MORPHOLOGICAL AND PHYSIOLOGICAL RESPONSES OF VEGETABLE TRANSPLANTS, HERBS, AND LEAFY GREENS TO LIGHT QUALITY, QUANTITY, AND DURATION

By

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ABSTRACT

MORPHOLOGICAL AND PHYSIOLOGICAL RESPONSES OF VEGETABLE TRANSPLANTS, HERBS, AND LEAFY GREENS TO LIGHT QUALITY, QUANTITY, AND DURATION

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Controlled-environment (CE) production of vegetables, herbs, and leafy greens is quickly expanding. However, knowledge gaps exist on how to manage them in CEs. Thus, we evaluated developmental parameters of 10 different basil (*Ocimum* spp.) species and cultivars and 8 herbs and leafy greens under a truncated 9-h short day (SD), day-extension lighting, and a 4-h night interruption utilizing red+white+far-red (R+W+FR) light-emitting diodes (LEDs). All basil cultivars, excluding 'Red Rubin' can be classified as day-neutral plants (DNP) under a low photosynthetic daily light integral (DLI). Coriander, dill, lavender, and marjoram can be classified as facultative long-day plants (LDPs). While watercress, oregano 'Kirigami' and 'Greek', and spearmint can be categorized as obligate LDPs. Furthermore, six basil cultivars were evaluated under a 9-h SD and 16-h LD utilizing a moderate DLI of ≈13 $mol \cdot m^{-2} \cdot d^{-1}$ and a high DLI of ≈23 $mol \cdot m^{-2} \cdot d^{-1}$. Time to visible bud and open flower were hastened under high DLIs and node number below the first open flower were reduced indicating that basil exhibited a facultative irradiance response (FIR). In a separate experiment, cucumber 'Elsie', tomato 'Climstar', and pepper 'Kathia' seedlings were grown under LED supplemental lighting (SL) providing spectral qualities beyond B and R radiation. Fresh weight and leaf area of all three species was greater when G radiation replaced R and B radiation. However, other plant parameters evaluated in response to radiation quality were found to be species-specific. Results from these studies can provide growers with information on how to manage growth and development of vegetable transplants, culinary and ornamental herbs, and leafy greens in CEs.

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Introduction

Greenhouses and other controlled environments (CEs) are essential for year-round production of vegetables, culinary herbs, and leafy greens in northern latitudes. CEs offer many advantages over open field production, including increased fruit quality and yield; reduced water usage, protection from pest and weed control pressure, and climatic extremes such as drought, flooding, and low- and high-temperature stress. Additionally, the ability to control environmental parameters such as temperature and light can be used to manage crop timing (McCartney and Lefsrud, 2018). As a result, food crop production within greenhouses is quickly expanding in the United States (U.S.) (Indoor Crop Production Feeding the Future, 2015). For example, from 2012 to 2017, the number of operations involved in greenhouse production of fresh cut culinary herbs and vegetables increased by 24%, from 8,750 to 10,849, thus resulting in a 15% increase in production area (9.1 to 10.5 million m^2) (USDA, 2019). Furthermore, during the same period the total value of sales increased by 18%, from $634 to $748 million U.S. dollars (USDA, 2019).

Due to year-round demand for fresh vegetables, herbs, and leafy greens, production occurs during times of the year when solar radiation is limited or excessive in northern regions. Therefore, production during the winter months requires supplemental lighting (SL) using high-intensity discharge (HID) lamps or light-emitting diodes (LEDs) to increase the photosynthetic daily light integral (DLI), thus increasing crop growth, yield, and quality. Electromagnetic radiation from the sun is a form of energy that is used for plant growth and development. The electromagnetic radiation spectrum encompasses a wide range of short and long wavelengths including ultraviolet [UV (100-380)], visible (380-770 nm), far-red [FR (700-800 nm)], and infra-red [IR (770-2500 nm)] radiation (Bird and Riordan, 1986; Iqbal, 1983). All wavebands can influence plant growth and development, however, radiation within the 400 to 700 nm range, known as photosynthetically active radiation (PAR) generally has the greatest impact on photochemical reactions such as photosynthesis (Lopez et al., 2017; Zhu et al., 2008). Photosynthetic pigments such as chlorophyll a and b absorb light energy (photons) within the PAR spectrum to convert water and carbon dioxide (CO_2) into sugars and oxygen (O_2) (van Iersel, 2017). These carbohydrates are the building blocks or chemical energy used for the production of roots, leaves, storage, and reproductive organs.

There are three primary properties of the plant light environment including quantity (intensity, irradiance), quality (spectrum), and duration (photoperiod). Irradiance refers to the amount of photons within a specific waveband falling on a unit area per unit time, and is expressed as micromoles per square meter per second ($\mu mol \cdot m^{-2} \cdot s^{-1}$) (Blanchard et al., 2006). Radiation quality refers to the color or wavelength distribution of electromagnetic radiation from the sun or electrical lamps. Duration or photoperiod, refers to the number of light hours within a 24-h period, available for plant growth, and its effect on photoperiodic crops. Generally speaking, radiation quantity, quality, and duration are associated with plant biomass accumulation, morphology, and flowering, respectively. However, all three properties interact to control plant growth and development.

Radiation Quality

Wavebands within PAR used by plants for photosynthesis include blue [B (400-500 nm)] green [G (500-600)], and red [R (600-700)] radiation. They can also utilize UV-A (320-380 nm) and FR radiation for other processes. Although PAR accounts for less than half (~43%) of the solar spectrum it is the most important waveband utilized for photosynthesis (Lopez et al., 2017). Radiation acts as both an energy source and a signal for plant growth and development. For instance, photomorphogenesis is a light mediated process by which the radiation spectrum (color) affects plant morphology and development. Radiation quality has a greater impact on photomorphogenesis, whereas irradiance used as an energy source, has a greater impact on photosynthesis (Han et al., 2007; Hernandez and Kubota, 2017).

Specialized photoreceptors such as cryptochromes, phytochromes, phototropins, and more recently described UV RESISTANCE LOCUS 8 (UVR8) enable plants to sense and respond to external signals (Li et al., 2012; Rizzini et al., 2011). Light signals, perceived by these photoreceptor families govern multiple developmental processes including seed germination, seedling de-etiolation, phototropism, shade avoidance, circadian rhythms, and flowering time (Deng and Quail, 1999; Wang and Deng, 2003; Jiao et al., 2007). Phytochromes primarily absorb R and FR wavelengths (and to a lesser extent B radiation), cryptochromes and phototropins absorb B and UV-A (320–500 nm), and UVR8 has recently been shown to perceive UV-B (282–320 nm) (Rizzini et al., 2011).

Blue radiation

Cryptochrome mediated plant responses to B radiation include the inhibition of stem elongation, promotion of stomatal opening, phototropism, and anthocyanin accumulation (Fankhauser and Chory, 1997; Hernandez and Kubota, 2017). *Arabidopsis* has two cryptochrome genes, *cry1* and *cry2*. Both genes are involved in resetting the circadian rhythm, and in de-etiolation responses (Chen et al., 2004). During stomatal opening, Schwartz and Zeiger (1984) discovered that for Asiatic dayflower (*Commelina communis*) and faba bean ‘Long pod’ (*Vicia faba*) stomatal apertures were higher under B radiation in comparison to white (W) and R radiation. Previous studies have reported that with increasing B radiation, stem and hypocotyl length were reduced (Brown et al., 1995; Hernandez and Kubota, 2016). For instance, pepper 'Hungarian Wax' (*Capsicum annuum*) seedlings grown under sole-source lighting (SSL) providing a ratio (%) of 10:90 B:R radiation at a photosynthetic photon flux density (*PPFD*) of 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$, had shorter stem lengths compared to plants grown under 0:100 B:R radiation (Brown et al., 1995). Liu et al. (2011) reported that cherry tomato (*Lycopersicon esculentum*) grown under SL providing a ratio (%) of 0:100 B:R radiation with a *PPFD* of 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$ were 95% taller than those under 50:50 B:R radiation. In a separate study, cucumber 'Cumlaude' (*Cucumis sativus*) 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 (75:25 B:R radiation). Interestingly, under 100:0 B:R radiation, hypocotyl length was 69% and 346% greater than under 0:100 B:R and 75:25 B:R radiation, respectively. The unexpected extension growth observed under 100:0 B:R radiation could be due to the lack of the coaction effect, where the absence of R radiation, prevents the inhibition of stem elongation that is usually associated with additions of B radiation (Hernandez and Kubota, 2016).

Green radiation

Green radiation was previously believed to have a minimal effect on plant growth and development (McCree, 1972). However, recent research indicates that G radiation may be involved in CO_2 assimilation and in promoting biomass and thus yield (Smith et al., 2017). Furthermore, G radiation can induce shade avoidance responses (Zhang et al., 2011), similar to FR light, by inactivating B absorbing cryptochromes (Banerjee et al., 2007; Bouly et al., 2007, Sellaro et al., 2010), thus resulting in hypocotyl extension growth (Folta, 2004). However, G radiation can also inhibit the accumulation of anthocyanins (Bouly et al., 2007; Zhang and Folta, 2012) and stomatal opening (Frenchilla et al., 2000). An estimated 10 to 50% of G radiation is reflected by chloroplasts (Nishio, 2000; Terashima et al., 2009). The remainder is either transmitted to the lower canopy or is absorbed by plant pigments such as chlorophyll and accessory pigments including carotenoids. Consequently, inner plant canopies can be rich in G radiation, meaning that photosynthesis in lower canopy leaves is mainly driven by G wavelengths. Furthermore, G radiation can penetrate deeper into the mesophyll layer of leaves, thereby potentially increasing photosynthesis where other wavelengths are limited (Smith et al., 2017). Chlorophyll exists in two forms chlorophyll *a* and chlorophyll *b* (Bollivar, 2006). Maximum absorption of dissolved chlorophyll *a* and *b* is in the B and R waveband range, and more weakly in the G range. Up to 80% of all G radiation is presumed to be transmitted through the chloroplast. Thus, G radiation can reach lower into leaf cells due to chlorophyll's weak absorption (Evans and Vogelmann, 2003; Vogelmann and Han, 2000). Vogelmann and Han (2000) treated spinach (*Spinacia oleracea*) with brief 2000 $\mu mol \cdot m^{-2} \cdot s^{-1}$ flashes of monochromatic B, R, and G radiation to determine maximum absorption depths. Adaxial to abaxial maximum absorption depths for B, R, and G radiation were 50, 100, and 150 µm, respectively.

Kim et al. (2004) grew lettuce 'Waldmann's Green' (*Lactuca sativa*) under four lighting treatments consisting of B+R, B+R supplemented with G fluorescent lamps, G fluorescent lamps, and under cool-white fluorescent (CWF) lamps, which provided 0, 24, 86, and 51% G radiation, respectively (18-h photoperiod; 9.7 $mol \cdot m^{-2} \cdot d^{-1}$). The addition of 24% G radiation to the B+R LEDs resulted in an increase for leaf area, shoot fresh weight, and shoot dry weight by 31, 45 and 47%, respectively. However, leaf area, shoot fresh and dry weight of lettuce was significantly reduced when grown under the G fluorescent lamps, compared to both the R+B and the R+B+G treatments. A benefit of adding G radiation to B+R radiation is that plants appear G, instead of grey or black, and pest, disease and nutritional deficiencies are easier to see.

Red and far-red radiation

The phytochrome family consists of five members, phytochromes A, B, C, D, and E, and are designated *phyA*, *phyB*, *phyC*, *phyD*, and *phyE* (Sharrock and Quail, 1989; Dehesh et al., 1991). The *phyA* gene is the primary photoreceptor involved in the perception and mediation of various plant responses to FR radiation, such as stem elongation and the shade avoidance response (Dehesh et al., 1993; Parks and Quail, 1993). Phytochrome is a photoreversible pigment with peak absorbance in the R and FR range (Rizzini et al., 2011). Phytochrome exists as two interconvertible forms, an active and inactive form. The FR absorbing form (P_{FR}) is biologically active, and the R absorbing form (P_R) is inactive (Hendricks et al., 1962, Sager et al., 1988). Therefore, when P_{FR} is illuminated with R radiation or kept in dark conditions, it converts to the P_R form, and when P_R is illuminated with FR radiation, it converts back to the P_{FR} form. Additionally, when phytochrome exists at an equilibrium between the active state (P_{FR}) and the inactive state (P_R), it is referred to as the phytochrome photostationary state (P_{FR}/P_{Total}, where P = P_R+ P_{FR}), relative to a specific spectral quality (Sager et al., 1988). P_{FR} formation culminates in altered expression of pytochrome responsive genes responsible for driving non-photosynthetic radiation responses including a shade avoidance response, seed germination, inhibition of stem elongation and flowering (Hendricks et al., 1962; Hendricks and Borthwick, 1967; Mancinelli et al., 2007). Reconversion to P_R can halt this process. Thus, R and FR emitting LEDs can be used to artificially manipulate the photoperiod and either delay or induce flowering responses in photoperiodic crops.

Photoperiodic lighting

Plants have evolved and developed the ability to perceive changes in day length during the growing season. The plant's developmental response or physiological reaction to changes in the length of day and night is known as photoperiodism (Thomas and Vince-Prue, 1997). The rotation of the earth and the tilting of the axis results in different amounts of solar radiation falling onto the earth, thereby causing different seasons and durations of light hours. Since the earth is tilted at an axis of 23.5º, as one moves farther from the equator and closer to the earth's poles the length of day and night can change dramatically. In the northern hemisphere day length becomes longer during the summer solstice and shorter during the winter solstice (Jackson, 2009).

The ability of plants to perceive and respond to these changes in day length proves to be beneficial, because it allows them to anticipate adverse environmental conditions. For example, in northern latitudes autumnal short days (SD) precede winter. Short days can act as a signal to induce bud dormancy and cold hardiness (Thomas and Vince-Prue, 1997). Plant responses triggered by seasonal changes of the natural photoperiod include seed germination, leaf expansion, stem elongation, tuberization, dormancy, bud set, and most importantly flowering (Densmore, 1997; Hay and Heide, 1983; Jackson, 2009, Lopez and Runkle, 2006; Runkle et al., 2017).

Based on photoperiodic flowering responses plants are categorized as long day (LDP), short day (SDP), or day-neutral plants (DNP) (Thomas and Vince-Prue, 1997). Plants with a LD response will flower when the night length is shorter than the critical duration, while SDPs will flower faster when the night length is longer than the critical duration (Runkle et al., 2017). Both LDP and SDPs can be further classified as having an obligate (qualitative) or facultative (quantitative) response. For example, a facultative SDP will flower faster when the night length is long, but will eventually flower under all photoperiods. On the contrary, an obligate LDP will only flower when the night length is longer than the critical duration (Blanchard and Runkle, 2010). DNPs flower regardless of the day or night length (Thomas and Vince-Prue, 1997).

Greenhouse growers can use low-intensity (1-2 $\mu mol \cdot m^{-2} \cdot s^{-1}$) electric lighting when the skotoperiod is long or a 4-h night interruption (NI) to induce or prevent flowering of LDPs or SDPs, respectively (Blanchard and Runkle, 2010; Mattson and Erwin, 2005). The use of blackout systems can also be employed to create truncated SDs to induce flowering of SDPs or prevent flowering of LDPs. Low R:FR, promote both stem elongation and flowering of LDPs. On the contrary, high R:FR (FR deficient environments) can inhibit flower initiation of LDPs such as snapdragon (*Antirrhinum majus*), campanula (*Campanula carpatica*), coreopsis (*Coreopsi grandiflora*), and petunia (*Petunia ×hybrida*) (Downs and Thomas, 1982; Kim et al., 2002; Runkle and Heins, 2001). FR radiation alone is not usually perceived as a LD, and thus a combination of R and FR radiation are commonly used to promote flowering of LDPs. Incandescent (INC) lamps emit a mixture of R and FR radiation, that create an intermediate phytochrome photoequilibria [PPE (0.60-0.75)], which has been shown to be the most effective at promoting flowering of some LDPs (Craig and Runkle, 2012; Thomas and Vince-Prue, 1997).

Until recently, INC lamps were commonly used for day extension (DE) and NI lighting to successfully promote flowering of the LDPs such as campanula, coreopsis, and lavender (*Lavandula angustifolia*) (Damann and Lyons, 1996; Runkle et al., 1998). However, they are electrically inefficient and thus have been phased out of production. LED fixtures containing R+FR are more efficient, have a longer operating life, and provide a PPE similar to that of INC lamps (Yeh and Chung, 2009). Kohyama et al. (2014) compared the flowering response of ageratum (*Ageratum houstonianum*), calibrachoa (*Calibrachoa ×hybrida*), two cultivars of dianthus (*Dianthus chinensis*) petunia under NI lighting using INC lamps or two LED lamps (R+W or R+W+FR). Time to flower, node number and plant height for all crops was similar under the INC lamps and R+W+FR LEDs. For example, dianthus 'Floral Lace Purple' flowered 5 days sooner when treated with a NI provided with INC or the R+W+FR lamps compared to a SD. Furthermore, time to flower for dianthus, under the R+W lamps was similar to plants under SDs.

Supplemental Lighting

Peak young plant (vegetative cuttings) and seed propagated vegetable and bedding plant production in northern latitudes, usually occurs when the ambient photosynthetic DLI can be as low as 1 to 5 $mol \cdot m^{-2} \cdot d^{-1}$ (Lopez and Runkle, 2008; Pramuk and Runkle, 2005; Styer, 2003). Low DLIs can lead to production issues such as inconsistent and excessive stem elongation, poor performance after transplant, and delayed rooting and germination (Lopez and Runkle, 2008). Furthermore, the DLI provided to the growing area within the greenhouse can be reduced by 50% or more, due to glazing materials and other greenhouse structures (Hanan, 1998). Therefore, greenhouse operations use SL to increase the DLI, thus increasing plant photosynthesis and quality. The most cost effective time to provide SL will depend on the plant density and the type of plant species being grown (shade vs. sun), but most importantly, whether or not ambient radiation levels are low. This is because at lower radiation levels even small increases in irradiance can dramatically increase the net photosynthetic rate (Faust et al., 2017). SL is less effective when radiation levels are higher, since the light saturation point will likely be reached sooner and thus any further SL will not increase photosynthesis. Thereby indicating that the net photosynthetic rate has been maximized and further increases in PAR is not economically feasible (Helma et al., 2004).

Benefits of SL include increased cutting quality and yields from stock plants (Chong et al., 2014), shorten production time of plugs, liners, and potted plants (Lopez et al., 2017), and compact growth with thicker stems, increased branching and earlier flowering of bedding plants (Erwin et al., 2017). To produce high-quality vegetable seedlings for transplant, defined by well-developed root and shoot systems, compact growth, and thick stems, a DLI ranging from 13 to 16 $mol \cdot m^{-2} \cdot d^{-1}$ is recommended (Fan et al., 2013; Moe et al., 2006). However mature fruiting vegetable plants require even higher DLIs usually ≥30 $mol \cdot m^{-2} \cdot d^{-1}$. Increased DLIs can shorten cultivation time, improve productivity and product quality, and allow for year-round production (Dorais and Ehret, 2008). Thus, allowing growers to meet year-round consumer demand. Similarly, previous research has determined that annual bedding plant seedlings also require a DLI of 10 to 12 $mol \cdot m^{-2} \cdot d^{-1}$ for optimal growth (Currey et al., 2012; Lopez and Runkle, 2008; Oh et al., 2010). Optimal vegetative growth of culinary herbs such as basil (*Ocimum* spp.), require a DLI of ≥10 $mol \cdot m^{-2} \cdot d^{-1}$ for optimal growth (Beaman et al., 2009; Chang et al., 2008, Dou et al., 2018; Walters and Currey, 2018). Young plants provided with SL have increased rooting, more branching, thicker stems, reduced extension growth, and potentially more crops cycles per season. Additionally, young plants grown under SL generally flower earlier during finishing (Lopez et al., 2017).

Plant height of various bedding plants has been shown to decrease with an increase in DLI. For example, height of impatiens ‘Accent Red’ (*Impatiens wallerana*) and salvia ‘Vista Red’ (*Salvia splendens*) seedlings grown under SSL decreased by 27% and 37%, respectively, as DLI increased from 4.1 to 14.2 $mol \cdot m^{-2} \cdot d^{-1}$ (Pramuk and Runkle, 2005). Furthermore, seedling shoot dry weight of celosia 'Gloria Mix' (*Celosia argentea*), impatiens, marigold 'Bonanza Yellow' (*Tagetes patula*), and pansy 'Crystal Bowl Yellow' (*Viola*) increased by 64, 47, 64, and 68%, respectively under the same DLIs (Pramuk and Runkle, 2005). Walters and Currey (2018) reported a 144, 205, and 208% increase in fresh weight for greenhouse grown sweet basil 'Nufar' (*Ocimum basilicum*), lemon basil 'Lime' (*O. ×citriodorum*) and holy basil 'Holy' (*O. tenuiflorum*), when the DLI increased from 7 to 15 $mol{\cdot}m^{-2}{\cdot}d^{-1}$. Furthermore, dry weight, height, node and branch number, and SPAD levels for all three species also increased with the increase in DLI. In a separate study, Dou et al. (2018) grew sweet basil 'Improved Genovese Compact' under varying irradiance. Similar to Walters and Currey (2018), fresh weight of sweet basil increased as DLI was increased from 9.3 to 17.8 $mol{\cdot}m^{-2}{\cdot}d^{-1}$. For example, fresh weight under DLIs of 12.9, 16.5, and 17.8 $mol{\cdot}m^{-2}{\cdot}d^{-1}$ was 54, 79 and 78% higher than that of those grown under a DLI of 9.3 $mol{\cdot}m^{-2}{\cdot}d^{-1}$ (Dou et al., 2018).

LITERATURE CITED

LITERATURE CITED

Banerjee, R., E. Schleicher, S. Meier, R.M. Viana, R. Pokorny, M. Ahmad, R. Bittl, and A. Batschauer. 2007. The signaling state of *Arabidopsis* cryptochrome 2 contains flavin semiquinone. J. Biol. Chem. 282:14916-14922.

Beaman, A.R., R.J. Gladon, and J.A. Schrader. 2009. Sweet basil requires an irradiance of 500 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for greatest edible biomass production. HortScience 44:64–67.

Bird, R.E and C. Riordan. 1986. Simple solar spectral model for direct and diffuse irradiance on horizontal and tilted planes at the earth's surface for cloudless atmospheres. J. Climate Appl. Meteorol. 25:87–97.

Blanchard, M.G. and E.S. Runkle. 2010. Intermittent light from a rotating high-pressure sodium lamp promotes flowering of long-day plants. HortScience 45:236–241.

Blanchard. M.G., J.A. Chong, J.E. Faust, and E.S. Runkle. 2006. Temperature and light, p. 51–60. In: J.M. Dole and J.L. Gibson (eds.). Cutting propagation: a guide to propagating and producing floriculture crops. Ball Publishing, Batavia, IL.

Bollivar, D.W. 2006. Recent advances in chlorophyll biosynthesis. Photosyn. Res. 90:173–194.

Both, A.J. and J.E. Faust. 2017. Light transmission: the impact of glazing material and greenhouse design, p. 59–66. In: R. Lopez and E.S. Runkle (eds.). Light management in controlled environments. Meister Media Worldwide, Willoughby, OH.

Bouly, J.P., E. Schleicher, M. Dionisio-Sese, F. Vandenbussche, D. Van Der Straeten, N. Bakrim, S. Meier, A. Batschauer, P. Galland, R. Bittl, and M. Ahmad. 2007. Cryptochrome blue light photoreceptors are activated through interconversion of flavin redox states. J. Biol. Chem. 282:9383–9391.

Brown, C.S., A.C. Schuerger, and J.C. Sager. 1995. Growth and photomorphogenesis of pepper plants under red light-emitting diodes with supplemental blue or far-red lighting. J. Amer. Soc. Hort. Sci. 120(5):808–813.

Chang, X., P.G. Alderson, and C.J. Wright. 2008. Solar irradiance level alters the growth of basil (*Ocimum basilicum* L.) and its content of volatile oils. Environ. Expt. Bot. 63:216–223.

Chen, M., J. Chory, and C. Fankhauser. 2004. Light signal transduction in higher plants. Annu. Rev. Genet. 38:87–117.

Chong, J.C., U.C. Samarakoon, and J.E. Faust. 2014. Effects of daily light integral and canopy density on shoot growth and development in a poinsettia (*Euphorbia pulcherrima* Willd. Ex. Klotsch) stock plant canopy. HortScience 49:51–54.

Craig, D.S. and E.S. Runkle. 2012. Using LEDs to quantify the effect of the red to far-red ratio of night-interruption lighting on flowering of photoperiodic crops. Acta Hort. 956:179–186.

Currey, C.J., V.A. Hutchinson, and R.G. Lopez. 2012. Growth, morphology, and quality of rooted cuttings of several herbaceous annual bedding plants are influenced by photosynthetic daily light integral during root development. HortScience 47:25–30.

Damann, M.P. and R.E. Lyons. 1996. Natural chilling and limited inductive photoperiod affect flowering in two Asteraceae genera. J. Amer. Soc. Hor. Sci. 121:694–698.

Dehesh, K., C. Franci, B.M. Parks, K.A. Seeley, T.W. Short, J.M. Tepperman, and P.H. Quail. 1993. Arabidopsis *HY8* locus encodes phytochrome A. The Plant Cell 5:1081–1088.

Dehesh, K., J.M. Tepperman, A.H. Christensen, and P.H. Quail. 1991. *phyB* is evolutionarily conserved and constitutively expressed in rice seedling shoots. Mol. Gen. Genet. 225:305–313.

Deng, X.W. and P.H. Quail. 1999. Signalling in light-controlled development. Seminars Cell Dev. Biol. 10:121–129.

Densmore, R.V. 1997. Effect of day length on germination of seeds collected in Alaska. Amer. J. Bot. 84:274–278.

Dorais, M. and D.L. Ehret. 2008. Chapter 14, Agronomy and the nutritional quality of fruit, p. 346–391. In: F.T. Barberan and M.I. Gil (eds.). Improving the health-promoting properties of fruits and vegetable products. Woodhead Publishing Ltd, Cambridge, England.

Dou, H., G. Niu, M. Gu, and J.G. Masabni. 2018. Responses of sweet basil to different daily light integrals in photosynthesis, morphology, yield, and nutritional quality. HortScience 53:496–503.

Downs, R.J. and J.F. Thomas. 1982. Phytochrome regulation of flowering in the long-day plant *Hyoscyamus niger*. Plant Physiol. 70:898–900.

Evans J.R. and T.C. Vogelmann. 2003. Profiles of C-14 fixation through spinach leaves in relation to light absorption and photosynthetic capacity. Plant Cell Environ. 26:547–560.

Erwin, J., N. Mattson, and R. Warner. 2017. Light effects on bedding plants, p. 119–134. In: R. Lopez and E.S. Runkle (eds.). Light management in controlled environments. Meister Media Worldwide, Willoughby, OH.

Fankhauser, C. and J. Chory. 1997. Light control of plant development. Annu. Rev. Cell Dev. Biol. 13:203–229.

Fan, X.-X., Z.-G. Xu, X.-Y. Liu, C.-M. Tang, L.-W. Wang, and X.-l. Han. 2013. Effects of light intensity on the growth and leaf development of young tomato plants grown under a combination of red and blue light. Scientia Hort. 153:50–55.

Faust, J.E., H. Verberkt, R. Heins, and T. Blom. 2017. Supplemental lighting of potted plants, p. 146–151. In: R. Lopez and E.S. Runkle (eds.). Light management in controlled environments. Meister Media Worldwide, Willoughby, OH.

Folta, K.M. 2004. Green light stimulates early stem elongation, antagonizing light-mediated growth inhibition. Plant Physiol. 135:1407–1416.

Frenchilla, S., L.D. Talbott, R.A. Bogomolni, and E. Zeiger. 2000. Reversal of blue light-stimulated stomatal opening by green light. Plant Cell Physiology. 41:171–176.

Han, Y-J., P-S. Song, and J-I, Kim. 2007. Phytochrome-mediated photomorphogenesis in plants. J. Plant Biol. 50:230–240.

Hanan, J. 1998. Greenhouses: advanced technology for protected horticulture. CRC Press, Boca Raton, Fla.

Hay, R.K.M. and O.M. Heide. 1983. Specific photoperiodic stimulation of dry matter production in a high-latitude cultivar of *Poa pratensis*. Physiol. Plant. 57:135–142.

Helma, V., R. Heins, and T. Blom. Supplemental lighting on potted plants, p. 72–78. In: P.R. Fisher and E. Runkle (eds.). Lighting up profits. Meister Media Worldwide, Willoughby, OH.

Hendricks, S.B. and H.A. Borthwick. 1967. The function of phytochrome in regulation of plant growth. Proc. Natl. Acad. Sci. 58:2125–2130.

Hendricks, S.B., W.L. Butler, and H.W. Siegelman. 1962. A reversible photoreaction regulating plant growth. J. Phys. Chem. 66:2550–2555.

Hernandez, R. and C. Kubota. 2016. Physiological responses of cucumber seedlings under different blue and red photon flux ratios using LEDs. Environ. Expt. Bot. 121:66–74.

Hernandez, R. and C. Kubota. 2017. Light quality and photomorphogenesis, p. 29–36. In: R. Lopez and E.S. Runkle (eds.). Light management in controlled environments. Meister Media Worldwide, Willoughby, OH.

Indoor Crop Production Feeding the Future. 2015. Newbean Capitol. Accessed 06 March 2019. <https://www.arguscontrols.com/articles/indoor-crop-production-feeding-the-future/>.

Iqbal, M. 1983. An introduction to solar radiation. Academic Press Canada, Don Mills, Ontario.

Jackson, S.D. 2009. Plant responses to photoperiod. New Phytologist 181:517–531.

Jiao, Y., O.S. Lau, and X.W. Deng. 2007. Light-regulated transcriptional networks in higher plant. Nature Rev. Genet. 8:217–230.

Kim, H.-H., G.D. Goins, R.M. Wheeler, and J.C. Sager. 2004. Green-light supplementation for enhanced lettuce growth under re- and blue-light-emitting diodes. HortScience 39:1617–1622.

Kim, H.-H., R.D. Heins, and W.H. Carlson. 2002. Development and flowering of petunia grown in a far-red deficient light environment. Acta Hort. 580:127–135.

Kim, H.-H., R.M. Wheeler, J.C. Sager, G.D. Goins, and J.H. Norikane. 2006. Evaluation of lettuce growth using supplemental green light with red and blue light-emitting diodes in a controlled environment-a review of research at Kennedy Space Center. Acta Hort. 711:111–119.

Kohyama, F., C. Whitman, and E.S. Runkle. 2014. Comparing flowering responses of long-day plants under incandescent and two commercial light-emitting diode lamps. HortTechnology 24:490–495.

Li, J., W. Terzaghi, X.W. Deng. 2012. Genomic basis for light control of plant development. Protein Cell 3:106–116.

Lopez, R.G. and E.S. Runkle. 2006. Temperature and photoperiod regulate flowering of potted *Miltoniopsis* orchids. HortScience 41:593–597.

Lopez, R.G. and E.S. Runkle. 2008. Photosynthetic daily light integral during propagation influences rooting and growth of cutting and subsequent development of New Guinea impatiens and petunia. HortScience 43:2052–2059.

Lopez, R., P. Fisher, and E. Runkle. 2017. Introduction to specialty crop lighting, p. 12–20. In: R. Lopez and E.S. Runkle (eds.). Light management in controlled environments. Meister Media Worldwide, Willoughby, OH.

Mancinelli, A.L., H.A. Borthwick, and S.B. Hendricks. 2007. Phytochrome action in tomato-seed germination. Bot. Gaz. 127:1–5.

Mattson, N.S. and J.E. Erwin. 2005. The impact of photoperiod and irradiance on flowering of several herbaceous ornamentals. Sci. Hort. 104:275–292.

McCartney, L., and M.G. Lefsrud. 2018. Protected agriculture in extreme environments: A review of controlled environment agriculture in tropical, arid, polar, and urban locations. Appl. Eng. in Agr. 34:455–473.

McCree, K.J. 1972. Action spectrum, absorptance and quantum yield of photosynthesis in crop plants. Agr Meteorol. 9:191–216.

Moe, R., S.O. Grimstad, and H.R. Gislerød. 2006. The use of artificial light in year round production of greenhouse crops in Norway. Acta Hort. 711:35–42.

Nishio, J.N. 2000. Why are higher plants green? Evolution of the higher plant photosynthetic pigment complement. Plant Cell Environ. 23:539–548.

Oh, W., E.S. Runkle, and R.M. Warner. 2010. Timing and duration of supplemental lighting during the seedling stage influence quality and flowering in petunia and pansy. HortScience 45:1332–1337.

Parks, B.M. and P.H. Quail. 1993. *hy8*, a new class of Arabidopsis long hypocotyl mutants deficient in functional phytochrome A. The Plant Cell 5:39–48.

Pinho, P. and L. Halonen. 2017. Agricultural and horticultural lighting, p. 703–720. In: R. Karlicek, C.-C. Sun, G. Zissis, R. Ma (eds.). Handbook of advanced lighting technology. Springer International Publishing, Switzerland.

Pramuk, L.A. and E.S. Runkle. 2005. Photosynthetic daily light integral during the seedling stage influences subsequent growth and flowering of *Celosia, Impatiens, Salvia, Tagets,* and *Viola*. HortScience 40:1336–1339.

Rizzini, L., J-J. Favory, C. Cloix, D. Faggionato, A. O'Hara, E. Kaiserli, R. Baumeister, E. Schafer, F. Nagy, G.I. Jenkins, and R. Ulm. 2011. Perception of UV-B by the *Arabidopsis* UVR8 protein. Sci. 332:103–106.

Runkle. E. and B. Bugbee. 2013. Problems with foot-candles, lux and lumens. GPN. 23.9.78.

Runkle, E., R. Lopez, and P. 2017. Fisher. Photoperiodic control of flowering, p. 38–47. In: R. Lopez and E.S. Runkle (eds.). Light management in controlled environments. Meister Media Worldwide, Willoughby, OH.

Runkle, E.S. and R.D. Heins. 2001. Specific functions of red, far red, and blue light in flowering and stem extension of long-day plants. J. Amer. Soc. Hort. Sci. 126:275–282.

Runkle, E.S., R.D. Heins, A.C. Cameron, and W.H. Carlson. 1998. Flowering of herbaceous perennials under various night interruption and cyclic lighting treatments. HortScience 33:672–677.

Sager, J.C., W.O. Smith, J.L. Edwards and K.L. Cyr. 1988. Photosynthetic efficiency and phytochrome photoequilibria determination using spectral data. Trans ASAE 31.

Schwartz, A. and E. Zeiger. 1984. Metabolic energy for stomatal opening. Roles of photophosphorylation and oxidative phosphorylation. Planta 161:129–136.

Sharrock, R.A., and P.H. Quail. 1989. Novel phytochrome sequences in *Arabidopsis thaliana*: structure, evolution, and differential expression of a plant regulatory photoreceptor family.

Genes Dev. 3:1745–1757.

Smith, H.L., L. McAusland, and E.H. Murchie. 2017. Don't ignore the green light: exploring diverse roles in plant processes. J. Expt. Bot. 68:2099–2110.

Styer, C. 2003. Propagating seed crops, p. 151–163. In: D. Hamrick (ed.). Ball redbook crop production: Volume two. 17th ed. Ball Publishing, Batavia, IL.

Terashima, I., T. Fujita, T. Inoue, W.S. Chow, and R. Oguchi. 2009. Green light drives leaf photosynthesis more efficiently than red light in strong white light: revisiting the enigmatic question of why leaves are green. Plant Cell Physiol. 50:684–697.

Thomas, B. and D. Vince-Prue. 1997. Photoperiodism in plants. 2nd ed. Academic Press, San Diego, CA.

U.S. Department of Agriculture (USDA), 2019. Census of Agriculture. National Agricultural Statistic Service. Washington DC. 25 April. 2019. <https://www.nass.usda.gov/Publications/AgCensus/2017/Full_Report/Volume_1,_Chapter_1_US/usv1.pdf>.

van Iersel, M. 2017. Light, photosynthesis, and plant growth, p. 21–28. In: R. Lopez and E.S. Runkle (eds.). Light management in controlled environments. Meister Media Worldwide, Willoughby, OH.

Vogelmann, T.C. and T. Han. 2000. Measurement of gradients of absorbed light in spinach leaves from chlorophyll fluorescence profiles. Plant Cell Environ. 23:1303–1311.

Walters, K.J. and C.J. Currey. 2018. Effects of nutrient solution concentration and daily light integral on growth and nutrient concentration of several basil species in hydroponic production. HortScience 53:1319–1325.

Wang, H. and X.W. Deng. 2003. Dissecting the phytochrome A-dependent signaling network in higher plants. Trends Plant Sci. 8:172–178.

Yeh, N. and J.-P. Chung. 2009. High-brightness LEDs—Energy efficient lighting sources and their potential in indoor plant cultivation. Renewable Sustainable Energy Rev. 13:2175–2180.

Zhang, T. and K.M. Folta. 2012. Green light signaling and adaptive response. Plant Signaling Behavior 7:1–4.

Zhang, T., S.A. Maruhnich, and K.M. Folta. 2011. Green light induces shade avoidance symptoms. Plant Physiol. 157:1528–1536.

Zhu, X.-G., S.P. Long, and D.R. Ort. 2008. What is the maximum efficiency with which photosynthesis can convert solar energy into biomass?. Current Opinion Biotechnol. 19:153–159.

SECTION II

FLOWERING DEVELOPMENT PARAMETERS OF CULINARY AND ORNAMENTAL HERBS AND LEAFY GREENS IN RESPONSE TO PHOTOPERIOD

Flowering development parameters of culinary and ornamental herbs and leafy greens in response to photoperiod

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Abstract

Increasingly, retailers and consumers are demanding non-flowering fresh cut culinary herbs and leafy greens and flowering potted ornamental herbs. However, few publications have documented environmental parameters that promote or inhibit flowering of these crops. Therefore, the objectives of this study were 1) to quantify how photoperiod influences flowering development parameters of culinary and ornamental herbs and leafy greens and 2) to determine the critical photoperiod of those crops that flower in response to photoperiod. Coriander 'Santo' (*Coriandrum sativum*), dill 'Bouquet' (*Anethum graveolens*), lavender 'Bandera Pink' (*Lavandula stoechas*), marjoram (*Origanum majorana*), oregano 'Kirigami' (*O. rotundifolium*), watercress (*Nasturtium officinale*), oregano 'Greek' (*O. vulgare hirtum*), and spearmint 'Spanish' (*Mentha spicata*) were grown in a greenhouse at 20 °C. Photoperiods consisted of a 9-h short day (SD) or an SD extended to 12, 13, 14, or 16 h with red+white+far-red (R+W+FR) light-emitting diode (LED) lamps (R:FR = 0.8) providing a total photon flux density of ≈2 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Additionally, an SD with a 4-h night interruption (NI) from the same R+W+FR lamps was included. Plants were assessed daily for time to first visible flower bud (VB) and open flowers (OF). Node number below the first OF and plant height were recorded at first OF. Node number at flowering was greater under 9-h SDs for coriander, dill, lavender, and marjoram, and generally decreased as day length increased to 16 h or under an NI. Coriander and dill grown under a 9-h SD were more compact at flowering in comparison to plants grown under photoperiods ≥13 h. Time to first VB occurred more rapidly under LDs for coriander, dill, lavender, and marjoram. Watercress and oregano 'Kirigami' only produced VBs and OFs under ≥13-h day lengths. Oregano 'Greek' and spearmint only flowered under 16 h or NI treatments. Therefore, coriander, dill, lavender, and marjoram can be classified as facultative long day plants

(LDPs). While watercress, oregano 'Kirigami', oregano 'Greek', and spearmint can be categorized as obligate LDPs, requiring ≥14-h, ≥13-h, and 16, or NI, respectively, for VB formation and flowering to occur.

Keywords: critical photoperiod, day-extension lighting, far-red radiation, light-emitting diodes, long-day plants, night-interruption lighting.

Abbreviations: ADT, average daily temperature; B, blue; CWF, cool-white fluorescent; DE, day-extension lighting; DLI, daily light integral; DN, day-neutral; FR, far red; G, green; HPS, high-pressure sodium; INC, incandescent; LED, light-emitting diode; LD, long-day; LDP, long-day plant; MH, metal halide; NI, night-interruption; OF, open flower; PPE, phytochrome photoequilibria; *PPFD*, photosynthetic photon flux density; PSS, phytochrome photostationary state; R, red; Rep., replication(s); SD, short-day; SDP, short-day plant; *TPFD*, total photon flux density; VB, visible bud; W, white.

Introduction

An increased health conscious attitude and curiosity in culinary cuisine from different cultures have increased the popularity and consumption of culinary herbs and leafy greens (Behe et al., 2013; Simon, 1990; Yue et al., 2012). To meet this growing demand, the number of operations involved in greenhouse vegetable, fresh cut culinary herb and leafy green production in the U.S. more than doubled to 8,750 from 2007 to 2012 (USDA, 2014). This has resulted in a 59% increase in production area under glass or other protection (USDA, 2014). In the same time period, sales increased by more than $81 million (+16%) (USDA, 2014).

Fresh culinary herbs and leafy greens are valued for their overall visual quality, flavor, texture, and aroma, and used as garnish, while ornamental herbs are valued for their flowers or essential oils. Additionally, herbs such as lavender (*Lavendula* spp.), mint (*Mentha* spp.), basil (*Ocimum* spp.), coriander (*Coriandrum sativum*), marjoram (*Origanum majorana*), and oregano (*Origanum* spp.) have cosmetic and/or medicinal properties (Aburjai and Natsheh, 2003; Baratta et al., 1998; Cavanagh and Wilkinson, 2002). For example, lavender is used for its essential oils in soaps, lotions, and perfumes (Aburjai and Natsheh, 2003). Furthermore, lavender, mint, basil, coriander, and oregano are known to have antimicrobial and/or anti-inflammatory properties (Baratta et al., 1998; Cavanagh and Wilkinson, 2002). Depending on the market, flowers can be advantageous or undesirable. Flower initiation and development is often undesirable during fresh cut production of crops such as mint, coriander, watercress (*Nasturtium officinale*), and oregano. For instance, premature flowering is such a major issue in coriander that seed companies are now offering slow-to-bolt cultivars. Although these cultivars are less susceptible to premature flowering, none are completely unresponsive to temperature and long days (LD) (Simon, 1990). Additionally, consumers may not buy, and retailers may reject fresh cut herbs and leafy greens with flower buds or flowers. Studies have shown that the composition of essential oils changes with the onset of flowering, leading to potential changes in flavor, and thereby affecting their use as a culinary herb or leafy green (Skrubis and Markakis, 1976; Vazquez and Dunford, 2005). On the contrary, if herbs are grown for ornamental purposes or for essential oil production, then flower initiation and development may be desired, since an increase in the number of flowers and oil yield can increase profitability (Burbot and Loomis, 1957; Hassiotis et al., 2014).

Greenhouse growers of ornamental crops often delay or promote flowering by manipulating the natural photoperiod or temperature. Photoperiod refers to the number of light hours within a

24-h period, and acts as an environmental signal for bud dormancy and break, formation of storage organs, and flowering of some crops (Thomas and Vince-Prue, 1984). However, the length of the dark period (or skotoperiod) is the determining factor of the flowering response (Thomas and Vince-Prue, 1997). Plants can be categorized as having an LD, short-day (SD), or day-neutral (DN) flowering response to day length (Thomas and Vince-Prue, 1997). Long-day and SD plants (LDPs and SDPs) can be further classified as qualitative or obligate if a certain photoperiod is absolutely required for flowering, or quantitative or facultative if the photoperiod accelerates but is not required for flowering (Blanchard and Runkle, 2010).

The use of red (R) and far-red (FR) radiation at low intensities (1-2 $\mu mol \cdot m^{-2} \cdot s^{-1}$) can be applied at the end of the day [day-extension lighting (DE)], during the middle of the night [night-interruption light (NI)], or before dawn to promote flowering responses in LDPs or inhibit flowering of SDPs (Runkle et al., 2012; Whitman et al., 1998). Before the introduction of light-emitting diode (LED) lamps, incandescent (INC) lamps were the conventional choice for DE and NI lighting because they were inexpensive and emitted an effective mixture of R and FR radiation that promoted flowering of LDPs (Vince-Prue and Canham, 1983). Unfortunately, they were also highly energy-inefficient, had a short life span, and were subsequently phased out of production (Waide, 2010). Although more expensive, LED flowering lamps have a longer-life span, are more energy efficient and provide a similar R to FR ratio as INC lamps are an alternative for greenhouse growers (Mitchell et al., 2015; Owen et al., 2018).

The majority of photoperiodic studies on specialty crops have been conducted on ornamental greenhouse crops. However, Downs et al. (1958) conducted photoperiodic studies with dill (*Anethum graveolens*) and found that when R and FR radiation were used as DE lighting, flowering was accelerated. Subsequently, dill and peppermint have been classified as LDPs

(Burbott and Loomis, 1967; Thomas and Vince-Prue, 1997). Bleasdale (1964) conducted a study on watercress, where plants were placed under 9-, 13-, 16-, and 20-h day lengths. Flower bud initiation was hastened under a 20-h photoperiod compared to a 13-h photoperiod, and no plants formed visible buds (VBs) under a 9-h SD. Spanish lavender 'Chica Purple', 'Chica Rose', 'Coco Purple', and 'Coco Blue and White' (*Lavandula stoechas*) was classified as a facultative LDP that did not require vernalization (Whitman and Padhye, 2009). However, another study conducted on *Lavandula angustifolia* determined that an increase in the duration of vernalization increased flowering percentage. Furthermore, flowering percentage also increased with a 4-h NI, in comparison to a 9-h SD (Whitman et al., 1996). Although photoperiodic studies have been conducted on some common culinary and ornamental herbs and leafy greens, the critical photoperiod of new cultivars and many other genera have not yet been determined. Therefore, the objectives of this study were 1) to determine how photoperiod influences flowering development parameters of economically important culinary and ornamental herbs and leafy greens and 2) to determine the critical photoperiod of those crops that flower in response to photoperiod.

Materials and methods

Plant material

Cuttings of spearmint 'Spanish' (*M. spicata*) were placed in 72-cell trays filled with a propagation substrate composed of (v/v) 50% perlite (Horticultural Perlite; Perlite Vermiculite Packaging, North Bloomfield, OH) and 50% soilless medium containing 70% peat moss, 21% perlite, and 9% vermiculite (Suremix; Michigan Grower Products, Inc., Galesburg, MI) on 25 Jan. 2018 and 17 Dec. 2018. The trays were then placed in a glass-glazed greenhouse under a 16-

h photoperiod with air and substrate temperature set points of 21 °C and 27 °C, respectively. After 14 d, rooted cuttings were transplanted into round 15-cm diameter (1,300-mL) containers filled with a soilless medium (Suremix; Michigan Grower Products Inc., Galesburg, MI) and then placed under their respective photoperiodic treatments. Seven days later, shoot tips were pinched, leaving 3 nodes per plant.

On 08 Feb. 2018 and 07 Jan. 2019, seeds of coriander ‘Santo’, oregano ‘Greek’ (*O. vulgare hirtum*), dill ‘Bouquet’, watercress, and marjoram were sown into 128-cell (12.0-mL) plug trays. Cells were filled with a seed sowing mix composed of 50% vermiculite (Vermiculite Premium Grade; Sungro Horticulture, Agawam, MA) and 50% of the soilless medium (Suremix; Michigan Grower Products Inc., Galesburg, MI) previously mentioned. Each tray was placed onto capillary mats in their respective treatments. After germination, seedlings were thinned to one plant per cell.

On 08 Mar. 2018 and 04 Feb. 2019 dill and watercress were transplanted into 11-cm round (600-mL) containers and subsequently transplanted into 15-cm round (1,300-mL) containers on 20 Apr. 2018 and 19 Mar. 2019. Coriander, oregano ‘Greek’, and marjoram were transplanted into 11-cm round containers on 09 Mar. 2018 and 05 Feb. 2019. Because of low germination rates in Rep. 1, cuttings of oregano ‘Greek’ were taken on 02 Feb. 2019 from pre-established stock plants of the same cultivar. The same environmental parameters and methods utilized for spearmint were utilized to root oregano ‘Greek’ cuttings.

Plugs of oregano ‘Kirigami’ (*O. rotundifolium*) and lavender ‘Bandera Pink’ (*L. stoechas*) obtained from a young plant propagator (Raker-Roberta's Young Plants, Litchfield, MI) were transplanted on 09 Mar. 2018 and on 05 Jan. 2019 into 11-cm containers. Lavender plants had the apical meristem excised 7 d after transplant, to 4 nodes per plant.

Plants were top irrigated with reverse osmosis water supplemented with water-soluble fertilizer ($mg \cdot L^{-1}$) 60 nitrogen (N), 23 phosphorus (P), 60 potassium (K), 28 calcium (Ca), 5 magnesium (Mg), 1 iron (Fe), 0.6 manganese (Mn), 0.6 zinc (Zn), 0.6 copper (Cu), 0.4 boron (B), and 0.1 molybdenum (Mo) (MSU Plug Special; Blackmore Company, Kankakee, IL) during the seedling stage and after transplant with reverse osmosis water supplemented with 14N-3P-14K water-soluble fertilizer ($mg \cdot L^{-1}$) 125 N, 12 P, 100 K, 65 Ca, 12 Mg, 1.0 Fe and Cu, 0.5 Mn and Zn, 0.3 B, and 0.1 Mo (MSU Orchid RO Water Special; Blackmore Company).

Greenhouse environment and lighting treatments

Plants were grown in a glass-glazed greenhouse at Michigan State University (East Lansing, MI; lat. 42º N) with exhaust fans, evaporative-pad cooling, radiant hot-water heating, and supplemental lighting controlled by an environmental control system (Priva Office version 725-3030; Priva North America, Vineland Station, ON, Canada). The greenhouse air temperature set point was a constant 20 °C. An aspirated thermocouple [36-gauge (0.127-mm diameter) type E] located in the middle of each bench measured the air temperature at plant height every 10 s, and a data logger (CR1000; Campbell Scientific, Logan, UT) recorded hourly means. The data logger controlled a 1500-W electric heater underneath each bench to provide supplement heat when the nighttime temperature was <18.9 °C. The air average daily temperature (ADT) (±SD) for the greenhouse during the duration of the study was 20.8 ± 3.5 °C for replication (Rep.) 1 and 19.6 ± 2.9 °C for Rep. 2 (data not provided). The actual bench ADT at plant height of each treatment during the two Reps. of the experiment is provided in Table 1.

Supplemental lighting provided by R+white (W) LEDs (Philips GP-TOPlight DRW-MB; Koninklijke Philips N.V., Eindhoven, the Netherlands) delivered a supplemental photosynthetic photon flux density (*PPFD*) of 90 ± 14 $\mu mol \cdot m^{-2} \cdot s^{-1}$ between 0800 and 1700 HR when the outdoor light intensity was below ≈440 $\mu mol \cdot m^{-2} \cdot s^{-1}$. On each bench, a line quantum sensor (LI-191R, LI-COR, Lincoln, NE) or a quantum sensor (LI-190R, LI-COR, Lincoln, NE) positioned horizontally at plant height measured *PPFD* every 10 s and a datalogger recorded hourly averages. The daily light integral (DLI) of each treatment during the two Reps. of the experiment were calculated and are provided in Table 1.

Each day, opaque black cloths were pulled over each bench at 1700 HR and opened at 0800 HR to create a truncated 9-h SD. Treatments consisted of the 9-h SD, or a 9-h day extended by four R+W+FR LED lamps (GreenPower LED flowering DR/W/FR 14 W, E26; Philips, Eindhoven, The Netherlands) beginning at 1700 HR to create 12-, 13-, 14-, or 16-h photoperiods or a 4-hour NI (from 2200 to 0200 HR). Each LED fixture was covered with multiple layers of aluminum wire mesh to achieve a total photon flux density (*TPFD*) of ≈2 $\mu mol \cdot m^{-2} \cdot s^{-1}$. The spectral distribution of the LED lamps was measured in five random locations throughout each bench with a spectroradiometer (PS-200; Stellar-Net, Tampa, FL), and the phytochrome photoequilibrium was estimated according to Sager et al.1988 (Fig. 1).

Data collection and analysis

All plants were monitored daily and the date of first VB and first open flower (OF) were recorded for all plants under each treatment. Plants that did not flower after 20 weeks were considered non-flowering. The number of nodes below the first OF, and plant height (from the media surface to the plant apical meristem) were recorded at first OF.

The experiment was a randomized complete block design. The two Reps. were performed over time and considered the blocking factor in the experiment. The six photoperiodic treatments were the single factor in the experiment. Eight or 10 plants (sub-units) of spearmint and all other plant species, respectively, were randomly assigned to each treatment. Data were separately analyzed for each species and the interactions between species were not evaluated. Data were analyzed with the SAS version 9.4 (SAS Institute, Inc., Cary, NC) mixed-model (PROC GLIMMIX) procedure and pairwise comparisons between treatments were performed with adjusted Tukey-Kramer difference test ($P \leq 0.05$). Data were pooled when there was no interaction between Rep. and treatment, or if the response trends were similar between replications. Statistics were not included for spearmint and oregano 'Greek' because of variability between experimental replications.

Results

Flowering percentage

The percentage of coriander and dill that flowered ranged from 95 to 100% for all treatments (Fig. 2A and B). Flowering percentage for all other species generally increased with increasing day lengths (Fig. 2C-H). For example, flowering percentage of lavender was 0, 40, 40, 90, 100, and 100 under a 9-, 12-, 13-, 14-, and 16-h photoperiod or a 4-h NI, respectively (Fig. 2C). The flowering percentage of watercress was 25, 80, and 90% under 14 and 16-h photoperiods and NI lighting, respectively (Fig. 2F). For marjoram, apart from the 9-h SD, there was an increase in flowering percentage from 12 to 16 h and the NI treatment (Fig. 2D). For oregano 'Kirigami' the percentage of plants that flowered was 53, 100, 100, and 100 under 13-, 14-, and 16-h photoperiods and a 4-h NI, respectively (Fig. 2E). During Rep. 1 flowering percentage of oregano 'Greek' was 40% and only flowered under the 16-h photoperiod, during Rep. 2 flowering percentage was 50% and only flowered under NI lighting (Fig. 2G and 4G). Spearmint flowering percentage was 100% under the 16 h and NI treatments during Rep. 1, but did not flower under any treatment during Rep. 2 (Fig. 2H and 4H).

Time to first visible bud

Generally, time to first VB occurred most rapidly under photoperiods ≥13 h compared to 9 h for coriander, dill, lavender, marjoram, and watercress (Fig. 3A-D, and F). As day length increased, time to first VB for coriander, dill, and lavender decreased, but not for marjoram (Fig. 3D). For marjoram, time to first VB increased from 95 to 107 d as the day length increased from 9 to 12 h, but then progressively decreased to 80 d as the photoperiod increased to 16 h (Fig. 3D). For coriander, dill, and lavender, time to first VB was hastened by 7, 6, and 36 d, respectively, under a 16-h LD compared to a 9-h SD (Fig. 3A, B, and C). For watercress, no VBs formed under day lengths <14 h. Additionally, VBs appeared 10 and 11 d earlier when watercress was grown under a 16-h LD or 4-h NI, respectively, compared to a 14-h photoperiod (Fig. 3F). Only data for Rep. 2 is presented for oregano 'Kirigami' as missing data prevented us from including Rep. 1. Photoperiod influenced time to first VB for oregano 'Kirigami (Fig. 3E). For oregano 'Greek', time to first VB was 3 d faster under the NI treatment for Rep. 2 when compared to the 16-h treatment in Rep. 1 (Fig. 3G). For spearmint, time to VB was hastened by 4 d under the 16-h LD in comparison to the NI treatment for Rep. 1 (Fig. 3H).

Time to first open flower

Time to first OF of coriander decreased as day length increased, with a 6-d difference between plants under 16-h and 9-h photoperiods (Fig. 4A). Under a 16-h photoperiod, dill and marjoram flowered 7 and 13 d faster than under a 9-h SD, respectively (Fig. 4B and D). Lavender followed the same general trend, but plants did not flower when grown under a 9-h SD (Fig. 4C). As photoperiod increased from 13 to 16 h, time to first OF of oregano 'Kirigami' decreased from 62 to 45 d (Fig. 4E) Time to first OF was not significantly different for coriander, dill, lavender, marjoram, oregano 'Kirigami', and watercress grown under a 16-h photoperiod or NI lighting (Fig. 4A-F). Watercress did not flower under 9-, 12-, or 13-h photoperiods and no significant difference for time to first OF were observed for plants grown under the 14, 16 h or NI treatments (Fig. 4F). Although all species flowered faster under LDs, watercress, oregano ‘Greek’, and spearmint only flowered under photoperiods ≥14-h long (Fig. 4F, G, and H). Nevertheless, as previously mentioned, both oregano ‘Greek’ and spearmint had inconsistent flowering during Reps. 1 and 2.

Node number below the first open flower

At flowering, coriander, dill, and marjoram had the greatest number of nodes below the first OF when grown under a 9-h SD and node number generally decreased with increasing day length (Fig. 5A, B, D). For instance, dill grown under a 9-h photoperiod had two more nodes than plants grown under 13-, 14-, 16-h and NI treatments (Fig. 5B). Marjoram grown under a 9-, 12-, 13-, 14-, or 16-h photoperiod or under NI lighting averaged 21, 20, 19, 17, 15, and 14 nodes, respectively (Fig. 5D). For lavender, no plants flowered under a 9-h SD; from 12 to 16 h or under a NI, node number decreased by 1 to 5 nodes (Fig. 5C). Watercress did not flower under 9-, 12-, or 13-h photoperiods and there was no significant difference in node number for plants under 14- or 16-h photoperiods, or under NI lighting (Fig. 5F).

Stem length at first open flower

Stem length at flowering of 9-h grown coriander and dill was 24.4 (25%) to 32.2 cm (31%) and 23.1 (17%) to 32.9 cm (23%) shorter compared to all the other treatments, respectively. (Fig. 6A and B). Stem length of 16 h and NI grown oregano ‘Kirigami’ was significantly shorter in comparison to 13-h grown plants (Fig. 6E). Lavender and watercress stem length was not affected by photoperiod (Fig. 6C and F).

Discussion

Phytochrome are photoreversible pigments found in all higher plants used to detect radiation, with peak absorbance in the R (600 to 700 nm) and FR (700 to 800 nm) radiation wavebands, and to a lesser extent in the blue [B (400 to 500 nm) waveband (Sager et al., 1988; Smith, 1983). They exist as two interconvertible forms, an active biological form (P_{FR}) and an inactive form (P_R) (Hendricks et al., 1962, Sager et al., 1988). When the R:FR is low it exists as the P_R form, and shade avoidance responses, such as stem elongation and leaf expansion occur. When the R:FR is high, P_R is converted to P_{FR} culminating in altered expression of phytochrome-responsive genes resulting in a flowering response in LDPs (Hendricks et al., 1962; Hendricks and Borthwick, 1967; Mancinelli et al., 2007).

Depending on the radiation quality provided, P_{FR} and P_R reach an equilibrium, which is referred to as the phytochrome photostationary state (PSS) or phytochrome photoequilibrium [PPE (P_{FR}/P_{Total}, where $P_{Total} = P_R + P_{FR}$)] (Sager et al., 1988). A PPE of 0.10-0.50 creates a low R:FR (high FR spectrum), while a high PPE of 0.75-0.89 creates a high R:FR (high R spectrum). A PPE between 0.60-0.75 is considered an intermediate PPE (Sager and Mc Farlane, 1997). Incandescent lamps emit a low R:FR, which creates an intermediate PPE. The LED lamps employed in our study had a PPE of 0.66, thereby providing an intermediate PPE that promoted flowering of the LD culinary and ornamental herbs and leafy greens evaluated. Craig and Runkle (2016) reported similar findings; as snapdragon 'Liberty Classic Cherry' (*Antirrhimun majus*) and three cultivars of petunia 'Shock Wave Ivory', 'Easy Wave White', and 'Wave Purple Improved' (*Petunia* × *hybrida*) flowered fastest under NI lighting provided by INC or LED lamps with a PPE of 0.64 or 0.63, respectively (intermediate PPE).

Excessive stem elongation and suppressed lateral branching can be a major drawback of utilizing FR radiation, since stem breakage and undesirable phenotypic traits can occur (Bleasdale, 1964; Moe and Heins, 1990; Whitman et al., 1998). For example, Torres and Lopez (2011), reported that stem elongation of the LDP *Tecoma stans* 'Mayan Gold' increased by 38% when photoperiod was extended to 12 or 16 h under INC lamps providing a *TPFD* of ≈2 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Whitman et al. (1998) found that *Campanula carpatica* 'Blue Clips' and *Coreopsis grandiflora* 'Early Sunrise' were both taller when grown under INC lamps in comparison to cool-white fluorescent (CWF), metal halide (MH), or high-pressure sodium (HPS) lamps providing 7-h DE lighting. Additionally, Kohyama et al. (2014) compared growth and development of dianthus 'Super Parfait Strawberry' (*Dianthus chinensis*) under a 9-h SD and NI lighting utilizing INC lamps or LED lamps emitting R+W radiation with or without FR radiation. They reported that plants grown under INC or R+W+FR radiation were ≈24 to 33% taller than those grown under SD or R+W LEDs (without FR radiation). Photoperiods >9 h increased stem length for coriander and dill. For instance, stem length of coriander and dill was 32.2 and 27.4 cm greater, respectively, for plants grown under a 16-h LD in comparison to a 9-h SD (Fig. 6A, and B). The increase in stem length is directly associated to the increased duration of exposure to FR radiation under the 16-h LD. Conversely, stem elongation may not always be associated with low R:FR for certain species. For example, Whitman et al. (1998) reported that stem of *Coreopsis verticillata* 'Moonbeam' grown under INC or HPS lamps were significantly shorter than those grown under CWF and MH lamps.

Time to VB was generally comparable to time to first OF for all species evaluated (Fig. 3A-H, and 4A-H). Visible bud formation and subsequent flowering of coriander, dill, and marjoram was generally hastened under ≥13 h photoperiods (Fig. 3A, B, and D, 4A, B, and D). Watercress, oregano 'Greek', and spearmint only produced VBs and flowers under LDs ≥14 h or a NI (Fig. 3F-H and 4F-H). Although oregano 'Kirigami' flowered under 13 h, flowering percentage was incomplete compared to ≥14 h or a NI, under which flowering was 100% (Fig. 2E). Thus, oregano 'Kirigami' requires ≥14 h or an NI for uniform flowering. Our results for watercress are similar to those previously mentioned by Bleasdale (1964), who reported VB formation was hastened under 20-h LDs versus shorter photoperiods. Similarly, VBs were not observed under a 9-h SD in either study. However, they reported that watercress produced VBs when grown under a 13-h photoperiod achieved with INC lamps, whereas in the current study, VBs and OFs did not initiate under 9 to 13-h photoperiods created with LEDs (Fig. 3F and 4F). Our lavender flowering data is in agreement to an industry report by Whitman and Padhye (2009), who classified Spanish lavender as a facultative LDP. Although plants produced VBs under a 9-h SD in our study, no OFs were observed and furthermore time to VB and OF decreased with increasing day length or a 4-h NI (Fig. 3C and 4C).

Although there were inconsistencies between Reps. related to flowering for oregano 'Greek' and spearmint, VBs and OFs only developed under either a 16-h or NI treatment (Fig. 3G-H and 4G-H). Langston and Leopold (1954) suggested that peppermint (*M. piperita* var. *vulgaris*) is an LDP, with a critical day length of 16 or 18 h required for floral differentiation and development. This contrasts with Burbott and Loomis (1957) who reported that peppermint (*M. piperita* var. Black Mitcham) flowered under a 14-h photoperiod created from a combination of fluorescent and INC lamps. Furthermore, Allard (1941) conducted DE photoperiodic studies utilizing natural sunlight or INC lamps for 18 h to evaluate multiple *Mentha* species. Spearmint (*M. spicata*) remained vegetative under 10 h but did flower when exposed to a 12-h photoperiod, whereas peppermint (*M. piperita*) produced few flowers when grown under a 14-h day length.

After 120 d, only 40 and 50% of oregano ‘Greek’ flowered under a 16-h photoperiod (Rep. 1) or a 4-h NI (Rep. 2), respectively (Fig. 2G). These inconsistent flowering responses between Reps. may have been influenced by the methods of propagation employed between Rep. 1 and 2. In Rep. 1, germination was low and seedling growth was slow. Therefore, we harvested cuttings in Rep. 2 from our stock plants that were maintained under a 9-h SD. Nevertheless, further studies are required to evaluate the length of the juvenile phase, temperature, and initial establishment (seed vs. cuttings) and their effect on flower development of LDPs.

Similar to other studies, we have shown that a 4-h NI can be as effective at promoting flowering of LDPs to DE lighting providing a 16-h photoperiod. Under a 4-h NI, flowering percentage was 100 and statistically occurred at the same time as plants under the 16-h photoperiod for coriander, dill, lavender, marjoram, oregano ‘Kirigami’, and spearmint (Fig. 2A-E, H, 4A-E, H). Runkle and Heins (2003) found similar results for pansy ‘Crystal Bowl Yellow’ (*Viola ×wittrockiana*), where flowering percentage was similar under DE (16-h photoperiod) and NI lighting created by INC lamps.

In conclusion, coriander ‘Santo’, dill ‘Bouquet’, lavender ‘Bandera Pink’, and marjoram can be considered facultative LDPs because time to VB and OF were generally hastened under LDs (≥13 h) or an NI, in comparison to a 9-h SD (Fig. 3A-D, 4A-D). Furthermore, node number below the first OF for coriander, dill, lavender, and marjoram decreased as photoperiod increased from 9 to 16 h or under an NI (Fig. 5A-D). Also, flowering percentage of lavender, marjoram, oregano ‘Kirigami’, and watercress increased from 9 to 16 h or under an NI (Fig. 2C-F). From our study oregano ‘Kirigami’, watercress, oregano ‘Greek’, and spearmint ‘Spanish’ can be classified as obligate LDPs, requiring ≥14-h for flowering to occur (Fig. 4E-H). Additionally, the critical photoperiod of watercress, oregano ‘Kirigami’, oregano ‘Greek’ and spearmint ‘Spanish’ is 14, 13, 16, and 16 h, respectively. Although time to VB and OF of oregano ‘Greek’ and spearmint was inconsistent between Reps., both species exhibited obligate LDP responses, requiring either 16 h or an NI to form buds and subsequently flower (Fig. 3G, H, 4G, and H). Results from this study can prove beneficial to growers who seek to prevent or delay flowering of herbs, while also providing valuable information for the promotion of flowering of ornamental crops such as lavender or oregano ‘Kirigami’.

Acknowledgements

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APPENDIX

Table II-1. Photoperiod (h), mean (±SD) bench average daily temperature (ADT), and daily light integral (DLI) (±SD) during two experimental replications (Rep.) for culinary and ornamental herbs and leafy greens. Plants were grown under a truncated 9-h short day (SD) or under a 9-h SD extended with red+white+far-red (R+W+FR) light-emitting diode (LED) lamps to achieve 12-, 13-, 14-, and 16-h photoperiods or a 4-h night interruption (NI).

Photoperiod (h)	Rep. 1 bench ADT [mean ± SD (ºC)]	Rep. 2 bench ADT [mean ± SD (ºC)]	Rep. 1 DLI ($mol \cdot m^{-2} \cdot d^{-1}$)	Rep. 2 DLI ($mol \cdot m^{-2} \cdot d^{-1}$)
9	20.6 ± 2.3	20.9 ± 2.0	-[z]	-[z]
12	20.7 ± 2.3	20.5 ± 2.4	10.7 ± 4.6	9.1 ± 4.3
13	20.4 ± 2.1	20.7 ± 1.9	10.8 ± 4.5	10.5 ± 4.9
14	20.8 ± 2.5	20.7 ± 1.9	10.2 ± 4.8	10.0 ± 4.5
16	20.5 ± 2.3	21.0 ± 2.0	9.7 ± 5.6	9.4 ± 4.4
NI	20.9 ± 2.5	20.3 ± 2.5	9.1 ± 4.3	9.9 ± 4.6

[z] No data collected

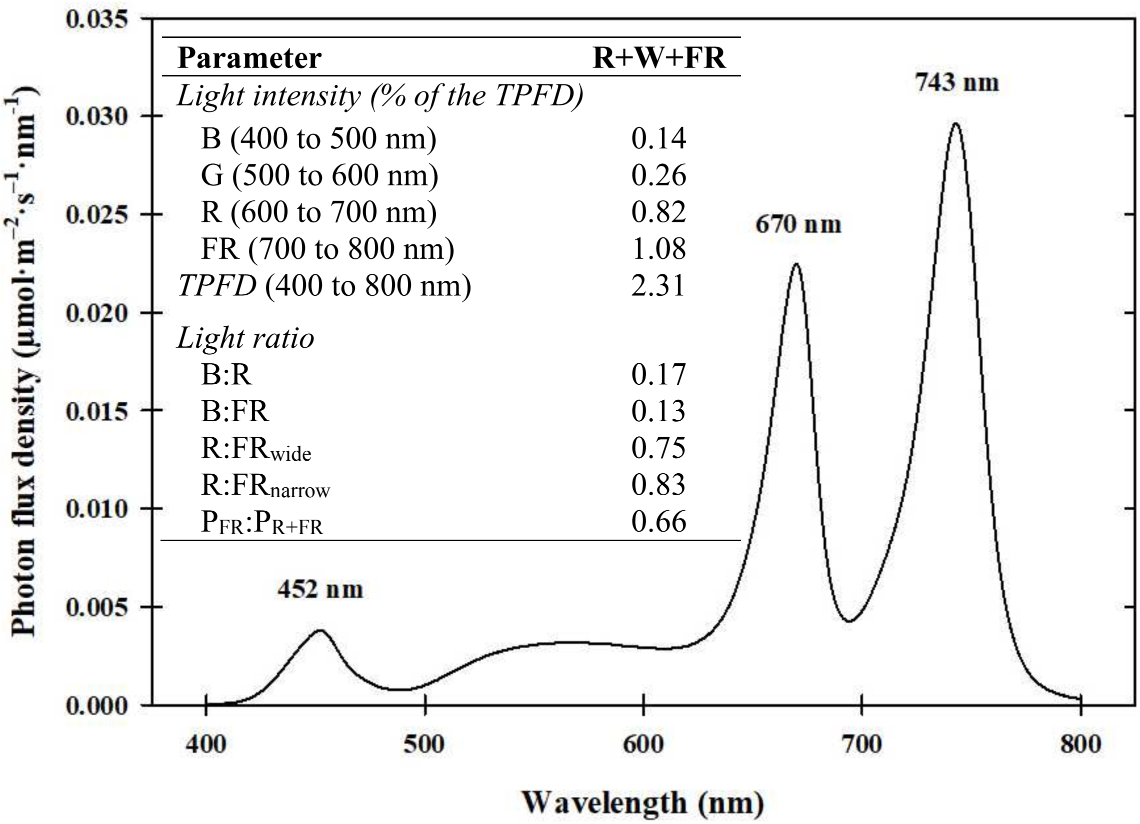

Figure II-1. Spectral distribution, intensity of blue [B (400–500 nm)], green [G (500–600 nm)], red [R (600–700 nm)], and far-red [FR (700–800 nm)] radiation, total photon flux density (*TPFD*), light ratio, and estimated phytochrome photoequilibria [P_{FR}/P_{R+FR} (the proportion of FR-absorbing phytochromes in the pool of R- and FR-absorbing phytochromes; Sager et al., 1988)] of R+W+FR light-emitting diode (LED) lamps covered with multiple layers of wire mesh. $R:FR_{wide}$ was calculated as 600 to 700 nm:700 to 800 nm; $R:FR_{narrow}$ was calculated as 655 to 665 nm:725 to 735 nm.

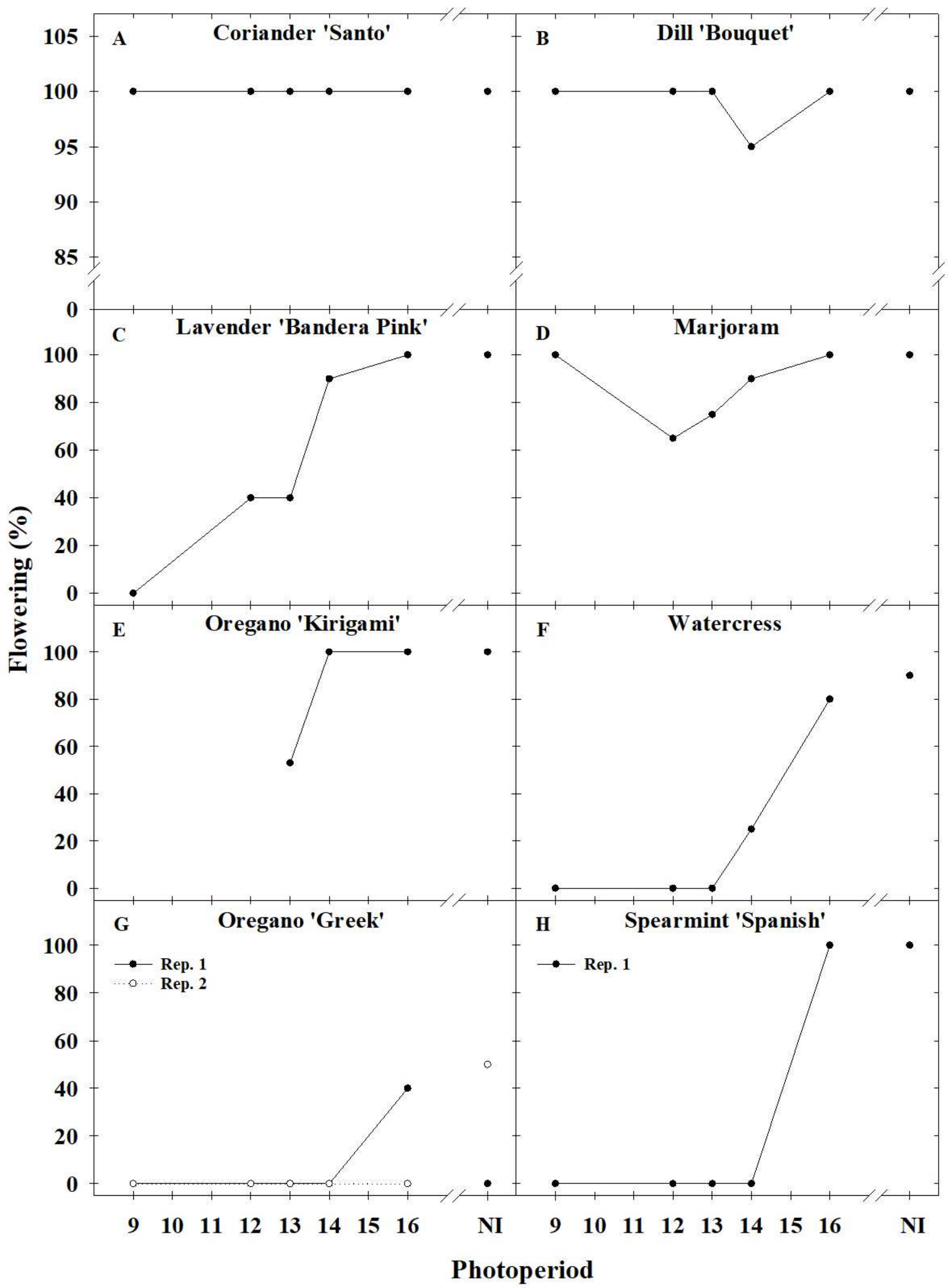

Figure II-2. Flowering percentage for eight herbs and leafy greens grown under a truncated 9-h short day (SD) or under a 9-h SD extended with red+white+far-red (R+W+FR) light-emitting diode (LED) lamps to achieve 12-, 13-, 14-, and 16-h photoperiods or a 4-h night interruption (NI). Flowering percentage of oregano ‘Greek’ and spearmint ‘Spanish’ are presented by replication (Rep.) due to variability between experimental Reps.

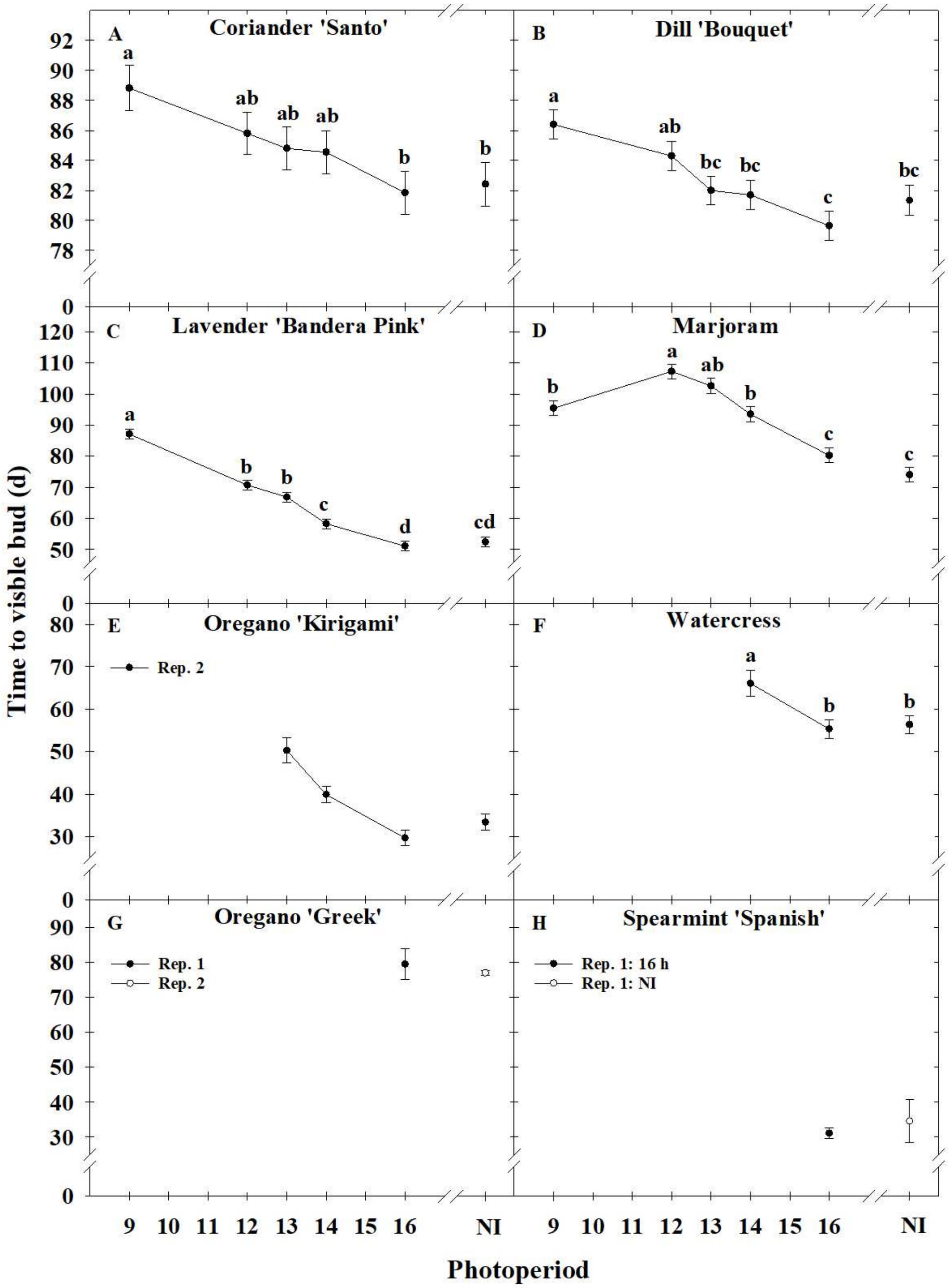

Figure II-3. Time to first visible bud (VB) for eight herbs and leafy greens grown under a truncated 9-h short day (SD) or under a 9-h SD extended with red+white+far-red (R+W+FR) light-emitting diode (LED) lamps to achieve 12-, 13-, 14-, and 16-h photoperiods or a 4-h night interruption (NI). Data were pooled when there was no interaction between replication (Rep.) and treatment, or if the response trends were similar between Reps. Letters indicate mean separations across photoperiodic treatments using Tukey-Kramer difference test at $P \leq 0.05$. Error bars indicate standard error. Mean separations were excluded due to variability between experimental Reps. for oregano ‘Kirigami’, oregano ‘Greek’ and spearmint ‘Spanish’.

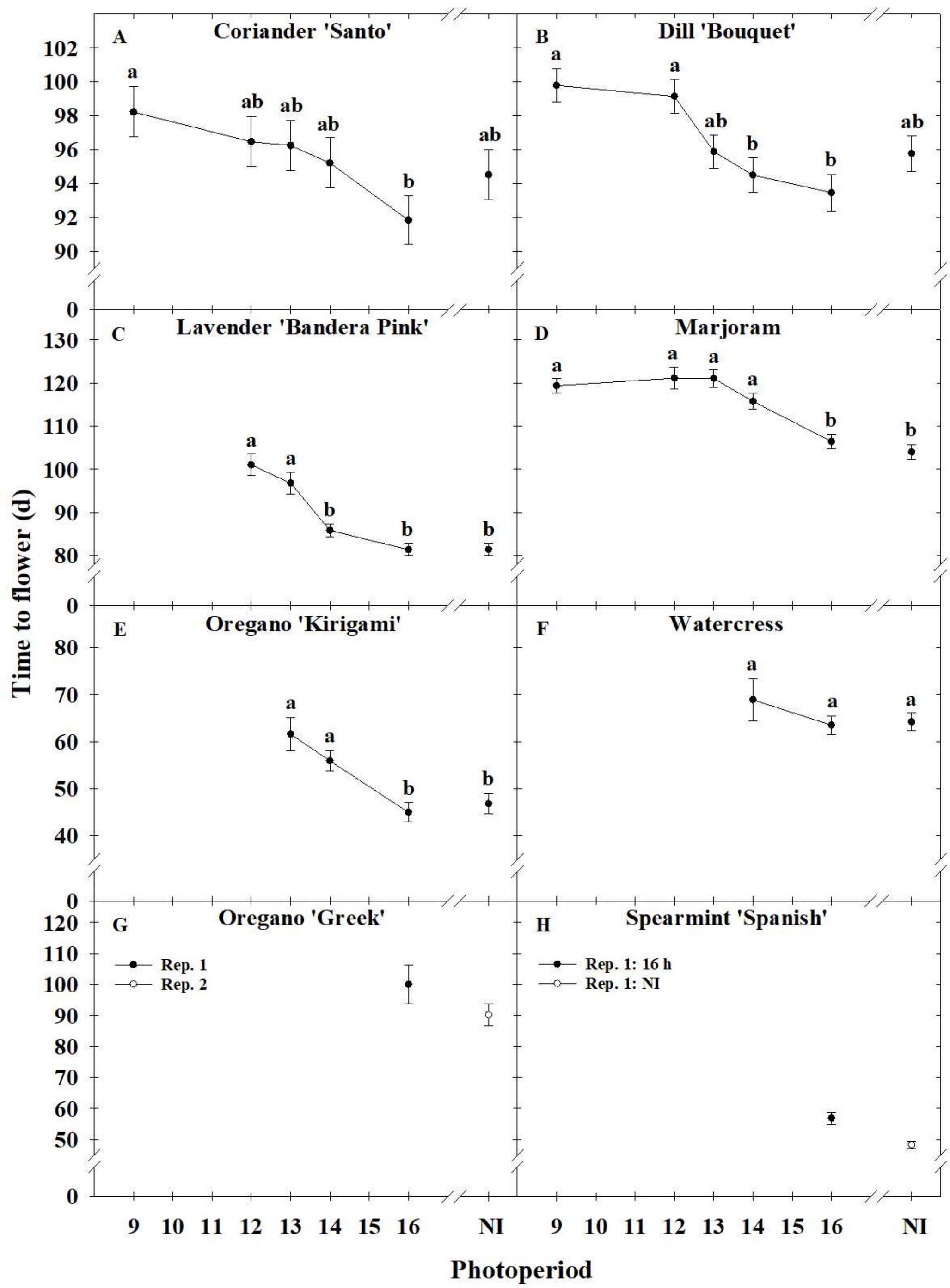

Figure II-4. Time to first open flower (OF) for eight herbs and leafy greens grown under a truncated 9-h short day (SD) or under a 9-h SD extended with red+white+far-red (R+W+FR) light-emitting diode (LED) lamps to achieve 12-, 13-, 14-, and 16-h photoperiods or a 4-h night interruption (NI). Data were pooled when there was no interaction between replication (Rep.) and treatment, or if the response trends were similar between Reps. Letters indicate mean separations across treatments using Tukey-Kramer difference test at $P \leq 0.05$. Error bars indicate standard error. Mean separations were excluded due to variability between experimental Reps. for oregano ‘Greek’ and spearmint ‘Spanish’.

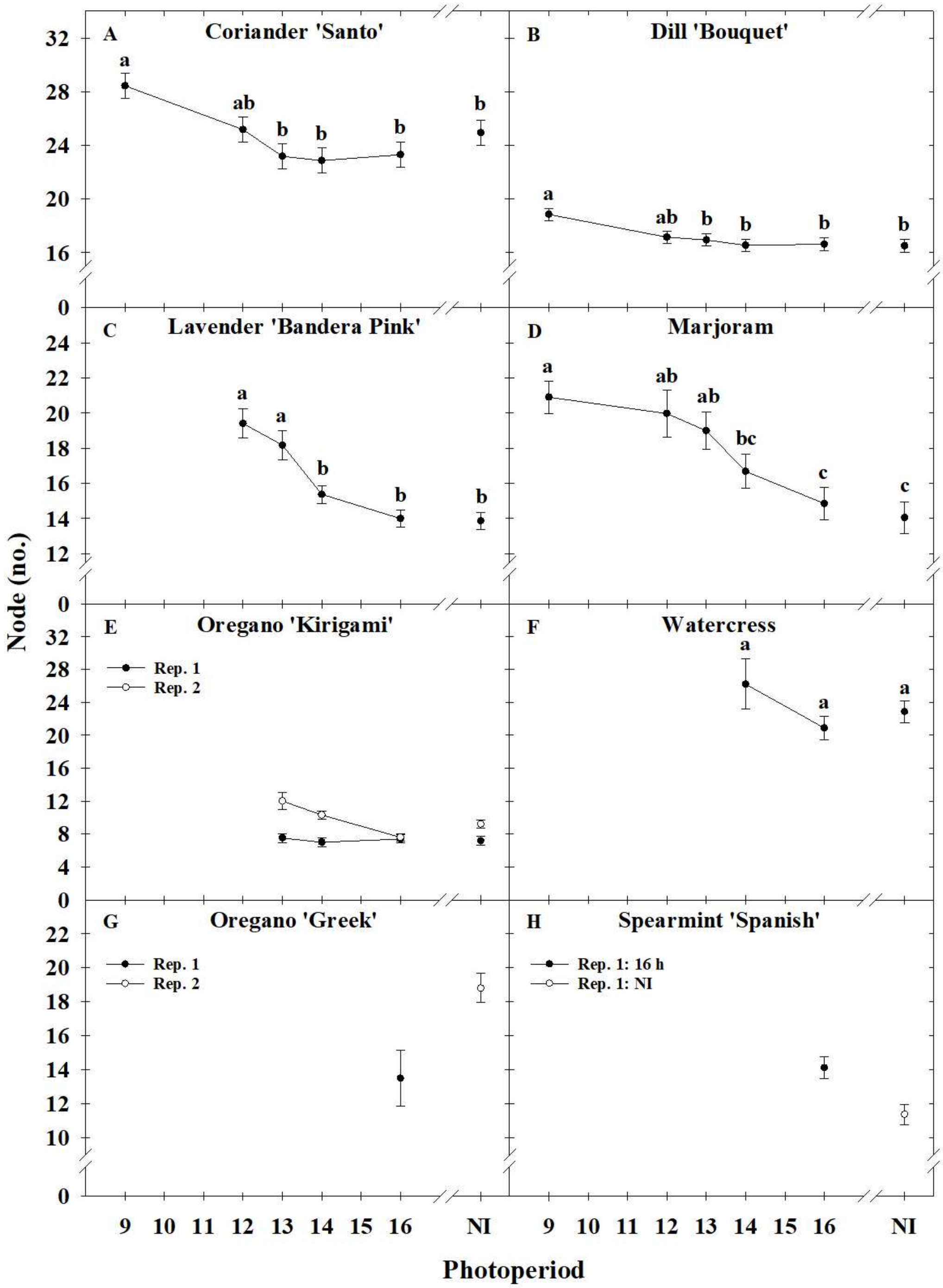

Figure II-5. Node number for eight herbs and leafy greens grown under a truncated 9-h short day (SD) or under a 9-h SD extended with red+white+far-red (R+W+FR) light-emitting diode (LED) lamps to achieve 12-, 13-, 14-, and 16-h photoperiods or a 4-h night interruption (NI). Data were pooled when there was no interaction between replication (Rep.) and treatment, or if the response trends were similar between Reps. Letters indicate mean separations across photoperiodic treatments using Tukey-Kramer difference test at $P \leq 0.05$. Error bars indicate standard error. Mean separations were excluded when there were interactions or due to variability between experimental Reps. for oregano ‘Kirigami’, oregano ‘Greek’ and spearmint ‘Spanish’.

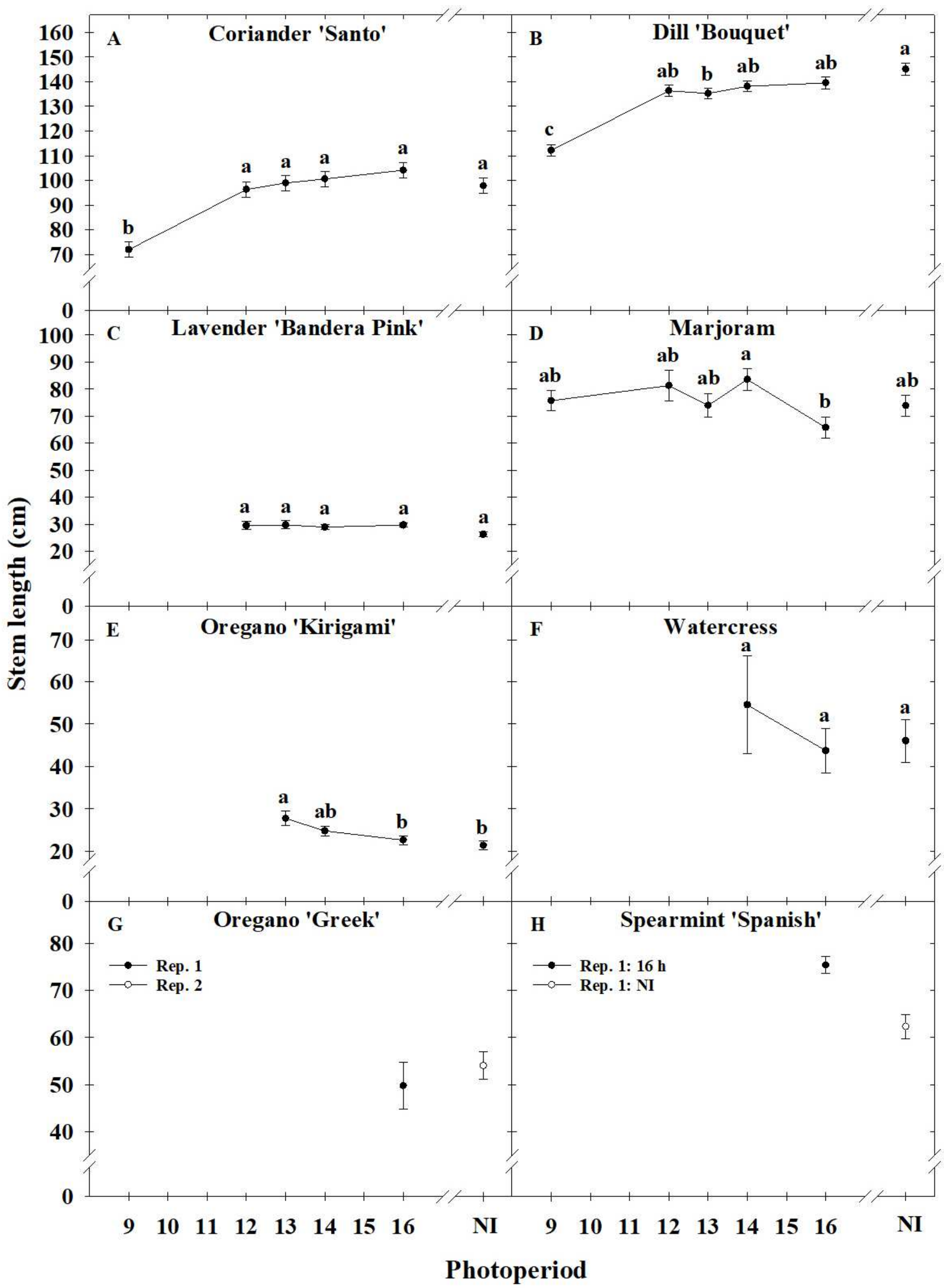

Figure II-6. Stem length at first open flower (OF) of eight herbs and leafy greens grown under a truncated 9-h short day (SD) or under a 9-h SD extended with red+white+far-red (R+W+FR) light-emitting diode (LED) lamps to achieve 12-, 13-, 14-, and 16-h photoperiods or a 4-h night interruption (NI). Data were pooled when there was no interaction between replication (Rep.) and treatment, or if the response trends were similar between Reps. Letters indicate mean separations across photoperiodic treatments using Tukey-Kramer difference test at $P \leq 0.05$. Error bars indicate standard error. Mean separations were excluded due to variability between experimental Reps. for oregano ‘Greek’ and spearmint ‘Spanish’.

LITERATURE CITED

LITERATURE CITED

Aburjai, T. and F.M. Natsheh. 2003. Plants used in cosmetics. Phytotherapy Res. 17:987–1000.

Allard, H.A. 1941. Further studies of the photoperiodic behavior of some mints (Labiatae). J. Agr. Res. 63:55–64.

Baratta, M.T., H.J.D. Dorman, S.G. Deans, D.M. Biondi, and G. Ruberto. 1998. Chemical composition, antimicrobial and antioxidative activity of laurel, sage, rosemary, oregano and coriander essential oils. J. Essent. Oil Res. 10:618–627.

Behe, B.K., B.L. Campbell, C.R. Hall, H. Khachatryan, J.H. Dennis, and C. Yue. 2013. Consumer preferences for local and sustainable plant production characteristics. HortScience 48:200–208.

Biggs, R.H. and A.C. Leopold. 1955. The effects of temperature on peppermint. Proc. Am. Soc. Hort. Sci. 66:315–321.

Blanchard, M.G. and E.S. Runkle. 2010. Intermittent light from a rotating high-pressure sodium lamp promotes flowering of long-day plants. HortScience 45:236–241.

Bleasdale, J.K.A. 1964. The Flowering and growth of watercress (*Nasturtium Officinale* R. BR.). J. Hort. Sci. 39:277–283.

Burbott, A.J. and W.D. Loomis. 1967. Effects of light and temperature on the monoterpenes of peppermint. Plant Physiol. 42:20–28.

Cavanagh, H.M.A. and J.M. Wilkinson. 2002. Biological activities of lavender essential oil. Phytotherapy Res. 16:301–308.

Craig, D.S. and E.S. Runkle. 2016. An intermediate phytochrome photoequilibria from night-interruption lighting optimally promotes flowering of several long-day plants. Environ. Expt. Bot. 121:132–138.

Downs, R.J., Borthwick, H.A., and A.A. Piringer.1958. Comparison of incandescent and fluorescent lamps for lengthening photoperiods. Proc. Am. Soc. Hort. Sci. 71:568–578.

Hassiotis, C.N., F. Ntana, D.M. Lazari, S. Poulios, and K.E. Vlachonasios. 2014. Environmental and developmental factors affect essential oil production and quality of *Lavandula angustifolia* during flowering period. Ind. Crops Prod. 62:359–366.

Hendricks, S.B. and H.A. Borthwick. 1967. The function of phytochrome in regulation of plant growth. Proc. Natl. Acad. Sci. 58:2125–2130.

Hendricks, S.B., W.L. Butler, and H.W. Siegelman. 1962. A reversible photoreaction regulating plant growth. J. Phys. Chem. 66:2550–2555.

Kohyama, F., C. Whitman, and E.S. Runkle. 2014. Comparing flowering responses of long-day plants under incandescent and two commercial light-emitting diode lamps. HortTechnology 24:490–495.

Langston, R. and A.C. Leopold. 1954. Photoperiodic responses of peppermint. Proc. Am. Soc. Hort. Sci. 63:347–352.

Mancinelli, A.L., H.A. Borthwick, and S.B. Hendricks. 2007. Phytochrome action in tomato-seed germination. Bot. Gaz. 127:1–5.

Mitchell, C.A., M.P. Dzakovich, C. Gomez, R. Lopez, J.F. Burr, R. Hernandez, C. Kubota, C.J. Currey, Q. Meng, E.S. Runkle, and C.M. Bourget. 2015. Light-emitting diodes in horticulture. Hort. Rev. 43. pp. 1–87.

Moe, R. and R.D. Heins. 1990. Control of plant morphogenesis and flowering by light quality and temperature. Acta Hort. 272:81–89.

Owen, W.G., Q. Meng, and R.G. Lopez. 2018. Promotion of flowering from far-red radiation depends on the photosynthetic daily light integral. HortScience 53:465–471.

Runkle, E.S. and R.D. Heins. 2003. Photocontrol of flowering and extension growth in the long-day plant pansy. J. Amer. Hort. Sci. 128:479–485.

Runkle, E.S., S.R. Padhye, W. Oh, K. Getter. 2012. Replacing incandescent lamps with compact fluorescent lamps may delay flowering. Scientia Hort. 143:56–61.

Sager, J.C. and C. Mc Farlane. 1997. Radiation. In plant growth chamber handbook, R.W. Langhans, and T.W. Tibbitts, eds. (Iowa: North Central Regional Research Publication).

Sager, J.C., W.O. Smith, J.L. Edwards and K.L. Cyr. 1988. Photosynthetic efficiency and phytochrome photoequilibria determination using spectral data. Trans ASAE 31.

Simon, J.E. 1990. Essential oils and culinary herbs. In: J. Janick and J.E. Simon (eds). Advances in new crops. Timber Press, Portland, OR.

Skrubis, B. and P. Markakis. 1976. The effect of photoperiod on the growth and the essential oil of *Ocimum basilicum* (Sweet Basil). Economic Bot. 30:389–393.

Smith, W.O. 1983. Phytochrome as a molecule, p. 96-118. In: W. Shropshire and H. Mohr (eds.) Encyclopedia of Plant Physiology. Springer, Berlin, Heidelberg.

Thomas, B. and D. Vince-Prue. 1984. Juvenility, photoperiodism, and vernalization, p. 408–439.

In: M.B. Wilkins (ed.). Advanced plant physiology. Longman Scientific & Technical, Essex, UK.

Thomas, B. and D. Vince-Prue. 1997. Photoperiodism in plants. 2nd ed. Academic Press, San Diego, CA.

Torres, A.P. and R.G. Lopez. 2011. Photoperiod and temperature influence flowering responses and morphology of *Tecoma stans*. HortScience 46:416–419.

U.S. Department of Agriculture (USDA). 2014. Census of Agriculture (2012). National Agricultural Statistic Service. Washington DC. 04 Mar. 2019. <https://www.nass.usda.gov/Publications/AgCensus/2012/Full_Report/Volume_1,_Chapter_1_US/usv1.pdf>.

Vazquez, R.S. and N.T. Dunford. 2005. Bioactive components of Mexican oregano oil as affected by moisture and plant maturity. J. Essent. Oil Res. 17:668–671.

Vince-Prue, D., and A.E. Canham. 1983. Horticultural significance of photomorphogenesis. p. 518-544 In: W. Shropshire, Jr., and H. Mohr (eds.). Photomorphogenesis. Encyclopedia of Plant Physiology (New Series). Vol 16. Springer, Berlin, Heidelberg.

Waide, P. 2010. Phase out of incandescent lamps: Implications for international supply and demand for regulatory compliant lamps. IEA Energy Papers. No. 2010/05, OECD Publishing, Paris. <https://doi.org/10.1787/5kmh3nhp62s0-en>.

Whitman, C. and S. Padhye. 2009. Production tips for top performers *Lavandula stoechas*. Greenhouse Grower. p:75–78.

Whitman, C.M., R.D. Heins, A.C. Cameron, and W.H. Carlson. 1996. Cold treatments, photoperiod, and forcing temperature influence flowering of *Lavandula angustifolia*. HortScience 31:1150–1153.

Whitman, C.M., R.D. Heins, A.C. Cameron, and W.H. Carlson. 1998. Lamp type and irradiance level for day length extensions influence flowering of Campanula carpatica ‘Blue Clips’, Coreopsis grandiflora ‘Early Sunrise’, and Coreopsis verticillata ‘Moonbeam’. J. Amer. Soc. Hort. Sci. 123:802–807.

Yue, C., J. Dennis, B. Behe, C. Hall, B. Campbell, and R. Lopez. 2012. Investigating consumer preference for organic, local, or sustainable plants. HortScience 46:610–615.

SECTION III

PHOTOSYNTHETIC DAILY LIGHT INTEGRAL AND PHOTOPERIOD INFLUENCE DEVELOPMENT OF BASIL SPECIES AND CULTIVARS

Photosynthetic daily light integral and photoperiod influence development of basil species and cultivars

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Abstract

Limited controlled environment studies have been conducted on common culinary herbs such as basil (*Ocimum* spp.) to determine how changes in day length and daily light integral (DLI) influence developmental parameters. Therefore, the objectives of this study were to quantify how photoperiod and DLI influence flowering development parameters of 10 basil species and cultivars. For experiment (Expt.) 1, photoperiodic response of *O. basilicum* 'Genovese', 'Sweet Thai', 'Cinnamon', 'Red Ruben', 'Sweet Dani Lemon', and 'Nufar', *O.* ×*citriodorum* 'Lime Basil', *O. tenuiflorum* 'Holy Basil', *O. basilicum* var. *citriodora* 'Mrs. Burns' Lemon', and *O. minimum* 'Pluto' were quantified. In Expt. 2 responses to photoperiod and DLI were evaluated for 'Genovese', 'Sweet Thai', 'Red Ruben', 'Nufar', 'Lime Basil' and 'Holy Basil'. In both Expts. seeds were germinated in plug trays and grown at 25 °C. Photoperiods for Expt. 1 consisted of a 9-h short-day (SD) or a 9-h SD extended to 11-, 12-, 13-, 14-, 15-, 16-h or a 4-h night interruption (NI) utilizing red+white+far-red (R+W+FR) light-emitting diode (LED) lamps (R:FR = 0.8) providing a total photon flux density (*TPFD*) of ≈2 $\mu mol \cdot m^{-2} \cdot s^{-1}$. In Expt. 1, the DLI was low ≈8 $mol \cdot m^{-2} \cdot d^{-1}$. For Expt. 2, a 9-h SD and a 16-h long-day (LD) were created under a moderate DLI of ≈13 $mol \cdot m^{-2} \cdot d^{-1}$ and high DLI of ≈23 $mol \cdot m^{-2} \cdot d^{-1}$. All cultivars, with the exception of 'Red Rubin' can be classified as day-neutral plants (DNPs) under a low DLI, because there were no discernible flowering trends among treatments. During Expt. 1 'Red Rubin' exhibited a facultative SD response and a day neutral response under a moderate and high DLI. Under moderate and high DLIs, 'Genovese', 'Nufar', and 'Sweet Thai' exhibited a facultative LD response as time to first open flower was hastened under a 16-h photoperiod. In Expt. 2, time to first open flower and node number below the first open flower were reduced when the DLI was increased from a moderate to a high DLI for all cultivars excluding 'Lime

Basil', thus indicating a facultative irradiance response.

Keywords: Culinary herbs, day-neutral plants, DLI, facultative, long-day plants, *Ocimum basilicum*, short-day plants

Abbreviations: ADT, average daily temperature; B, blue; CE, controlled environment; CWL, cool white fluorescent; DE, day-extension; DLI, daily light integral; DNP, day-neutral plant; Expt., experiment(s); FIR, facultative irradiance response; FR, far red; G, green; HPS, high-pressure sodium; LD, long-day; LDP; long-day plant; LED, light-emitting diode; NI, night interruption; OF, open flower; *PFD*, photon flux densities; PL, photoperiodic lighting; *PPFD*, photosynthetic photon flux density; R, red; SD; short-day; SDP, short-day plant; SL, supplemental lighting; *TPFD*, total photon flux density; VB, visible bud; W, white.

Introduction

The genus *Ocimum*, composed of 30 (Simon et al., 1999) to 150 (Evans, 2009) species, is collectively known as basil, and is a member of the mint family, Lamiaceae. Basil is believed to be native to India, Asia, and Africa (Darrah, 1980; Putievsky and Galambogi, 1999; Simon, 1985), but its exact origin is uncertain. *Ocimum* spp. have several uses, including as a medicinal herb, for religious purposes, for the production of essential oils, and as a landscape ornamental or cut flower (Dole and Wilkins, 2005; Grayer et al., 1996; Kalita and Khan, 2013; Simon et al., 1990; Simon et al., 1999). However, sweet basil (*O. basilicum*) is the most common species and is used as a culinary herb, either as a fresh-cut, container grown, or dried product.

The market for fresh culinary herbs in the United States (U.S.) has increased by 10 to 12% annually from 2004 to 2014 (USAID, 2014). Total production of field and controlled environment (CE) grown fresh cut herbs is valued at $109 million (certified organic) and $200 million (not certified organic) (USDA, 2015). Of this production, CE production expanded by 190% between 1998 and 2014, and the number of commercial operations increased by 173% to 524 operations (USDA, 2015). Basil is the most popular culinary herb grown in CE greenhouses and indoor vertical farms due to its high market value (DeKalb et al., 2014). This includes both hydroponic and container production (Adam, 2005). However, statistics individual commodities such as basil not collected.

Prevention of flower initiation and development in culinary herbs such as basil is important (Davis, 1995), as retailers often will not accept fresh-cut herbs if buds or flowers are present. Retailers and consumers perceive fresh-cut basil with buds and flowers as old, off flavored, and bitter (Williamson, 2019). In contrast, field producers of other *Ocimum* spp. used for their essential oils will want their crops to flower quickly to maximize aromatic oil concentrations (Simon, 1995), since the greatest amount of essential oils are primarily accumulated in the leaves and flowers (Nurzynska-wierdak et al., 2013).

Flowering of many horticulture crops can be influenced by changes in day length and photosynthetic daily light integral (DLI) that occur with seasonal changes (Erwin and Warner, 2002; Mattson and Erwin, 2005, Runkle and Heins, 2003). Photoperiod refers to the number of light hours within a 24-hour period. However, the skotoperiod or critical night length regulates flowering responses (Thomas and Vince-Prue, 1997). Seasonal responses, as a result of photoperiodism include the onset of dormancy, the formation of storage organs, asexual reproduction, leaf development, stem elongation, germination, and the initiation or prevention of flowering (Taiz and Zeiger, 2010; Thomas and Vince-Prue, 1984).

Horticultural crops are classified into three major photoperiodic classes including short-day (SDP), long-day (LDP) and day-neutral plants (DNP) (Runkle et al., 2017; Thomas and Vince-Prue, 1997). Both LDP and SDP can be further classified depending on whether the photoperiod is required for flowering (qualitative or obligate) or if the photoperiod accelerates but is not required for flowering (quantitative or facultative) (Blanchard and Runkle, 2010). In CEs, growers can manipulate the day length based on the flowering response desired. For example, day-extension (DE) or night interruption (NI) lighting can be employed to induce flowering of LD species such as coreopsis 'Moonbeam' (*Coreopsis verticillata)*, bellflower 'Deep Blue Clips' (*Campanula carpatica*), and coreopsis 'Early Sunrise' (*Coreopsis grandiflora*) when natural day lengths are short (Padhye and Runkle, 2011; Whitman et al., 1998). While the use of blackout systems can be used to truncate natural LDs to provide inductive conditions for SD species, such as creeping zinnia (*Sanvitalia procumbens*) and Mexican sunflower 'Sundance' *Tithonia rotundifolia* (Mattson and Erwin, 2005). DNPs such as New Guinea impatiens (*Impatiens hawkeri*), summer snapdragon (*Angelonia angustifolia*), and tomato (*Lycopersicon esculentum*) are insensitive to day length and flower regardless of the photoperiod provided (Currey et al., 2011).

A limited number of studies have examined how photoperiod influences growth and development of culinary herbs. Burbott and Loomis (1967) reported that peppermint (*Mentha piperita*) grown under a 12-h day length remained vegetative. Langston and Leopold (1954), reported that flower induction of peppermint occurred when day length was extended to 14 or 18 h. When sweet basil was grown at 30/12 ºC, 24/12 ºC, and 18/12 ºC (day and night temperatures) and under 10- or 16-h photoperiods, plants flowered faster under LDs and higher temperatures (Putievsky, 1983). In a separate study, sweet basil grown under an 18-h photoperiod flowered 8, 5, and 3 d faster compared to plants grown under a 9-, 12-, and 15-h photoperiod, respectively (Skrubis and Markakis, 1976).

Herb production within greenhouses and other semi CEs can occur year-round, however during the winter months in northern latitudes ambient DLIs can be low. Thus, the only feasible way to appreciably increase the DLI is with the use of supplemental lighting (SL) (Currey et al., 2017). Beaman et al. (2009) reported a yield increase for sweet basil, cilantro (*Coriandrum sativum*), dill (*Anethum graveolens*), and parsley (*Petroselenium crispum*) by 144, 154, 241, and 120%, respectively when the DLI was increased from 6.3 to 7.5 $mol{\cdot}m^{-2}{\cdot}d^{-1}$ to 14.5 to 19.2 $mol{\cdot}m^{-2}{\cdot}d^{-1}$. Walters and Currey (2018) reported fresh and dry weight, height, and node number of *O. basilicum* 'Nufar' increased by 144, 178, 20, and 18%, respectively, as DLI increased from 7 to 15 $mol{\cdot}m^{-2}{\cdot}d^{-1}$. In a separate study, sweet basil 'Improved Genovese Compact' grown under sole-source lighting providing 5 different DLIs resulted in larger and thicker leaves when the DLI was increased (Dou et al., 2018).

Previous studies have established that an increase in DLI can accelerate time to first open flower (OF) of certain bedding crops (Erwin et al., 2017; Mattson and Erwin, 2005; Oh et al., 2009). For example, time to flower of cyclamen (*Cyclamen persicum*) 'Metis Scarlet Red' decreased from 133 to 75 d as DLI was increased from 1.4 to 17.3 $mol{\cdot}m^{-2}{\cdot}d^{-1}$ (Oh et al., 2009). For sweet pea 'Royal White' (*Lathyrus odoratus*), leaf number below the first flower decreased from 16 to 11, and time to flower decreased from 78 to 57 d when grown under an 18-h photoperiod with a DLI of 9.7 $mol{\cdot}m^{-2}{\cdot}d^{-1}$ provided by high-pressure sodium (HPS) lamps in comparison to a NI treatment (Mattson and Erwin, 2005). Furthermore, flowering did not occur under 9-h SDs, regardless of supplemental lighting.

Studies investigating how photoperiod and DLI interact to affect developmental parameters of popular basil species grown in CEs are needed; considering there are more than 60 cultivars (Simon, 1995) of *O. basilicum*, not including other *Ocimum* spp., (Evans, 2009) and that previous studies have focused on growth (fresh and dry weight, height, leaf area) and not flowering parameters. Therefore, the objectives of this study were to: 1) quantify how photoperiod influences flowering of 10 basil species and cultivars and 2) determine if photoperiod and DLI interact to influence flowering responses.

Materials and methods

Plant material (Expt. 1)

Seeds of various genotypes of basil including *O. basilicum* 'Genovese', 'Sweet Thai', 'Cinnamon', 'Red Ruben', 'Sweet Dani Lemon', and 'Nufar', *O. tenuiflorum* 'Holy Basil', *O. basilicum* var. *citriodora* 'Mrs. Burns' Lemon', *O.* ×*citriodorum* 'Lime Basil', and *O. minimum* 'Pluto' were sown on 13 Oct. 2017 and 20 Aug. 2018 into 128-cell plug trays (2.7 × 2.7 cm; 12.0-mL cell volume). Each cell was filled with a soilless substrate composed of 50% vermiculite (Vermiculite Premium Grade; Sungro Horticulture, Agawam MA) and 50% soilless medium containing 70% peat moss, 21% perlite, and 9% vermiculite (Suremix; Michigan Grower Products, Inc., Galesburg, MI).

Seeded trays of each cultivar were placed under each lighting treatment and on capillary mats. Seeded trays were overhead irrigated as needed with reverse osmosis water supplemented with water-soluble fertilizer (mg·L^{-1}) 60 nitrogen (N), 23 phosphorus (P), 60 potassium (K), 28 calcium (Ca), 5 magnesium (Mg), 1 iron (Fe), 0.6 manganese (Mn), 0.6 zinc (Zn), 0.6 copper (Cu), 0.4 boron (B), and 0.1 molybdenum (Mo) (MSU Plug Special; Blackmore Company, Kankakee, IL). After cotyledon emergence, seedlings were thinned, so that only one plant per cell remained.

Once plugs were pullable, 10 randomly selected seedlings were transplanted into 11-cm round (600-mL) containers filled with a soilless medium (Suremix; Michigan Grower Products Inc.). Twenty-one days after sowing 'Genovese', 'Cinnamon', 'Sweet Dani Lemon', 'Nufar', 'Mrs. Burns' Lemon', 'Lime Basil', and 'Pluto' were transplanted and 'Red Rubin', 'Sweet Thai', and 'Holy Basil' were transplanted 28 d after sowing. After transplant, plants were irrigated as needed with reverse osmosis water supplemented with water-soluble fertilizer ($mg \cdot L^{-1}$) 125 N, 12 P, 100 K, 65 Ca, 12 Mg, 1.0 Fe and Cu, 0.5 Mn and Zn, 0.3 B, and 0.1 Mo (MSU Orchid RO Water Special; Blackmore Company).

Plant material (Expt. 2)

Seeds of 'Genovese', 'Holy Basil', 'Lime Basil', 'Nufar', 'Sweet Thai', and 'Red Ruben' were sown on 10 Sept. 2018 and 12 Mar. 2019. Sowing, germination, thinning, and irrigation of seedlings and transplants followed the same protocol as in Expt. 1. However, once plugs were pullable after 21 d, 9 seedlings were randomly selected and transplanted into round 15-cm diameter (1,300-mL) containers filled with the same soilless medium (Suremix; Michigan Grower Products Inc.).

Greenhouse environment and lighting treatments (Expt. 1)

Plants were grown in a glass-glazed greenhouse with exhaust fans, evaporative-pad cooling, radiant hot-water heating, and SL controlled by an environmental control system (Priva Office version 725-3030; Priva North America, Vineland Station, ON, Canada). The greenhouse air average daily temperature (ADT) set point was a constant 25 ºC. Space heaters provided supplemental heat for each bench under black cloth when the air temperature fell under 24.8 °C. The photoperiod was 9 h (0800 to 1700 HR) consisting of natural photoperiods (lat. 42º N) and supplemental lighting from 200-W light-emitting diodes (LEDs) (Philips GP-TOPlight DRW-MB; Koninklijke Philips N.V., Eindhoven, the Netherlands) that provided a photosynthetic photon flux density (*PPFD*) (±SD) of 90 ± 14 $\mu mol \cdot m^{-2} \cdot s^{-1}$ when the outdoor light intensity was below ≈440 $\mu mol \cdot m^{-2} \cdot s^{-1}$ to achieve a DLI of <8 $mol \cdot m^{-2} \cdot d^{-1}$, hence forward referred to as a low DLI (Table 1). The 100-nm waveband ratios (%) of the LED fixtures, defined by their blue [B (400-500 nm)], green [G (500-600 nm)], and red [R (600-700 nm)] photon flux densities (*PFD*), were 10:5:85.

Opaque black cloths were pulled over each bench daily at 1700 HR and opened at 0800 HR to create a truncated 9-h short day (SD) for all treatments. Treatments consistent of the 9-h SD or a 9 h extended by four R+W+Far-red (R+W+FR) LED lamps (GreenPower LED flowering DR/W/FR 14 W, E26; Philips) on each bench to create 11-, 12-, 13-, 14-, 15-, or 16-h photoperiods or a 4-h NI from 2200 to 0200 HR. Each LED lamp was covered with multiple layers of aluminum wire mesh to achieve an average total photon flux density (*TPFD*) of ≈2 $\mu mol \cdot m^{-2} \cdot s^{-1}$ between 400 and 800 nm. The 100-nm waveband ratios (%) of the R+W+FR LED lamps, defined by their B, G, R, and FR radiation, were 7:12:35:46. The spectral distribution of the LED lamps was measured in five random locations throughout each bench by a spectroradiometer (PS-200; Stellar-Net, Tampa, FL), and the phytochrome photoequilibrium was estimated according to Sager et al. (1988) (Fig. 1).

Greenhouse environment and lighting treatments (Expt 2).

Plants were grown in two separate glass-glazed greenhouse compartments. Environmental parameters such as heating, cooling, and SL were controlled by the same environmental control system previously mentioned from Expt. 1. The greenhouse air ADT was set at a constant 25 ºC. Continuous SL was provided to one of the greenhouse compartments for 9 $h \cdot d^{-1}$ (0800 to 1700 HR) utilizing six 200-W LED arrays (Philips GP-TOPlight DRW-LB and DRW-HB; Koninklijke Philips N.V., Eindhoven, the Netherlands) that provided a supplemental *PPFD* (±SD) of ≈250 ± 1.7 $\mu mol \cdot m^{-2} \cdot s^{-1}$, to provide a DLI of ≈23 $mol \cdot m^{-2} \cdot d^{-1}$, hence forward referred to as a high DLI (Table 2). The 100-nm waveband ratios (%) of the LED arrays, defined by the combined B (peak wavelength 449 nm) and R (peak wavelength 665 nm) *PFDs*, was 15:85. All LED arrays providing SL were placed ≈147 cm above the benches. The second greenhouse compartment did not receive any SL, and the average DLI was ≈13 $mol \cdot m^{-2} \cdot d^{-1}$, hence forward referred to as a moderate DLI (Table 2).

There were two benches per greenhouse compartment, over which two photoperiodic lighting (PL) treatments were delivered. Treatments consisted of a truncated 9-h SD created by pulling an opaque black cloth as previously described. DE lighting provided by R+W+FR LED lamps (as previously described) were used to create a 16-h (0800 to 2400 HR) photoperiod.

Data collection and analysis

In both experiments, plants were assessed daily and the date of first visible bud (VB) and date of first OF were recorded. At first OF, the number of nodes below the first OF and plant height were recorded (from the media surface to the plant apex). Plants that did not flower 105 d after sowing were considered non-flowering. A shielded and aspirated 0.13-mm type E thermocouple (Omega Engineering, Stamford, CT, USA) at canopy height recorded the air temperatures on each bench and a line quantum sensor (LI-191R, LI-COR, Lincoln, NE) (Apogee Instruments, Inc., Logan, UT) or a quantum sensor (LI-190R, LI-COR, Lincoln, NE) placed at canopy height recorded the light intensity. A CR-1000 datalogger (Campbell Scientific, Logan, UT) collected the environmental data every 15 s and hourly means were recorded. Actual mean air temperatures and DLI during Expt. 1 and 2 are reported in Table 1 and 2, respectively.

Expt. 1 was a randomized complete block design (RBCD) with 10 plants of each cultivar assigned to each treatment. Each Rep. was regarded as a blocking factor. Benches with different photoperiodic treatments were considered the experimental units and pots randomly placed throughout the benches were considered sub samples. Expt. 2 was also a RCBD with 9 plants per cultivar. Each plant was considered an experimental unit in the data analysis. Experiment one had one factor (photoperiodic treatment) and eight levels (9, 11, 12, 13, 14, 15, 16 h and NI) and Expt. 2 had two factors 1) photoperiod, and 2) light intensity, each with two levels (9 and 16-h photoperiods, and presence or absence of SL). For both Expt., data were separately analyzed for each cultivar, therefore species and cultivars were not considered another factor. Data for Expt. 1 was pooled if no interaction between Rep. and treatments was present, or if similar response trends were observed between Reps. Data for both Expts. was analyzed with the SAS version 9.4 (SAS Institute, Inc., Cary, NC) using the PROC GLIMMIX procedure and pairwise comparisons between treatments were performed with adjust Tukey-Kramer difference test ($P \leq 0.05$).

Results

Expt. 1: Time to first visible bud

No significant differences for time to first VB were observed for ‘Cinnamon’, ‘Genovese’, ‘Lime Basil’, ‘Pluto’, and ‘Sweet Thai’ under a low DLI (Fig. 2A, B, D, G, and J). Although there were significant differences among photoperiodic treatments, for 'Nufar' and 'Sweet Dani Lemon' there were no discernable trends (Fig. 2F and I). For 'Holy Basil' time to first VB occurred 9 d faster under a 9-h SD in comparison to a 16-h LD (Fig. 2C). Similarly, time to first VB was hastened by 7 and 6 d for 'Red Ruben' grown under a 9- or 12-h SD in comparison to a 16-h LD (Fig. 2H).

Expt. 1: Time to first open flower

Under a low DLI (<8 $mol \cdot m^{-2} \cdot d^{-1}$) no significant difference for time to first OF were observed for 'Cinnamon', 'Genovese', "Holy Basil' and 'Pluto' (Fig. 3A-C, and G). Although there were significant differences, no discernable trend was evident for time to first OF for the remaining cultivars (Fig. 3D-F, I, and J). However, time to first OF occurred most rapidly for 'Red Rubin' grown under 9 and 12-h SDs (Fig. 3H). For instance, time to first OF for 'Red Rubin' was hastened by 7 d for plants grown under 9 and 12-h photoperiods, when compared to plants grown under the 16-h LD.

Expt. 1: Node number below the first open flower

There was no significant difference in the number of nodes below the first OF for 'Genovese', 'Lime Basil', 'Pluto', and Sweet Dani Lemon' under a low DLI (Fig. 4B, D, G, and I). For the remaining cultivars, there were significant differences in the node number below the first open flower (Fig. 4A, C, E, F, H, J). However, differences were minor, ranging from 1 to 3 nodes. For 'Holy Basil', with the exception of the 13-h photoperiod, plants grown under the 9-h SD had the least number of nodes compared to all other photoperiodic treatments (Fig. 4C). 'Red Rubin' under the 9-h SD had one less node below the first OF compared to the 16-h LD (Fig. 4H).

Expt. 1: Height at first open flower

Under a low DLI, excluding ‘Genovese’, significant differences in height were observed for all species and cultivars (Fig. 5A-J). Height at first open flower was significantly shorter under the 9-h SD compared to all other photoperiodic treatments for ‘Holy Basil’, ‘Mrs. Burns’ Lemon’ and ‘Sweet Dani Lemon’ (Fig. 5C, E, and I). For example, under a 9-h SD ‘Holy Basil’ and ‘Mrs. Burns’ Lemon’ plants were 18 to 26% and 18 to 23% shorter, respectively in comparison to all other photoperiodic treatments (Fig. 5C and E). Furthermore, excluding the 4-h NI treatment, ‘Nufar’, ‘Red Rubin’, and ‘Sweet Thai’ were shortest under a 9-h SD compared to the remaining DE lighting treatments (Fig. 5F, H, and J).

Expt. 2: Time to first visible bud

Time to first VB was hastened under a 16-h LD with a high DLI compared to a 9-h SD with a moderate DLI for ‘Genovese’, ‘Holy Basil’, ‘Nufar’, ‘Red Rubin’ and ‘Sweet Thai’ (Fig. 6A, B, D-F). Under a moderate DLI photoperiod significantly affected time to first VB of ‘Holy Basil’, ‘Nufar’, and ‘Sweet Thai’ (Fig. 6B, D, and F). Where time to first VB occurred more rapidly for ‘Holy Basil’ under a 9-h SD compared to a 16-h LD (Fig. 6B). Whereas, time to first VB was hastened under a 16-h LD and delayed under a 9-h SD for ‘Nufar’ and ‘Sweet Thai’ (Fig. 6D and F). Under a high DLI there was no significant difference among photoperiodic treatments for all basil cultivars (Fig. 6A-F).

Expt. 2: Time to first open flower

For all cultivars, except ‘Lime Basil’ time to first OF occurred most rapidly when plants were grown under a 16-h LD and a high DLI (≈23 $mol \cdot m^{-2} \cdot d^{-1}$) in comparison to the 9-h SD and a moderate DLI (≈13 $mol \cdot m^{-2} \cdot d^{-1}$) (Fig. 7A-F). Time to first OF for ‘Nufar’, under a moderate and high DLI was hastened by 10 and 6 d under a 16-h LD compared to a 9-h SD, respectively (Fig.

7D). ‘Genovese’ and ‘Sweet Thai’ followed similar trends to that of ‘Nufar’ (Fig. 7A, D, F). Under a moderate DLI, time to first OF for ‘Holy Basil’ occurred most rapidly (8 d) under a 9-h SD, compared to a 16-h LD. However, under a high DLI there was no significant difference between LD and SDs (Fig. 7B). For ‘Red Rubin’ under moderate and high DLIs, photoperiod did not significantly affect time to first OF. However, an increase in DLI hastened flowering of both SD and LD grown plants compared to the 9-h SD under a moderate DLI (Fig. 7E).

Expt. 2: Node number below the first open flower

Node number below the first OF was reduced under a high DLI regardless of photoperiod, compared to a moderate DLI for ‘Lime Basil’ and Sweet Thai’ (Fig. 8C and F). Under a moderate and high DLI photoperiod did not significantly affect node number below the first OF, for all cultivars, excluding ‘Holy Basil’ and ‘Nufar’ under a moderate DLI (Fig. 8A-F). For instance, under a moderate DLI and 16-h LD, node number below the first OF increased by two nodes for ‘Holy Basil’compared to a 9-SD with a moderate DLI (Fig. 8B). Whereas, under a moderate DLI and 16-h LD, node number below the first OF decreased by two nodes for ‘Nufar’ compared to a 9-h SD with a moderate DLI (Fig. 8D).

Expt. 2: Height at first open flower

Regardless of DLI, photoperiod did not significantly affect height of ‘Holy Basil’, ‘Nufar’, ‘Red Rubin’, and ‘Sweet Thai’ at first OF (Fig. 9B, D-F). However, with an increase in DLI, height of ‘Holy Basil’ and ‘Nufar’ was reduced (Fig. 9B and D). For instance, under a high DLI, the combined average height of 9- and 16-h grown ‘Holy Basil’ decreased by 19.8 (22%), compared to the combined average height of 9- and 16-h grown plants under a moderate DLI (Fig. 9B). Under a high DLI, height of ‘Genovese’, decreased by 15.2 (18%) cm when grown under a 16-h LD compared to a 9-h SD (Fig. 9A).

Discussion

Flower inhibition or induction of basil is desirable depending on its intended use; be it for culinary, ornamental, or the production of essential oils. An understanding of the environmental parameters that influence developmental parameters could be beneficial for growers who seek to induce flowering when basil is to be used as an ornamental or for essential oil production. However, inhibition of flowering could be desired by CE growers. Numerous studies conducted on bedding plants have demonstrated how DE and NI lighting can effectively induce or inhibit flowering of LDPs and SDPs, respectively, while truncated SDs using blackout systems can promote or inhibit flowering (Mattson and Erwin, 2005; Torres and Lopez, 2011). Based on the results for time to first OF from Expt. 1, under a low DLI (<8 $mol \cdot m^{-2} \cdot d^{-1}$) all cultivars excluding 'Red Rubin' exhibited DNP responses (Fig 3A-J). Generally, there were no significant differences in time to first OF, and when there were significant differences, no discernable trends were observed. 'Red Rubin' exhibited facultative SD responses under a low DLI as flowering occurred under all photoperiodic treatments and the NI, however time to first OF occurred more rapidly under a 9 and 12-h SD (Fig 3H).

Results from Expt. 1 for 'Genovese' and 'Lime Basil' are in agreement with Erwin et al. (2017), who describe these two cultivars as DNP; however, information regarding specific photoperiodic treatments were not provided. In contrast to our results, Skrubis and Markakis (1976) reported that *O. basilicum* var. *citriodora* displayed LD responses, since flower development and subsequent anthesis occurred more rapidly under an 18-h photoperiod compared to 9-, 12-, and 15-h photoperiods, utilizing cool white fluorescent (CWF) lamps. However, in their study plants were grown under ambient sunlight for 9 h (0800 to 1700 HR), and then moved into a growth chamber where the CWF lamps provided DE lighting. The ambient

DLI was not provided and DE lighting did not increase the final DLI by more than 0.6 $mol·m^{-2}·d^{-1}$ for those treatments.

In addition to photoperiod, DLI can also influence flowering of plants (Mattson and Erwin, 2005; Owen et al., 2018, Zhang et al., 1996). For instance, Zhang et al. (1996) reported a decrease in time to flower of the facultative LDP yarrow 'Summer Pastels' (*Achillea millefolum*) from 57 to 37 d as DLI increased from 5.8 to 17.3 $mol·m^{-2}·d^{-1}$ under a 16-h photoperiod. Similarly, an increase in DLI from 5 to 20 $mol·m^{-2}·d^{-1}$ hastened flowering of the LDP petunia (*Petunia ×hybrida* Vilm.-Andr.) (Faust et al., 2005). In Expt. 2, time to first OF of 'Genovese' under a moderate DLI occurred 7 d faster under a 16-h LD compared to a 9-h SD. Under a high DLI time to first OF occurred 9 d faster under a 16-h LD compared to a 9-h SD. Therefore, under moderate and high DLIs 'Genovese' exhibited facultative LDP responses (Fig. 7A). 'Nufar' and 'Sweet Thai' followed similar trends and can also be classified as facultative LDPs, under moderate and high DLIs (Fig. 7D and F).

Although 'Red Rubin' displayed facultative SD responses under a low DLI in Expt. 1, the response was diminished under moderate and high DLIs (Expt. 2) as there were no significant differences in time to first OF among the photoperiodic treatments (Fig. 3H and 7E). 'Lime Basil' responded as a DNP under the low DLI treatment in Expt. 1 and under the moderate and high DLIs in Expt. 2 (Fig. 3D and 7C).

An increase in DLI has been associated with the acceleration of growth and development of numerous crops due to an increase in photosynthesis (Nemali and van Iersel, 2004). The hastening of time to VB and OF in our study can be attributed to an increase in photosynthesis resulting from the additional irradiance that would increase metabolic activity, thus accelerating plant growth and development and possibly reducing the juvenile phase (Adams et al., 1999). A facultative irradiance response (FIR) could further explain and validate this hypothesis. An FIR can occur within the three primary photoperiodic response groups, SDP, LDP, and DNP (Erwin et al., 2017). An FIR referrers to a decrease in time to first OF and node number below the first OF, resulting from an increase in DLI (Mattson and Erwin, 2005). Plants exhibiting an FIR flower faster because the juvenile phase is shortened under high radiation levels (Adams et al., 1999). Warner (2010) described faster flowering and fewer nodes in four *Petunia* spp. (*Petunia axillaris*, *P. exserta*, *P. ×hybrida* 'Mitchell', and *P. integrifolia*) grown under 16-h LDs with a DLI of 16.5 $mol{\cdot}m^{-2}{\cdot}d^{-1}$ compared to 9-h SDs at 11.4 $mol{\cdot}m^{-2}{\cdot}d^{-1}$. For instance, node number below the first flower for *P. axillaris* and *P. exserta* decreased from 38 and 26 to 20 and 13, while time to flower decreased from 70 and 64 d to 45 and 53 d, respectively, as irradiance and day length increased. Therefore, 'Genovese', 'Holy Basil', 'Nufar', 'Red Rubin', and 'Sweet Thai' exhibited an FIR, as time to first OF was hastened, and node number below the first OF was reduced, when the DLI was increased from a moderate to a high DLI (Fig. 7A, B, D-F, 8A, B, D-F).

From Expt. 1, the increase in plant height at flowering generally observed under DE lighting can be associated to an increased exposure to FR radiation from the R+W+FR LED lamps. The use of FR radiation promotes stem elongation and suppresses lateral branching (Moe and Heins, 1990) of crops such as watercress (Bleasdale, 1964), pansy 'Matrix Yellow' (*Viola ×wittrockiana*), and petunia 'Dreams Midnight' (*P. ×hybrida*) (Owen et al., 2018) when grown under incandescent (INC) or R+W+FR LEDs. Similarly, in our study, all cultivars excluding 'Genovese' were significantly taller when grown under a 16-h LD compared to a 9-h SD (Fig. 5A-J). Therefore, the increase in height was likely evoked by the shade avoidance response, mediated by the R and FR absorbing photoreceptor phytochrome. Plants in a greenhouse are generally exposed to nearly equal amounts of B, G, R, and FR radiation from the sun. However, the R+W+FR LED lamps employed during our study had a low R:FR (R:FR ratio = 0.8) which created a FR rich environment, resulting in taller plants.

Generally, photoperiod did not significantly affect plant height at first OF during Expt. 2 (Fig. 9A-F). However, 'Holy Basil' and 'Nufar', plant height decreased with an increase in DLI, regardless of photoperiodic treatment (Fig. 9B and D). Similar to our findings for these to cultivars, Hurt et al. (2019) reported a decrease in stem length under SL in comparison to PL and ambient light for impatiens 'Accent Premium Salmon' (*I. walleriana*) and petunia 'Ramblin Peach Glo' (*P. ×hybrida*) plants. A decrease in stem height resulting from an increase in DLI can be of great benefit to growers who struggle with canopy management, by helping to reduce stem breakage, which would otherwise be common for herbs grown under FR rich environments.

In conclusion, under a low DLI we have classified *O. basilicum* 'Genovese', 'Sweet Thai', 'Cinnamon', 'Sweet Dani Lemon', and 'Nufar', *O. ×citriodorum* 'Lime Basil', *O. tenuiflorum* 'Holy Basil', *O. basilicum* var. *citriodora* 'Mrs. Burns' Lemon', and *O. minimum* 'Pluto' as DNPs since photoperiod either did not significantly affect time to first OF or no discernable trend was evident under DE or NI lighting. However, under a low DLI 'Red Rubin' can be classified as a facultative SDP because time to first OF occurred most rapidly under SDs in comparison to a 16-h LD (Fig. 3H). These results were diminished in Expt. 2, under moderate and high DLIs as 'Red Rubin' exhibited DN responses (Fig. 7E). Under moderate and high DLIs 'Genovese', 'Nufar', and 'Sweet Thai' exhibited facultative LD responses (Fig. 7A, D, and F). Furthermore, in Expt. 2 under a 9-h SD all cultivars excluding 'Lime Basil' exhibited an FIR, where higher DLIs induced faster flowering while reducing the number of nodes below the first OF (Fig. 7A-F, 8A-F). Our results indicate that photoperiod alone is not a feasible option for reproductive management of the basil cultivars evaluated. However, DLI generally had a greater impact on time to first OF, VB, node number, and height. Thus, the management of DLI could be a more effective strategy for managing plant development. Additionally, we have demonstrated that basil should not be grown under DLIs <13 $mol \cdot m^{-2} \cdot d^{-1}$ in order to avoid excessive stem elongation, especially if growing under a FR radiation rich environment. Under high DLIs, basil should be harvested earlier to prevent undesirable flowering.

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APPENDIX

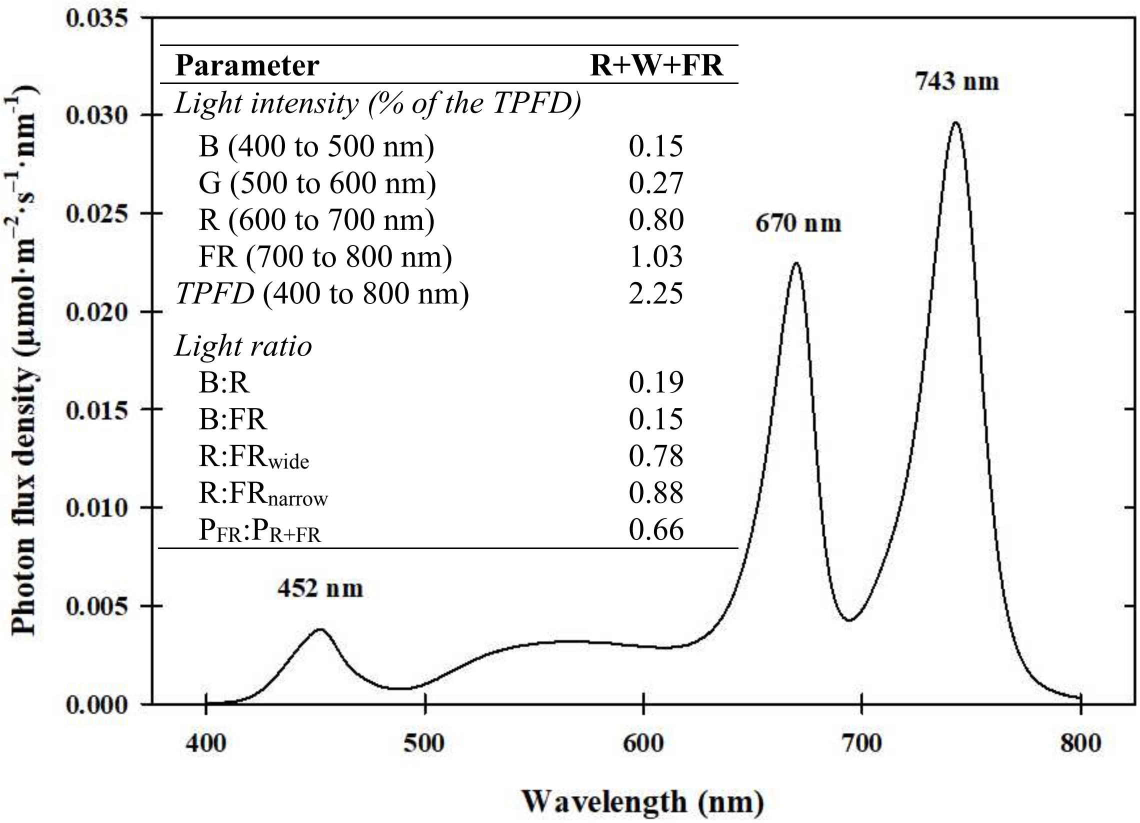
Table III-1. Expt. 1. photoperiod (h), mean (±SD) bench average daily temperature (ADT), and daily light integral (DLI) (±SD) during two experimental replications (Rep.) for basil. Plants were grown under a truncated 9-h short day (SD) and day length was extended with red+white+far-red (R+W+FR) light-emitting diode (LED) lamps to achieve 11-, 12-, 13-, 14-, 15-, 16-h or a 4-h night interruption (NI).

Photoperiod (h)	Rep 1 ADT [mean ± SD (ºC)]	Rep 2 ADT [mean ± SD (ºC)]	Rep 1 DLI ($mol \cdot m^{-2} \cdot d^{-1}$)	Rep 2 DLI ($mol \cdot m^{-2} \cdot d^{-1}$)
9	23.6 ± 1.3	24.4 ± 2.1	- [z]	-
11	24.0 ± 1.2	24.7 ± 2.0	-	7.1 ± 3.6
12	24.5 ± 1.2	24.2 ± 1.9	-	6.8 ± 3.1
13	24.1 ± 1.6	24.9 ± 2.4	7.2 ± 4.4	-
14	23.9 ± 1.5	24.3 ± 2.0	-	6.2 ± 3.0
15	24.2 ± 1.4	24.3 ± 2.3	6.6 ± 4.5	-
16	24.0 ± 1.3	24.6 ± 2.2	-	6.7 ± 3.5
NI	23.1 ± 1.8	24.3 ± 1.8	7.5 ± 4.1	-

[z] No data collected.

Table III-2. Expt. 2. daily light integral (DLI) treatment, photoperiod (h), average DLI (±SD), and greenhouse mean (±SD) air average daily temperature (ADT) delivered to six basil cultivars. Plants were grown under a truncated 9-h short day (SD) or a 16-h long-day (LD), with moderate or high photosynthetic DLIs. Day extension photoperiodic lighting (PL) was delivered by light-emitting diode (LED) lamps. LED lamps emitted red+white+far-red (R+W+FR) radiation and were used to extend the photoperiod by 7 h [16 h (1700 to 2400 HR)].

DLI treatment	Photoperiod (h)	Avg. DLI ($mol \cdot m^{-2} \cdot d^{-1}$)	Greenhouse air ADT [mean ± SD (ºC)]
Moderate	9	12.8 ± 8.0	25.7 ± 1.2
	16	13.7 ± 8.0	25.7 ± 1.2
High	9	22.2 ± 7.9	25.2 ± 2.4
	16	23.2 ± 8.0	25.2 ± 2.4



Parameter	R+W+FR
Light intensity (% of the TPFD)	
B (400 to 500 nm)	0.15
G (500 to 600 nm)	0.27
R (600 to 700 nm)	0.80
FR (700 to 800 nm)	1.03
TPFD (400 to 800 nm)	2.25
Light ratio	
B:R	0.19
B:FR	0.15
$R:FR_{wide}$	0.78
$R:FR_{narrow}$	0.88
$P_{FR}:P_{R+FR}$	0.66

Figure III-1. Expt. 1 and 2. spectral distribution, intensity of blue [B (400–500 nm)], green [G (500–600 nm)], red [R (600–700 nm)], and far-red [FR (700–800 nm)] radiation, total photon flux density (*TPFD*), light ratio, and estimated phytochrome photoequilibria [P_{FR}/P_{R+FR} (the proportion of FR-absorbing phytochromes in the pool of R- and FR-absorbing phytochromes; Sager et al., 1988)] of R+W+FR light-emitting diode (LED) lamps covered with multiple layers of wire mesh. $R:FR_{wide}$ was calculated as 600 to 700 nm:700 to 800 nm; $R:FR_{narrow}$ was calculated as 655 to 665 nm:725 to 735 nm.

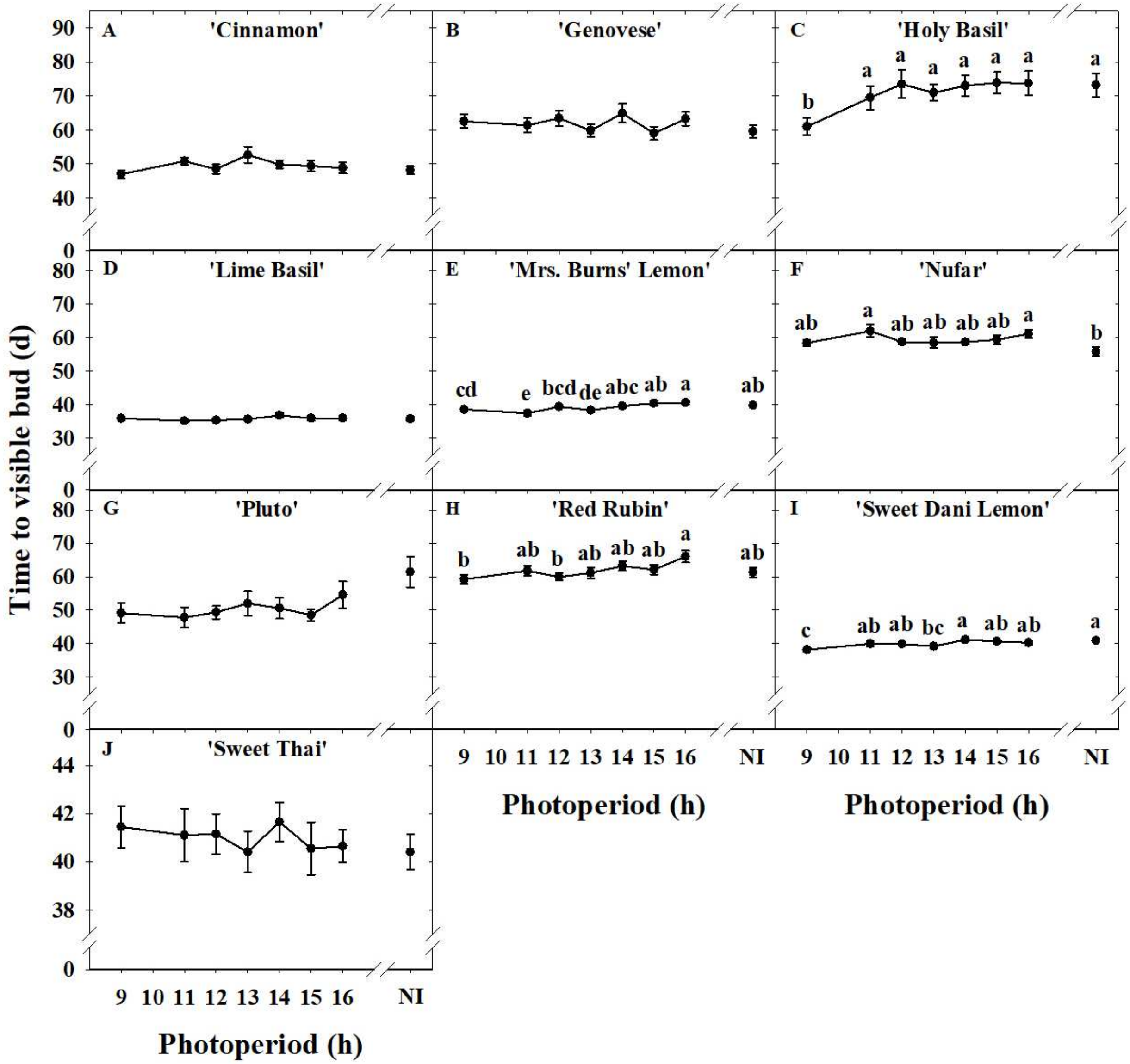


Figure III-2. Expt. 1. time to first visible bud (VB) for 10 basil cultivars grown under a truncated 9-h short-day (SD) or under a 9-h SD extended with red+white+far-red (R+W+FR) light-emitting diode (LED) lamps to achieve 11-, 12-, 13-, 14-, 15- and 16-h photoperiods or a 4-h night interruption (NI). Data were pooled when there was no interaction between replication (Rep.) and treatment, or if the response trends were similar between Reps. Letters indicate mean separations across treatments using Tukey-Kramer difference test at $P \leq 0.05$. Absences of letters indicate no significant difference $P \leq 0.05$. Error bars indicate standard error.

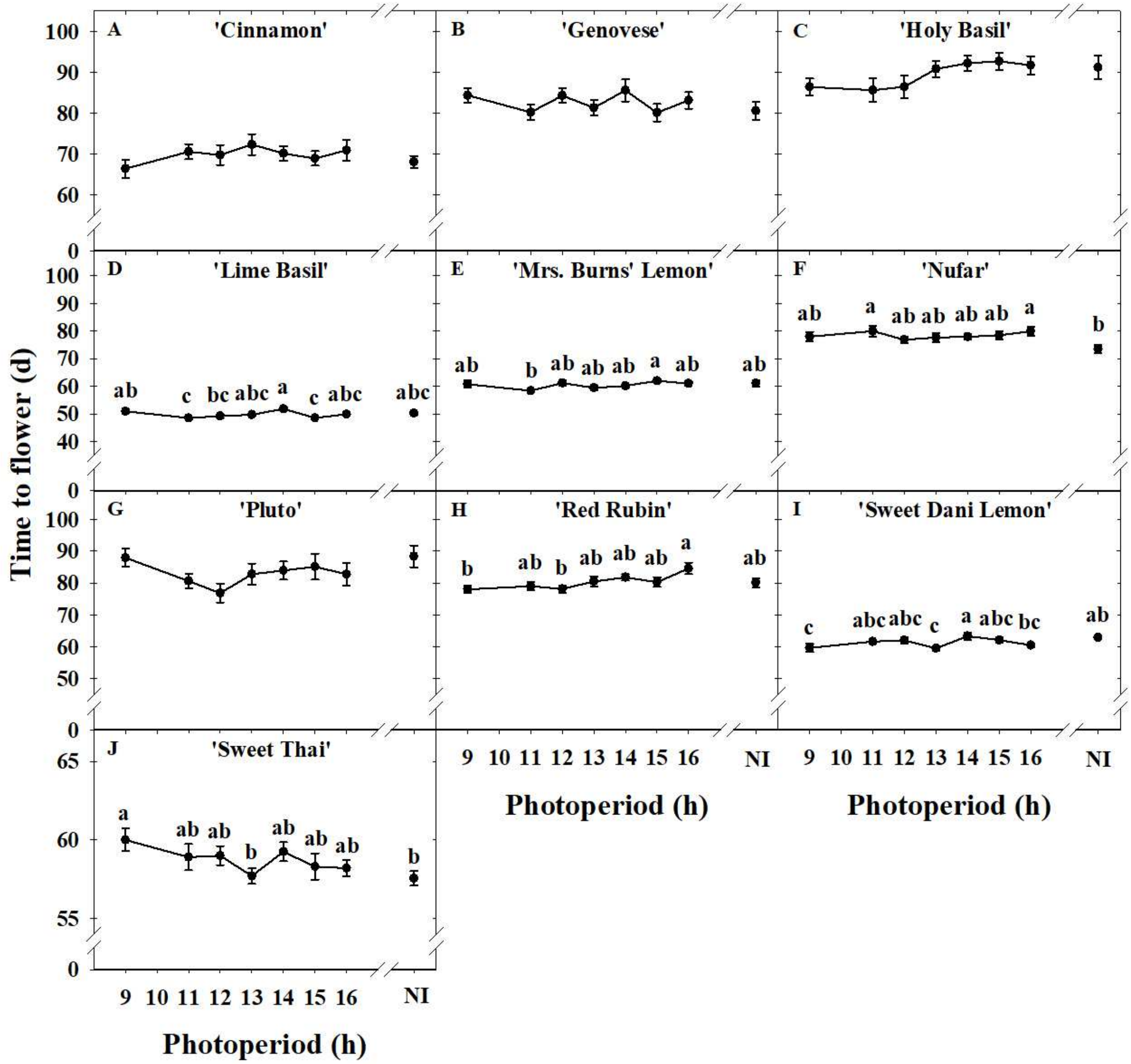


Figure III-3. Expt. 1. time to first open flower (OF) for 10 basil cultivars grown under a truncated 9-h short-day (SD) or under a 9-h SD extended with red+white+far-red (R+W+FR) light-emitting diode (LED) lamps to achieve 11-, 12-, 13-, 14-, 15- and 16-h photoperiods or a 4-h night interruption (NI). Data were pooled when there was no interaction between replication (Rep.) and treatment, or if the response trends were similar between Reps. Letters indicate mean separations across treatments using Tukey-Kramer difference test at $P \leq 0.05$. Absences of letters indicate no significant difference $P \leq 0.05$. Error bars indicate standard error.

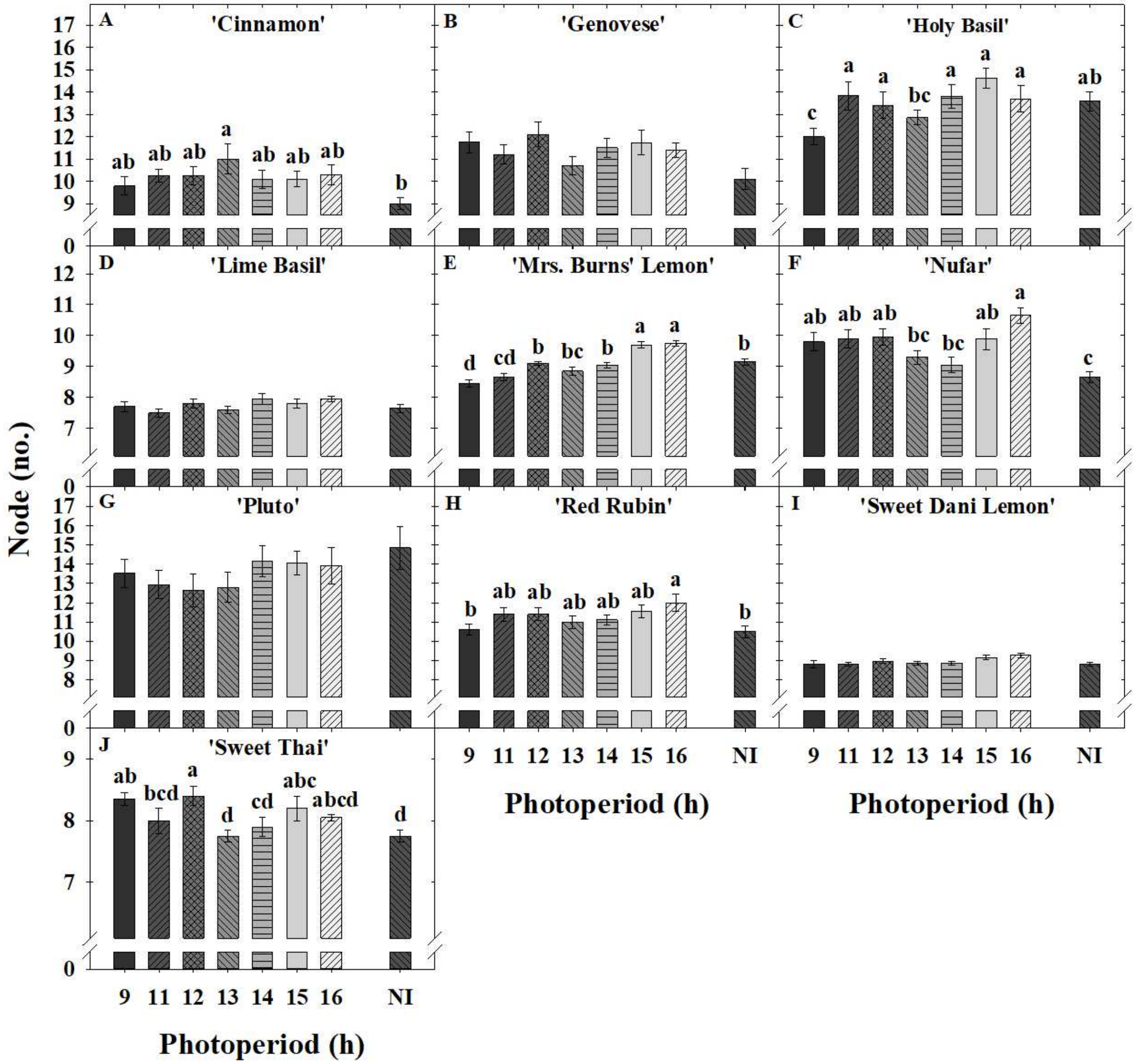


Figure III-4. Expt. 1. node number below the first open flower (OF) for 10 basil cultivars grown under a truncated 9-h short-day (SD) or under a 9-h SD extended with red+white+far-red (R+W+FR) light-emitting diode (LED) lamps to achieve 11-, 12-, 13-, 14-, 15- and 16-h photoperiods or a 4-h night interruption (NI). Data were pooled when there was no interaction between replication (Rep.) and treatment, or if the response trends were similar between Reps. Letters indicate mean separations across treatments using Tukey-Kramer difference test at $P \leq 0.05$. Absences of letters indicate no significant difference $P \leq 0.05$. Error bars indicate standard error.

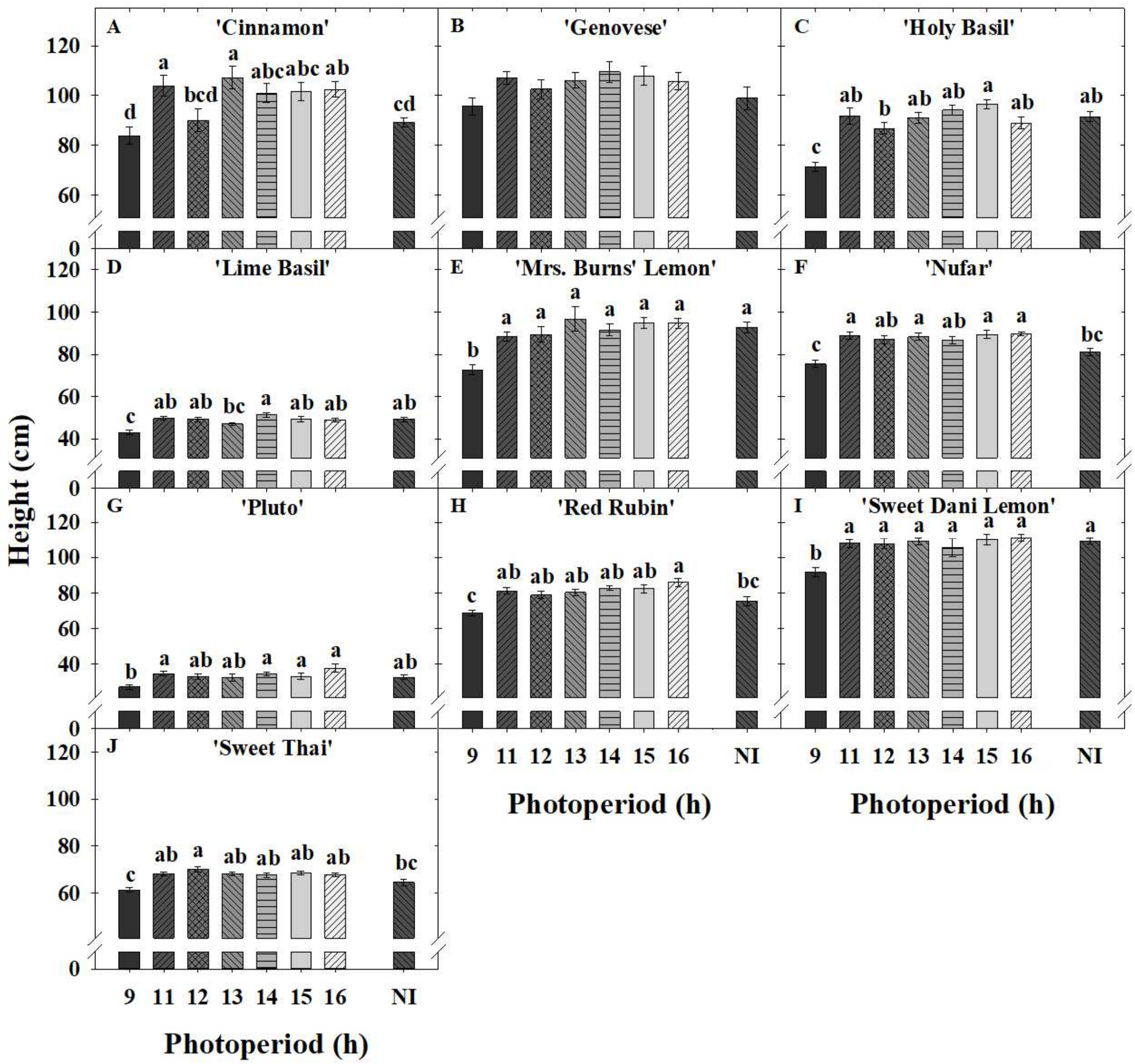


Figure III-5. Expt. 1. height at first open flower for 10 basil cultivars grown under a truncated 9-h short-day (SD) or under a 9-h SD extended with red+white+far-red (R+W+FR) light-emitting diode (LED) lamps to achieve 11-, 12-, 13-, 14-, 15- and 16-h photoperiods or a 4-h night interruption (NI). Data were pooled when there was no interaction between replication (Rep.) and treatment, or if the response trends were similar between Reps. Letters indicate mean separations across treatments using Tukey-Kramer difference test at $P \leq 0.05$. Absences of letters indicate no significant difference $P \leq 0.05$. Error bars indicate standard error.

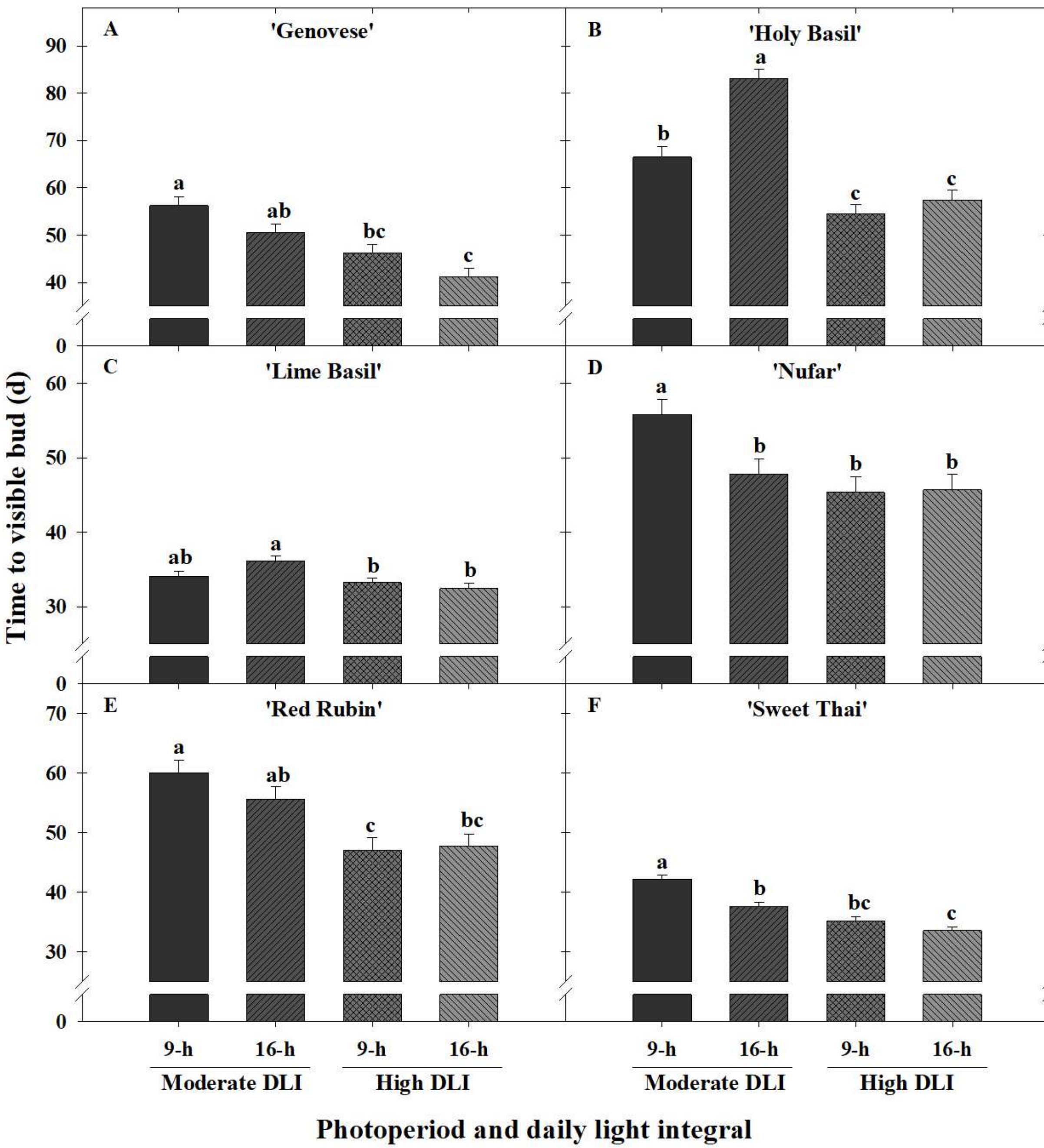


Figure III-6. Expt. 2. time to first visible bud (VB) for six basil cultivars grown under moderate or high photosynthetic daily light integrals (DLIs) and a truncated 9-h short-day (SD) or day-extension lighting from low-intensity light-emitting diode (LED) lamps emitting red+white+far-red (R+W+FR) radiation for 7 h (1700 to 2400 HR) to achieve a 16-h photoperiod. Letters indicate mean separations across treatments using Tukey-Kramer difference test at $P \leq 0.05$. Error bars indicate standard error.

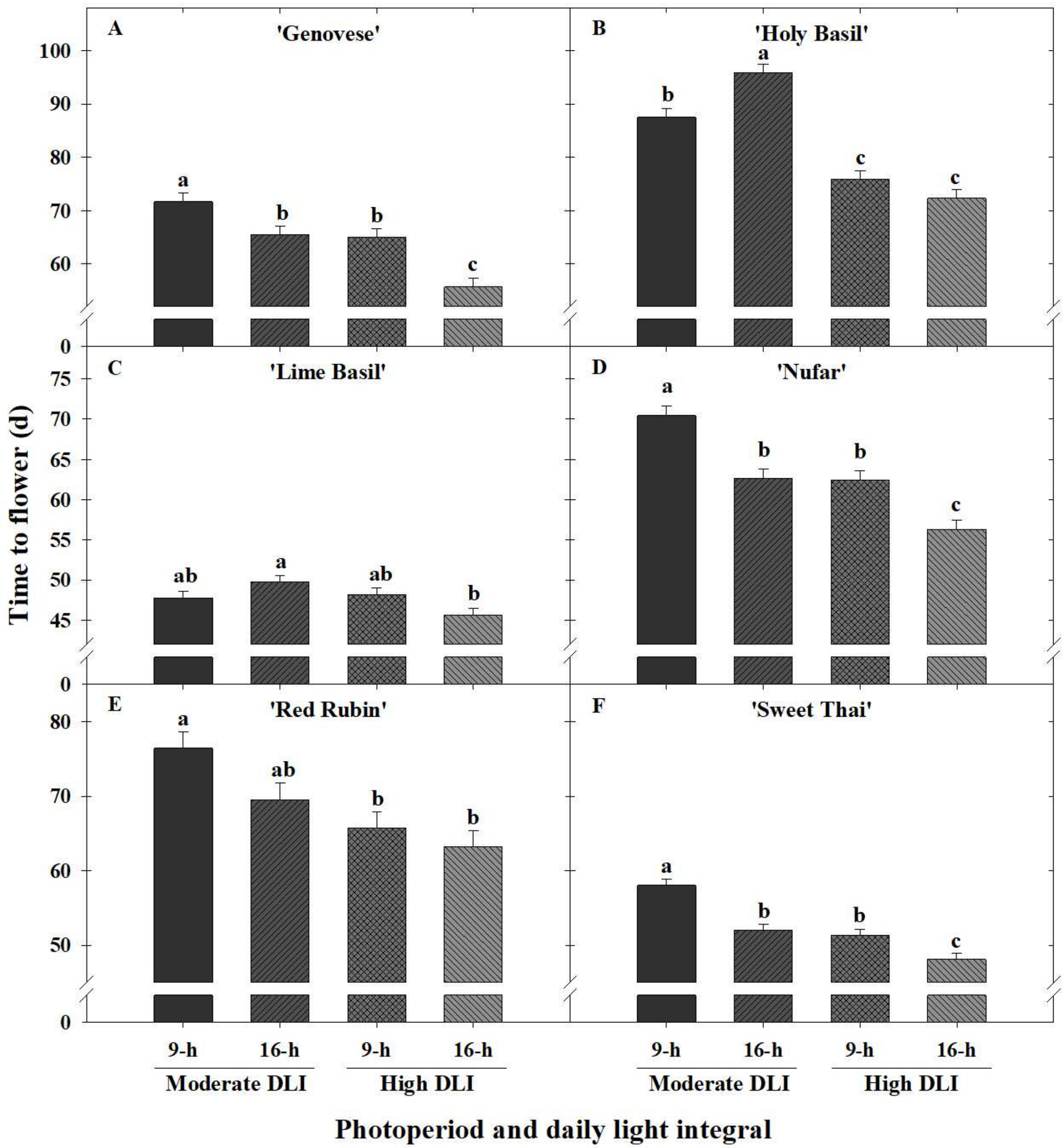


Figure III-7. Expt. 2. time to first open flower (OF) for six basil cultivars grown under moderate or high photosynthetic daily light integrals (DLIs) and a truncated 9-h short-day (SD) or day-extension lighting from low-intensity light-emitting diode (LED) lamps emitting red+white+far-red (R+W+FR) radiation for 7 h (1700 to 2400 HR) to achieve a 16-h photoperiod. Letters indicate mean separations across treatments using Tukey-Kramer difference test at $P \leq 0.05$. Error bars indicate standard error.

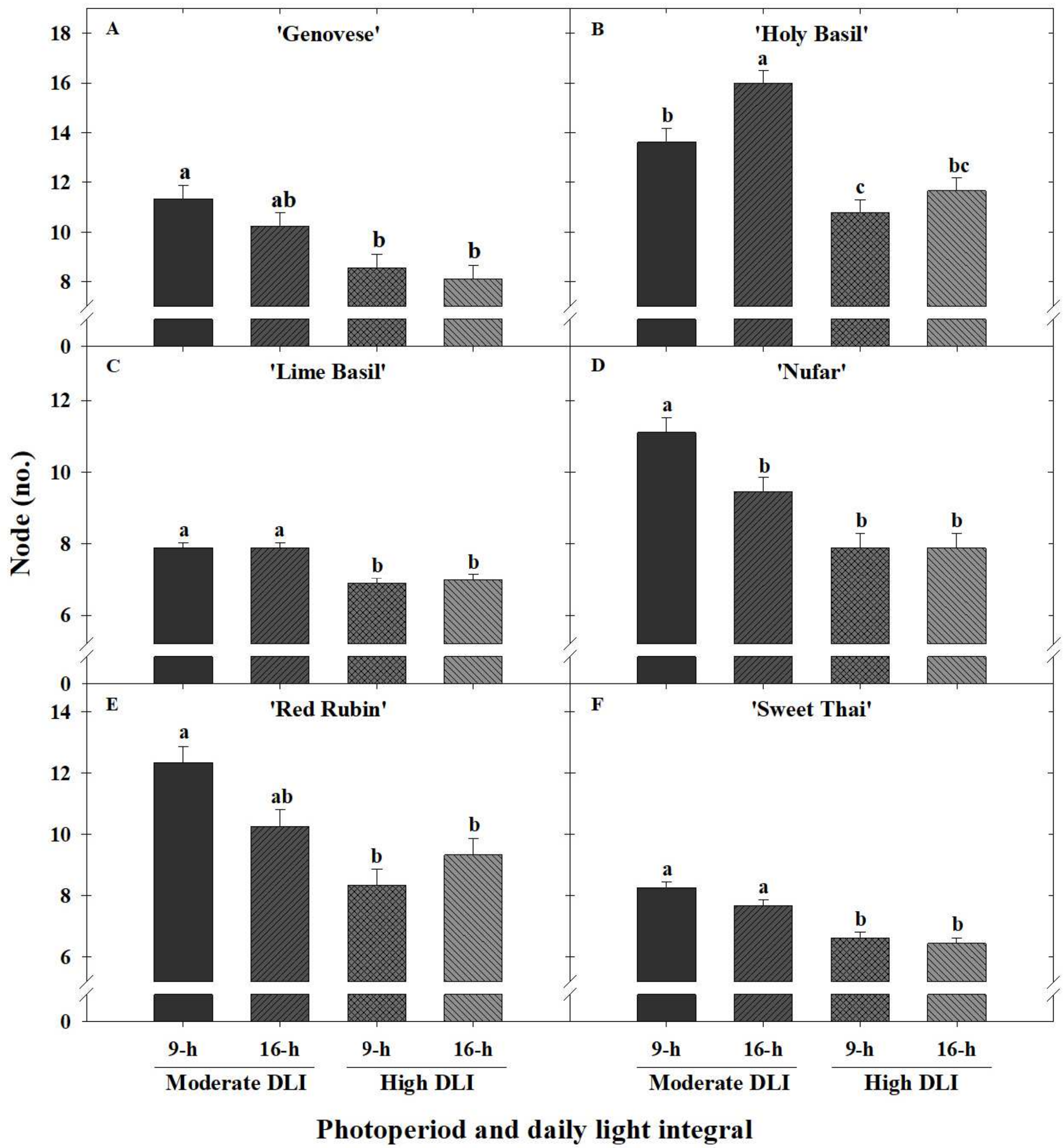


Figure III-8. Expt. 2. node number below the first open flower (OF) for six basil cultivars grown under moderate or high photosynthetic daily light integrals (DLIs) and a truncated 9-h short-day (SD) or day-extension lighting from low-intensity light-emitting diode (LED) lamps emitting red+white+far-red (R+W+FR) radiation for 7 h (1700 to 2400 HR) to achieve a 16-h photoperiod. Letters indicate mean separations across treatments using Tukey-Kramer difference test at $P \leq 0.05$. Error bars indicate standard error.

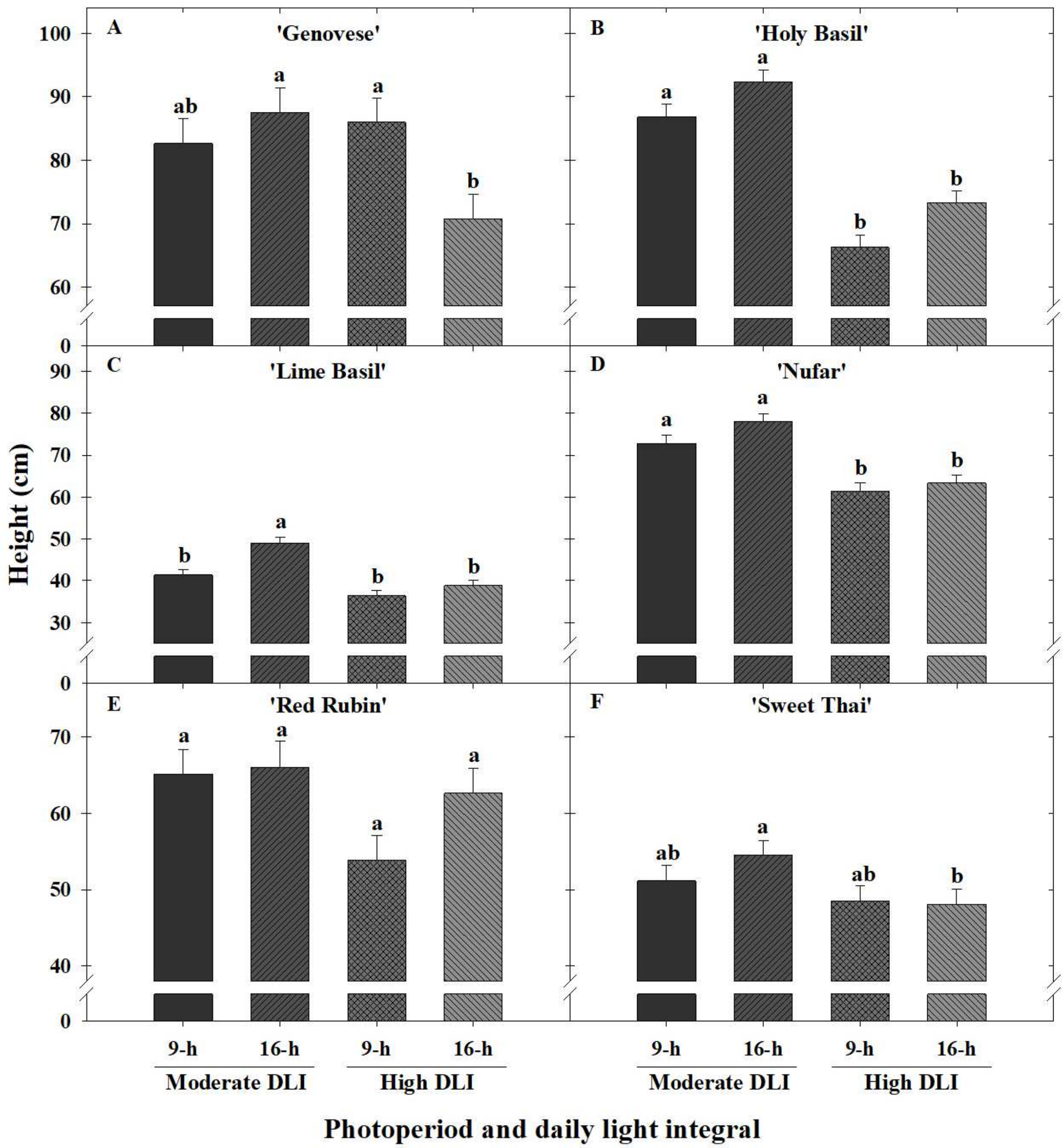


Figure III-9. Expt. 2. height at first open flower for six basil cultivars grown under moderate or high photosynthetic daily light integrals (DLIs) and a truncated 9-h short-day (SD) or day-extension lighting from low-intensity light-emitting diode (LED) lamps emitting red+white+far-red (R+W+FR) radiation for 7 h (1700 to 2400 HR) to achieve a 16-h photoperiod. Letters indicate mean separations across treatments using Tukey-Kramer difference test at $P \leq 0.05$. Error bars indicate standard error.

LITERATURE CITED

LITERATURE CITED

Adam, K.L. 2005. Herbs: organic greenhouse production. Appropriate Technology Transfer for Rural Areas. National Sustainable Agriculture Information Service. 1–16.

Adams, S.R., S. Pearson, P. Hadley, and W.M. Patefield. 1999. The effects of temperature and light integral on the phases of photoperiod sensitivity in *Petunia ×hybrida*. Annals of Bot. 83:263-269.

Beaman, A.R., R.J. Gladon, and J.A. Schrader. 2009. Sweet basil requires an irradiance of 500 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for greatest edible biomass production. HortScience 44:64–67.

Blanchard, M.G. and E.S. Runkle. 2010. Intermittent light from a rotating high-pressure sodium lamp promotes flowering of long-day plants. HortScience 45:236–241.

Bleasdale, J.K.A. 1964. The Flowering and growth of watercress (*Nasturtium Officinale* R. BR.). J. Hort. Sci. 39:277–283.

Burbott, A.J. and W.D. Loomis. 1967. Effects of light and temperature on the monoterpenes of peppermint. Plant Physiol. 42:20–28.

Currey, C.J., D.A. Kopsell, N.S. Mattson, J.K. Craver, R.G. Lopez, J.E. Erwin, and C. Kubota. 2017. Supplemental and sole-source lighting of leafy greens, herbs, and microgreens, p. 170–180. In: R. Lopez and E.S. Runkle (eds.). Light management in controlled environments. Meister Media Worldwide, Willoughby, OH.

Currey, C.J., R.G. Lopez, and N.S. Mattson. 2011. Flower induction of annuals. Purdue Extension Bulletin HO–249-W. <https://www.extension.purdue.edu/extmedia/ho/ho-249-w.pdf>.

Davis, J.M. 1995. *North Carolina Basil Production Guide.* N.C. Cooperative Extension, NC State University, Raleigh. AG-477. <https://content.ces.ncsu.edu/north-carolina-basil-production-guide>.

Darrah, H.H. 1980. The Cultivated basils. Thomas Buckeye Printing Company, Independence, Miss.

DeKalb, C.D., B.A. Kahn, B.L. Dunn, M.E. Payton, and A.V. Barker. 2014. Substitution of soilless medium with yard waste compost for basil transplant production. HortTechnology 24:668–675.

Dole, J.M. and H.F. Wilkins. 2005. Floriculture: Principles and species. 2nd ed. Prentice Hall, Upper Saddle River, NJ.

Dou, H., G. Niu, M. Gu, and J.G. Masabni. 2018. Responses of sweet basil to different daily light integrals in photosynthesis, morphology, yield, and nutritional quality. HortScience 53:496–503.

Erwin, J., N. Mattson, and R. Warner. 2017. Light effects on bedding plants, p. 119–134. In: R. Lopez and E.S. Runkle (eds.). Light management in controlled environments. Meister Media Worldwide, Willoughby, OH.

Erwin, J.E. and R.M. Warner. 2002. Determination of photoperiodic response group and effect of supplemental irradiance on flowering of several bedding plant species. Acta Hort. 580:95–99.

Evans, W.C. 2009. Trease and Evans pharmacognosy. 16th ed. Saunders Elsevier, Philadelphia, N.Y.

Faust, J.E., V. Holcombe, N.C. Rajapakse, and D.R. Layne. 2005. The effect of daily light integral on bedding plant growth and flowering. HortScience 40:6645–649.

Grayer, R. J., G. C. Kite, F. J. Goldstone, S. E. Bryan, A. Paton, and E. Putievsky. 1996. Infraspecific taxonomy and essential oil chemotypes in sweet basil, *Ocimum basilicum*. Pytochemistry 43:1033–1039.

Hurt, A., R.G. Lopez, and J.K, Craver. 2019. Supplemental but not photoperiodic lighting increased seedling quality and reduced production time of annual bedding plants. HortScience 54:289-296.

Kalita, J. and M.L. Khan. 2013. Commercial potentialities of essential oil of *Ocimum* members growing in North East India. Intl. J. Pharmacy Life Sci. 4:2559–2567.

Langston, R. and A.C., Leopold. 1954. Photoperiodic responses of peppermint. Proc. Amer. Soc. Hort. Sci. 63:347–352.

Mattson, N.S. and J.E. Erwin. 2005. The impact of photoperiod and irradiance on flowering of several herbaceous ornamentals. Sci. Hort. 104:275–292.

Moccaldi, L.A. and E.S. Runkle. 2007. Modeling the effects of temperature and photosynthetic daily light integral on growth and flowering of *Salvia splendens* and *Tagetes patula*. J. Amer. Soc. Hort. Sci. 132:283–288.

Moe, R. and R.D. Heins. 1990. Control of plant morphogenesis and flowering by light quality and temperature. Acta Hort. 272:81–89.

Nemali, K. and M. van Iersel. 2004. Acclimation of photosynthesis and growth of wax begonias grown at different light levels, p. 22–23. In: Fisher, P.R. and E.S. Runkle (eds.). Lighting up profits. Meister Media Worldwide, Willoughby, OH.

Nurzynska-wierdak, R., B. Borowski, K. Dzida, G. Zawislak, and R. Kowalski. 2013. Essential oil composition of sweet basil cultivars as affected by nitrogen and potassium fertilization. Turkish. J. Agr. For. 37:427–436.

Oh, W., E.S. Runkle, and R.M. Warner. 2010. Timing and duration of supplemental lighting during the seedling stage influence quality and flowering in Petunia and Pansy. HortScience 45:1332–1337.

Owen, W.G., Q. Meng, and R.G. Lopez. 2018. Promotion of flowering from far-red radiation depends on the photosynthetic daily light integral. HortScience 53:465–471.

Padhye, S.R. and E.S. Runkle. 2011. Use of compact fluorescent lamps to provide a long-day photoperiod to herbaceous perennials. Acta. Hort. 886:197–205.

Putievsky, E. 1983. Temperature and daylength influences on the growth and germination of sweet basil and oregano. J. Hort. Sci. 58:583–587.

Putievsky, E. and B. Galambosi. 1999. Production systems of sweet basil. Basil: the genus *Ocimum*, Vol. 10, p. 39–65. In: R. Hiltuen and Y. Holm (eds.). Basil the genus *Ocimum*. Harwood Academic Publishers. Australia.

Runkle, E.S. and R.D. Heins. 2003. Photocontrol of flowering and extension growth in the long-day plant pansy. J. Amer. Soc. Hort. Sci. 128:479–485.

Runkle, E., R. Lopez, and P. Fisher. 2017. Photoperiodic control of flowering, p. 38–47. In: R. Lopez and E.S. Runkle (eds.). Light management in controlled environments. Meister Media Worldwide, Willoughby, OH.

Simon, J. E. 1985. Sweet basil a production guide. Purdue University, Cooperative Extension Service, Indiana. 13 June 2018. <https://www.extension.purdue.edu/extmedia/HO/HO-189.html>.

Simon, J.E. 1995. Basil. Purdue University, Cooperative Extension Service, Indiana. 13 June 2018. < https://www.hort.purdue.edu/newcrop/CropFactSheets/basil.html>.

Simon, J. E., J. Quin, and R. G. Murray. 1990. Basil: A source of essential oils, p. 484–489. In: J. Janick and J.E. Simon (eds.). Advances in new crops. Timber Press, Portland, Ore.

Simon, J.E., M.R. Morales, W.B. Phippen, R.F. Vieira, and Z. Hao. 1999. Basil: A source of aroma compounds and a popular culinary and ornamental herb, p. 499–505. In: J. Janick (eds.). Perspectives on new crops and new uses. ASHS Press, Alexandria, Va.

Skrubis, B. and P. Markakis. 1976. The effect of photoperiod on the growth and the essential oil of *Ocimum basilicum* (Sweet Basil). Economic Bot. 30:389-393.

Taiz, L. and E. Zeiger. 2010. Plant physiology. 5th ed. Sinauer Associates, Inc, Sunderland, Mass.

Thomas, B. and D. Vince-Prue. 1997. Photoperiodism in plants. Academic Press, San Diego, Calif.

Thomas, B. and D. Vince-Prue. 1984. Juvenility, photoperiodism, and vernalization, p. 408–439. In: M.B. Wilkins (ed.). Advanced plant physiology. Longman Scientific and Technical, Essex, UK.

Torres, A.P. and R.G. Lopez, 2011. Photoperiod and temperature influence flowering responses and morphology of *Tecoma stans*. HortScience 46:416–419.

U.S. Department of Agriculture (USDA). 2015. Census of Horticultural Specialties (2014). National Agricultural Statistics Service. Washington DC. 30 Mar. 2019. <https://www.nass.usda.gov/Publications/AgCensus/2012/Online_Resources/Census_of_Horticulture_Specialties/HORTIC.pdf>.

Walters, K.J. and C.J. Currey. 2018. Effects of nutrient solution concentration and daily light integral on growth and nutrient concentration of several basil species in hydroponic production. HortScience 53:1319–1325.

Warner, R.M. 2010. Temperature and photoperiod influence flowering and morphology of four *Petunia* spp. HortScience 45:365–368.

Whitman, C.M., R.D. Heins, A.C. Cameron, and W.H. Carlson. 1998. Lamp type and irradiance level for day length extensions influence flowering of *Campanula carpatica* 'Blue Clips', *Coreopsis grandiflora* 'Early Sunrise', and *Coreopsis verticillata* 'Moonbeam'. J. Amer. Soc. Hort. Sci. 123:802–807.

Williamson, J. 2019. Basil. 18 July 2019. <https://hgic.clemson.edu/factsheet/basil/>.

Zhang, D., A.M. Armitage, J.M. Affolter, and M.A. Dirr. 1996. Environmental control of flowering and growth of *Achillea millefolium* L. 'Summer Pastels'. HortScience 31:364–365.

SECTION IV

SUPPLEMENTAL LIGHTING RADIATION QUALITY INFLUENCES CUCUMBER, TOMATO, AND PEPPER TRANSPLANT GROWTH AND DEVELOPMENT

Supplemental lighting radiation quality influences cucumber, tomato, and pepper transplant growth and development

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Abstract

Supplemental lighting (SL) is required for the production of high-quality vegetable transplants in greenhouses when 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 SL spectral quality beyond blue (B) and red (R) radiation influence plant growth and development. Seeds of hybrid greenhouse seedless cucumber 'Elsie' (*Cucumis sativus*), tomato 'Climstar' (*Lycopersicon esculentum* Mill.), 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 SL treatments delivered a total photosynthetic 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 (700–800 nm) LEDs] and a control that delivered 25 $\mu mol \cdot m^{-2} \cdot s^{-1}$ from HPS lamps with matching photoperiod. The LED treatments defined by their wavebands (photon flux density in $\mu mol \cdot m^{-2} \cdot s^{-1}$) of B, green (G, 500–600 nm), R and far-red (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, tomato, and pepper transplants under $B_{30}G_{30}R_{60}$ and HPS_{120} SL had the greatest stem diameter. Fresh weight and leaf area of all three species was significantly greater when G radiation replaced R or B radiation. For example, leaf area and fresh weight of cucumber, tomato, and pepper increased by 33, 49, and 22% and 35, 56, and 14%, respectively, for plants under $B_{30}G_{30}R_{60}$ SL compared to plants under $B_{25}R_{95}$ SL. Generally, both cucumber and pepper transplants were most compact under $B_{25}R_{95}$ SL and tomatoes under the HPS_{25} (low intensity control) and $B_{25}R_{95}$ SL. The inclusion of FR radiation

reduced the incidence of leaf necrosis. From this study, one can conclude that plant responses to SL quality are generally species-specific, and therefore high-wire transplants should be grown separately to optimize production, however more studies are required.

Keywords: *Capsicum annuum*, *Cucumis sativus*, greenhouse, hydroponic, *Lycopersicon esculentum*, seedlings.

Abbreviations: ADT, average daily temperature; B, blue; CE, controlled-environment; DLI, daily light integral; FR, far red; G, green; HPS, high-pressure sodium; INC, incandescent; IR, infra-red; LED, light-emitting diode; PL, photoperiodic lighting; *PPFD*, photosynthetic photon flux density; PSII, photosystem, R, red; SL, supplemental lighting; SSL, sole-source lighting *TPFD*, total photon flux density; UV, ultraviolet; W, white.

Introduction

Controlled-environment (CE) greenhouse and protected production of fruiting vegetable crops offers many advantages over open field production, including: increased fruit quality and yield; predictable crop timing; year-round production; reduced water usage, pest and weed control pressure, and climatic extremes such as drought, flooding, and low- and high-temperature stress (McCartney and Lefsrud, 2018). Therefore, CE production of food crops, within greenhouses and other protected structures, is gaining interest in the United States (U.S.) (Indoor Crop Production Feeding the Future, 2015). From 2009 to 2014, CE and protected food crop production area increased by 31% 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 metric tons of produce grown under protection in 2014, high-wire fruiting vine crops such as tomato (*Solanum lycopersicum*), cucumber (*Cucumis sativus*), and pepper (*Capsicum* spp.) accounted for 37, 14, and 1%, 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; 543 of which utilized 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).

Nonetheless, the need for a reliable domestic source of high-quality grafted transplants for CE production has out-paced current availability (Kubota et al., 2004). As a result, greenhouse vegetable growers are purchasing grafted transplants from specialized producers, mainly sourced from Canadian propagators (Kubota and Kroggel, 2004). Imported transplants can potentially to be denied entry into the U.S. based on phytosanitary grounds. Furthermore, prolonged shipping by truck increases the risk of transplant deterioration, resulting in successive delayed growth, flower abortion and delayed fruit development from low light, ethylene exposure, chilling, and/or freezing injury (Kubota et al., 2004; Kwack et al., 2016).

Transplants used for CE production are grown in soilless media (i.e. rock wool or coco coir) (Boyhan and Granberry, 2017), irrigated using subirrigation systems (i.e. ebb and flow or flood floors), and grown under high-intensity supplemental lighting (SL) (Demers and Gosselin, 2002; Hernandez, and Kubota, 2012; Mitchell et al., 2015; McCall, 1992). Supplemental lighting is used to increase the daily light integral (DLI) in greenhouses when solar radiation intensities and day lengths are limited, especially during winter months (Hernandez, and Kubota, 2012; Mitchell et al., 2015; McCall, 1992). 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, can be produced under SL (Fisher et al., 2017).

High-pressure sodium (HPS) lamps have been the industry standard for greenhouse SL for many decades. However, the recent availability of high-intensity and energy-efficient, light-emitting diode (LED) fixtures, have made them a promising alternative as their prices continue to decrease and energy efficacies increase. LEDs are solid-state, semiconducting devices (Bourget, 2008), with a narrow- or broad-band radiation spectrum (Currey and Lopez, 2013;

Mitchell et al., 2015). Their long lifetime, small size, and cool-emitting temperatures can make them well suited for CE horticultural production (Mitchell et al., 2015).

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

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 $mol·m^{-2}·d^{-1}$) with HPS or monochromatic B or R LED SL that increased the DLI by 3.7 $mol·m^{-2}·d^{-1}$ (Hernandez and Kubota, 2015). No significant differences in shoot fresh and dry mass 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 mass than plants grown under LEDs that provided B or R radiation, respectively. Presumably the increased fresh mass was due to higher leaf temperatures, resulting from infra-red (IR) radiation emitted from HPS SL. More importantly, 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 maybe species dependent (Hernandez and Kubota, 2014b).

Green radiation was long considered the least efficient waveband within the PAR spectrum for photosynthesis (McCree, 1972). However, G radiation's low absorption rate 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, fresh and dry mass of cucumber hybrid 'Mandy' transplants (Novičkovas et al., 2012). However, plant responses to SL containing G radiation have been contradictory. For example, Kim et al. (2004) found that a high percentage of green radiation [>50% of total 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 were increased when G radiation was filtered from W radiation provided by cool-white fluorescent (CWF) lamps. Furthermore, when supplementary G radiation was added to W light the fresh weight of marigold was reduced, but height was unaffected (Klein et al., 1965).

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 the production of economically significant cultivars of cucumber, tomato, and pepper for transplant production. We postulate that supplemental lighting including green or far-red radiation will increase vegetable transplant quality by increasing leaf area and fresh mass, but will also increase stem length and decrease stem diameter.

Materials and methods

Plant material

Hybrid greenhouse cucumber ‘Elsie’, tomato ‘Climstar’, and pepper ‘Kathia’ (*Capsicum annuum*) 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 05 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 Hyro 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. 42 °N). Plants were rotated daily to mitigate any positional effects within the greenhouses. After ten days under SL for cucumber and fourteen 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 tote reservoir (HDX, The Home Depot, Atlanta, GA), and a submersible water pump (Kedsum-3500 65 Watt pump; Xiolan, China) that delivered 49-L·m^{-1} to their respective flood bench. The pH and EC of the nutrient solution within reservoirs were adjusted daily using a hand-held meter (HI 991301 pH/EC/TDS Meter: Hanna Instruments). The pH was adjusted to 6.0 using sulfuric acid (pH down) and potassium bicarbonate (pH up). The EC was adjusted using reverse osmosis water to 0.88 dS·m^{-1}. The mean pH and EC (±SD) during the experiment were 6.1 ± 0.1 and 0.9 ± 0.01 dS·m^{-1}, respectively. Actual values pH and EC values, per greenhouse compartment are reported in Table 1.

Greenhouse environmental conditions

Whitewash (ReduSol; Baarle-Nassau, 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 also 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, USA) 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 means 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 ≈440 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (on for a minimum of 25 minutes and off for a minimum of 20 minutes)]. Four 400-W HPS lamps (LR48877; P.L. Light Systems, Beamsville, Ontario, Canada) or three 600-W LEDs 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. The 100-nm waveband ratios of the three LED SL treatments, delivered by cool W and R LEDs and defined by their wavebands (photon flux density in $\mu mol \cdot m^{-2} \cdot s^{-1}$) of B, G, R, and FR radiation, were $B_{20}G_{10}R_{75}FR_{15}$, $B_{25}R_{95}$, and $B_{30}G_{30}R_{60}$. Additionally, the $B_{30}G_{30}R_{60}$ SL treatment also provided 2 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of FR radiation. The HPS lamps emitted intensities of $B_1G_{13}R_9FR_2$ (HPS_{25}) and $B_7G_{57}R_{47}FR_9$ (HPS_{120}). For cucumber, tomato, and pepper, the total number of lamp hours of operation was 325, 407, and 370 (Rep 1), 426, 521, and 478 (Rep 2), and 431, 522, and 468 (Rep 3). For all sections, spectral quality and *TPFD* at plant height were measured in twelve separate locations throughout the growing area with a portable spectroradiometer (PS-200; Stellar-Net, Tampa, FL) (Figure 1). Spectral scans and radiation intensity measurements of the SL were taken at night, at the beginning or end of each replication to ensure consistency from one replication to another. The total DLIs are reported in Table 1. The phytochrome photoequilibrium was estimated for all five lighting treatments following Sager et al. (1988).

Plant measurements and experimental design

Excluding germination, cucumber plants were harvested after 28 days under SL, while tomato and pepper plants were harvested after 35 days. Plant height (measured from the medium surface to 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 Switzerland). The number of nodes and fully expanded leaves (greater than 1 cm in length) per plant were also recorded at harvest. Internode length was calculated by 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). The reproductive status of each plant was also recorded. Plants were deemed either reproductive or non-reproductive, 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 replications, and the number of leaves with necrotic lesions were divided by the total number of leaves per plant to calculate incidence of leaf necrosis (%). Plants were excised just above the medium, and total shoot (stems and leaves) fresh weight was measured using a digital scale. Stems and leaves were put into paper envelopes and placed inside a drying oven set at ≥70 °C for ≥ 6 d. Dry weights for each plant were recorded after drying. Prior to the destructive plant measurements, chlorophyll fluorescence of five plants, per species, per treatment were measured using a portable chlorophyll fluorescence meter (Handy Plant Efficiency Analyzer (PEA); Hansatech Instruments Ltd., King's Lynn, 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 1,200 µmol·m^{-2}·s^{-1}) for 5 s to saturate photosystem II (PSII). Chlorophyll fluorescence was expressed as F_v/F_m.

The experiment was a randomized complete block design (RCBD), with three replications over time. Plants were blocked by SL treatments with 10 experimental units (individual plants) of each species per treatment and replication. 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 replication 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, with the exception of dry weight, were analyzed and presented as pooled results. Data for dry weight was pooled for Rep. 1 and 2, while Rep. 3 was analyzed separately due to inconsistencies between Reps. 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 significantly lower than all the other treatments. Height, hypocotyl, and internode length were greatest 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 $B_{30}G_{30}R_{60}$ SL, and the least were recorded under $B_{25}R_{95}$ SL (Fig. 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, with the exception of 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 the $B_{25}R_{95}$ 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 greater under HPS_{120}, $B_{20}G_{10}R_{75}FR_{15}$, and $B_{30}G_{30}R_{60}$, and shorter 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 to 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 (986cm^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, 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, fresh weight of plants grown under the control was 5.8 (17.1%), 17.2 (38.2%), 17.4 (38.4%), and 24.5 g (46.7%) 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 days, all plants under SL had 100% visible flower buds, while plants under the low intensity control only had 6.7% (Fig. 4B). For tomato plants grown under HPS_{120} and $B_{30}G_{30}R_{60}$ SL, the incidence of leaf necrosis was 20.7% and 16.9%, respectively (Fig. 5).

Pepper

Data for stem diameter, internode length, leaves, leaf area, fresh weight, F_v/F_m and visible flower bud formation were pooled (Fig. 2C, L, 3C, F, I, O, and 4C). Data from Rep. 2 and 3 were pooled together for height, hypocotyl, and dry weight (Fig. 2F, I, and 3L). For node number, Rep. 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 Rep. 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). From the un-pooled results hypocotyl length was still the greatest under the control (4.1 cm) (Fig. 2I). Internode length was greatest under the control, and was significantly greater compared to HPS_{120}, $B_{25}R_{95}$, and $B_{30}G_{30}R_{60}$, but not $B_{20}G_{10}R_{75}FR_{15}$ 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 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). From the un-pooled results, the greatest dry weight was observed in plants grown under $B_{25}R_{95}$, but was not significantly different from plants grown under HPS_{120} and $B_{30}G_{30}R_{60}$ SL (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 mass (Oh et al., 2010; Randall and Lopez, 2014). 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 non-grafted transplants (Lee, 1994). Grafted seedlings benefit from extended hypocotyl length, since it helps to increase grafting success and hence survival rate, and reduce rooting from the scion after transplant (Chai and Kubota, 2010). However, elongated hypocotyls are not desired for non-grafted seedlings, because it 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; Poel and Runkle, 2017; Hernandez and Kubota, 2012). Gomez and Mitchell (2015) evaluated multiple tomato cultivars under varying DLIs throughout the year. Ambient DLIs were supplemented with HPS lamps or LEDs providing (%) 20:80, 5:95, or 0:100 B:R radiation at a *PPFD* of 61 ± 2 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for 23 $h \cdot d^{-1}$ to achieve a SL DLI of 5.1 $mol \cdot m^{-2} \cdot d^{-1}$. For tomato cultivars grown under SL, hypocotyl diameter, epicotyl length, leaf number, leaf area, and shoot dry weight increased, while hypocotyl elongation was decreased (Gomez and Mitchell, 2015). In another study conducted by Poel and Runkle (2017), petunia (*Petunia ×hybrida*) 'Wave Misty Lilac', snapdragon (*Antirrhinum majus*) 'Montego Yellow', and tomato 'Supersweet' seedlings were grown under PL providing 10 $\mu mol \cdot m^{-2} \cdot s^{-1}$ or SL providing a *PPFD* of 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for 16 $h \cdot d^{-1}$. A 16 to 40% increase in DLI from SL generally increased the number of leaves, dry root and shoot weight. For tomato seedlings, shoot and root dry weight was 27 and 38% lower, respectively, when grown under PL in comparison to HPS SL (Poel and Runkle, 2017).

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 (≈11.8 $mol \cdot m^{-2} \cdot d^{-1}$) stem diameter of cucumber and pepper increased, compared to the low intensity control (≈6.1 $mol \cdot m^{-2} \cdot d^{-1}$) by 17 to 27% and 14 to 25%, respectively (Fig. 2A, 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 'Titan Red Dark' (*Catharanthus roseus*), impatiens 'Super Elfin XP Blue Pearl' (*Impatiens walleriana*), and geranium 'Bullseye Red' (*Pelargonium ×hortorum*) under ambient solar radiation (control) to SL from HPS lamps or LEDs providing a ratio (%) 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 was increased from ≈6.1 to ≈11.8 $mol \cdot m^{-2} \cdot d^{-1}$ shoot dry weight of tomato transplants increased by 107 to 183% compared to 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 that 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, 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; McCall, 1992). However, studies have not always 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 that greater than 40% of the total DLI needs to come from SL to elicit morphological responses. For instance, 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' were observed. In the current study, SL provided ≈43% of the total DLI for cucumber, tomato, and pepper transplants. Hernandez and Kubota (2014a) also reported that under B and R LED SL spectral quality treatments only elicited morphological responses when the solar DLI was low.

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 to the $B_{25}R_{95}$ (Fig. 3D-I). A possible explanation could be the replacement of R or B radiation for G. The increased leaf area and fresh weight can be in part attributed to G radiation's ability to be transmitted more deeply into the plant canopy compared to R and B radiation (Klein, 1992;

Smith, 1993). For example, chlorophyll weakly absorbs G radiation, meaning that up to 80% G radiation is transmitted through the chloroplast (Terashima et al., 2009), thereby allowing more G photons to pass deeper into the mesophyll (Smith et al., 2017; Sun et al., 1998) and thus helping to further increase photosynthetic efficiency, biomass accumulation, and yield (Smith et al., 2017). Kim et al. (2004) observed similar results, where growth of lettuce (*Lactuca sativa* 'Waldmann's Green') 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 (PGRs) (Currey and Lopez, 2011; Lopez and Runkle, 2007) or day/night differentials (DIF) (Ecke et al., 2004) for the control of extension growth or plant height (Randall and Lopez, 2014; Wollaeger and Runkle, 2015). For instance, under monochromatic red 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 prevent 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 to 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 to monochromatic R LEDs, and increased by 346% compared to the 75:25 B:R SSL treatment (Hernandez and Kubota, 2016). Similarly, we observed reductions in height of vegetable transplants grown under $B_{25}R_{95}$, which were not as apparent in other LED treatments that contained G and FR radiation (Fig. 2D-F).

SL and SSL radiation intensity can have varying results on extension growth and height depending on the plant species (Randall and Lopez, 2014; 2015; Poel and Runkle, 2017). We found that by increasing the DLI from ≈6.1 to 11.8 $mol \cdot m^{-2} \cdot d^{-1}$, height of cucumber and pepper transplants was generally more compact under SL compared to 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 to the low intensity control (Fig. 2E). Similarly, Pramuk and Runkle (2005) found species-dependent responses for height in ornamental seedlings when the DLI was increased from 4.1 to 14.2 $mol \cdot m^{-2} \cdot d^{-1}$ under SSL. For instance, height of impatiens 'Accent Red' and *Salvia splendens* 'Vista Red' decreased by 27% and 37%, respectively, while the height of *Tagetes patula* 'Bonanza Yellow' and *Celosia argentea* var. *plumosa* 'Gloria Mix' increased by 10% and 12%, respectively. 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 to 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. 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). When DLI was 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 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).

Considering all three species are categorized as DNPs, and because the duration of SL and PL were equal (16 $h \cdot d^{-1}$), differences in visible bud percentage observed for tomato and pepper can be associated with an increase in DLI. For example, visible flower bud percentage for tomato under the low intensity control was 7%, compared to 100% for plants under SL, regardless of the spectral quality (Fig. 4). For cucumber and pepper there was a small reduction in visible flower bud percentage under $B_{25}R_{95}$ and $B_{20}G_{10}R_{75}FR_{15}$ SL, respectively. Further studies are required to evaluate the spectral quality influence on flower initiation and development of vegetable transplants.

Considering 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 were 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. The incidence of leaf necrosis was 2% for tomato transplants grown under the low intensity control providing 25 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Therefore, the reduction in leaf necrosis can be associated to the lower DLI, in comparison to the SL treatments, which averaged ≈11.8 $mol \cdot m^{-2} \cdot d^{-1}$ across treatments (Fig. 5). Additionally, low fertility can be ruled out as the reason for necrotic symptoms since, low N during transplant production is considered between 50 to 75 $mg \cdot L^{-1}$, and we provided 100 $mg \cdot L^{-1}$. The optimal range for tomato transplant production is 100 to 150 $mg \cdot L^{-1}$ (Whipker et al., 2018).

No biotic factors were identified by a diagnostic lab that might have caused these symptoms; therefore, we suspect that these symptoms were caused by a physiological disorder such as intumescence. This non-pathogenic disorder has been observed previously in susceptible cultivars of tomato grown under ultraviolet (UV)- and/or B-deficit light environments, such as under SSL LEDs (Lang et al. 1983; Eguchi et al. 2016). Under UV-deficit environments it has also been suggested that phytochrome is involved in the regulation of intumescence development in tomato (Morrow, 1987; Morrow and Tibbitts, 1988). In a study by Morrow (1987), intumescence developed under R radiation, but was inhibited under combinations of R and FR. It was also reported that tomato 'Early Girl' plants did not develop intumescence injury when grown under SSL LEDs providing only B radiation (Wollaeger and Runkle, 2014).

HPS lamps have been the industry standard for providing SL to vegetable transplants (Gomez and Mitchell, 2015; Mitchell et al., 2015). However, HPS lamps primarily emit radiation within the 565 to 700 nm range (Randall and Lopez, 2014). LEDs have emerged as a viable alternative SL source, due to their electrical efficacy (Nelson and Bugbee, 2014; Wallace and

Both, 2016) and ability to provide specific light spectra for the optimization of transplant production (Gomez and Mitchell, 2015). From our study, LED SL provided by the $B_{30}G_{30}R_{60}$ provided similar results for many of the parameters evaluated for all three species (Fig. 2A-O and 3A-O). For instance, stem diameter, internode length, and number of nodes for all three species were similar when grown under the HPS_{120} and $B_{30}G_{30}R_{60}$ (Fig. 2A-C, J-O). Additionally, for cucumber and pepper, no significant differences were observed for leaf area and fresh weight when grown under HPS_{120} or $B_{30}G_{30}R_{60}$ (Fig. 3D, F, G, and I). Furthermore, leaf area, fresh and dry weight of tomato was greater when grown under $B_{30}G_{30}R_{60}$ compared to HPS_{120} (Fig. 3E, H, and K). Based on results from our study, transplant quality was equivalent or greater when grown under $B_{30}G_{30}R_{60}$ compared to HPS_{120} SL. Thus, the use of LEDs for SL are a viable and economically feasible alternative to HPS lamps for the production of vegetable transplants in CEs.

In conclusion, the results from our study help to quantify how SL quality influences the morphological and physiological properties of vegetable transplants. 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. For example, stem diameter of cucumber was greatest under the HPS_{120} and $B_{30}G_{30}R_{60}$. 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 G and/or FR 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 the $B_{25}R_{95}$

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 the $B_{25}R_{95}$ SL for both species. 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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APPENDIX

Table IV-1. Supplemental lighting (SL) treatments, replication (Rep.), supplemental radiation, average daily light integral (DLI) from 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} (on for a minimum of 25 minutes and off for a minimum of 20 minutes)], greenhouse canopy air and leaf temperature, and nutrient solution pH and electrical conductivity (EC). Cucumber, pepper, and tomato were placed under treatments on 26 Sept. 2018, 24 Oct. 2018, and 07 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	26.8 ± 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

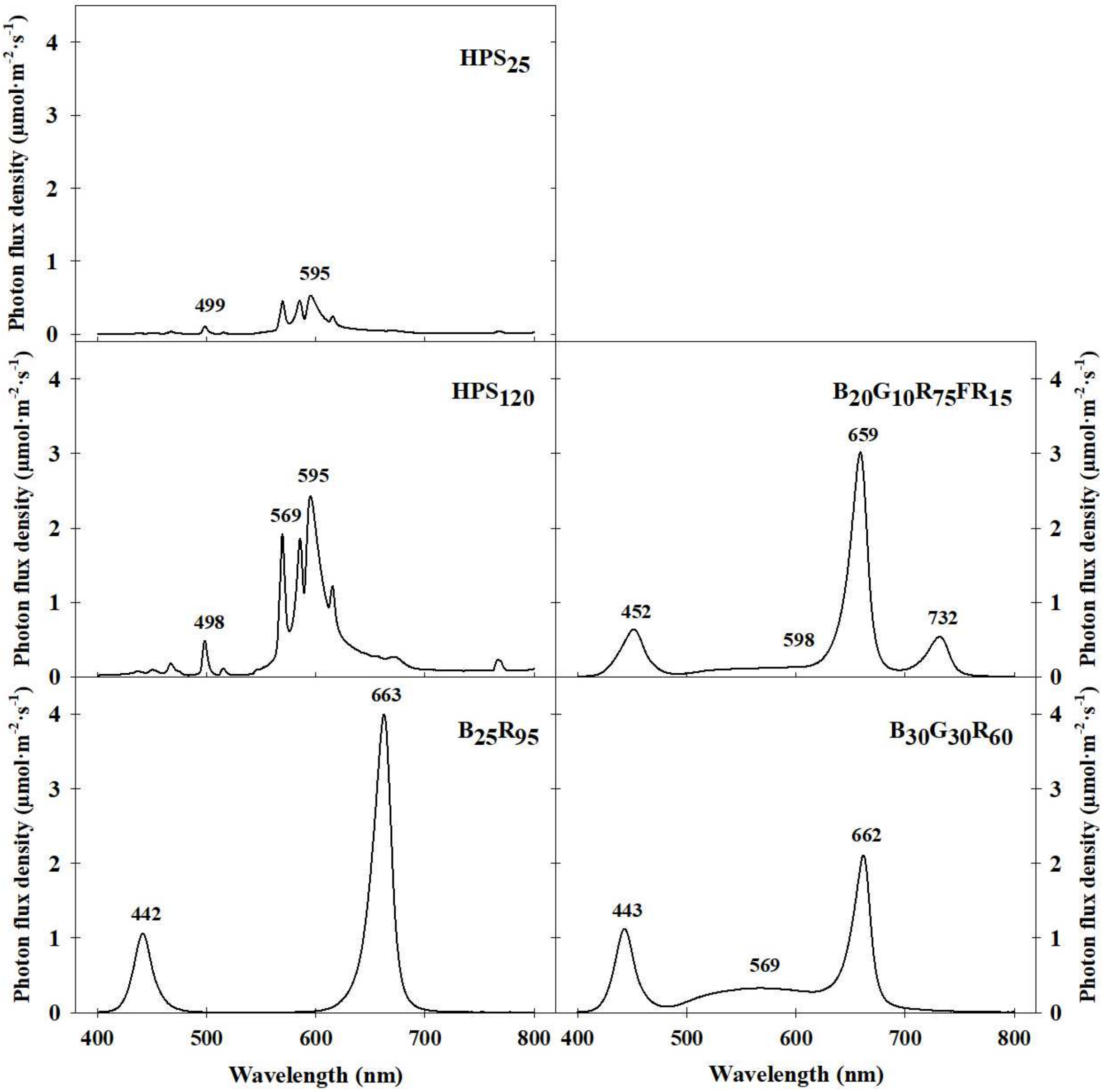

Figure IV-1. Spectral quality delivered from high-pressure sodium (HPS) lamps providing photoperiodic and supplemental lighting (SL) and light-emitting diode (LED) fixtures delivering SL. Blue (B, 400-500 nm) represents the blue photon flux (PF), G (500-600 nm) the green PF, R (600-700 nm) the red PF and FR (700-800 nm) the far-red PF from LEDs. 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 B, G, R, and FR.

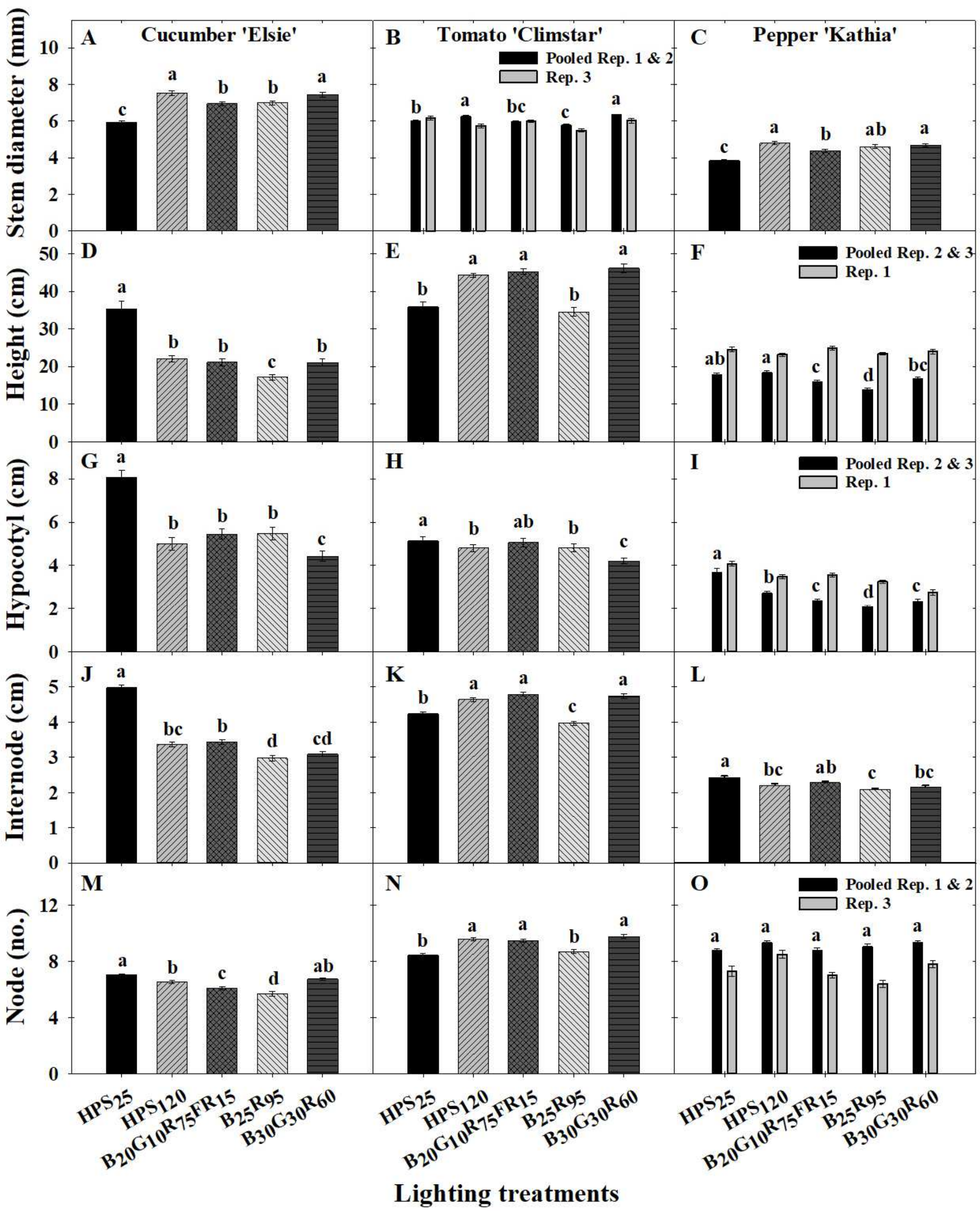

Figure IV-2. Stem diameter (mm), height (cm), hypocotyl (cm), internode length (cm), and average number of nodes per plant of cucumber, tomato, and pepper. Data were collected 28, 35, and 35 days after treatment under high-pressure sodium (HPS) or light-emitting diode (LED) supplemental lighting (SL)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

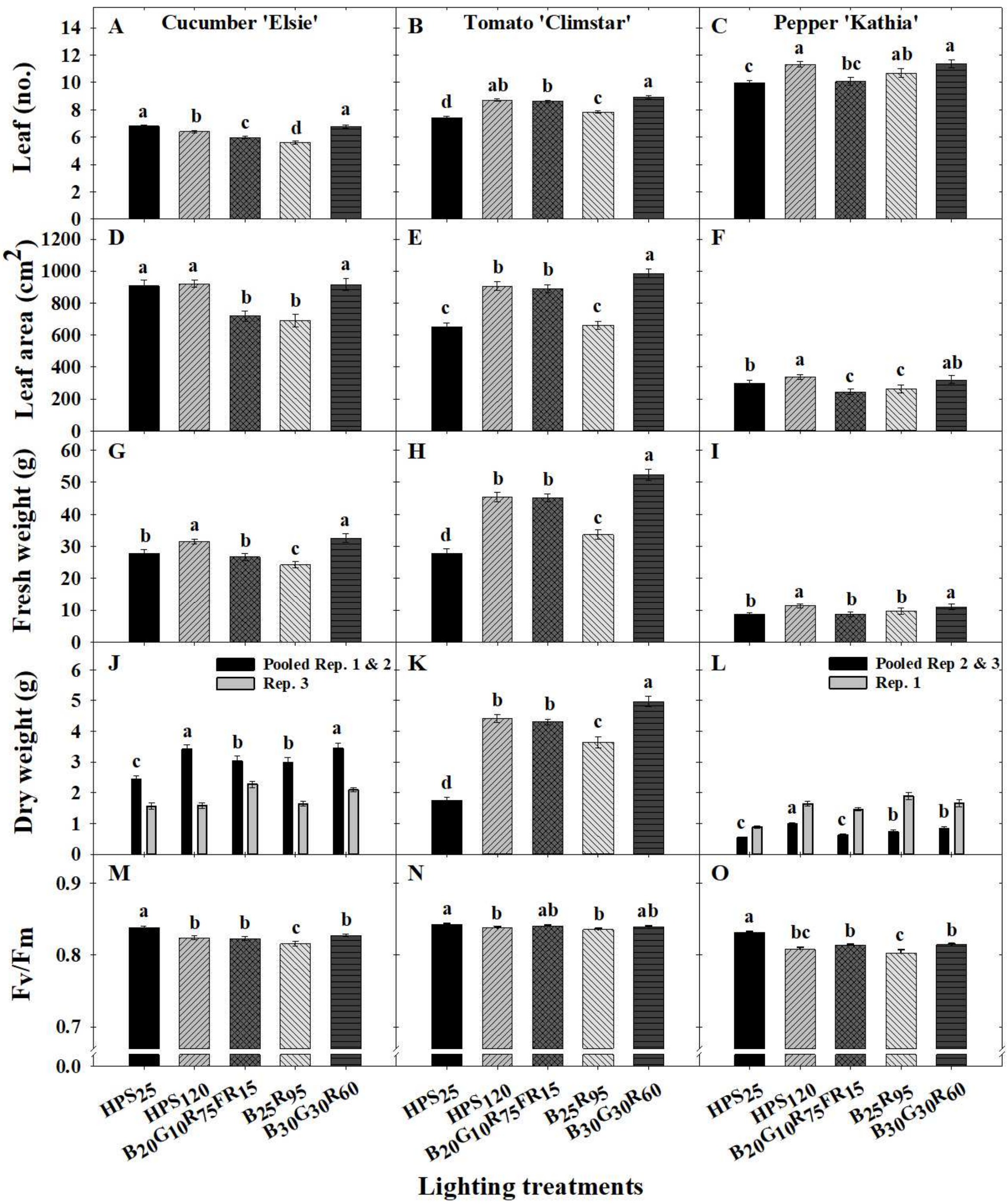

Figure IV-3. Number of leaves, leaf area (cm^2), fresh weight (g), dry weight (g), and chlorophyll fluorescence (F_v/F_m) per plant of cucumber, tomato, and pepper. Data were collected 28, 35, and 35 days after treatment under high-pressure sodium (HPS) or light-emitting diode (LED) supplemental lighting (SL) treatments for cucumber, tomato, and pepper, respectively. Data were pooled when there was no interaction between replication (Rep.) and treatment, or if the response trends were similar between Reps. Letters indicate mean separations across treatments using Tukey-Kramer difference test at $P \leq 0.05$. Error bars indicate standard error. Mean separations were excluded for un-pooled data.

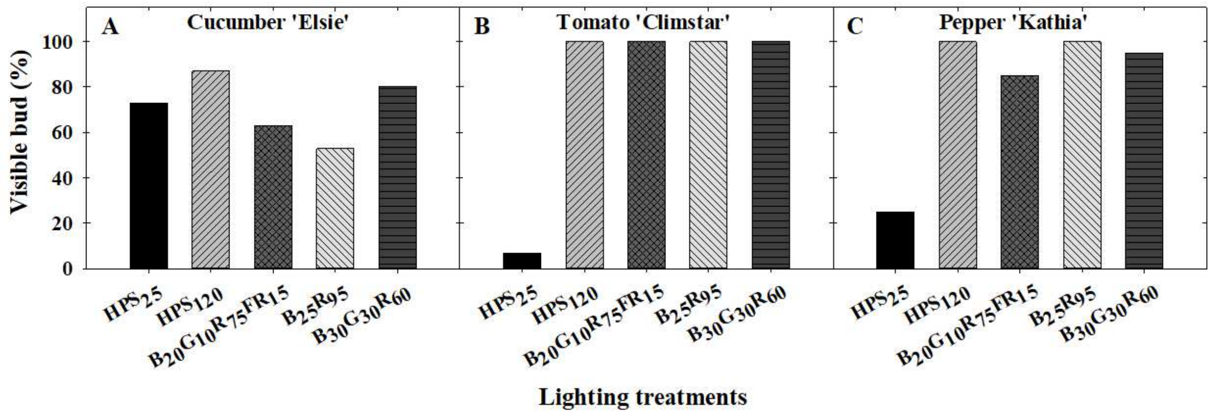

Figure IV-4. Visible bud percentage of 28, 35, and 35 day-old cucumber, tomato, and pepper transplants, grown under different high-pressure sodium (HPS) and light-emitting diode (LED) supplemental lighting (SL) treatments.

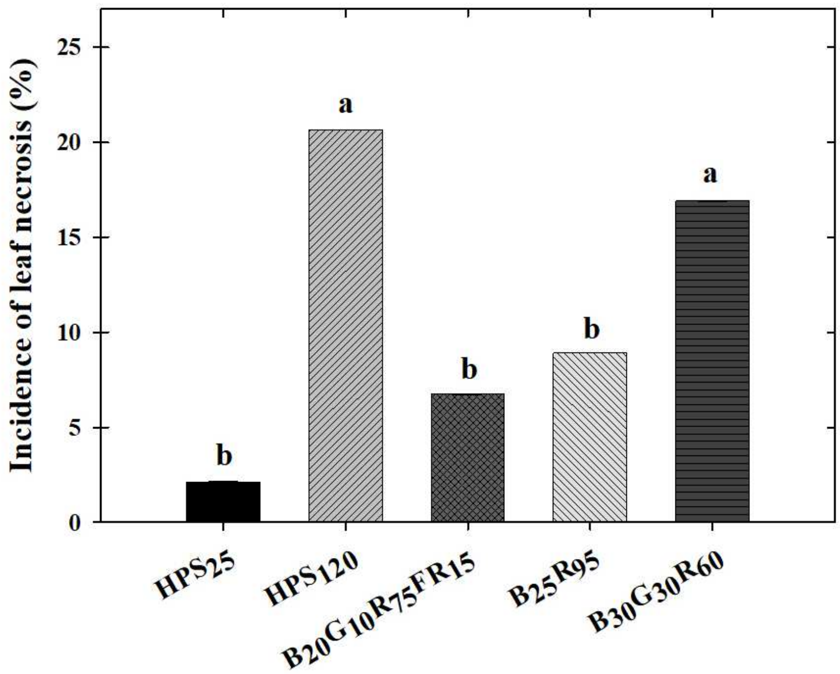

Figure IV-5. The incidence of leaf necrosis resulting from high-pressure sodium (HPS) and light-emitting diode (LED) supplemental lighting (SL) treatments on tomato (‘Climstar’ *L. lycopersicum*), after 35 days of SL. Percentage of leaves damaged (%) was calculated by dividing the number of leaves showing necrotic lesions by the total number of leaves, and multiplying by 100.

LITERATURE CITED

LITERATURE CITED

Bourget, C.M. 2008. An introduction to light emitting diodes. HortScience 43:1944–1946.

Boyhan, G.E. and D.M. Granberry. 2017. Commercial production of vegetables transplants. University of Georgia. Bulletin 1144.

Brown, C.S., A.C. Schuerger, and J.C. Sager. 1995. Growth and photomorphogenesis of pepper plants under red light-emitting diodes with supplemental blue or far-red lighting. J. Am. Soc. Hort. Sci. 120:808–813.

Chia, P.-L. and C. Kubota. 2010. End-of-day far-red light quality and dose requirements for tomato rootstock hypocotyl elongation. HortScience 45:1501–1506.

Currey, C.J. and R.G. Lopez. 2011. Early flurprimidol drench applications suppress final height of four poinsettia cultivars. HortTechnology 21:35–40.

Currey, C.J. and R.G. Lopez. 2013. Cuttings of *Impatiens, Pelargonium*, and *Petunia* propagated under light-emitting diodes and high-pressure sodium lamps have comparable growth, morphology, gas exchange, and post-transplant performance. HortScience 48(4):428–434.

Demers, D.A. and A. Gosselin. 2002. Growing greenhouse tomato and sweet pepper under supplemental lighting: optimal photoperiod, negative effects of long photoperiod and their causes. Acta Hort. 580:83–88.

Dorais, M., C.A. Mitchell, and C. Kubota. 2017. Lighting greenhouse fruiting vegetables, p. 159–169. In: R. Lopez and E.S. Runkle (eds.). Light management in controlled environments. Meister Media Worldwide, Willoughby, OH.

Ecke, III, P., J. Faust, A. Higgins, and J. Williams. 2004. The Ecke poinsettia manual. Ball Publ., Batavia, IL.

Eguchi, T., R. Hernandez, and C. Kubota. 2016. Far-red and blue light synergistically mitigate intumescence injury of tomato plants grow under ultraviolet- deficit light environment. HortScience 51(6):712–719.

Fan, X.X., Z.G. Xu, X.Y. Liu, C.M. Tang, L.W. Wang, and XI. Han. 2013. Effects of light intensity on the growth and leaf development of young tomato plants grown under a combination of red and blue light. Sci. Hort. 153:50–55.

Fausey, B.A., R.D. Heins, and A.C. Cameron. 2005. Daily light integral affects flowering and quality of greenhouse-grown *Achillea*, *Gaura*, and *Lavandula*. HortScience 40:114–118.

Fisher, P., A.J. Both, and B. Bugbee. 2017. Supplemental lighting technology, costs, and efficiency, p. 74–81. In: R. Lopez and E.S. Runkle (eds.). Light management in controlled environments. Meister Media Worldwide, Willoughby, OH.

Gomez, C. and C.A. Mitchell. 2015. Growth responses of tomato seedlings to different spectra of supplemental lighting. HortScience 50(1):112–118.

Greenhouse Management. 2013. U.S. greenhouse produce market to flourish. Greenhouse Management. Accessed 06 March 2019. <https://www.greenhousemag.com/article/greenhouse-produce-market-in-united-states-grows-to-four-billion/>

Hernandez, R. and C. Kubota. 2012. Tomato seedling growth and morphological response to supplemental LED lighting red:blue ratios under varied daily solar light integrals. Acta Hort. 956:187–194.

Hernandez, R. and C. Kubota. 2014a. Growth and morphological response of cucumber seedlings to supplemental red and blue photon flux ratios under varied solar daily light integrals. Scientia Hort. 173:92–99.

Hernandez, R. and C. Kubota, 2014b. LEDs supplemental lighting for vegetable transplant production: Spectral evaluation and comparisons with HID technology. Acta Hort. 1037:829–836.

Hernandez, R. and C. Kubota. 2015. Physiological, morphological, and energy-use efficiency comparisons of LED and HPS supplemental lighting for cucumber transplant production. HortScience 50(3):351–357.

Hernandez, R. and C. Kubota. 2016. Physiological responses of cucumber seedlings under different blue and red photon flux ratios using LEDs. Environ. and Expt. Bot. 121:66–74.

Hurt, A., R.G. Lopez, and J.K. Craver. 2019. Supplemental but not photoperiodic lighting increased seedling quality and reduced production time of annual bedding plants. HortScience 54(2):289–296.

Indoor Crop Production Feeding the Future. 2015. Newbean Capitol. Accessed 06 March 2019. <https://www.arguscontrols.com/articles/indoor-crop-production-feeding-the-future/>.

Jones, J.B., Jr. 2008. Tomato plant culture: In the field, greenhouse, and home garden. 2nd Ed. CRC Press, Boca Raton, FL.

Kim, H.H., R.M. Wheeler, J.C. Sager, G.D. Goins, and J.H. Norikane. 2006. Evaluation of lettuce growth using supplemental green light with red and blue light-emitting diodes in a controlled environment - a review of research at Kennedy Space Center. Acta Hort. 711:111–119.

Klein, R.M. 1992. Effects of green light on biological systems. Biol. Rev. 67:199–284.

Klein, R.M., P.C. Edsall, and A.C. Gentile. 1965. Effects of near ultraviolet and green radiations on plant growth. Plant Physiol. 40:903–906.

Kubota, C. and M. Kroggel. 2004. Optimization of long distance transportation conditions for high quality tomato seedlings: effects of air temperature and light inside trailers. HortScience 39:896.

Kubota, C., M. Kroggel, D. Solomon, and L. Benne. 2004. Analysis and optimization of long distance transportation conditions for high quality tomato seedlings. Acta Hort. 659:227–234.

Kwack, Y., J.H. Lee, and C. Chun. 2016. Proper period and temperature for transportation of cucumber and tomato transplants. Hort. Environ. Biotechnol. 57(6):554–559.

Lang, S.P., B.E. Stuckmeyer, and T.W. Tibbitts. 1983. Morphology and anatomy of intumescence development on tomato plants. J. Amer. Soc. Hort. Sci. 108:266–271.

Lee, J.-M. 1994. Cultivation of grafted vegetables I. current status, grafting methods, and benefits. HortScience 29(4)235–239.

Liu, X.Y., T.T. Chang, S.R. Guo, Z.G. Xu, and J. Li. 2011. Effect of different light quality of LED on growth and photosynthetic character in cherry tomato seedling. Acta Hort. 907:325–330.

Lopez, R.G. and E.S. Runkle. 2007. Early PGR drench applications on poinsettias. Greenhouse Product News 17(8):22–29.

Lopez, R.G. and E.S. Runkle. 2008. Photosynthetic daily light integral during propagation influences rooting and growth of cutting and subsequent development of New Guinea impatiens and petunia. HortScience 43:2052–2059.

Massa, G.D., H.H. Kim, R.M. Wheeler, and C.A. Mitchell. 2008. Plant productivity in response to LED lighting. HortScience 43(7):1951–1956.

McCall, D. 1992. Effect of supplementary light on tomato transplant growth, and the after-effects on yield. Scientia Hort. 51:65–70.

McCartney, L. and M.G. Lefsrud. 2018. Protected agriculture in extreme environments: A review of controlled environment agriculture in tropical, arid, polar, and urban locations. Appl. Eng. in Agr. 34(2):455–473.

McCree, K.J. 1972. Action spectrum, absorptance and quantum yield of photosynthesis in crop plants. Agr Meteorol. 9:191–216.

Mitchell, C.A., M.P. Dzakovich, C. Gomez, R. Lopez, J.F. Burr, R. Hernandez, C. Kubota, C.J.

Currey, Q. Meng, E.S. Runkle, and C.M. Bourget. 2015. Light-emitting diodes in horticulture. Hort. Rev. 43:1–87.

Morrow, R.C. 1987. Environmental factors regulating intumescence development (oedema) in tomatoes. Univ. Wis., Madison, PhD Diss.

Morrow, R.C., and T.W. Tibbitts. 1988. Evidence for involvement of phytochrome in tumor development on plants. Plant Physiol. 88:1100–1114.

Nelson, J.A. and B. Bugbee. 2014. Economic analysis of greenhouse lighting: Light emitting diodes vs. high intensity discharge fixtures. PLoS One. 9:e99010, doi: 10.1371/journal.pone.0099010.

Novičkovas A., A, Brazaitytė, P. Duchovskis, J. Jankauskienė, G. Samuolienė, A. Viršilė, R. Sirtautas, Z. Bliznikas, and A. Žukauskas. 2012. Solid-state lamps (LEDs) for the short-wavelength supplementary lighting in greenhouses: experimental results with cucumber. Acta. Hort. 927:723–730.

Oh, W., E.S. Runkle, and R.M. Warner. 2010. Timing and duration of supplemental lighting during the seedling stage influence quality and flowering in petunia and pansy. HortScience 45:1332–1337.

Poel, B.R. and E.S. Runkle. 2017. Spectral effects of supplemental greenhouse radiation on growth and flowering of annual bedding plants and vegetable transplants. HortScience 52(9):1221–1228.

Pramuk, L.A. and E.S. Runkle. 2005. Photosynthetic daily light integral during the seedling stage influences subsequent growth and flowering of *Celosia*, *Impatiens*, *Salvia*, *Tagetes*, and *Viola*. HortScience 40:1336–1339.

Randall, W.C. and R.G. Lopez. 2014. Comparison of supplemental lighting from high-pressure sodium lamps and light emitting-diodes during bedding plant seedling production. HortScience 49:589–595.

Randall, W.C. and R.G. Lopez. 2015. Comparison of bedding plant seedlings grown under sole-source light-emitting diodes (LEDs) and greenhouse supplemental lighting from LEDs and high-pressure sodium lamps. HortScience 50(5):705-713.

Schrader, W.L. 2000. Using transplants in vegetable production. Publication 8013. Univ. of Calif., Division of Agriculture and Natural Resources.

Smith, H. 1993. Sensing the light environment: the functions of the phytochrome family, p. 377–416. In: R.E. Kendrick and G.H.M. Kronenberg (eds.). Photomorphogenesis in plants. Kluwer Academic Publ., Dordrecht.

Smith, H.L., L. McAusland, and E.H. Murchie. 2017. Don't ignore the green light: exploring diverse roles in plant processes. J. of Exp. Bot. 68(9):2099–2110.

Snowden, M.C., Cope, K.R. and B. Bugbee. 2016. Sensitivity of seven diverse species to blue and green light: interactions with photon flux. PloS one, 11(10):1–32.

Sun, J., J.N. Nishio, and T.C. Vogelmann. 1998. Green light drives CO_2 fixation deep within leaves. Plant Cell Physiol. 39(10):1020–1026.

Terashima, I., Fujita, T., Inoue, T., Chow, W.S. and Oguchi, R. 2009. Green light drives photosynthesis more efficiently than red light in strong white light: revisiting the enigmatic question of why leaves are green. Plant and Cell Physiology. 50(4):684–697.

U.S. Department of Agriculture (USDA). 2010. Census of Horticultural Specialties (2009). National Agricultural Statistic Service. Washington DC. 30 Mar. 2019. <https://www.nass.usda.gov/Publications/AgCensus/2007/Online_Highlights/Census_of_Horticulture_Specialties/HORTIC.pdf>.

U.S. Department of Agriculture (USDA). 2015. Census of Horticultural Specialties (2014). National Agricultural Statistics Service. Washington DC. 30 Mar. 2019. <https://www.nass.usda.gov/Publications/AgCensus/2012/Online_Resources/Census_of_Horticulture_Specialties/HORTIC.pdf>.

Wallace, C. and A.J. Both. 2016. Evaluating operating characteristics of light sources for horticultural applications. Acta Hort. 1134:435–444.

Whipker, B.E., P. Cockson, J. Henry, and W.G. Owen. 2018. Nutritional monitoring series tomato transplants (*Solanum lycopersicum*). 30 Mar. 2019. < https://urbanagnews.com/wp-content/uploads/2018/05/Nutritional-Factsheet-Tomato-Transplants.pdf>.

Wollaeger, H.M. and E.S. Runkle. 2014. Growth of impatiens, petunia, salvia, and tomato seedlings under blue, green, and red light-emitting diodes. HortScience 49:734–740.

Wollaeger, H.M. and E.S. Runkle. 2015. Growth and acclimation of impatiens, salvia, petunia, and tomato seedlings to blue and red light. HortScience 50:522–529.