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Supplemental Radiation Quality Influences Cucumber, Tomato, and Pepper Transplant Growth and Development

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***Abstract*. Supplemental lighting is required for the production of high-quality vegetable transplants in greenhouses when the photosynthetic daily light integral (DLI) is low. Light-emitting diodes (LEDs) are a promising alternative to high-pressure sodium (HPS) lamps. However, there are a limited number of studies that have evaluated how LED supplemental lighting spectral quality beyond blue (B) and red (R) radiation influences plant growth and development. Seeds of hybrid greenhouse seedless cucumber 'Elsie' (*Cucumis sativus*), tomato 'Climstar' (*Solanum lycopersicum*), and pepper 'Kathia' (*Capsicum annuum*) were sown and placed into a dark growth chamber until radicle emergence. Seedlings were grown in a greenhouse at a 25 °C constant temperature set point and under five lighting treatments. The supplemental lighting treatments delivered a total photon flux density (*TPFD*) of 120 $\mu mol\cdot m^{-2}\cdot s^{-1}$ for 16 $h\cdot d^{-1}$ based on an instantaneous threshold from HPS lamps or LEDs [three treatments composed of B (400–500 nm), R (600–700 nm), white, and/or far-red (FR; 700–800 nm) LEDs], and a control that delivered 25 $\mu mol\cdot m^{-2}\cdot s^{-1}$ from HPS lamps (HPS_{25}). The LED treatments defined by their wavebands (*TPFD* in $\mu mol\cdot m^{-2}\cdot s^{-1}$) of B, green (G, 500–600 nm), R, and FR radiation were $B_{20}G_{10}R_{75}FR_{15}$, $B_{25}R_{95}$, and $B_{30}G_{30}R_{60}$; whereas the HPS treatments emitted $B_{7}G_{57}R_{47}FR_{9}$ (HPS_{120}) and $B_{1}G_{13}R_{9}FR_{2}$ (HPS_{25}). Generally, cucumber, pepper, and tomato transplants under $B_{30}G_{30}R_{60}$ and HPS_{120} supplemental lighting had the greatest stem diameter. Fresh weight and leaf area of all three species was greater when G radiation replaced R or B radiation. For example, leaf area and fresh weight of cucumber, tomato, and pepper increased (by 33%, 22%, and 49%; and 35%, 14%, and 56%, respectively) for plants under $B_{30}G_{30}R_{60}$ supplemental lighting compared with plants under $B_{25}R_{95}$ supplemental lighting. The most compact cucumber and pepper transplants were those grown under $B_{25}R_{95}$ supplemental lighting, and the most compact tomatoes were those grown under the HPS_{25} (control) and $B_{25}R_{95}$ supplemental lighting. Tomato transplants under treatments providing ≥30 $\mu mol\cdot m^{-2}\cdot s^{-1}$ of G radiation had an increased incidence of leaf necrosis. From this study, we conclude that plant responses to supplemental lighting quality are generally genera-specific, and therefore high-wire transplants should be separated by genera to optimize production and quality. However, additional studies are required to provide complete LED supplemental lighting recommendations.**

Controlled-environment (CE) greenhouse and protected production of fruiting vegetable crops is gaining interest in the United States (Indoor Crop Production Feeding the Future, 2015). From 2009 to 2014, CE and protected food crop production area increased by 30%, from 6.6 million to over 8.6 million m^2 (USDA, 2010, 2015). Additionally, during the same period, the total value of sales of food crops grown under protection increased by 44%, from \$553 to \$797 million (USDA, 2010, 2015). Of the more than 265,000 t of produce grown under protection in 2014, high-wire fruiting vine crops such as cucumber (*Cucumis sativus*), pepper (*Capsicum* spp.), and tomato (*Solanum lycopersicum*) accounted for 14%, 1%, and 37%, respectively (USDA, 2015). From 2010 to 2014, cucumber and pepper production increased by 174% and 323%, respectively (USDA, 2010, 2015); and although tomato production decreased by 40%, greenhouse-grown tomatoes accounted for as much as 70% of tomato sales (Greenhouse Management, 2013). The combined wholesale and retail value of these three commodities totaled over \$484 million, or 61% of all CE food crop sales in 2014 (USDA, 2015).

Successful CE and field vegetable production is dependent on high-quality young plants, commercially referred to as "transplants" (Mitchell et al., 2015). For example, earlier and multiple harvests per growing season, better stand development, and increased profitability are a result of using high-quality transplants (Schrader, 2000). Consequently, the demand for vegetable transplants is increasing (Kubota et al., 2004; Kwack et al., 2016). In 2014, the number of operations commercially producing vegetable and strawberry transplants increased to 693, of which 543 used greenhouses or other protected structures (USDA, 2015). In 1988, sales from transplants were valued at \$50.7 million. By 2014, sales were nearly \$372 million. Total sales of pepper and tomato transplants (grown under protection and from open field) accounted for 22% of all transplant sales in 2014 (USDA, 2015).

Transplants used for CE production are generally grown in soilless media (i.e., rock wool or coco coir) (Boyhan and Granberry, 2017), boom irrigated, and grown under high-intensity supplemental lighting (SL) (Demers and Gosselin, 2002; Hernandez and Kubota, 2012; Mitchell et al., 2015). Supplemental lighting is used to increase the daily light integral (DLI) in greenhouses when solar radiation intensities and daylengths are limited, especially during winter months (Hernandez and Kubota, 2012; Mitchell et al., 2015). To produce high-quality vegetable transplants, a DLI of 13 $mol\cdot m^{-2}\cdot d^{-1}$ or greater is recommended (Dorais et al., 2017; Fan et al., 2013). However, in greenhouses located in northern latitudes, the DLI can average <5 $mol\cdot m^{-2}\cdot d^{-1}$ during winter months (Fausey et al., 2005; Lopez and Runkle, 2008). Under low-light conditions, stem diameter is reduced, extension growth is promoted, flowers are aborted, and subsequently fruit abortion can occur leading to economic losses (Dorais et al., 2017). However, compact transplants with short internodes and thick stems (Mitchell et al., 2015), and shortened production times of transplants, can be produced under SL (Fisher et al., 2017).

Blue [B (400–500 nm)] and red [R (600–700)] LEDs have dominated horticultural lighting because B and R radiation are considered the most photosynthetically efficient wavebands (McCree, 1972). However, plants perceive and use a broader range of radiation for growth and development, including green [G (500 to 600 nm)] and far-red [FR (700–800 nm)] radiation. Furthermore, when B and R radiation are used together, plants appear purple or gray to the human eye, making diseases, pest infestations, and nutritional deficiencies difficult to identify (Massa et al., 2008). One solution could be the addition of G or white (W) radiation. When added to R and B radiation, it increases the color-rendering index, thereby creating a more pleasant working environment without compromising plant growth

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(Snowden et al., 2016; Terashima et al., 2009).

Limited SL studies have been published to evaluate vegetable seedling responses to different supplemental radiation qualities (Mitchell et al., 2015). One such study sought to evaluate high-wire cucumber 'Cumlaude' transplant growth under a low solar DLI ($6.3\ mol{\cdot}m^{-2}{\cdot}d^{-1}$), with HPS or monochromatic B or R LED SL that increased the DLI by $3.7\ mol{\cdot}m^{-2}{\cdot}d^{-1}$ (Hernandez and Kubota, 2015). No significant differences in shoot fresh and dry weight or number of leaves were observed between plants grown under SL providing B or R radiation. Conversely, plants grown under HPS lamps had 28% and 32% greater shoot fresh weight than plants grown under LEDs that provided B or R radiation, respectively. Presumably the increased fresh weight was due to higher leaf temperatures, resulting from infrared (IR) radiation emitted from HPS SL. When SL contributes <40% of the DLI (Hurt et al., 2019), morphological responses may be less pronounced than under sole-source lighting (SSL) (Hernandez and Kubota, 2015) and may be species dependent (Hernandez and Kubota, 2014).

Green radiation was long considered the least efficient waveband within the photosynthetically active radiation (*PAR*) spectrum for photosynthesis (McCree, 1972). However, the low absorption rate of G radiation allows for better penetration into the plant canopy and can potentially further increase photosynthesis and plant growth (Klein, 1992). Green radiation can reduce hypocotyl elongation and increase leaf area and fresh and dry weight of the cucumber hybrid 'Mandy' transplants (Novičkovas et al., 2012). However, plant responses to SL containing G radiation have been contradictory. For example, Kim et al. (2006) found that a high percentage of G radiation [>50% of the photosynthetic photon flux density (*PPFD*)] reduced growth of lettuce (*Lactuca sativa*), while a lower percentage (24%) of G radiation in combination with B and R LEDs increased leaf area and shoot fresh and dry weight. In another study with tomato and French marigold (*Tagetes patula*), fresh and dry weight, height of plants and lengths of peduncle increased when G radiation was filtered from W radiation provided by cool-white fluorescent lamps (Klein et al. 1965). Furthermore, when supplementary G radiation was added to W radiation, the fresh weight of marigold was reduced, but height was unaffected. Therefore, the objective of this study was to build upon previous SL studies by quantifying physiological and morphological responses to different B, G, R, and FR radiation intensities for economically significant cultivars of cucumber, tomato, and pepper for transplant production.

Materials and Methods

Plant material. Hybrid greenhouse seedless cucumber 'Elsie', tomato 'Climstar', and pepper 'Kathia' seeds (Syngenta Seeds, Inc. Minneapolis, MN) were sown into 120-cell rockwool plug trays (2 × 2.7 cm; 8.5-mL individual cell volume) (GroPlug; Grodan, Roermond, The Netherlands) and covered with a layer of vermiculite on 24 Sept. 2018, 22 Oct. 2018, and 5 Jan. 2019. Seeded plug trays were placed into a dark growth chamber that had an air average daily temperature (ADT) and relative humidity set point of 28 °C and 60%, respectively, until radicle emergence. The trays were overhead irrigated as needed with a nutrient solution consisting of reverse osmosis water supplemented with a combination of magnesium sulfate [$25\ mg{\cdot}L^{-1}$ sulfur (S)] and 12N–4P–16K water-soluble fertilizer, supplying ($mg{\cdot}L^{-1}$): 100 nitrogen (N), 33 phosphorus (P), 133 potassium (K), 58 calcium (Ca), 36 magnesium (Mg), 27 S, 0.1 boron (B), 0.4 copper (Cu), 1 iron (Fe), 0.4 manganese (Mn), 0.1 molybdenum (Mo), and 0.4 zinc (Zn) (RO Hydro FeED; JR Peters Inc., Allentown, PA). The pH and EC were adjusted to 6.0 and $0.88\ dS{\cdot}m^{-1}$, respectively.

Upon radicle emergence, trays of each species were randomly assigned to one of four SL treatments or a low-intensity control, each within one of five separate glass-glazed greenhouse compartments in the Plant Science Research Greenhouse ranges at Michigan State University (East Lansing, MI; lat. 43 °N). Plants were rotated daily to mitigate any positional effects within the greenhouses. After 10 days under SL for cucumber and 14 days for tomato and pepper, 10 seedlings per species were transplanted into rockwool cubes (10 × 10 × 6.5 cm; 650-mL individual volume) (Delta Blocks; Grodan). After transplant, plants were irrigated daily using an ebb and flow system with reverse osmosis water supplemented with the same nutrient solution previously mentioned. Each greenhouse compartment had a 208-L reservoir and a submersible water pump (Kedsum-3500 65-W pump; Xiolan, China) that delivered $49\ L{\cdot}m^{-1}$ to their respective flood bench. The pH and EC of the nutrient solution within reservoirs were monitored daily using a hand-held meter (HI 991301 pH/electrical conductivity (EC)/total dissolved solids meter; Hanna Instruments, Smithfield, RI). The pH was adjusted to 6.0 using sulfuric acid and potassium bicarbonate. The average pH and EC (±SD) during the experiment were 6.1 ± 0.1 and $0.9 \pm 0.01\ dS{\cdot}m^{-1}$, respectively. Actual pH and EC values, per greenhouse compartment, are reported in Table 1.

Greenhouse environmental conditions. Whitewash (ReduSol; Baarle-Nassau, The Netherlands) was applied to the glass exterior of the five east-to-west–orientated greenhouse sections, to decrease radiation intensity and improve uniformity. To avoid radiation contamination from adjacent SL treatments, whitewash was applied to the glass between greenhouse compartments. Radiation intensity in each section was measured by a quantum sensor (LI-190/R; LI-COR, Lincoln, NE) placed at plant canopy height. A shielded and aspirated 0.13-mm type E thermocouple (Omega Engineering, Stamford, CT) measured air temperature at canopy height, and an IR sensor (Type T, OS36-01; Omega Engineering) measured leaf temperature. A CR-1000 datalogger (Campbell Scientific, Logan, UT) collected environmental data in each compartment every 15 s, and hourly averages were recorded. Exhaust fans, roof vents, evaporative pad cooling, and radiant hot-water heating were controlled by an environmental control system (Integro version 725-3030; Priva North America, Vineland Station, ON, Canada) to maintain an air ADT set point of 25 °C. The actual air ADT and leaf temperatures are reported in Table 1.

Supplemental lighting treatments. Four SL treatments and a low-intensity control, providing a photoperiodic lighting (PL) treatment, were delivered for $16\ h{\cdot}d^{-1}$ based on an instantaneous threshold [on from 0600 to 2200 HR when the outside *PPFD* was below $\approx 440\ \mu mol{\cdot}m^{-2}{\cdot}s^{-1}$ (on for a minimum of 25 min and off for a minimum of 20 min)]. Four 400-W HPS lamps (LR48877; P.L. Light Systems, Beamsville, Ontario, Canada) or three 600-W LED fixtures (LX601G TL1002 R2A or LX601C HLB607-l2-B-L1-RC; Heliospectra, Göteborg, Sweden) (42.5 cm L × 21.9 cm W × 19.9 cm H; 286 diodes) per treatment provided a total photon flux density (*TPFD*) of $120\ \mu mol{\cdot}m^{-2}{\cdot}s^{-1}$ in an experimental area of $1.9\ m^2$. The low-intensity control was delivered by one 150-W HPS light fixture (HPS_{25}) (LU150; Acuity Lithonia Lighting, Conyers, GA) and provided a *TPFD* of $25\ \mu mol{\cdot}m^{-2}{\cdot}s^{-1}$ in an experimental area of $1.9\ m^2$. Three LED SL treatments, delivered by cool W and R or FR LEDs and defined by their 100-nm wavebands (radiation intensity in $\mu mol{\cdot}m^{-2}{\cdot}s^{-1}$) of B (400–500 nm), G (500–600 nm), R (600–700 nm), and FR (700–800 nm) radiation, were $B_{20}G_{10}R_{75}FR_{15}$, $B_{25}R_{95}$, and $B_{30}G_{30}R_{60}$. The HPS lamps emitted intensities of $B_1G_{13}R_9FR_2$ (HPS_{25}) and $B_7G_{57}R_{47}FR_9$ (HPS_{120}). The total number of lamp hours of operation for three replications (Rep.) was 325, 370, and 407 (Rep. 1), 426, 478, and 521 (Rep. 2), and 431, 468, and 522 (Rep. 3), for cucumber, tomato, and pepper, respectively. For all treatments, spectral quality and radiation intensity at plant height were measured in twelve separate locations throughout the growing area with a portable spectroradiometer (PS-200; Stellar-Net, Tampa, FL) (Fig. 1). Spectral scans and radiation intensity measurements of the SL were taken at night, at the beginning or end of each Rep. to ensure consistency from one Rep. to another. The total DLIs (sunlight + SL) are reported in Table 1.

Plant measurements and experimental design. Excluding germination, cucumber plants were harvested after 28 d under SL, while tomato and pepper plants were harvested after 35 d. Plant height (measured from the medium surface to the apical meristem) and hypocotyl length were measured using a ruler. Stem diameter, ≈1 cm below the cotyledons, was measured using a digital caliper (41101 DigiMax; Wiha, Buchs, Switzerland). The number of nodes and leaves greater than 1 cm in length were also recorded at harvest. Internode length was calculated by

Table 1. Supplemental lighting (SL) treatments, replication (Rep.), supplemental radiation, average total daily light integral (DLI) from solar radiation and SL provided by high-pressure sodium (HPS) lamps or light-emitting diodes (LEDs) for 16 h·d^{-1} based on an instantaneous threshold (on from 0600 to 2200 HR when the outside *PPFD* was below ≈440 µmol·m^{-2}·s^{-1}). Average greenhouse canopy air and leaf temperature, and nutrient solution pH and electrical conductivity (EC) ±SD. Cucumber, pepper, and tomato were placed under treatments on 26 Sept. 2018, 24 Oct. 2018, and 7 Jan. 2019.

Lighting treatment	Rep.	Supplemental radiation (µmol·m^{-2}·s^{-1})	Total DLI (mol·m^{-2}·d^{-1})	Temperature (°C)		Nutrient solution pH	Nutrient solution EC (dS·m^{-1})
				Air	Leaf		
HPS_{25}	1	—	6.9	24.1 ± 1.4	25.9 ± 1.5	6.13 ± 0.07	0.89 ± 0.03
	2	25 ± 2.7	5.3	25.2 ± 0.9	27.2 ± 1.0	6.06 ± 0.08	0.89 ± 0.02
	3	25 ± 3.1	6.2	25.0 ± 1.4	26.4 ± 2.2	6.08 ± 0.07	0.89 ± 0.02
HPS_{120}	1	120 ± 3.3	12.0	24.1 ± 1.3	25.9 ± 1.3	6.09 ± 0.07	0.90 ± 0.02
	2	123 ± 2.5	11.5	24.6 ± 1.4	26.0 ± 1.5	6.06 ± 0.10	0.89 ± 0.03
	3	124 ± 5.7	11.9	24.8 ± 3.3	25.9 ± 3.3	6.06 ± 0.09	0.89 ± 0.03
$B_{25}R_{95}$	1	119 ± 6.6	12.2	24.8 ± 1.5	25.5 ± 1.6	6.05 ± 0.11	0.89 ± 0.02
	2	121 ± 6.8	11.9	24.6 ± 1.4	24.7 ± 1.5	6.05 ± 0.12	0.88 ± 0.03
	3	120 ± 5.3	12.0	23.4 ± 3.4	24.5 ± 3.5	6.04 ± 0.08	0.89 ± 0.03
$B_{30}G_{30}R_{60}$	1	119 ± 5.3	12.6	25.5 ± 1.1	25.8 ± 1.5	6.05 ± 0.11	0.89 ± 0.03
	2	120 ± 4.5	11.6	25.1 ± 1.1	25.9 ± 1.4	6.05 ± 0.11	0.89 ± 0.03
	3	122 ± 6.1	11.6	24.5 ± 2.6	25.8 ± 2.8	6.03 ± 0.10	0.89 ± 0.02
$B_{20}G_{10}R_{75}FR_{15}$	1	119 ± 3.0	13.2	23.5 ± 1.2	25.1 ± 1.5	6.09 ± 0.10	0.89 ± 0.02
	2	120 ± 4.0	10.7	24.1 ± 1.9	25.4 ± 2.0	6.06 ± 0.09	0.89 ± 0.02
	3	120 ± 3.0	10.5	23.7 ± 3.3	24.8 ± 3.5	6.06 ± 0.09	0.89 ± 0.03

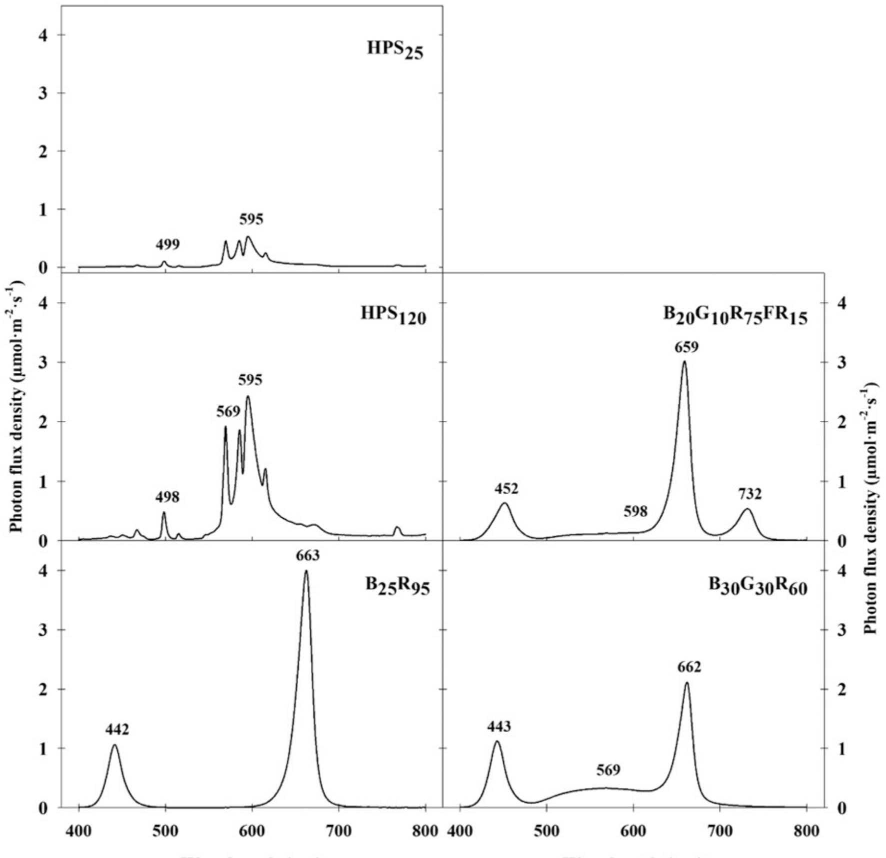

Fig. 1. Spectral quality delivered from high-pressure sodium (HPS) lamps providing photoperiodic and supplemental lighting (SL) and light-emitting diode fixtures delivering SL. Number subscripts after HPS denote the total photon flux density (*TPFD*) in µmol·m^{-2}·s^{-1}. Number subscripts in the LED treatments denote the photon flux density (*PFD*) in µmol·m^{-2}·s^{-1} of blue (B, 400–500 nm), green (G, 500–600 nm), red (R, 600–700 nm), and far-red (FR, 700–800 nm) radiation.

dividing the number of nodes by plant height. Total leaf area per plant was measured using a leaf-area meter (LI-300; LI-COR, Lincoln, NE). Plants were deemed either reproductive or nonreproductive, depending on the presence or absence of visible flower buds. The number of tomato leaves per plant with necrotic lesions was recorded for the second and third Rep., and the number of leaves with necrotic lesions were divided by the total number of leaves per plant to calculate incidence of leaf necrosis (%). Before the destructive plant measurements, chlorophyll fluorescence (F_v/F_m) of five plants, per species, per treatment were measured using a portable chlorophyll fluorescence meter [Handy Plant Efficiency Analyzer (PEA); Hansatech Instruments 229 Ltd., Norfolk, U.K.]. Fully expanded leaves were dark-acclimated for a minimum of 15 min. using the manufacturer's plastic and foam clips before measurements were recorded. Fluorescence was measured by opening the shutter of the dark-acclimating clip and exposing the leaf to R radiation (peak wavelength of 650 nm at 1200 µmol·m^{-2}·s^{-1}) for 5 s to saturate photosystem II (PSII). Plants were excised just above the medium, and total shoot (stems and leaves) fresh weight was measured using a digital balance. Stems and leaves were put into paper envelopes and placed inside a drying oven set at ≥70 °C for ≥6 d, after which dry weights were recorded.

The experiment was organized in a randomized complete block design, with three Reps. over time. Plants were blocked by randomized SL treatments with 10 experimental units (individual plants) of each species per treatment and Rep. The data for each plant species were analyzed separately using the PROC GLIMMIX procedure in SAS (version 9.4; SAS Institute, Cary, NC). In the analysis, the SL treatment was considered the fixed factor, whereas Rep. was regarded as a random factor in the analysis. Mean separations were analyzed using adjusted Tukey–Kramer HSD ($P = 0.05$). Data were pooled when there was no interaction between Rep. and treatment, or if the response trends were similar between Reps.

Results

Cucumber. All data parameters except dry weight were analyzed and presented as pooled results. Data for dry weight was pooled for Reps. 1 and 2, while Rep. 3 was analyzed separately. Transplants grown under HPS_{120} and $B_{30}G_{30}R_{60}$ SL exhibited the greatest stem diameter (Fig. 2A). The stem diameter of plants under HPS_{25} (control) SL was lower than the other treatments. Height, hypocotyl, and internode length were greatest for plants grown under the control, averaging 35.3, 8.1, and 5.0 cm in length, respectively (Fig. 2D, G, and J). The greatest number of nodes and leaves were under HPS_{25} and

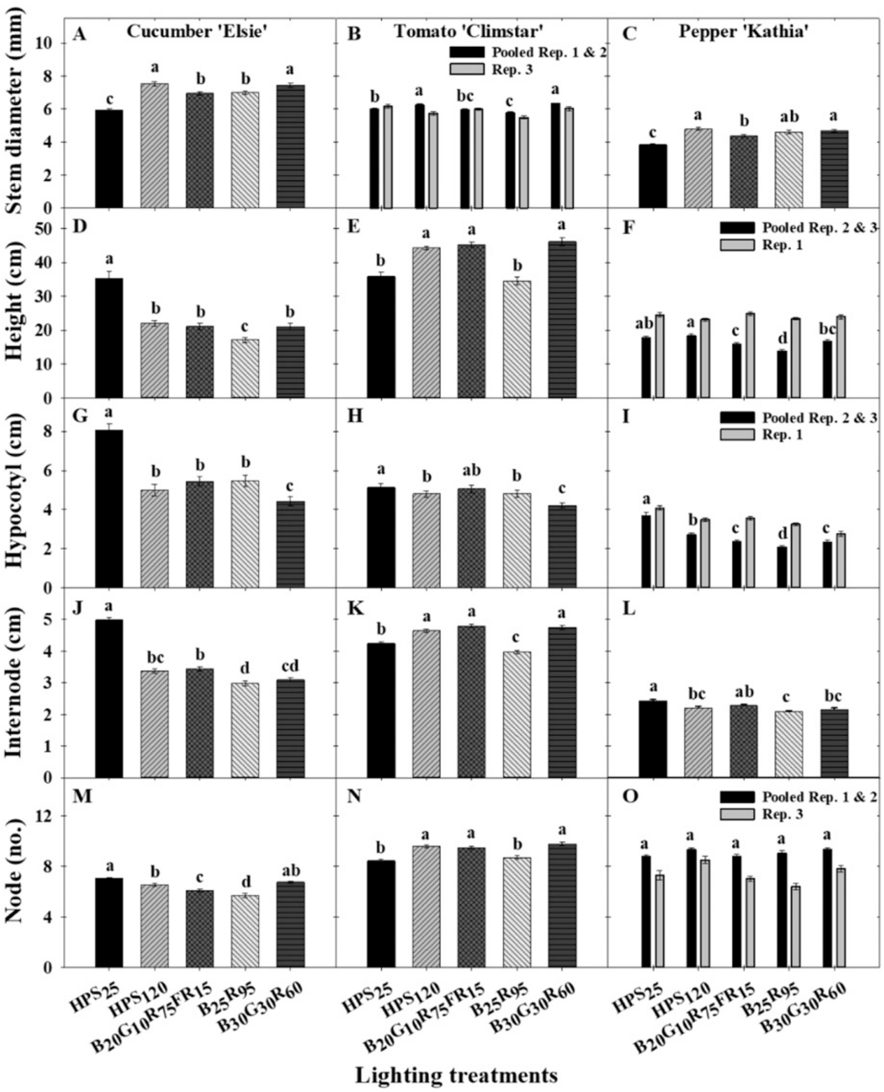

Fig. 2. Stem diameter (mm), height (cm), hypocotyl (cm), internode length (cm), and average number of nodes per plant of cucumber, tomato, and pepper. Data were collected after 28, 35, and 35 d under high-pressure sodium (HPS) photoperiodic and supplemental lighting (SL) or light-emitting diode SL treatments for cucumber, tomato, and pepper, respectively. Data were pooled when there was no interaction between replication (Rep.) and treatment. Letters indicate mean separations across treatments using Tukey–Kramer difference test at $P \leq 0.05$. Error bars indicate standard error.

$B_{30}G_{30}R_{60}$ SL, and the fewest were recorded under $B_{25}R_{95}$ SL (Figs. 2M and 3A). Leaf area was similar among transplants under HPS_{25}, HPS_{120}, and $B_{30}G_{30}R_{60}$ SL (Fig. 3D). SL providing $B_{20}G_{10}R_{75}FR_{15}$ and $B_{25}R_{95}$ significantly reduced leaf area. For example, leaf area of transplants grown under $B_{25}R_{95}$ was 225 (25%), 227 (25%), and 231 (25%) cm^2 less than transplants grown under the control, $B_{30}G_{30}R_{60}$, and HPS_{120}, respectively (Fig. 3D).

Transplants grown under HPS_{120} and $B_{30}G_{30}R_{60}$ SL exhibited the greatest fresh weight (Fig. 3G). In the pooled results for Reps. 1 and 2, the greatest seedling shoot dry weight was under HPS_{120} and $B_{30}G_{30}R_{60}$, and the lowest was under the low-intensity control. In Rep. 3, the greatest shoot dry weight was under $B_{20}G_{10}R_{75}FR_{15}$ and $B_{30}G_{30}R_{60}$ SL (Fig. 3J). The efficiency of PSII, denoted by F_v/F_m, was greatest for transplants grown under the control (0.84), and not significantly different between HPS_{120} (0.82), $B_{20}G_{10}R_{75}FR_{15}$ (0.82), and $B_{30}G_{30}R_{60}$ (0.83) (Fig. 3M). After 28 d of SL, the percentage of cucumber plants having visible flower buds averaged 53%, 63%, 80%, and 87% for $B_{25}R_{95}$, $B_{20}G_{10}R_{75}FR_{15}$, $B_{30}G_{30}R_{60}$, and HPS_{120}, respectively, and 73% for the control (Fig. 4A).

Tomato. All data parameters except stem diameter were analyzed and presented as pooled results. From the pooled results (Reps. 1 and 2), tomato seedlings under $B_{30}G_{30}R_{60}$ and HPS_{120} SL had the greatest stem diameter (6.3 and 6.3 mm) (Fig. 2B). However, for Rep. 3, plants grown under the control had the greatest stem diameter (6.2 mm) (Fig. 2B). No significant difference in height was observed among transplants grown under HPS_{120}, $B_{20}G_{10}R_{75}FR_{15}$, and $B_{30}G_{30}R_{60}$ SL (Fig. 2E). Transplants grown under the control and $B_{25}R_{95}$ were significantly shorter than all the other treatments. For example, transplants grown under $B_{25}R_{95}$ were 9.7 (22%), 10.7 (24%), and 11.6 (25%) cm shorter than those grown under HPS_{120}, $B_{20}G_{10}R_{75}FR_{15}$, and $B_{30}G_{30}R_{60}$ SL, respectively (Fig. 2E). Hypocotyl length was greatest under the control (5.1 cm) and shortest under $B_{30}G_{30}R_{60}$ (4.2 cm) (Fig. 2H). Internode length was greatest under HPS_{120}, $B_{20}G_{10}R_{75}FR_{15}$, and $B_{30}G_{30}R_{60}$, and shortest under the control and $B_{25}R_{95}$ (Fig. 2K). Additionally, internode length of $B_{25}R_{95}$ grown transplants was significantly less in comparison with all other treatments. Transplants grown under HPS_{120}, $B_{20}G_{10}R_{75}FR_{15}$, and $B_{30}G_{30}R_{60}$ SL did not differ significantly in the number of nodes and averaged between 9 to 10 nodes (Fig. 2N).

Transplants under $B_{30}G_{30}R_{60}$ SL had the greatest leaf area (986 cm^2) and fresh (52.4 g) and dry weight (5.0 g) (Fig. 3E, H, and K). There was no significant difference in leaf area or fresh and dry weight between transplants grown under HPS_{120} and $B_{20}G_{10}R_{75}FR_{15}$ SL (Fig. 3E, H, and K). Under the control, transplants had the fewest number of leaves and lowest fresh and dry weight (Fig. 3B, H, and K). For example, the fresh weight of plants grown under the control was 5.8 (17%), 17.2 (38%), 17.4 (38%), and 24.5 (47%) g less than those under $B_{25}R_{95}$, $B_{20}G_{10}R_{75}FR_{15}$, HPS_{120}, and $B_{30}G_{30}R_{60}$ SL, respectively (Fig. 3H). F_v/F_m was slightly higher for plants grown under HPS_{25} but was not significantly different from $B_{20}G_{10}R_{75}FR_{15}$ and $B_{30}G_{30}R_{60}$ grown plants (Fig. 3N). After 35 d, all plants under SL had visible flower buds, while only 7% of plants under the low-intensity control had visible buds (Fig. 4B). For tomato plants grown under HPS_{120} and $B_{30}G_{30}R_{60}$ SL, the incidence of leaf necrosis was 21% and 17%, respectively (Fig. 5).

Pepper. Data for stem diameter, internode length, number of leaves, leaf area, fresh weight, F_v/F_m, and visible flower bud formation were pooled (Figs. 2C, L, 3C, F, I, O, and 4C). Data from Reps. 2 and 3 were pooled together for height, hypocotyl, and dry weight (Figs. 2F, I, and 3L). For node number, Reps. 1 and 2 were pooled and Rep. 3 was analyzed separately (Fig. 2O). Stem diameter of pepper transplants grown under the control was 12% to 20% smaller than transplants grown under $B_{20}G_{10}R_{75}FR_{15}$, $B_{25}R_{95}$, $B_{30}G_{30}R_{60}$, and HPS_{120} (Fig. 2C). Height of pepper transplants from Reps. 1 and 2 was significantly reduced under $B_{25}R_{95}$ SL, but there was no significant difference in height among treatments in Rep. 3 (Fig. 2F). Hypocotyl length, from the pooled results (Reps. 2 and 3), was greatest for HPS_{25} grown plants (Fig. 2I). Internode length was greatest under the control and was significantly greater compared with HPS_{120}, $B_{25}R_{95}$, and $B_{30}G_{30}R_{60}$, but not with $B_{20}G_{10}R_{75}FR_{15}$ grown transplants (Fig. 2L). There was no significant difference in the number of nodes for the pooled data (Reps. 1 and 2) among all SL treatments (Fig. 2O). However, in Rep. 3, HPS_{120} had the greatest number of nodes (9), while $B_{25}R_{95}$ had the least (6) (Fig. 2O).

Pepper transplants grown under the control had the least number of leaves, and there was no significant difference in leaf number among the transplants under HPS_{120}, $B_{25}R_{95}$, and $B_{30}G_{30}R_{60}$ SL (Fig. 3C). Leaf area was

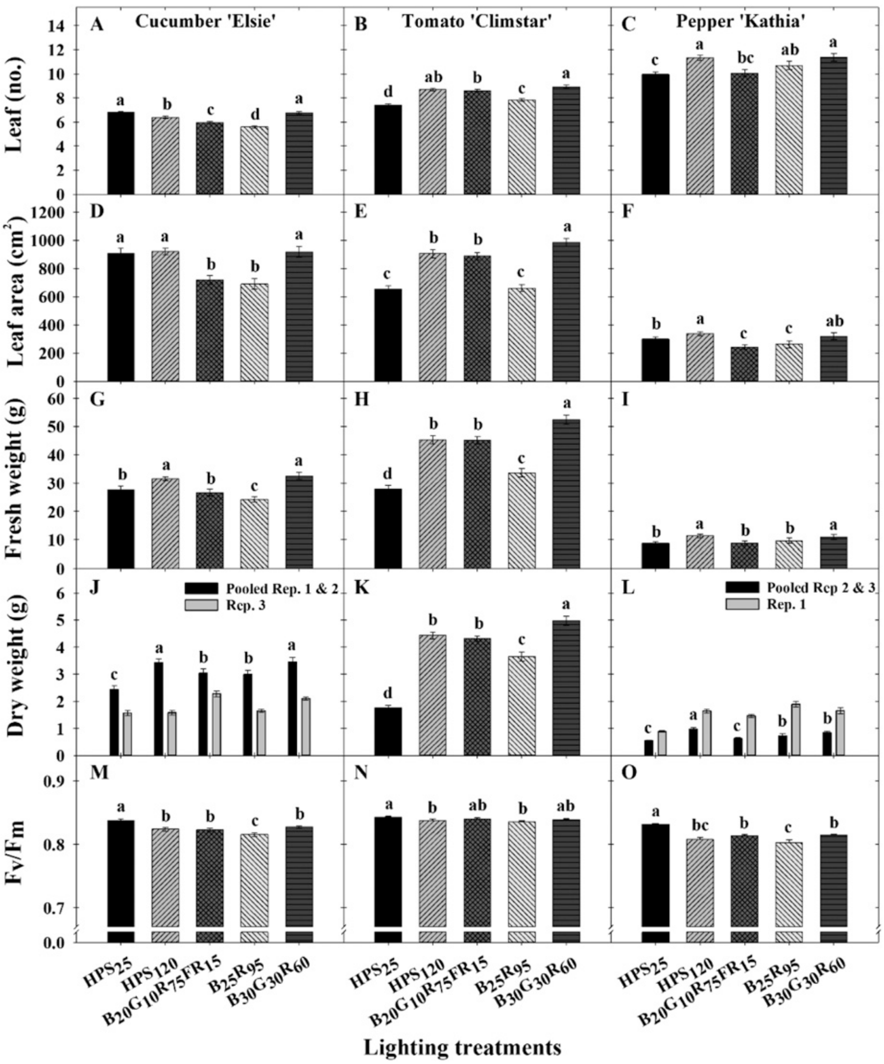

Fig. 3. Number of leaves, leaf area (cm^2), fresh weight (g), dry weight (g), and chlorophyll fluorescence (F_v/F_m) of cucumber, tomato, and pepper. Data were collected after 28, 35, and 35 d under high-pressure sodium (HPS) photoperiodic and supplemental lighting (SL) or light-emitting diode SL treatments for cucumber, tomato, and pepper, respectively. Data were pooled when there was no interaction between replication (Rep.) and treatment. Letters indicate mean separations across treatments using Tukey–Kramer difference test at $P \leq 0.05$. Error bars indicate standard error.

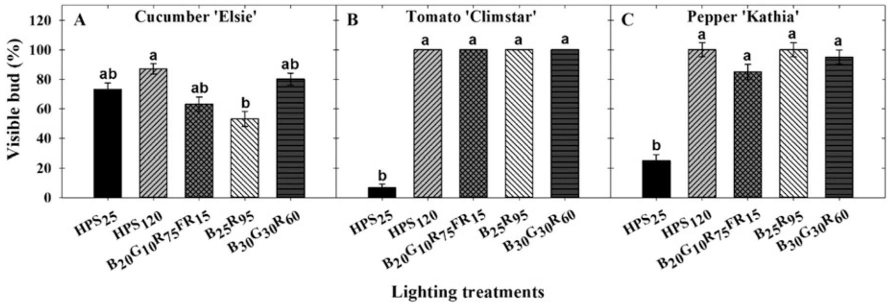

Fig. 4. Percent of cucumber, tomato, and pepper transplants with a visible flower bud. Data were collected after 28, 35, and 35 d under high-pressure sodium (HPS) photoperiodic and supplemental lighting (SL) or light-emitting diode SL treatments for cucumber, tomato, and pepper, respectively.

greatest among transplants grown under HPS_{120} and $B_{30}G_{30}R_{60}$, while those under $B_{20}G_{10}R_{75}FR_{15}$ and $B_{25}R_{95}$ SL had the lowest leaf area (Fig. 3F). In Reps. 2 and 3, HPS_{120} grown transplants had greater dry weight than all other SL treatments and the control (Fig. 3L). F_v/F_m of transplants grown under the control averaged 0.83 and was significantly greater than all other treatments (Fig. 3O). The visible flower bud percentages for pepper were 25%, 85%, 95%, 100%, and 100% for transplants grown under HPS_{25}, $B_{20}G_{10}R_{75}FR_{15}$, $B_{30}G_{30}R_{60}$, $B_{25}R_{95}$, and HPS_{120} SL (Fig. 4C).

Discussion

High-quality ornamental transplants are defined as having large stem diameters, are compact in size, fully rooted, and have high root and shoot dry weight (Randall and Lopez, 2014), and a reduced leaf area to avoid mutual shading. Similar morphological characteristics define a high-quality, greenhouse-grown vegetable transplant, including well-developed leaves, straight stems, and deep-green leaves (Gomez and Mitchell, 2015). However, certain features can differ depending on the intended use of the transplant (Chia and Kubota, 2010). For example, seedlings can be used as rootstocks, scions, or as nongrafted transplants (Lee, 1994). Grafted seedlings benefit from extended hypocotyl length, because it helps to increase grafting success (and hence survival rate) and to reduce rooting from the scion after transplant (Chia and Kubota, 2010). However, elongated hypocotyls are not desired for nongrafted seedlings, because this trait may lead to weak transplants (Gomez and Mitchell, 2015; Jones, 2008) and logistical challenges for shipping.

Numerous studies have documented the positive effects of SL during both ornamental and vegetable young plant production in greenhouse environments (Currey and Lopez, 2013; Gomez and Mitchell, 2015; Hernandez and Kubota, 2012; Poel and Runkle, 2017). Additionally, SL and SSL radiation intensity can have species-dependent impacts on extension growth and height (Poel and Runkle, 2017; Randall and Lopez, 2014, 2015). We found that by increasing the DLI from ≈6.1 to 11.8 $mol \cdot m^{-2} \cdot d^{-1}$, cucumber and pepper transplants were generally shorter under SL compared with the low-intensity control (Fig. 2D and F). For instance, under SL, cucumber transplants were 38% to 52% shorter than those under the low-intensity control (Fig. 2D). On the contrary, increasing the DLI resulted in a 23% to 29% increase in plant height of tomato transplants under SL (excluding $B_{25}R_{95}$), compared with the low-intensity control (Fig. 2E). Contrary to our results for tomato, but consistent with our results for cucumber, Fan et al. (2013) reported a reduction in height as DLI increased. For example, tomato was 28% to 47% shorter when grown under DLIs, ranging from 6.5 to 23.8 $mol \cdot m^{-2} \cdot d^{-1}$, in comparison with 2.2 $mol \cdot m^{-2} \cdot d^{-1}$. The underlying difference between the two studies is that Fan et al. (2013) grew plants under SSL, while the current study was conducted under SL in a greenhouse with background solar radiation that provided different spectral radiation qualities.

Height of plants is influenced by internode length, not node number. For instance, internode length of cucumber transplants was greatest under the control, averaging ≈5.0 cm, resulting in the tallest plants (Fig. 2D and J). As DLI increased from ≈6.1 to 11.8 $mol \cdot m^{-2} \cdot d^{-1}$, internode length was reduced by 31% to 40%, thus resulting in a significant decrease in

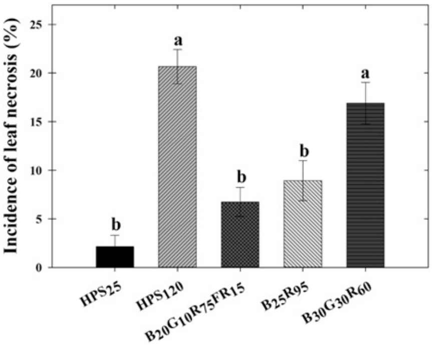

Fig. 5. The incidence of leaf necrosis resulting from high-pressure sodium (HPS) lamp photoperiodic and supplemental lighting (SL) and light-emitting diode SL treatments on tomato seedlings, after 35 d. The percentage of leaves damaged was calculated by dividing the number of leaves showing necrotic lesions by the total number of leaves and multiplying by 100.

height (Fig. 2D and J). A similar reduction of internode length was observed for pepper transplants; however there was no significant difference between the low-intensity control and $B_{20}G_{10}R_{75}FR_{15}$ (Fig. 2L). For tomato transplants, excluding $B_{25}R_{95}$, increasing the DLI resulted in a 9% to 13% increase in internode length, and thus taller plants were observed (Fig. 2E and K).

Our study confirms that an increase in DLI from SL has a positive impact on many of the morphological traits measured. For instance, under higher DLIs ($\approx$11.8 $mol \cdot m^{-2} \cdot d^{-1}$), stem diameter of cucumber and pepper increased, compared with the low-intensity control ($\approx$6.1 $mol \cdot m^{-2} \cdot d^{-1}$), by 17% to 27% and 14% to 25%, respectively (Fig. 2A and C). Fan et al. (2013) observed similar results when cherry tomato seedlings were grown under LED SSL, providing a 1:1 of B:R radiation at a *PPFD* of 50 to 550 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Stem diameter increased incrementally, by 14% to 23%, as the DLI increased from 2.2 to 23.8 $mol \cdot m^{-2} \cdot d^{-1}$. Randall and Lopez (2015) compared growth of vinca (*Catharanthus roseus*) 'Titan Red Dark', impatiens (*Impatiens walleriana*) 'Super Elfin XP Blue Pearl', and geranium (*Pelargonium ×hortorum*) 'Bullseye Red' under ambient solar radiation (control) to SL from HPS lamps or LEDs providing a ratio (%) of 13:87 B:R radiation at a *PPFD* of 70 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Additionally, the same species were grown under SSL consisting of (%) 13:87 B:R or 30:70 B:R radiation at 185 $\mu mol \cdot m^{-2} \cdot s^{-1}$ to evaluate if there were differences in plant quality between plants grown under SSL and greenhouse SL. Under SL and SSL, stem diameter of vinca, impatiens, and geranium was 12% to 17%, 26% to 45%, and 8% to 15% greater, respectively, compared with those seedlings under the control.

From our study, as DLI increased from $\approx$6.1 to 11.8 $mol \cdot m^{-2} \cdot d^{-1}$, shoot dry weight of tomato transplants increased by 107% to 183% compared with the low-intensity control (Fig. 3K) The same trend was generally observed for the pooled results of cucumber and pepper, however minor variabilities existed (Fig. 3J and L). The increase in shoot dry weight can be attributed to increased biomass accumulation from SL as it increased the DLI (Hernandez and Kubota, 2014; Pramuk and Runkle, 2005). For example, Pramuk and Runkle (2005) found that average shoot dry weight increased as DLI increased from 4.1 to 14.2 $mol \cdot m^{-2} \cdot d^{-1}$ for celosia (*Celosia argentea*), impatiens, marigold, and viola by 64%, 47%, 64%, and 68%, respectively.

Both SSL and SL studies have shown how the use of specific radiation wavebands can be used to manipulate hypocotyl length, plant height, stem diameter and length, and leaf area, among many other morphological properties of ornamental and vegetable plants (Chia and Kubota, 2010; Currey and Lopez, 2013; Fan et al., 2013; Klein et al., 1965; Liu et al., 2011; Lopez and Runkle, 2008; Massa et al., 2008). However, not all studies reported morphological changes in response to SL radiation quality. For instance, Poel and Runkle (2017) reported few (if any) differences when SL contributed 20% to 40% of the total DLI. Conversely, Randall and Lopez (2014, 2015) found that morphological responses to SL for bedding plant seedlings were observed when 40% to 60% of the DLI was provided by SL. Given this, Hurt et al. (2019) hypothesized and confirmed that greater than 40% of the total DLI needs to come from SL to elicit morphological responses. They reported when LED SL provided 40% to 55% of the total DLI, compact growth of gerbera (*Gerbera jamesonii*) 'Jaguar Deep Orange', impatiens 'Accent Premium Salmon', and petunia 'Ramblin Peach Glo' seedlings were observed. In the current study, SL provided $\approx$43% of the total DLI for cucumber, tomato, and pepper transplants. Hernandez and Kubota (2014) also reported that B and R LED SL spectral quality treatments only elicited morphological responses when the solar DLI was $\approx$5 $mol \cdot m^{-2} \cdot d^{-1}$.

Leaf area and fresh weight of cucumber, tomato, and pepper increased by 33%, 49%, and 22% and 35%, 56%, and 14%, respectively, under the $B_{30}G_{30}R_{60}$ SL treatment compared with the $B_{25}R_{95}$ (Fig. 3D–I). A possible explanation could be the replacement of R radiation with G radiation. The increased leaf area and fresh weight can be in part attributed to the fact that G radiation is transmitted more deeply into the plant canopy compared with R and B radiation (Klein, 1992; Smith, 1993). For example, chlorophyll weakly absorbs G radiation, meaning that up to 80% of G radiation is transmitted through the chloroplast (Terashima et al., 2009). This allows more G photons to pass deeper into the mesophyll to reach deeper chloroplasts that R and B radiation are unable to access, helping to further increase photosynthetic efficiency, biomass accumulation, and yield (Smith et al., 2017). For example, in the absence of G radiation, the F_v/F_m of both cucumber and pepper was significantly lower under $B_{25}R_{95}$ SL (Fig. 3M and O), indicating that the photosynthetic efficiency of plants was higher under the other treatments providing G radiation.

Kim et al. (2006) observed similar results, where lettuce 'Waldmann's Green' growth was compared under LED SSL, providing 150 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of B and R radiation or B and R radiation supplemented with G fluorescent lamps. An increase of 32%, 45%, and 47% in leaf area, shoot fresh weight, and shoot dry weight, respectively, were reported as a result of replacing R or B radiation with G radiation.

Spectral quality manipulation can be an effective alternative to using plant growth regulators or day/night air temperature differentials for the control of extension growth or plant height (Randall and Lopez, 2014; Wollaeger and Runkle, 2015). For instance, under monochromatic R LEDs, hypocotyl elongation of cucumber transplants was promoted (Hernandez and Kubota, 2016). Taller transplants can make handling and transportation more difficult because they run a greater risk of stem breakage (Kubota et al., 2004; Kwack et al., 2016; Pramuk and Runkle, 2005). Therefore, the addition of B to R radiation can be a useful tool for preventing excessive stem elongation (Hernandez and Kubota, 2016; Randall and Lopez, 2014; Wollaeger and Runkle, 2015).

Previous studies have reported that with increasing B radiation, stem and hypocotyl length are reduced (Brown et al., 1995; Hernandez and Kubota, 2016; Liu et al., 2011). For instance, Brown et al. (1995) reported shorter pepper seedlings under SSL providing 10:90 B:R radiation at a *PPFD* of 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$ in comparison with monochromatic R radiation. Similarly, cherry tomato plants grown under SL providing 0:100 B:R radiation at a *PPFD* of 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$ were 95% taller than plants grown under 50:50 B:R radiation (Liu et al., 2011). When cucumber plants were grown under SSL providing an increasing B:R radiation ratio, ranging from 0:100 to 100:0 B:R at a *PPFD* of 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$, plant height, hypocotyl, and epicotyl length decreased as the proportion of B radiation increased up to 75:25 B:R radiation. However, under monochromatic B LEDs, height increased by 69% compared with monochromatic R LEDs and increased by 346% compared with the 75:25 B:R SSL treatment (Hernandez and Kubota, 2016). Although the $B_{30}G_{30}R_{60}$ SL treatment provided the greatest amount of B radiation of any of the treatments in this study, plants were generally taller. Zhang et al. (2011) reported that the addition of G radiation to R and B radiation under higher radiation intensities induced a shade-avoidance syndrome. Therefore, this study further illustrates that G radiation has an antagonistic effect on the growth inhibition response of B radiation. Not surprisingly, we observed reductions in height of vegetable transplants grown under $B_{25}R_{95}$ SL that did not contain FR and/or G radiation (Fig. 2D–F).

Considering all three species are categorized as day-neutral plants, and because the duration of SL and PL were equal (16 $h \cdot d^{-1}$), differences in the number of plants with visible flower buds for tomato and pepper can be associated with an increase in DLI. For example, only 7% of tomatoes grown under the low-intensity control had flower buds, compared with 100% of plants grown under SL, regardless of the spectral quality (Fig. 4). Fewer cucumber and pepper plants had visible flower buds when grown under $B_{25}R_{95}$, $B_{20}G_{10}R_{75}FR_{15}$ SL, and $B_{30}G_{30}R_{60}$ SL, respectively, compared with plants under HPS_{120}. This observation could be attributed to an increase in plant temperature under the HPS_{120} lamps. Further studies are required to evaluate the spectral quality influence on flower initiation and development of vegetable transplants.

Given that tomato plants can develop physiological disorders such as chlorosis and necrosis under photoperiods >16 h or continuous lighting, it has been suggested that long photoperiods with low radiation intensities can be an alternative method to prevent symptoms on young transplants (Gomez and Mitchell, 2015). In the current study, the incidence of small and irregular necrotic lesions was observed on tomato leaves under all SL treatments, with the highest percentage of symptoms observed under HPS_{120} and $B_{30}G_{30}R_{60}$ SL. Previous studies have suggested that radiation quality and constant temperatures can influence leaf chlorosis of tomato (Demers, 1998; Demers and Gosselin, 2002). In the present study, tomato transplants under HPS_{120} and $B_{30}G_{30}R_{60}$ SL received $\geq 30\ \mu mol \cdot m^{-2} \cdot s^{-1}$ of G radiation. Additionally, transplants were grown under constant temperatures. No biotic factors were identified by a diagnostic laboratory, that might have caused these symptoms; and low fertility can be ruled out as the reason for necrotic symptoms because we provided $100\ mg \cdot L^{-1}$ N when fertilizing. The optimal range for tomato transplant production is 100 to $150\ mg \cdot L^{-1}$ (Whipker, 2018).

Conclusions

The results from our study help to quantify how SL quality influences the morphological and physiological properties of vegetable transplants when the ambient solar DLI is low. Spectral quality significantly influenced the parameters evaluated for cucumber, tomato, and pepper. Increasing the DLI resulted in an increase of stem diameter of cucumber and pepper transplants. Stem elongation of cucumber was promoted under the low-intensity control, while it was reduced for tomato transplants under the low-intensity control. Furthermore, the replacement of B or R radiation with FR and/or G radiation increased plant height of cucumber and tomato. Generally, $B_{25}R_{95}$ was the most effective at reducing internode length of all three species. Fresh weight of cucumber and pepper was greatest under HPS_{120} and $B_{30}G_{30}R_{60}$ SL. Leaf area and fresh weight of tomato was greatest under the $B_{30}G_{30}R_{60}$ SL. The results from our study suggest that $B_{25}R_{95}$ SL produces the most compact cucumber and tomato transplants, which is a desired trait for preventing breakage during transport. However, parameters such as leaf area and fresh weight were negatively impacted under $B_{25}R_{95}$ SL. Finally, the $B_{30}G_{30}R_{60}$ LED treatment was equally effective as the HPS_{120} for the promotion of desirable traits for vegetable transplants, thus indicating that LED SL is both a viable and economically feasible alternative to the current industry standard.

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