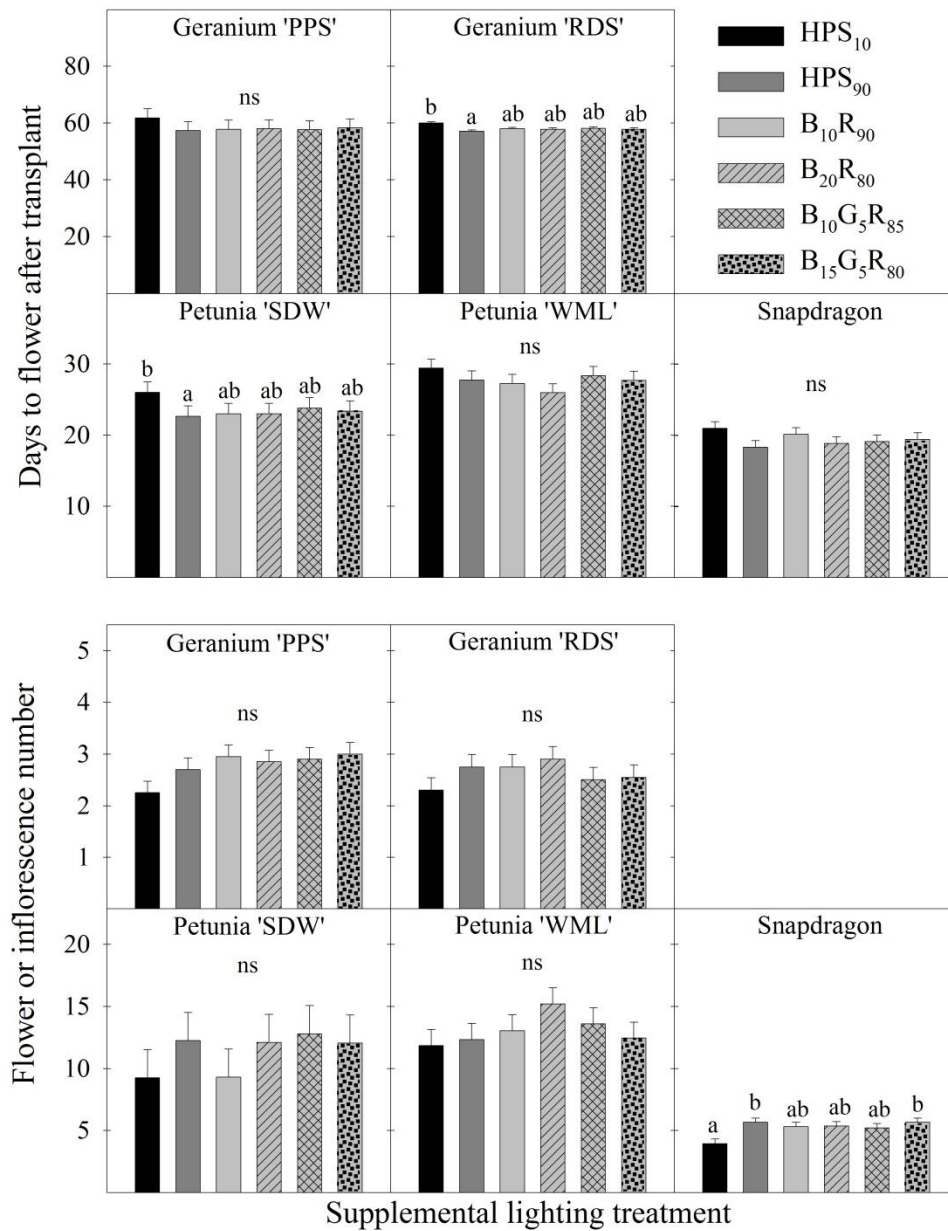
Figure 2.5. Days to flower after transplant and total flower or inflorescence number (old and existing) 7-10 d after flowering of seven seedling cultiva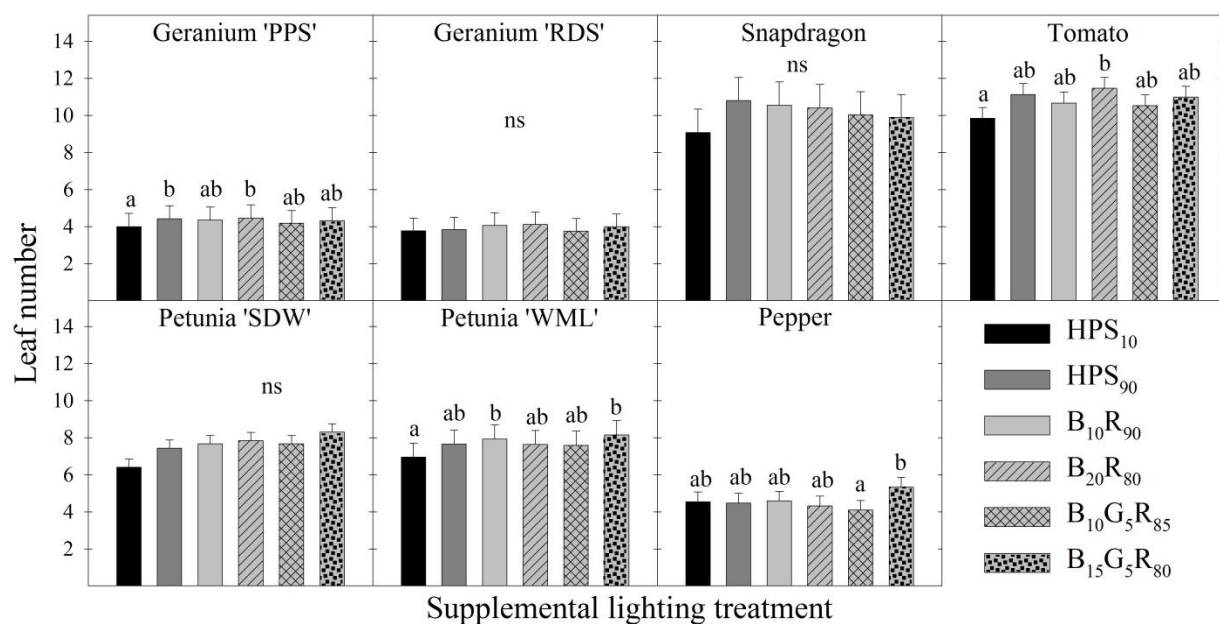rs grown under ambient light and supplemental lighting from two high-pressure sodium (HPS) or four light-emitting diode (LED) treatments delivering different proportions of blue (B, 400 to 500 nm), green (G, 500 to 600 nm), and red (R, 600 to 700 nm). All treatments were delivered at a *PPFD* of 90 μmol·m^{-2}·s^{-1}, except HPS$_{10}$ delivered at 10 μmol·m^{-2}·s^{-1}. Numbers in subscript denote proportion of intensity in 100 nm wavebands. Means sharing a letter are not statistically different by Tukey's honest significant difference test at *P* ≤ 0.05. Error bars indicate standard error. 'PPS', 'Pinto Premium Salmon'. 'RDS', 'Ringo 2000 Deep Scarlet'. 'SDW', 'Single Dreams White'. 'WML', 'Wave Misty Lilac'.

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SECTION III

THE UTILITY OF BLUE, RED, AND FAR-RED RADIATION FROM LIGHT-EMITTING
DIODES FOR SUPPLEMENTAL LIGHTING OF ANNUAL BEDDING PLANTS

The Utility of Blue, Red, and Far-red Radiation from Light-emitting Diodes for Supplemental Lighting of Annual Bedding Plants

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Abstract

Supplemental lighting (SL), traditionally provided by high-pressure sodium (HPS) lamps, is recommended for greenhouse production of seedlings during light-limiting conditions. Light-emitting diodes (LEDs) have emerged as an appealing alternative to HPS lamps primarily because they can provide SL at improved energy efficiencies and have longer fixture lifetimes. The specific emission spectra of LEDs also provide an opportunity to manipulate plant morphology through targeting light absorption of specific photoreceptors. Our objective was to quantify how the spectral quality of SL affected plant growth and subsequent flowering. We grew seedlings of geranium (*Pelargonium ×hortorum*), pepper (*Capsicum annuum*), petunia (*Petunia ×hybrida*), snapdragon (*Antirrhinum majus*) and tomato (*Solanum lycopersicum*) in greenhouses at 20 °C under a 16-h photoperiod under six SL treatments: five that delivered a photosynthetic photon flux density (*PPFD*) of 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$ from HPS lamps (HPS$_{90}$) or LEDs [four treatments composed of (B, 400-500 nm), red (R, 600-700 nm), far red (FR, 700-800 nm) and/or white LEDs] and one that delivered 10 $\mu mol \cdot m^{-2} \cdot s^{-1}$ from HPS (HPS$_{10}$) lamps. The LED treatments defined by their relative amounts of B, green (G, 500-600 nm), and R light were B$_{10}$R$_{90}$, B$_{45}$R$_{55}$, B$_{10}$G$_5$R$_{85}$, and B$_{12}$G$_{20}$R$_{68}$+FR (FR at 12 $\mu mol \cdot m^{-2} \cdot s^{-1}$). At transplant, leaf area and seedling height were similar among 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$ treatments in all species except snapdragon, where seedlings grown under B$_{12}$G$_{20}$R$_{68}$+FR had 62% greater leaf area than those grown under B$_{45}$R$_{55}$ and were 47%, 18%, 38%, and 62% taller than those grown under HPS$_{90}$, B$_{10}$R$_{90}$, B$_{10}$G$_5$R$_{85}$ and B$_{45}$G$_{55}$, respectively. After transplant and finishing under the same SL treatments, snapdragon flowered on average 7 d earlier under the B$_{12}$G$_{20}$R$_{68}$+FR treatment than the other LED treatments while geranium grown under B$_{45}$R$_{55}$ and B$_{12}$G$_{20}$R$_{68}$+FR flowered 7 to 9 d earlier than those under the B$_{10}$G$_5$R$_{85}$ and B$_{10}$R$_{90}$ treatments. Seedlings of each species grown under the

HPS$_{10}$ treatment accumulated less dry mass and took longer to flower compared to seedlings under the other SL treatments. We conclude that light quality of SL has relatively little effect on seedling and transplant development, and thus, the primary advantage of using LEDs is related to their operational properties such as electrical efficacy.

Introduction

The photosynthetic daily light integral (DLI) is the cumulative quantity of photons within the photosynthetically active waveband (400 to 700 nm) incident upon a square meter during a 24-h period and is usually expressed in the unit of mol·m^{-2}·d^{-1}. During commercial seedling production, a minimum DLI of 10 to 12 mol·m^{-2}·d^{-1} has been recommended to achieve suitable seedling quality and reduced time to flower after transplant (Lopez and Runkle, 2008; Pramuk and Runkle, 2005). Commercial production of annual (bedding plant and vegetable) seedlings primarily occurs during the winter and early spring, and in the northern U.S., the mean outdoor DLI is as low as 5 to 10 mol·m^{-2}·d^{-1} (Korczynski et al., 2002) and inside a greenhouse, values will be 30 to 50% lower. Therefore, supplemental lighting from electric lamps is commonly used by commercial growers to achieve the desired DLI. Supplemental lighting (SL) can be delivered by high-intensity discharge lamps, and most commonly from high-pressure sodium (HPS) lamps, and operate during cloudy conditions or at night to increase the DLI. Light-emitting diodes (LEDs) have increasing potential to be used for SL applications as the technology develops, particularly as their intensity and efficacy increase and cost decreases (Bourget, 2008).

Unlike HPS lamps, LEDs emit narrow wavebands based on their chip composition and can therefore emit specific wavebands of interest for a range of applications (Mitchell et al., 2016). Early focus of LED use in horticulture was on the application of red (R, 600-700 nm)

light because it is strongly absorbed by chlorophyll extracts and was the first color to become feasible for horticultural lighting (Bula et al., 1991). Growth under R alone in sole-source lighting (SSL) experiments produced plants with elongated hypocotyls and petioles or decreased chlorophyll development, which could be alleviated with the addition of a relatively low flux of blue (B, 400-500 nm) light (Hoenecke et al., 1992; Tripathy and Brown, 1995). Unlike broad-spectrum light sources, the LED spectral output can be tailored to emit only photosynthetic or photomorphogenic wavelengths (Morrow, 2008).

Plant growth and development are controlled by photoreceptors that regulate hypocotyl and internode extension, leaf expansion, chlorophyll orientation, and flowering in response to specific wavebands of light. For example, the cryptochrome receptors, cry1 and cry2, respond to wavelengths from 390 to 480 nm and regulate stem extension, guard cell opening, anthocyanin accumulation, and in at least some species, flower induction (Ahmad et al., 2002). In *Arabidopsis*, cryptochromes mediate hypocotyl elongation through B light regulation of gibberellic acid metabolism (Zhao et al., 2007). Phytochrome, a family of proteins that primarily absorb R and far-red (FR, 700-800 nm) radiation, signals shade avoidance and flowering control through gene-regulated control of transcription networks (Folta and Caravalho, 2015). Phytochrome exists in R- (Pr; inactive) and FR- (Pfr; active) absorbing forms and the incident light quality (particularly the R:FR) establishes a phytochrome photoequilibrium (PPE). In conditions depleted of R light, such as under a plant canopy, the PPE becomes low, which signals stem and petiole elongation (Franklin and Whitelam, 2005). With the narrow emission spectra of LEDs, one can target these photoreceptors to potentially control plant morphology, which can influence quality attributes important for commercial production of ornamental and vegetable seedlings.

Early plant experiments with R and FR LEDs and B light from blue fluorescent (BF) lamps showed including B or FR in SSL studies could manipulate plant morphology (Brown et al., 1995; Goins et al., 1997). Brown et al. (1995) grew 21-day old pepper (*Capsicum annuum* 'Hungarian Wax') seedlings under SSL from metal halide lamps, only R from R LEDs (peak=660 nm), 1% BF + 99% R LEDs, and R LEDs + 59 $\mu mol \cdot m^{-2} \cdot s^{-1}$ from FR LEDs (peak=735 nm), each providing a *PPFD* of 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for 12 $h \cdot d^{-1}$. Plants grown under R + BF were shorter than those grown under R alone, while those grown under R + FR were tallest. Plants grown without B light had negatively impacted leaf expansion and dry mass accumulation.

Far-red LEDs have been used in plant applications to manipulate extension growth of leaves and stems as well as regulating flowering of at least some long-day plants. For example, by adding FR to B and R SSL treatments from LEDs, Park and Runkle (2016) were able to increase photosynthetic efficiency in snapdragon (*Antirrhinum majus*) seedlings; those grown under increasing amounts of FR displayed greater leaf expansion that subsequently increased light capture. In addition, stem length of tomato (*Solanum lycopersicum*) rootstock seedlings increased from an end-of-day FR treatment from LEDs similar to that under incandescent bulbs (Chia and Kubota, 2010). Red+FR has been provided by incandescent bulbs to promote flowering in long-day plants, but R + white (W) + FR LEDs effectively promote flowering while consuming less energy than traditional sources (Meng and Runkle, 2014). By adding FR radiation from LEDs, it is possible to accelerate flowering in some long-day plants that are FR-sensitive.

High-quality seedlings suitable for shipping and transplanting should have a high dry weight per internode and be compact. Randall and Lopez (2014) reported decreases in seedling

height of six ornamental species grown under 15% B + 85% R from LEDs compared to those grown under HPS SL at a *PPFD* of 160 μmol·m^{-2}·s^{-1}. However, the same species grown under 30% B + 70% R LED SL were of similar height as those grown under 15% B + 85% R LED SL. Similarly, previous results growing annual seedlings under different LED SL treatments showed inconsistent or limited responses of seedling height, leaf area, and dry weight among HPS and LED treatments (Chapter 2). Providing SL with more pronounced differences in the B:R, the addition of FR, and longer treatment periods (from seedling emergence to flowering) could lead to greater differences in growth and development. Therefore, our objective was to evaluate SL from HPS or LEDs with increased B or added FR on seedling quality and plant performance after transplant until flowering.

Materials and Methods

Plant material. Seeds of geranium (*Pelargonium ×hortorum* 'Pinto Premium Salmon'), pepper 'Long Red Slim Cayenne', petunia (*Petunia ×hybrida* 'Single Dreams White'), snapdragon 'Montego Yellow' and tomato 'Supersweet' were sown into 128-cell plug trays (2.7 × 2.7 cm; 12.0-mL volume) at a commercial greenhouse (C. Raker and Sons, Inc., Litchfield, MI) and delivered to the Plant Science Research Greenhouses at Michigan State University (East Lansing, MI) four (replication 1) or five (replication 2) days after seed sow. The same seedling distribution, irrigation, and fertilization methods described in Chapter 2 were followed, with 64 seedlings in each of two blocks for each species.

Lighting treatments. Different SL treatments were delivered to each greenhouse section continuously for 16 h·d^{-1} (0600 to 2200 HR) at a *PPFD* of 90 μmol·m^{-2}·s^{-1} (five sections) or 10 μmol·m^{-2}·s^{-1} (one section) as measured at plant height in 9 different horizontal positions by a

portable spectroradiometer (PS-200, StellarNet Inc., Tampa, FL) (Figure 3.1). Two of the SL

treatments were delivered by HPS lamps using either one 150-W fixture (LU150; Acuity

Lithonia Lighting, Conyers, GA) or four 400-W fixtures (LR48877; P.L. Light Systems,

Beamsville, Ontario, Canada) to deliver 10 (HPS_{10}) or 90 (HPS_{90}) $\mu mol \cdot m^{-2} \cdot s^{-1}$, respectively. The

four remaining SL treatments were delivered by commercial fixtures that contained R (peak=660

nm), B (peak=453 nm), W, and/or far-red (FR, peak=737 nm) LEDs, three of which were

wrapped in a layer of flexible, neutral-density mesh (General purpose aluminum; New York

Wire, Grand Island, NY) to reduce light intensity by approximately 35%. Each LED fixture was

mounted horizontally 1.9 m above the bench height and the 400-W and 150-W HPS fixtures

were mounted 1.3 m and 2.5 m above the plants, respectively. Glass walls between greenhouse

sections were coated with a heavy layer of whitewash to prevent light treatment contamination.

The four LED treatments were defined by their 100-nm waveband ratios of B, G, and R

light (subscript values indicate the percentage of each waveband) and were $B_{10}R_{90}$, $B_{45}R_{55}$,

$B_{10}G_5R_{85}$, and $B_{12}G_{20}R_{68}$+FR. The $B_{10}R_{90}$ and $B_{10}G_5R_{85}$ treatments were delivered by top-

lighting fixtures (GP-TOPlight DR/B-LB2013 and GP-TOPlight DR/W-MB2013, Philips,

Eindhoven, The Netherlands) alone. The $B_{45}R_{55}$ treatment (Figure 3.1) was delivered by top-

lighting fixtures providing 20% B + 80% R (GP-TOPlight DR/B-HB2013, Philips) with two

layers of neutral-density mesh to reduce light intensity (by approximately 57%) along with 18 B-

emitting LED research modules (GreenPower LED research module blue, Philips) hung 60 cm

above the benches to provide the target *PPFD*. The fourth LED treatment $B_{12}G_{20}R_{68}$+FR was

provided by top-lighting fixtures that emitted 12 $\mu mol \cdot m^{-2} \cdot s^{-1}$ FR (GP-TOPlight DR/W/FR_2-

HB2013, Philips) and did not require mesh to obtain the target *PPFD*. The estimated

phytochrome photoequilibria (PPE) established under each treatment was calculated using

spectrodiometer software (SpectraWiz, StellarNet Inc.) that used the formula described in Sager et al. (1982) and ranged from 0.84 to 0.88 (Figure 3.2).

Environmental conditions. The experiment was performed in six glass-glazed greenhouse sections as described in Chapter 2. The set point for air temperature was 20 °C during the day and night and was maintained by steam heating, exhaust fans, and roof vents controlled by a greenhouse environmental control system (Integro 725, Priva North America, Vineland, Ontario, Canada). In each section, air temperature was recorded by an aspirated tube thermocouple (Type E; Omega Engineering, Stamford, CT) above canopy height. Leaf surface temperature was measured by an infrared thermocouple (Type K, OS36-01; Omega Engineering, Stamford, CT), placed 15 cm above one seeding tray in each section during the seedling phase and 5 cm above one plant during the transplant phase and oriented downward at a 45° angle. The *PPFD* was measured at bench height and recorded by a quantum sensor (LI-190SA, LI-COR, Lincoln, NE). Whitewash (Kool Ray Classic; Continental Products Co., Euclid, OH) was applied on the glass-glazed greenhouse exterior to decrease the intensity (by approximately 20%) and improve the uniformity of sunlight midway through the second replication. Environmental conditions in each section were monitored and logged using a data logger (CR-10; Campbell Scientific, Logan, UT) every 10 s and hourly averages were recorded. Environmental data during the seedling and transplant phases are reported in Tables 3.1 and 3.2, respectively.

Seedling measurements and transplant. After 14 to 26 days of lighting treatments (depending on species and seasonal conditions), eight seedlings from each block, 16 seedlings total, were sampled at random, excluding those in edge rows, and the following measurements were made: leaf area [using a leaf area meter (LI-3000; LI-COR, Lincoln, NE)], leaf number, and plant height (from substrate surface). Shoots were abscised at the media surface and roots,

separated from the media in a washbasin, were then placed in paper envelopes and into a drying oven (NAPCO 630, NAPCO Scientific Co., Tualatin, OR) at 80 °C for at least 48 h then measured for shoot and root dry weight. From the remaining seedlings, 10 (five from each block) each of geranium, petunia, and snapdragon from each treatment were transplanted into 10-cm pots containing 70% peat moss, 21% perlite and 9% vermiculite (SUREMIX, Michigan Grower Products Inc., Galesburg, MI) and returned to their respective SL treatment. Pots were irrigated with line-fed water-soluble fertilizer providing (in mg·L^{-1}) 125 N, 12 P, 100 K, 65 Ca, 12 Mg, 1 Fe and Cu, 0.5 Mn and Zn, 0.3 B, and 0.1 Mo (MSU RO Water Special; GreenCare Fertilizers, Inc., Kankakee, IL) as necessary and rotated positionally every two days. Date of first open flower or inflorescence, height at first flower, and total number of flowers or inflorescences (old and existing) approximately 7-10 d after flowering was recorded.

Experimental design and data analysis. The experiment was performed twice with seed sowings in Nov. and Dec. 2015. Data were analyzed as a randomized complete block design with subsamples to account for seasonal changes in daily light integral (DLI) and temperature, among other factors. Data were analyzed using the mixed model procedure (PROC MIXED) in SAS 9.4 (SAS Institute, Cary, NC) and pairwise comparisons between treatments were performed using Tukey's honest significant difference test ($P \leq 0.05$).

Results

Plant height. At transplant, seedlings of petunia, snapdragon, tomato, and pepper were shorter when grown under the HPS$_{10}$ treatment compared to those grown under HPS$_{90}$; height of geranium seedlings was similar under all treatments (Figure 3.3). Tomato, pepper, and petunia seedlings grown under any 90 µmol·m^{-2}·s^{-1} SL treatment were similar in height, however petunia

seedlings grown under $B_{45}R_{55}$ were similar in height to those grown under HPS_{10} SL. Snapdragon seedlings grown under $B_{12}G_{20}R_{68}$+FR were the tallest among treatments, followed by those grown under $B_{10}R_{90}$ and those under the remaining 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$ treatments were similar in height.

 Leaf number and leaf area. Tomato seedlings grown under $B_{45}R_{55}$ had more leaves at transplant than those grown under $B_{10}R_{90}$, $B_{10}G_5R_{85}$, and HPS_{10} SL while those under all of the 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$ SL treatments had more leaves than those grown under HPS_{10} (Figure 3.4). There were no other differences in leaf number among the other crops grown under the 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$ SL treatments. Total leaf area for all crops studied was similar among the 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$ SL treatments except for snapdragon seedlings, in which those grown under $B_{45}R_{55}$ had 37% less leaf area than seedlings grown under $B_{12}G_{20}R_{68}$+FR. Leaf area under HPS_{10} SL was 63%, 64%, 64% and 75% less than seedlings grown under HPS_{90} SL in pepper, tomato, snapdragon, and petunia, respectively. There were no differences in average leaf area (the quotient of total leaf area and average leaf number) among 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$ SL treatments (data not presented).

 Dry shoot weight. In all crops tested, dry shoot weight was significantly less in seedlings grown under the HPS_{10} treatment than those grown under the LED and HPS_{90} SL treatments (Figure 3.5). Seedlings grown under HPS_{10} accumulated 53%, 68%, 69%, 75%, and 79% less dry mass in geranium, pepper, tomato, petunia, and snapdragon, respectively, compared to those grown under HPS_{90}. Among the 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$ SL treatments, only pepper seedlings exhibited a difference in dry weight among LED SL treatments. The $B_{10}R_{90}$ LED SL treated seedlings accumulated less dry matter than seedlings grown under HPS_{90} SL.

Dry root weight. Root weights of tomato, petunia, pepper, and snapdragon were 40%, 57%, 68%, and 76% less when grown under HPS_{10} than those grown under HPS_{90} SL. Tomato seedling root weight was greater under HPS_{90} SL and $B_{12}G_{20}R_{68}$+FR LED SL compared to the HPS_{10} treatment, whereas those under the remaining LED SL treatments were similar. In all crops tested, there were no differences in dry root weights among the 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$ SL treatments.

Days to first flower. Seedlings grown under HPS_{10} continuously (during the seedling and transplant phases) took the longest to flower (Figure 3.6). On average, snapdragon, petunia, and geranium took 19, 23, and 24 more days to flower under the HPS_{10} treatment compared to those grown under the HPS_{90} treatment. Petunia transplants grown under 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$ SL treatments took a similar number of days to flower, while among LED SL treatments, snapdragon flowered earliest when grown under the $B_{12}G_{20}R_{68}$+FR treatment. Geranium transplants grown under $B_{10}R_{90}$ and $B_{10}G_5R_{85}$ took longer to flower than those grown under $B_{12}G_{20}R_{68}$+FR and $B_{45}R_{55}$, but flowering time was similar to those grown under HPS_{90}.

Plant height at first flower. Snapdragon plants were of similar height at flowering under all SL treatments. Petunia plants grown under HPS_{10} were taller at first flower than those grown under HPS_{90}, $B_{10}R_{90}$, and $B_{45}R_{55}$, but were of similar height as those grown under $B_{10}G_5R_{85}$ and $B_{12}G_{20}R_{68}$+FR. Petunia grown under $B_{10}R_{90}$ were shorter at first flower than those grown under $B_{12}G_{20}R_{68}$+FR, but were similar to those grown under the remaining treatments. Geranium was shorter at first flower when grown under the $B_{45}R_{55}$ treatment than those under the HPS_{10}, HPS_{90}, and $B_{12}G_{20}R_{68}$+FR treatments.

Total flower number. Snapdragon grown under HPS_{90} and $B_{12}G_{20}R_{68}$+FR had more inflorescences than those grown under HPS_{10} while those grown under the LED SL treatments

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had a similar inflorescence number. Petunia grown under $B_{12}G_{20}R_{68}$+FR SL had more flowers than those grown under HPS_{10} and $B_{10}G_5R_{85}$. Similarly, geranium had the most inflorescences when grown under the $B_{12}G_{20}R_{68}$+FR treatment and among the least under HPS_{10}. The $B_{10}R_{90}$ treatment was the only 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$ SL treatment in which plants had a similar number of inflorescences as those grown under HPS_{10}.

Discussion

One of our objectives was to determine if SL that emitted a relatively high percentage (>25%) of B light would inhibit extension growth of seedlings. In a prior experiment (Chapter 2), we observed limited effects of light quality from HPS and LED SL treatments on seedling growth and morphology when B was ≤20% of the total *PPFD*. Blue light can suppress stem extension and leaf expansion through a cryptochrome-mediated pathway altering gene expression (Folta and Childers, 2008) and perhaps through other B light-mediated photoreceptors. For example, Wollaeger and Runkle (2015) grew seedlings of impatiens (*Impatiens walleriana*), salvia (*Salvia splendens*), petunia, and tomato under SSL from LEDs providing six B:R ratios (from 100:0 to 0:100) and as little as 10 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of B was enough to elicit morphological effects, while cryptochrome receptors were likely saturated at 40 $\mu mol \cdot m^{-2} \cdot s^{-1}$ because plants receiving more than 25% B were similar in height.

Despite the increased ratio of B in the $B_{45}R_{55}$ treatment, there were few differences or inconsistent responses in leaf expansion and plant height under the 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$ treatments. Snapdragon seedlings grown under $B_{45}R_{55}$ were 26% and 37% shorter than those grown under $B_{10}R_{90}$ and $B_{12}G_{20}R_{68}$+FR, respectively, however the addition of FR may be a confounding factor in this second comparison. There were no differences in plant height or leaf area in the

other four species tested among the 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$ treatments. A lack of response in stem elongation and leaf expansion was reported under SL with 0 to 16% B delivered with R to tomato (Hernandez and Kubota, 2012) and cucumber (*Cucumis sativus*) seedlings (Hernandez and Kubota, 2014). In contrast, seedlings of snapdragon, vinca (*Catharanthus roseus*), impatiens, geranium, petunia, and marigold (*Tagetes patula*) were more compact when grown under LED SL delivering 15 and 30% B with R compared with those grown under HPS, but there were no differences in plant height between the two B+R LED SL treatments (Randall and Lopez, 2014). The lack of a clear B light response in our and other SL studies could be attributed to the saturation of B light-absorbing photoreceptors from background ambient sunlight. All plants received a DLI of approximately 3 to 5 $mol \cdot m^{-2} \cdot d^{-1}$ from sunlight (Table 3.1 and 3.2), which equates to approximately 0.7 to 1.2 $mol \cdot m^{-2} \cdot d^{-1}$ of B radiation to saturate photoreceptors across all treatments.

We were also interested in the effects of SL treatments (especially the different percentages of B light) on plant growth after transplant. After 12 weeks under SL, geranium plants grown under $B_{45}R_{55}$ were 27% shorter at flowering than those grown under HPS_{90}, but were similar to those under the other LED treatments without FR. Transplants of snapdragon were the same height at flowering and petunia plants were generally similar under 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$ SL treatments. In another SL experiment, shoot length of three poinsettia (*Euphorbia pulcherrima*) cultivars after 12 weeks was reduced by 20 to 34% under 20%B + 80%R from LEDs than under HPS lamps (Islam et al., 2012). They attributed the reduced plant height to the increased B in the LED treatment and cryptochrome-mediated elongation suppression. The lack of consistent differences in petunia and snapdragon, but shorter geranium plants at first flower under the $B_{45}R_{55}$ treatment, could be attributed to the increased time under the SL treatments;

geraniums flowered in an average of 66 days after transplant while petunia and snapdragon flowered in half that time. It is also possible that geranium is more sensitive to B light effects, and additional studies focusing on spectral sensitivity compared to other species is needed.

A second experimental objective was to investigate the effect of adding FR to SL on seedling extension growth and subsequent flowering. Through manipulation of the phytochrome photoreceptors, FR radiation can regulate plant growth and flowering. There is generally an inverse linear relationship of PPE to extension growth, however specific responses to R:FR ratio vary among species and depend on the inclusion of other wavelengths (Runkle and Heins, 2001). In our study, snapdragon seedlings grown under the FR-emitting SL treatment (PPE=0.84) were tallest among treatments and had a greater leaf area than those grown under $B_{45}R_{55}$ (PPE=0.86). Park and Runkle (2016) reported up to a 70% increase in snapdragon seedling height and 40% increase in leaf expansion as PPE decreased from 0.88 to 0.69 in SSL treatments when the intensity of B light was constant. While our SL treatments had slightly different PPEs, morphological responses could be confounded by the different intensities of B, G, and R delivered in each treatment. The effects of SL lighting on plant height at flowering were inconsistent, although plants grown under the $B_{12}G_{20}R_{68}$+FR treatment were always at least as tall as plants grown under the other LED SL treatments. The commercial fixtures used in this experiment did not have adjustable spectra, therefore further testing with fixed ratios of B, G, and R among treatments would be needed to isolate the effects from added FR radiation.

In the production of ornamental transplants, producing compact seedlings is a common objective, which can be achieved using light with a high R:FR, but a high R:FR can potentially delay flower initiation and development in some long-day plants (Runkle and Heins, 2001). Snapdragon grown under the $B_{12}G_{20}R_{68}$+FR treatment flowered 8 days earlier than those under

the remaining LED SL treatments, although time to flower was similar to those under the HPS_{90} treatment. Under a FR-intercepting filter creating a high R:FR, flower initiation was delayed in campanula (*Campanula carpatica*) and coreopsis (*Coreopsis ×grandiflora*) and flower development was inhibited in viola (*Viola ×wittrockiana*; Runkle and Heins, 2001). Runkle and Heins (2003) were successful in promoting flowering of viola by adding FR radiation inside an FR-deficient environment throughout the photoperiod, for four hours at the end of the photoperiod, or as night interruption lighting. However, treatments that promoted flowering also promoted extension growth. More experimentation is required to determine the usefulness of including FR radiation in SL lighting on plant growth and development, perhaps with higher FR intensities.

When the DLI from sunlight is low, SL can be used in greenhouses to increase DLI and thus quality parameters of seedlings (Pramuk and Runkle, 2005). The DLI under the HPS_{10} treatment was approximately 3 to 4 $mol·m^{-2}·d^{-1}$ lower than under the 90 $μmol·m^{-2}·s^{-1}$ SL treatments while the photoperiod was the same (16 h). In previous SL experiments that increased DLI during the seedling phase, growth (as measured by dry mass accumulation), stem caliper, and leaf area increased (Hernandez and Kubota, 2014; Randall and Lopez, 2015). For example, Hernandez and Kubota (2014) grew cucumber plants in a greenhouse with and without SL at a *PPFD* of 54 $μmol·m^{-2}·s^{-1}$ from LEDs at three different R and B ratios at two ambient DLIs, 5.2 and 16.2 $mol·m^{-2}·d^{-1}$. At both DLIs, the seedlings grown with SL had a greater dry and fresh mass, leaf number, leaf area, and stem diameter. Similarly, in our experiment, seedlings of each species had a greater dry shoot weight when grown under the 90 $μmol·m^{-2}·s^{-1}$ SL treatments. Root dry weight, leaf area, and leaf number were also greater for three of five species grown under SL.

Plants can exhibit shade-avoidance responses, such as increases in extension growth, in response to decreases in the R:FR, the incident light intensity, or both (Ballaré et al., 1991; Smith, 1982). Hernandez and Kubota (2014) reported an increase in hypocotyl length for seedlings grown without SL, but in this current study, seedlings grown under the lower DLI were of the same height or shorter than those grown under the 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$ SL treatments. Similarly, seedling height of five species was similar or shorter under ambient light compared to those grown under SL from HPS lamps or LEDs (Randall and Lopez, 2015). However in a separate study, stem length of impatiens and salvia decreased as DLI increased while the opposite occurred in marigold and celosia [*Celosia argentea* var. *plumosa* (Pramuk and Runkle, 2005]. We attribute the shorter seedlings in our study to the development of fewer nodes at the time of transplant. Compared to those grown under HPS_{90}, seedlings of pepper, tomato, petunia, and snapdragon grown under HPS_{10} were 37%, 44%, 46%, and 62% shorter and had 31%, 44%, 33%, and 31% fewer nodes, respectively. Therefore, a paradigm exists that while plant height increases under low light conditions, plants may be shorter than those grown under higher light because they are less mature.

Providing an increased DLI to plants during the finishing stage can decrease time to flower, increase finished plant quality, or both in many species (Blanchard et al., 2011). Therefore, we postulated that time to flower would be reduced by providing SL during the transplant and finishing phases. Faust et al. (2005) reported increasing DLI from 5 to 19 $mol \cdot m^{-2} \cdot d^{-1}$ during the transplant phase decreased days to flower for marigold, petunia, salvia, and zinnia. In our experiment, all species tested flowered earlier under the high-intensity SL treatments. Similarly, Sams et al. (2016) noted an increase in inflorescence number on marigold grown under SL that added 8.6 $mol \cdot m^{-2} \cdot d^{-1}$ to a natural DLI of 11.5 $mol \cdot m^{-2} \cdot d^{-1}$ from HPS lamps

or LEDs compared to those grown without SL. We observed an increase in inflorescence number in geranium under four SL treatments compared to those grown under HPS_{10} while flower and inflorescence number in petunia and snapdragon showed inconsistent responses to DLI. However, more light does not necessarily increase flower number at first flowering. Although an increased DLI decreased time to flower, there was also a decrease in total flower number at first flowering (Pramuk and Runkle, 2005). Plants that take longer to flower have a longer vegetative phase and therefore have more time to harvest light and accumulate photosynthate for flower production. A similar response in flower production occurred when plants were grown at lower temperatures; time to flower and flower number at first flowered generally increased as the average daily temperature decreased (Vaid et al., 2014).

Even with an increased percentage of B in our SL treatments, we were not able to elicit consistent responses in seedling or transplant growth and morphology. Growing geraniums for their complete lifecycle under $B_{45}R_{55}$ SL (with a higher percentage of B light) could be an effective tool for height control depending on the DLI conditions. The inclusion of FR with SL also showed inconsistent responses but it did accelerate flowering of snapdragon and may have a similar effect on other long-day crops when the natural photoperiod is short. Research with SL treatments with more extreme spectral differences in B and FR, and perhaps other wavebands, is needed to further explore the potential of how SL can be used to achieve more compact growth and early flowering of ornamental crops.

APPENDIX

Table 3.1. Means (±SD) of temperature and photosynthetic daily light integral (DLI) as measured in greenhouses by aspirated thermocouples, infrared sensors, and quantum sensors during the seedling phase under ambient solar radiation with supplemental lighting treatments delivered by high-pressure sodium (HPS) lamps or light-emitting diodes (LEDs). For the LED treatments, subscript values that follow each waveband of blue (B, 400 to 500 nm), green (G, 500 to 600 nm), red (R, 600 to 700 nm), and far-red (FR, 700 to 800 nm) radiation indicate their percentages. Numbers in subscript following HPS treatments denote their intensity ($\mu mol \cdot m^{-2} \cdot s^{-1}$).

Treatment initiation	Supplemental light treatment	Daytime air temperature (°C)	Daytime tray temperature (°C)	Air – tray temperature (°C)	DLI ($mol \cdot m^{-2} \cdot d^{-1}$)
4 Nov.	HPS_{10}	19.2 ± 0.9	14.0 ± 2.6	5.2	3.8 ± 1.7
	HPS_{90}	19.5 ± 1.2	17.2 ± 3.3	2.3	7.0 ± 1.7
	$B_{10}R_{90}$	19.4 ± 1.0	15.9 ± 2.9	3.4	7.3 ± 1.6
	$B_{10}G_5R_{85}$	20.0 ± 0.6	17.1 ± 2.9	2.8	7.6 ± 1.6
	$B_{12}G_{20}R_{68}$ + FR	19.5 ± 0.9	16.2 ± 2.1	3.3	7.2 ± 1.6
	$B_{45}R_{55}$	20.4 ± 1.5	18.1 ± 2.3	2.3	6.7 ± 1.5
29 Dec.	HPS_{10}	19.0 ± 0.7	11.5 ± 3.1	7.5	3.5 ± 1.2
	HPS_{90}	19.7 ± 1.1	15.3 ± 2.5	4.4	7.7 ± 1.0
	$B_{10}R_{90}$	18.8 ± 0.9	14.3 ± 2.0	4.5	7.7 ± 0.9
	$B_{10}G_5R_{85}$	18.8 ± 1.5	13.2 ± 1.8	5.6	8.7 ± 1.1
	$B_{12}G_{20}R_{68}$ + FR	19.7 ± 0.8	14.7 ± 1.9	5.1	7.2 ± 1.0
	$B_{45}R_{55}$	20.7 ± 0.8	12.1 ± 1.9	8.5	7.2 ± 0.9

Table 3.2. Means (±SD) of temperature and photosynthetic daily light integral (DLI) as measured in greenhouses by aspirated thermocouples, infrared sensors, and quantum sensors from transplant to flowering under ambient solar radiation with supplemental lighting treatments delivered by high-pressure sodium (HPS) lamps or light-emitting diodes (LEDs). For the LED treatments, subscript values that follow each waveband of blue (B, 400 to 500 nm), green (G, 500 to 600 nm), red (R, 600 to 700 nm), and far-red (FR, 700 to 800 nm) radiation indicate their percentages. Numbers in subscript following HPS treatments denote their intensity ($\mu mol \cdot m^{-2} \cdot s^{-1}$).

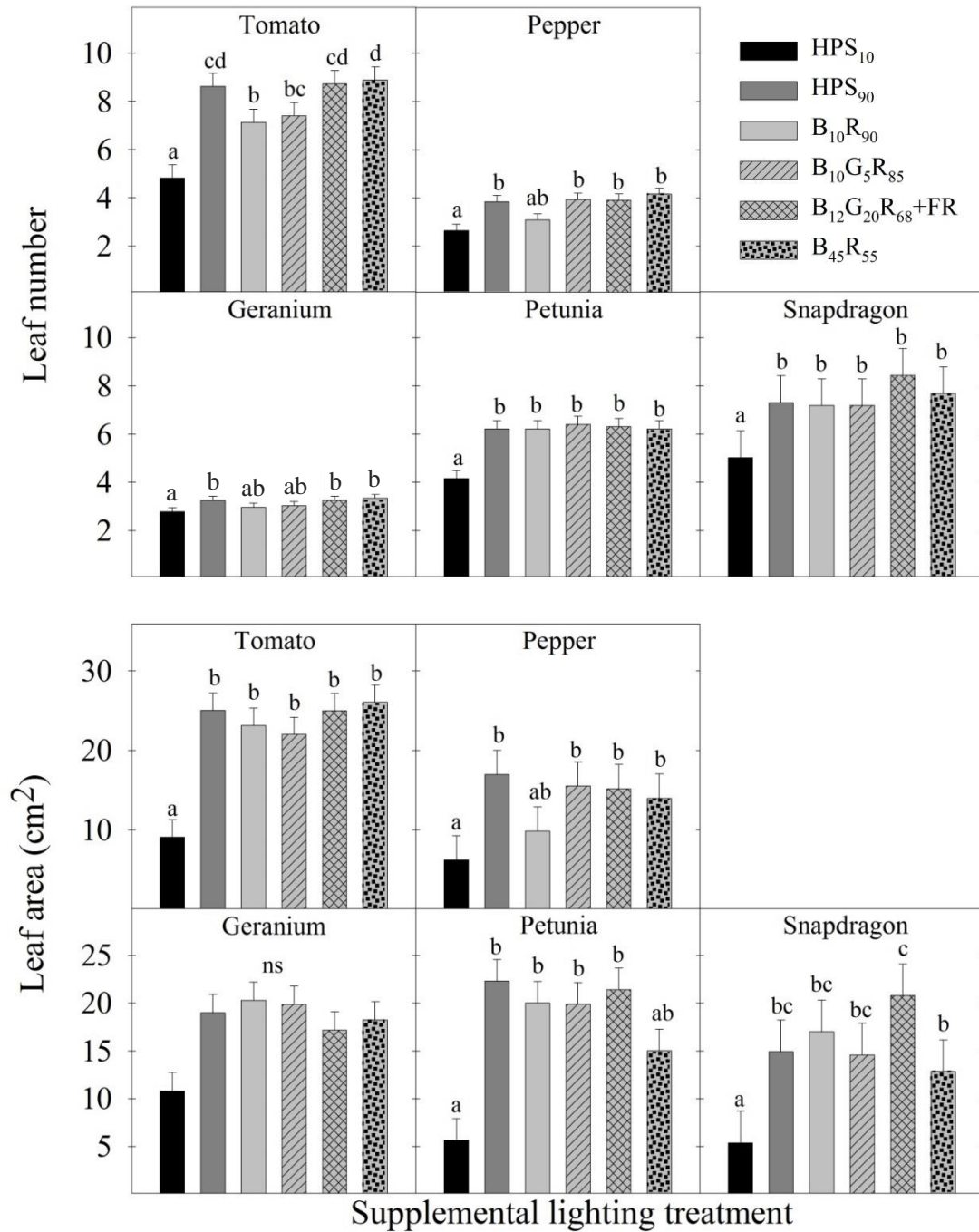| Transplant date	Supplemental light treatment	Daytime air temperature (°C)	Daytime pot temperature (°C)	Air – pot temperature (°C)	DLI ($mol \cdot m^{-2} \cdot d^{-1}$)
25 Nov.	HPS_{10}	19.0 ± 0.7	13.3 ± 1.1	5.6	3.5 ± 1.4
	HPS_{90}	19.8 ± 1.3	16.7 ± 3.1	3.2	7.6 ± 1.1
	$B_{10}R_{90}$	19.2 ± 1.0	16.0 ± 2.8	3.1	7.6 ± 1.1
	$B_{10}G_5R_{85}$	18.9 ± 0.9	15.4 ± 3.4	3.5	8.4 ± 1.5
	$B_{12}G_{20}R_{68} + FR$	19.8 ± 0.9	16.2 ± 2.7	3.6	7.4 ± 1.1
	$B_{45}R_{55}$	20.6 ± 0.8	13.7 ± 3.1	6.9	7.3 ± 1.0
20 Jan.	HPS_{10}	19.8 ± 1.4	15.2 ± 2.9	4.6	5.6 ± 2.3
	HPS_{90}	20.7 ± 1.7	21.1 ± 5.2	-0.4	9.1 ± 1.9
	$B_{10}R_{90}$	19.7 ± 1.2	18.9 ± 3.4	0.7	9.6 ± 1.9
	$B_{10}G_5R_{85}$	19.0 ± 1.2	16.6 ± 4.2	2.4	10.4 ± 1.7
	$B_{12}G_{20}R_{68} + FR$	20.4 ± 1.2	17.8 ± 4.2	2.6	9.3 ± 1.9
	$B_{45}R_{55}$	21.4 ± 1.0	14.7 ± 3.7	6.7	9.2 ± 1.8
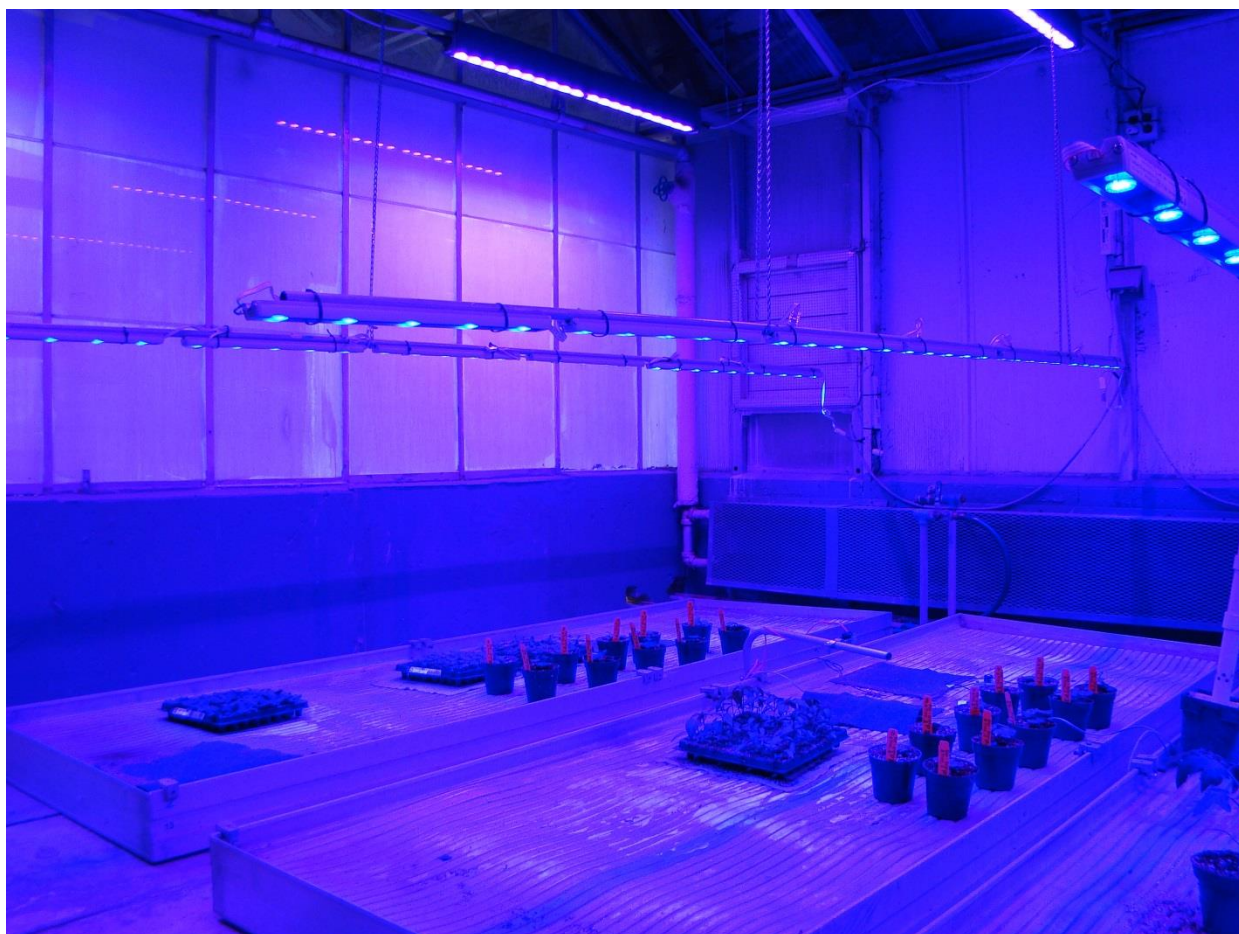
Figure 3.1. Supplemental lighting treatment delivered by a combination of light-emitting diode (LED) top-lighting fixtures and research modules to provide 45% blue and 55% red light at a total *PPFD* of 90 μmol·m^{-2}·s^{-1}.
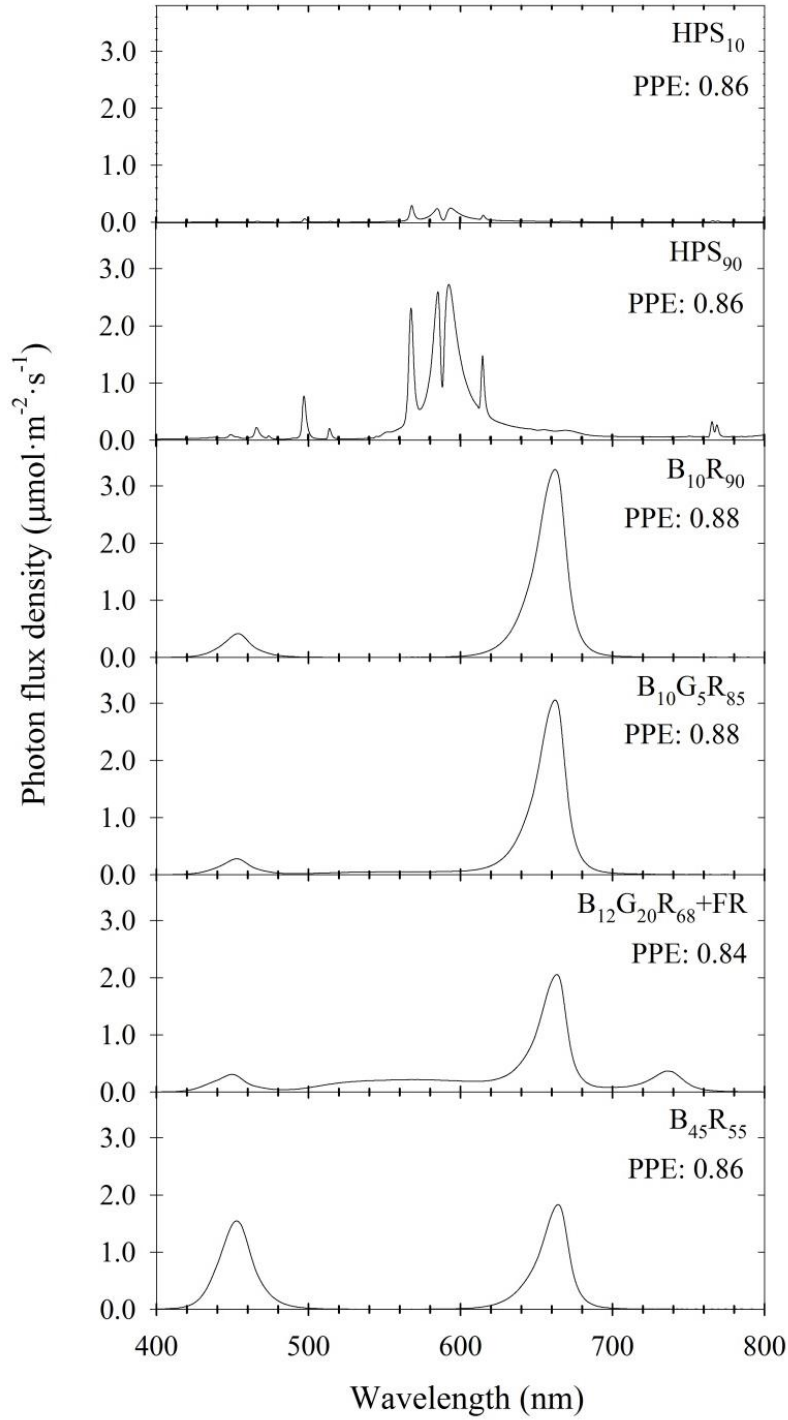
Figure 3.2. Spectral distribution and estimated phytochrome photoequilibria (PPE) of six supplemental lighting treatments between 400 and 800 nm from high-pressure sodium (HPS) and light-emitting diodes (LEDs) delivering different percentages (denoted in subscript) of blue (B, 400 to 500 nm), green (G, 500 to 600 nm), red (R, 600 to 700 nm), and far-red (FR, 700 to 800 nm) radiation. Numbers in subscript following HPS treatments denote their intensity (in μmol·m^{-2}·s^{-1}).
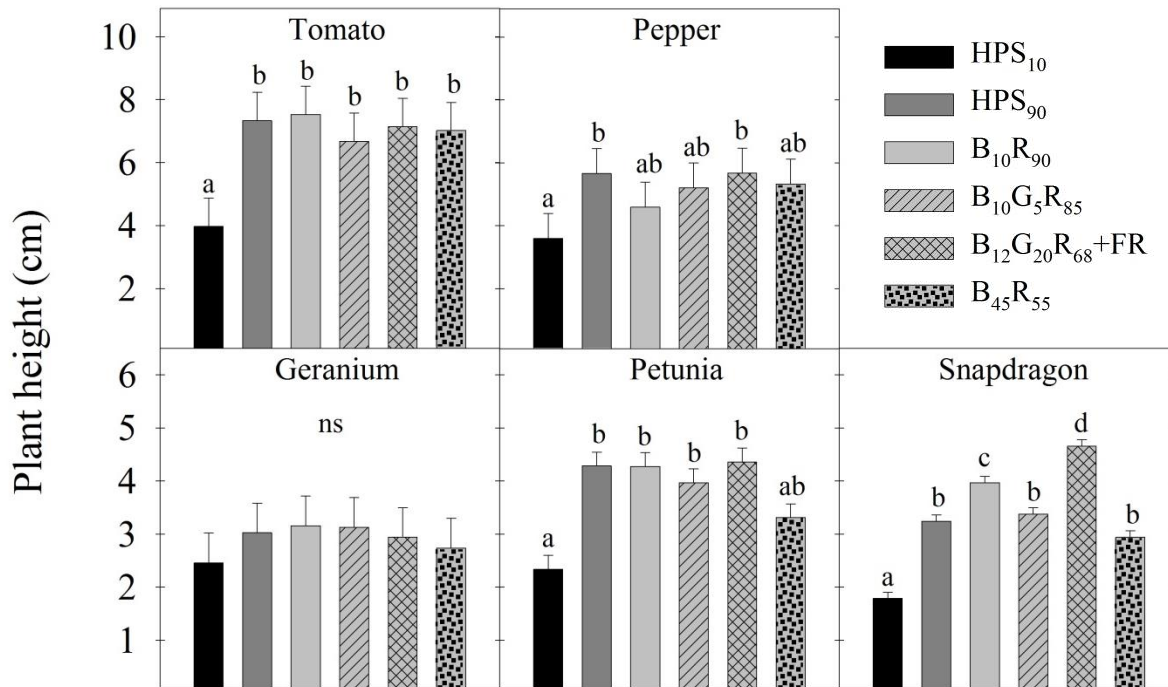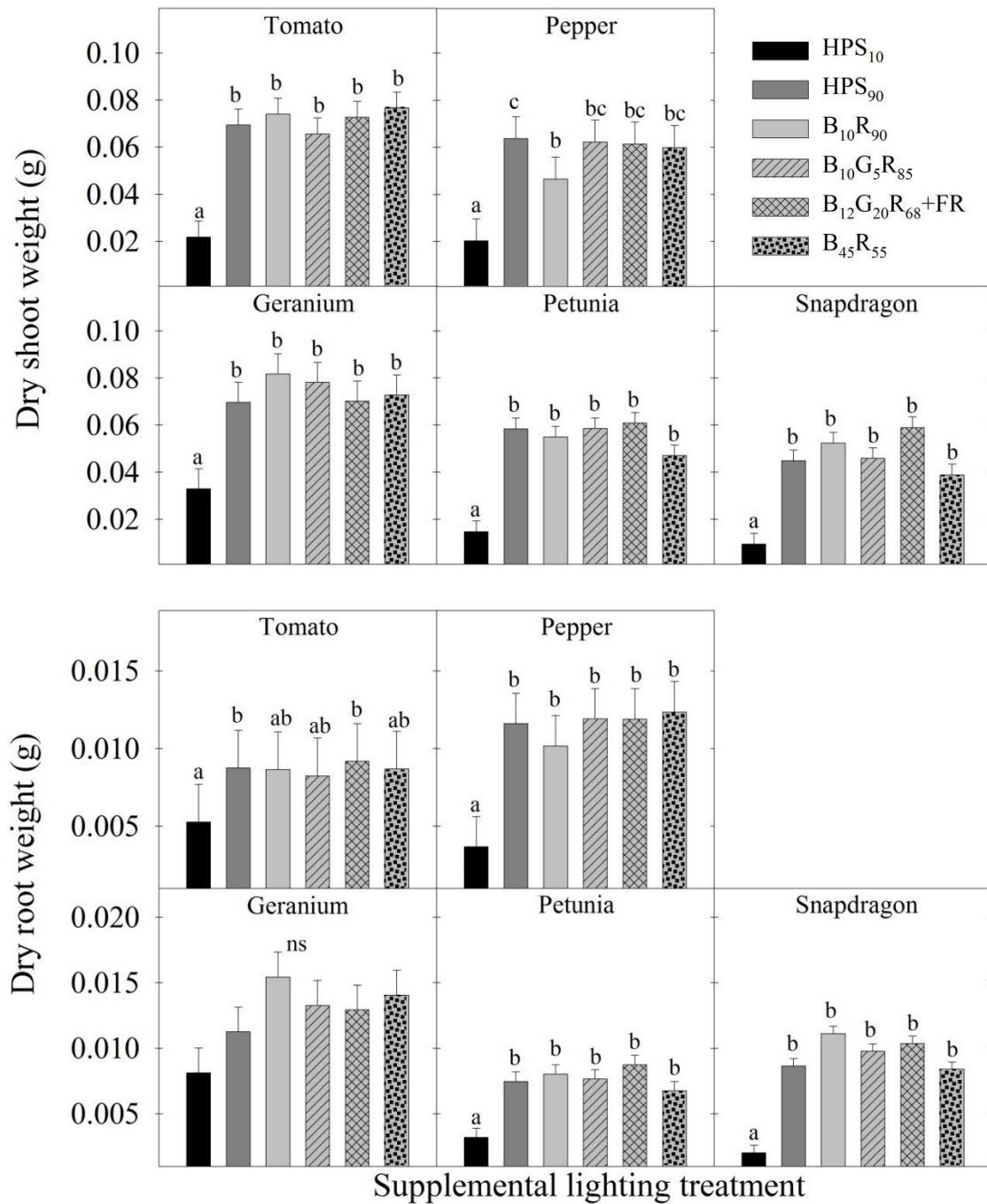
Figure 3.3. Plant height of five seedling crops grown under ambient greenhouse light and supplemental lighting from two high-pressure sodium (HPS) or four light-emitting diode (LED) treatments delivering different percentages of blue (B, 400 to 500 nm), green (G, 500 to 600 nm), red (R, 600 to 700 nm), and far-red (FR, 700 to 800 nm) radiation. All treatments delivered a *PPFD* of 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$, except HPS$_{10}$, which delivered a *PPFD* at 10 $\mu mol \cdot m^{-2} \cdot s^{-1}$. For the LED treatments, subscript values denote the waveband proportions. Means sharing a letter are not statistically different by Tukey's honest significant difference test at $P \leq 0.05$. Error bars indicate standard error.

Figure 3.4. Leaf number and leaf area of five seedling crops grown under ambient greenhouse light and supplemental lighting from two high-pressure sodium (HPS) or four light-emitting diode (LED) treatments delivering different percentages of blue (B, 400 to 500 nm), green (G, 500 to 600 nm), red (R, 600 to 700 nm), and far-red (FR, 700 to 800 nm) radiation. All treatments delivered a *PPFD* of 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$, except HPS_{10}, which delivered a *PPFD* at 10 $\mu mol \cdot m^{-2} \cdot s^{-1}$. For the LED treatments, subscript values denote the waveband proportions. Means sharing a letter are not statistically different by Tukey's honest significant difference test at $P \leq$ 0.05. Error bars indicate standard error.
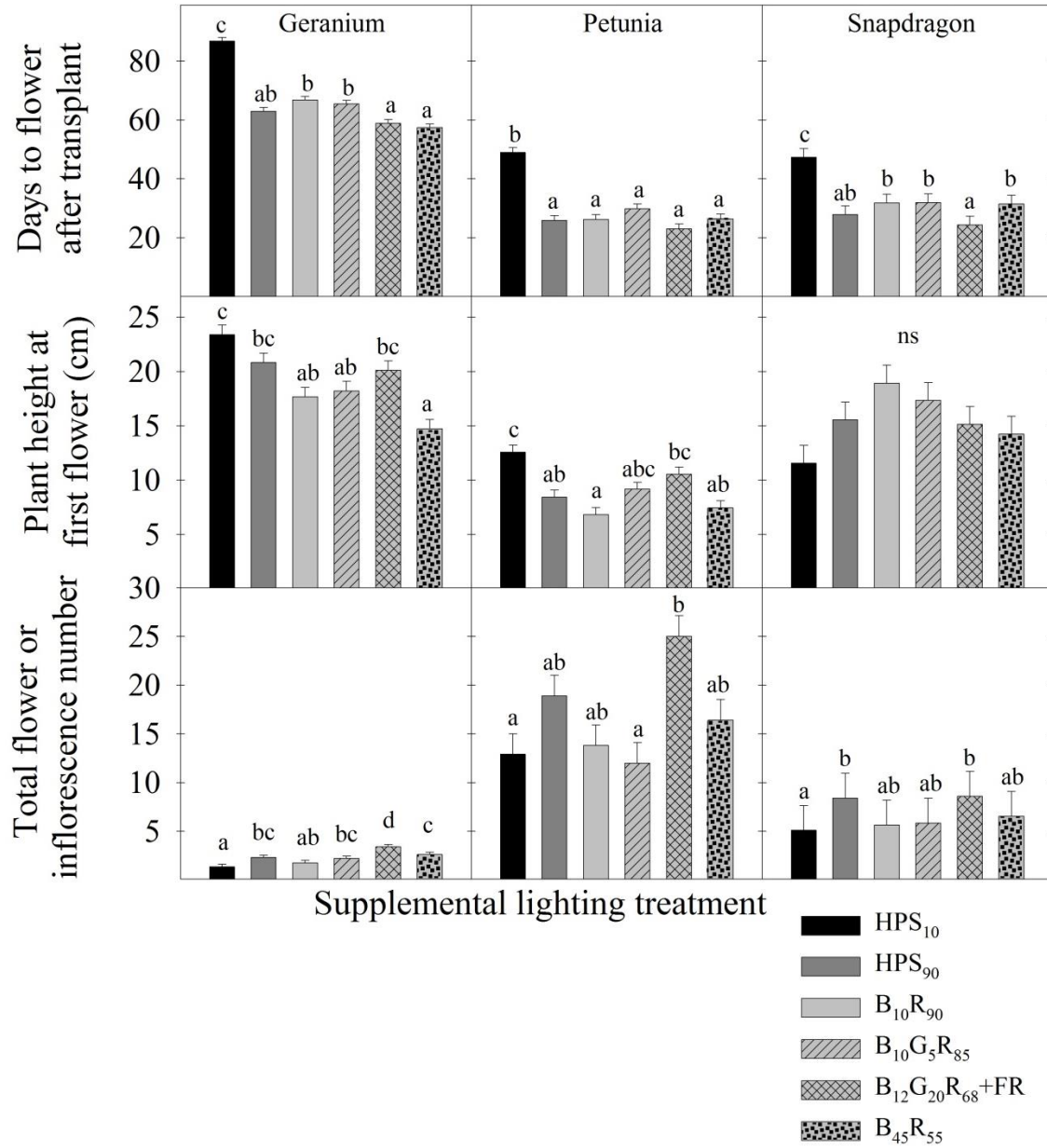
Figure 3.5. Dry shoot and root weights of five seedling crops grown under ambient greenhouse light and supplemental lighting from two high-pressure sodium (HPS) or four light-emitting diode (LED) treatments delivering different percentages of blue (B, 400 to 500 nm), green (G, 500 to 600 nm), red (R, 600 to 700 nm), and far-red (FR, 700 to 800 nm) radiation. All treatments delivered a *PPFD* of 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$, except HPS$_{10}$, which delivered a *PPFD* at 10 $\mu mol \cdot m^{-2} \cdot s^{-1}$. For the LED treatments, subscript values denote the waveband proportions. Means sharing a letter are not statistically different by Tukey's honest significant difference test at $P \le$ 0.05. Error bars indicate standard error.

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Figure 3.6. Days to flower after transplant, plant height at first flower and total flower or inflorescence number of three seedling crops grown under ambient greenhouse light and supplemental lighting from two high-pressure sodium (HPS) or four light-emitting diode (LED) treatments delivering different percentages of blue (B, 400 to 500 nm), green (G, 500 to 600 nm), red (R, 600 to 700 nm), and far-red (FR, 700 to 800 nm) radiation. All treatments delivered a *PPFD* of 90 μmol·m^{-2}·s^{-1}, except HPS$_{10}$, which delivered a *PPFD* at 10 μmol·m^{-2}·s^{-1}. For the LED treatments, subscript values denote the waveband proportions. Means sharing a letter are not statistically different by Tukey's honest significant difference test at *P* ≤ 0.05. Error bars indicate standard error.

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