MANIPULATING LIGHT QUALITY TO IMPROVE GROWTH ATTRIBUTES OF HIGH-VALUE SPECIALTY CROPS IN CONTROLLED ENVIRONMENTS

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ABSTRACT

MANIPULATING LIGHT QUALITY TO IMPROVE GROWTH ATTRIBUTES OF HIGH-VALUE SPECIALTY CROPS IN CONTROLLED ENVIRONMENTS

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Manipulating light quality with light-emitting diodes (LEDs) can regulate crop traits and responses including plant architecture, quality characteristics, and flowering time. We investigated how different radiation wavebands, especially far-red (FR; 700-800 nm), could be delivered in controlled environments to produce specialty crops with desired attributes. We utilized end-of-day (EOD) photoperiodic lighting in greenhouses to determine whether FR radiation would promote extension growth without influencing the flowering of poinsettia. EOD FR lighting promoted poinsettia extension growth, and at a low-intensity it was not perceived as a long day, but it was at a higher intensity. In another study, we determined the impacts of photoperiodic lighting (to increase leaf area) and supplemental lighting (SL) (to increase photosynthesis) on growth, pigmentation, and sensory attributes of greenhouse-grown lettuce. EOD lighting had few effects on lettuce growth, but greenhouse SL, especially from blue (B; 400-500 nm) and red (R; 600-700 nm) LEDs, increased lettuce growth and coloration but sensory attributes were less preferred by consumers than plants grown without SL. In a third study, we quantified how a variety of floriculture crop seedlings respond to the addition of FR radiation to B+R sole-source LED lighting. The addition of 40 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of FR radiation promoted stem elongation of some species and accelerated the flowering of snapdragon. Collectively, this research shows the potential applications of including FR in a radiation spectrum to elicit specific plant growth, quality, and flowering attributes of horticultural crops.

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Introduction

Greenhouses are commonly used in the commercial production of flowering plants (e.g., bedding plants, herbaceous perennials, and potted plants) and vegetables. The primary purpose of growing plants in greenhouses is to better control environmental factors that regulate plant growth and development so that growers can develop and implement production schedules to produce crops reliably and for specific market dates. Temperature in the greenhouse is relatively easily controlled while light, as one of the most important environmental factors for plant growth, is difficult to manage (Albright et al., 2000).

The natural photoperiod and photosynthetic daily light integral (DLI) depend on a number of factors, especially the time of year and the location. Photoperiod, which is the number of hours of light during a 24-h period, is involved in several physiological responses of plants including flowering. Plants can perceive light at a very low photosynthetic photon flux density (*PPFD*), for example at 0.1 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Whitman et al., 1998), so the biological photoperiod can be defined as the period from sunrise to sunset, plus 30 to 40 minutes of twilight (Faust and Heins, 1995). The photoperiod changes little at the equator but the seasonal variation increases as latitude increases. For example, the biological photoperiod at 30 degrees latitude varies from about 11 h during the winter to 14.5 h during the summer, while at 50 degrees, it varies from 9 to 17 h (Runkle et al., 2017).

Sunlight is the major light source inside most greenhouses. Radiation emitted by the sun passes through the earth's atmosphere, which modifies the spectrum once it reaches the earth's surface depending on the time of day and year, latitude, and cloud cover (Ehret et al., 1989). The DLI describes the total amount of photosynthetically active radiation (PAR; 400 to 700 nm)

delivered during a 24–h period in a square meter, and has the unit of mol·m^{-2}·d^{-1}. In the northern part of the U.S. and Canada, the maximum DLI is about 60 mol·m^{-2}·d^{-1} outdoors on a cloudless summer day, and is less than 5 mol·m^{-2}·d^{-1} in the winter on a dark, cloudy day. In greenhouses, within the U.S., variation in DLI is greatest between the north and south during the fall and winter, while during spring and summer, the DLI variation is greatest between the eastern and western regions (Korczynski et al., 2002). PAR accounts for approximately 43% of the total solar photosynthetic radiation energy (for around 1960 µmol·m^{-2}·s^{-1}) (Thimijan and Heins, 1983) and is further reduced by 10-40% because of the attenuation of light from the glazing material, structural frame, hanging baskets, and other obstructions (Monk and Molnar, 1987). Thus, the average DLI that enters the greenhouse varies from 5 to 30 mol·m^{-2}·d^{-1} (Runkle, 2006). Generally, glass has ≥10% greater light transmission than plastic films (Nijskens et al., 1985). Single layer glass provides a direct light transmittance of 90% compared to 80% for polyethylene (Both and Faust, 2017). Thus, during the winter and early spring, the DLI is often a limiting factor for plant growth in greenhouses >40 ºN latitude (Aldrich et al., 1969).

Plant growth typically increases with an increase in DLI. For example, the total dry weight of a wide range of crops, including ageratum (*Ageratum houstonianum*), begonia (*Begonia ×semperflorens-cultorum*), marigold (*Tagetes erecta*), petunia (*Petunia ×hybrida*), salvia (*Salvia coccinea*), vinca (*Catharanthus roseus*), and zinnia (*Zinnia elegans*) increased as the DLI increased from 5 to 43 mol·m^{-2}·d^{-1} at an average temperature of 23 ºC (Faust et al., 2005). Flower number of petunia, salvia, vinca, and zinnia also increased, by 419% to 558%, as the DLI increased from 5 to 43 mol·m^{-2}·d^{-1}. In addition, shoot dry mass of snapdragon (*Antirrhinum majus*), ruddles (*Calendula officinalis*), impatiens (*Impatiens wallerana*), mimulus (*Mimulus ×hybridu*), and torenia (*Torenia fournieri*) increased (102% to 240%) and flowering

time decreased (by 9% to 38%) as the DLI increased from 10.5 to 21.8 $mol \cdot m^{-2} \cdot d^{-1}$ at 20 ºC (Warner and Erwin, 2005).

Increasing DLI in greenhouses is usually achieved by delivery of supplemental, high-intensity lighting. For example, supplemental lighting increased photosynthetic rate more than 2-fold compared to non-lighted strawberries (*Fragaria ×ananassa*), resulting in an increased average fruit weight in 'Benihoppe' and fruit number in 'Benihoppe', 'Sagahonoka', and 'Akihime' (Hidaka et al., 2015). In lettuce (*Lactuca sativa*), day-extension lighting from 16 to 24 h at a *PPFD* of 50-100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ increased biomass by 20% and reduced the growth cycle by 7 d during the winter (Gaudreau et al., 1994). The phytochemicals of baby leaf lettuce including anthocyanins, carotenoids, and phenolics also increased, depending on the quality of supplemental lighting (Li and Kubota, 2009). Although supplemental lighting is effective for plant production, its utility depends, in part, on the location of the greenhouses, crop(s) grown, and lamp type. For example, supplemental lighting can significantly increase the DLI for a northern U.S. greenhouse, but not for a greenhouse in the Southwest (Korczynski et al., 2002).

Horticultural Lighting

Electrical lighting is usually used by growers to increase plant growth, regulate flowering, or both. Supplemental, photoperiodic, and sole-source lighting are three types of the most common lighting applications in horticulture. Supplemental lighting refers to delivery of moderate to high-intensity light in the greenhouse, usually from above. This system increases the DLI and promotes photosynthesis, resulting in increased plant growth of shoots, roots, flowers, and fruits, especially during low-light conditions. Photoperiodic lighting is typically delivered at a low intensity to regulate flowering; it accelerates flowering of long-day plants (LDPs) and inhibits flowering of short-day plants (SDPs) and thus, helps to regulate crop production

schedules and reduce production durations. Sole-source lighting is the delivery of a moderate to high intensity of light that is the only light source for plants. Sole-source lighting has been used successfully in vertical farming (plant factories) in Japan for over two decades, and for even longer inside growth chambers for controlled-environment research and for germination of seedlings by commercial growers.

Incandescent (INC) and fluorescent (FL) lamps have been traditionally used in greenhouse crop production, primarily as photoperiodic lighting. INC works on the principle of heating a metal to a high temperature to emit light. Commonly used as photoperiodic lighting to regulate flowering of SDPs and LDPs, it has a relatively low red (R, 600-700 nm) to far-red (FR, 700-800 nm) ratio (R:FR) of around 0.6, and thus, promotes stem elongation of most crops. However, INC has a very low electrical efficacy due to the loss of more than 90% of electric input into heat (Runkle and Both, 2017). Although INC is inexpensive to purchase and easy to install, it has been gradually phased out of production due to its inefficiency in converting electricity into radiation useful to plant production. Compact fluorescent lamps (CFL), which generate light by sending an electrical discharge through an ionized gas, were designed as a replacement for INC. It emits more blue (B; 400 to 500 nm) light and less FR light than INC, has an R:FR ratio around 6.0, and is more electrically efficient than INC lamps (Runkle and Both, 2017). However, petunia flowered 2-3 weeks later under CFL than INC, which indicates that for at least some LDPs, CFL lamps are less effective at promoting flowering than INC (Oh and Runkle, 2016; Runkle et al., 2012). In addition, the lifespan of CFLs depends on the number of on/off cycles and therefore, is not an appropriate product for cyclic lighting (Runkle and Both, 2017). In addition, FL lamps are sometimes used indoors for germination shelves to provide light without excessive heat (Mattson, 2015).

High-intensity discharge lamps are the most widely used lamps in modern greenhouse crop production. These lamps, which include high-pressure sodium (HPS) and metal halide (MH), work on the principle of passing an electric current through a gas. HPS is used for supplemental lighting to increase photosynthesis and thus promote the growth and yield. For example, the total yield of greenhouse tomato (*Lycopersicon esculentum*) fruit increased by 16% to 37% under 140 $\mu mol \cdot m^{-2} \cdot s^{-1}$ HPS compared to non-supplemented (ambient) light, and as the *PPFD* under HPS increased from 70 to 140 $\mu mol \cdot m^{-2} \cdot s^{-1}$, the weight of tomato fruit increased by 20-30% (McAvoy and Janes, 1984). HPS can also be effective as photoperiodic lighting to regulate flowering. For example, bellflower (*Campanula carpatica*), coreopsis (*Coreopsis grandiflora*), petunia, and black-eyed susan (*Rudbeckia hirta*) were studied under a 4-h NI with cyclic HPS lamps during a 15-h night (Blanchard and Runkle, 2010). All species promoted flowering under HPS lamps, while none of the long-day plants flowered under a 9-h short-day. However, HPS has an R:FR ratio of around 6.3 and thus when delivered at a low intensity, may not be as effective as lamps with a lower R:FR ratio at promoting the flowering of LDPs (Runkle and Both, 2017).

MH lamps are sometimes used in retail garden centers because they emit more of a white light than HPS lamps, which provides more true plant colors to consumers (Fisher et al., 2017). It has also been used as supplemental lighting to increase plant growth. However commercially, HPS is more suitable for large-scale supplemental lighting than FL and MH lamps because of its higher efficacy of transforming electricity into photosynthetic photons (Moe et al., 2005), as well as its longer bulb life.

Light-emitting diodes (LEDs) are a relatively new lighting technology that is increasingly being used in horticulture. LEDs work on the principle of light emission produced by passing a

current through different semiconductor materials such as indium gallium nitride (InGaN), aluminum gallium indium phosphide (AlGaInP), and aluminum gallium arsenide (AlGaAs). Early LEDs could only emit low-intensity infrared wavelengths while modern LEDs can emit wavebands of photosynthetic radiation (from 400 to 700 nm), as well as ultraviolet and far-red radiation, in somewhat narrow or broad wave bands. With the development, LEDs have a significantly longer lifetime than conventional lamps, ranging from 20,000 to 55,000 h compared with lifetimes for INC of 1,000 h, CFL of 8,000 to 10,000 h (Tähkämö et al., 2012), and HPS of 10,000 h (Nelson and Bugbee, 2014). In addition, LEDs are also developed to be safer than other bulb types because there is no fragile glass envelope to break, is no high touch temperature, and are fewer hazardous materials (Olle and Viršilė, 2013).

There are several advantages of LEDs compared to other lamp types, including their relatively high electrical efficacy that continues to increase. LEDs emit relatively little radiant heat, so they can be placed closer to the crop compared to conventional fixtures such as HPS lamps (Fisher et al., 2017). In addition, because light emitted is more directional than conventional lamps, there's the potential to focus the light and reduce illuminated areas not occupied by plants. The efficacy of LEDs continues to increase as the technology develops. In 2014, the efficacy of LED fixtures ranged from 0.9 to 1.7 $\mu mol \cdot J^{-1}$ (Nelson and Bugbee, 2014), and more recently, fixtures with efficacies of >2.0 $\mu mol \cdot J^{-1}$ have been developed (Fisher et al., 2017). The efficacy of LED intracanopy lighting for converting electricity into high-wire tomato biomass was 75% higher than overhead lighting from HPS lamps (Gómez et al., 2013). In addition, the electrical cost for the average fruit under HPS overhead lighting was 403% higher than from LED intracanopy lighting, without a compromise in fruit yield.

However, LED arrays used for horticultural applications are a relatively new technology and there are still barriers to commercial implementation. The relatively high cost of investment for LEDs is the greatest obstacle to the expansion of LED technology in horticulture. Thus, LEDs will become more popular as the technology develops, the efficacy continues to increase, and the cost is further reduced. A hybrid lighting system that combines some of the features of LEDs with conventional lamps could be an economically efficient option, depending on the crop and lamp characteristics desired for production (Olle and Viršilė, 2013). Additional considerations for LEDs to be used in greenhouses include adequate dissipation of heat (an excessively high temperature can overheat the LED package, reducing light output and fixture longevity) and tolerance to high humidity.

Different types of LEDs can be combined on arrays to emit a specific spectrum for supplemental or sole-source lighting to promote growth and yield. For example, lamb's lettuce (*Valerianella locusta*) was grown under 90% of red LEDs (peak = 660 nm) plus 10% blue LEDs (90R/10B), warm white LEDs, or HPS at a supplemental *PPFD* of 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ in the greenhouse (Wojciechowska et al., 2015). The yield was the greatest under 90R/10B and was 29-33% higher than under HPS or warm-white LEDs. In a study with hydroponically grown Boston lettuce, plants were grown in growth chambers under red+blue+white LEDs (RBW) and red+blue LEDs (RB) at a *PPFD* of 210 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Lettuce grown under RBW had 20% and 14% greater shoot fresh and dry weight as well as 48% and 44% greater root fresh and dry weight compared to that of RB (Lin et al., 2013).

LEDs can also be used to deliver photoperiodic lighting to regulate flowering responses. Manipulating the spectrum of LEDs can influence flowering attributes as well as increase the efficacy of delivering the long-day condition. For example, several LDPs were grown under 9-h

short-days (SDs) with or without a 2 μmol·m^{-2}·s^{-1} 4-h NI from LEDs with or without FR. NI including FR (R+W+FR) significantly promoted flowering of coreopsis, petunia, and snapdragon by ~12, 6, and 13 d, respectively, compared to those grown under NI without the FR (such as R, R+B, cool-white, and warm-white) (Meng and Runkle, 2015). In a separate study, under a photoperiod of 16 h, marigold and salvia had 43% and 100% more flower buds under 1:1 R+B LEDs than FL when delivered at a *PPFD* of 90 μmol·m^{-2}·s^{-1} (Heo et al., 2006). In addition, the number of open flowers of ageratum was 100% greater under R+B than L.

Supplemental Lighting

Supplemental lighting in greenhouses provides additional light when the solar DLI is not sufficient to maintain high yield and quality for crop production. Supplemental lighting increases photosynthesis, crop growth, and yield most efficiently when the DLI is low, especially from mid-November to mid-February in the Northern hemisphere. Typically, 50 to 75 μmol·m^{-2}·s^{-1} is delivered to floriculture crops, and a higher intensity of 100 to 200 μmol·m^{-2}·s^{-1} is provided to high-wire vegetables and cut flowers (Fisher et al., 2017). Specifically for vegetable crops, a photoperiod of 12 to 16 h of supplemental lighting at 50-75 μmol·m^{-2}·s^{-1} for lettuce, 75-100 μmol·m^{-2}·s^{-1} for sweet pepper (*Capsicum annum*), and 75-175 μmol·m^{-2}·s^{-1} for cucumber (*Cucumis sativus*) has been recommended for vegetable seedlings (Dorais and Gosselin, 2002). For tomatoes, 83 μmol·m^{-2}·s^{-1} was generally favorable for seedling production and a DLI of ≥ 30 mol·m^{-2}·d^{-1} was recommended for fruiting crops (Dorais, 2003).

Plant growth and biomass increase under supplemental lighting compared to natural light mainly because of greater photosynthesis that increases growth and yield. For example, Dorais and Gosselin (2002) reported that increasing the light intensity from 100 to 150 μmol·m^{-2}·s^{-1}

increased yield by 4 to 30%, depending on the plant species. In a separate study, shoot dry weight of celery (*Apium graveolens*), lettuce, broccoli (*Brassica oleracea*), and tomato transplants increased by 22%, 40%, 19%, and 24%, and root dry weight by 97%, 42%, 38%, and 21%, respectively, under 400-W HPS that delivered a *PPFD* of 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ compared to natural light (Masson et al., 1991). Similarly, the biomass of Boston-type lettuce increased up to 270%, along with a greater head firmness and a ~30% reduction of production cycle length, under 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ HPS lamps with a 24-h photoperiod than under natural light (Gaudreau et al., 1994). In cucumber, seedlings were grown under a 16-h photoperiod from 400-W HPS lamps with a *PPFD* of 65 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at planting, and increased to 350 $\mu mol \cdot m^{-2} \cdot s^{-1}$ when the plants reached the overhead wire (Hao and Papadopoulos, 1999). Supplemental lighting increased leaf chlorophyll content (by 14-23%), plant biomass accumulation (by 9-18%), and yield including 25-56% more fruit, 34-60% greater fruit weight, 11-23% increased fruit size, 10-12% greater fruit dry mass content, and 16-43% higher fruit skin chlorophyll content compared to ambient light conditions.

Although commercial producers sometimes use photoperiodic lighting to manipulate flowering of daylength-sensitive crops, supplemental lighting can also influence the flowering process. For example, supplemental lighting at 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$ from HPS lamps during either the last two-thirds or the entire plug stage accelerated subsequent flowering of petunia and pansy (*Viola ×wittrockiana*) by 5-6 d compared to the control, which was photoperiodic lighting at 3 $\mu mol \cdot m^{-2} \cdot s^{-1}$ provided by HPS (Oh et al., 2010). Similarly, days to the first flower of cyclamen decreased by 44% as DLI provided by sole-source cool-white FL lamps increased from 1.4 to 17.3 $mol \cdot m^{-2} \cdot d^{-1}$ (Oh et al., 2009). However, supplemental lighting from conventional lamps can also increase plant temperature by non-photosynthetic radiation (700-50,000 nm) (Faust and

Heins, 1997). For example, the shoot-tip temperature of vinca that received 100 μmol·m^{-2}·s^{-1} of supplemental HPS lighting was 1.7 °C higher than that without supplemental lighting (Faust and Heins, 1997). Thus, a reduction in time to flowering under supplemental lighting can at least partly be attributed to a higher plant temperature. Therefore, supplemental lighting can improve plant production and/or accelerate flowering by increasing photosynthesis as well as slightly increasing plant temperature when conventional lamps are used.

The spectral distribution of supplemental lighting can also influence branching, as well as other quality attributes of horticultural crops. Light with a high R:FR typically promotes branching, while a lower R:FR suppresses it. For example, poinsettia (*Euphorbia pulcherrima*) branching decreased by an average of 4.2 branches per plant under an R filter (creating a low R:FR), and increased it by 1.5 branches under an FR filter (creating a higher R:FR), compared to plants under a non-selective screen (Clifford et al., 2004). Cut rose (*Rosa ×hybrida*) produced 49% and 64% more flowering shoots under 70-75 μmol·m^{-2}·s^{-1} HPS and MH, respectively, compared to HPS filtered to provide a relatively low R:FR ratio (Roberts et al., 1993). Similarly, the axillary shoot number of rhododendron grown under a filter creating an R:FR ratio of 0.4 was 33% less than under an R:FR ratio of 2.0, both with a *PPFD* of around 25 μmol·m^{-2}·s^{-1} (Marks and Simpson, 1999).

Photoperiodic Lighting

Flowering is one of the most important developmental stages in a plant's life cycle. Photoperiodism, which refers to a physiological reaction of the plant to day length, is one of several factors that can mediate flowering responses. Day length is perceived primarily by the leaves, and for photoperiodic crops that have obtained the capacity to flower (i.e., are not

juvenile), an inductive photoperiod leads to transmission of the flowering signal from the leaves to the shoot meristem. Upon perceiving this signal, plants switch from vegetative to reproductive growth and initiate flower buds (Taiz and Zeiger, 2010). Circadian rhythms allow plants to program molecular events at specific times of the day. Photoperiod perception and circadian rhythms work collaboratively to drive the response to photoperiod and regulate the flowering process.

Different species, and even different cultivars of the same species, can have different inductive photoperiods, but photoperiodic flowering responses can generally be divided into five groups (Thomas and Vince-Prue, 1997). Flowering in SDPs is determined primarily by the duration of darkness (Taiz and Zeiger, 2010). They only flower, or flower earlier, when exposed to a long, uninterrupted dark period of a critical length, which is at least 12 h for most ornamental SDPs (Runkle and Fisher, 2004). LDPs are dark dominant and only flower, or flower earlier, when the length of the dark period is less than 8-11 h. Within each category (SDPs, LDPs), photoperiodically responsive plants have an obligate (qualitative) or a facultative (quantitative) response. Obligate plants only flower under a particular photoperiod, while facultative plants can flower under any photoperiod but flower earlier under some particular photoperiod. Day-neutral plants (DNPs) flower regardless of the day/night length (Thomas and Vince-Prue, 1997). In addition, intermediate day plants only flower when the day length is neither too long nor too short, while ambiphotoperiodic-day plants require a dual day length (e.g., short days and long days in a sequence) to initiate flowering.

In the commercial production of many photoperiodic floriculture crops, flowering is regulated by photoperiodic (low-intensity) lighting. For day-extension lighting, the threshold *PPFD* to regulate flowering of several herbaceous perennials ranged from 0.05 to 0.4

μmol·m^{-2}·s^{-1}, while the saturation *PPFD* ranged from 0.2 to 1 μmol·m^{-2}·s^{-1}, depending on the species (Whitman et al., 1998). Generally, a *PPFD* of 1-3 μmol·m^{-2}·s^{-1} during the night is recommended to accelerate flowering of LDPs and inhibit flowering of SDPs (Runkle, 2015). Using photoperiodic lighting to control flowering is crucial to coordinate marketability of crops with the time of high demand. For example, the production of poinsettia and carnation (*Dianthus caryophyllus*), which are targeted for Christmas and Mother's Day, respectively, utilizes photoperiod manipulation (Vince-Prue and Canham, 1983). Photoperiodic lighting can reduce production time, which can reduce overhead costs such as heating and cooling, as well as other inputs such as water and labor.

The day length is manipulated in commercial greenhouses in various ways. SD can be created using light-excluding materials to cover plants, such as blackout cloth or black plastic. However, heat absorbed from the sun can accumulate under the black cloth, which can delay flowering of at least some SDP such as poinsettia and chrysanthemum (*Chrysanthemum morifolium*). In contrast, there are two general strategies to create long-days (LDs). To deliver long days, short days can be extended to 14-16 h, an approach known as end-of-day (EOD) or day-extension (DE) lighting, or lighting can be provided during the middle of the dark period, which is known as night interruption (NI) lighting (Armitage, 1994; Vince-Prue and Canham, 1983). Although DE can effectively regulate flowering, it can require more electricity than NI when the natural days are short because operation time can be as long as 6 or 7 h.

NI lighting is typically delivered during the middle of a long (12-16 h) night (Lane et al., 1965; Thomas and Vince-Prue, 1997). NI lighting for a short duration (e.g., 30 min) and low irradiance (1 μmol·m^{-2}·s^{-1}) is sufficient to keep some (but not all) SDPs vegetative (Lane et al., 1963; Vince-Prue and Canham, 1983). In contrast, LDPs usually require a longer exposure (>2 h)

and/or higher irradiance to trigger flowering. Therefore, a 4-h NI at a minimum intensity of 2 $\mu mol \cdot m^{-2} \cdot s^{-1}$ is recommended to ensure saturation of the flowering response for most SDPs and LDPs (Runkle et al., 1998). Typically, an NI from 22:00-02:00 HR is widely used in commercial greenhouse crop production (Runkle and Fisher, 2004). However, the specific time period for this 4 h NI can be different. For example, dianthus (*Dianthus chinensis*), zinnia, and geranium (*Pelargonium zonale*) were investigated under 3-5 $\mu mol \cdot m^{-2} \cdot s^{-1}$ from white FL with NI during three time periods (18:00-22:00 HR, 22:00-02:00 HR, or 02:00-06:00 HR) (Park et al., 2013). In the LDP dianthus, NI from 02:00-06:00 HR was the most effective in promoting flowering (by 5 d) and in delaying flowering of the SDP zinnia (by 14 d). The flowering of geranium was not affected by the NI application time, which is not surprising because it is day neutral.

Cyclic lighting, which is the delivery of light on an intermittent basis, provides an opportunity to create LD while reducing electrical cost. There are three ways to create cyclic lighting (Runkle, 2007): INC lamps that turn on for 6 min and off for 24 min for 4 to 6 h during the night; HPS/MH/LEDs mounted on an irrigation boom that moves over the plants at least once every 15 min for at least 4 h; and a stationary HPS lamp with a rotating reflector. Cyclic INC with a timer is effective on most SDPs, but may not promote flowering of some LDPs as much as continuous NI (Runkle et al., 1998). For example, Blanchard and Runkle (2010) grew petunia and black-eyed susan under either a cyclic INC (6 min on every 30 min) or a continuous INC, each for 4 h, and at a *PPFD* of 3 $\mu mol \cdot m^{-2} \cdot s^{-1}$. The flowering of petunia and black-eyed susan was delayed by 9 to 16 d when grown under cyclic INC compared to continuous INC.

Different radiation wavebands can have distinctly different roles in the photoperiodic regulation of flowering. Generally, R is most effective at inhibiting flowering of SDPs, while the flowering of a wide range of LDPs is promoted most when R is combined with FR. For example,

LEDs with an R:FR ≥0.66 or INC (with an R:FR= 0.59), both at a photon flux density from 600-800 nm of 1.3-1.6 μmol·m^{-2}·s^{-1}, inhibited flowering of SDPs when used as a 4-h NI (Craig and Runkle, 2013). It delayed flowering of chrysanthemum, dahlia (*Dahlia hortensis*), and marigold by 42 d, 11 d, and 10-20 d respectively. In contrast, an 8-h DE from INC accelerated flowering of the LDP henbane (*Hyoscyamus niger*) by 9 to 18 d compared to cool-white FL with a high R:FR (Downs and Thomas, 1982). Similarly, a 2- or 4-h NI or 6-h DE from INC lamps, at a *PPFD* of 2.3 μmol·m^{-2}·s^{-1}, promoted flowering of pansy by up to 5-6 d compared to CFL lamps (Oh and Runkle, 2016). The efficacy of B light as a DE or NI varies among species. In a study with cyclamen, plants were grown under a 9-h short day with a 4-h NI provided by R, B, or R+B at a *PPFD* of 4 μmol·m^{-2}·s^{-1} in the greenhouse (Shin et al., 2010). NI with R+B, R, or B promoted flowering by 19, 12, and 11 d, respectively, compared to those without NI. However, in other SDPs [e.g., cosmos (*Cosmos sulfureus*)] and LDPs (e.g., dianthus), low intensity (0.6-1.6 μmol·m^{-2}·s^{-1}) B light, alone or when added to R light as a 4-h NI, did not influence flowering, and plants were similar to those under a 9-h SD (Meng and Runkle, 2015).

Light Quality

Plants perceive light quality with four main classes of photoreceptors: phytochromes, cryptochromes, phototropins, and UVR8. Phytochromes primarily absorb R and FR light, and to a much smaller extent, B light. Phytochromes interact with cryptochromes to regulate multiple physiological responses including photomorphogenesis, shade avoidance, circadian rhythms, flowering, and phototropism. Cryptochromes and phototropins are considered B light photoreceptors because they primarily absorb B, although cryptochromes also absorb ultraviolet A (UV-A, 320 to 400 nm). Phototropins are reported to regulate phototropism, chloroplast

movement, and stomatal opening. Peak absorption of UVR8 is by ultraviolet B (UV-B, 280 to 320 nm), and it mediates responses including UV-B acclimation and tolerance and hypocotyl growth inhibition (Favory et al., 2009).

Red and far-red light

The relative quantum efficiency curve for photosynthesis generated by McCree (1972) peaks in the orange-red region. Therefore, R is photosynthetically efficient at promoting plant growth. For instance, hydroponic lettuce under monochromatic R LEDs at either a low or high *PPFD* (85 or 170 $\mu mol \cdot m^{-2} \cdot s^{-1}$) developed an average of four more leaves compared to plants under monochromatic B LEDs at the same *PPFD* (Yanagi et al., 1996). In addition, plants under R LEDs were 77% and 52% taller than those under B LEDs at the high or low *PPFD*, respectively. While the proportion of R light from conventional lamps ranges from 24-40%, the percentage is commonly 75-85% in LED arrays developed for horticulture applications (Runkle, 2016).

Red and FR light are perceived by phytochromes, which are present in two forms: the R light-absorbing form (referred to as Pr) and the FR light-absorbing form (referred to as Pfr) (Taiz and Zeiger, 2010). The interconversion between these two forms of each phytochrome in plants is known as photoreversibility, and can regulate seed germination, extension growth, and flowering. The Pr form is a blue-colored, biologically inactive form, which can convert to the Pfr form, a blue-green biologically active form, and vice versa. One form cannot be fully converted into the other because their absorption spectra overlap. Depending on the light quality, these two forms of phytochromes reach an equilibrium called the photostationary state or phytochrome photoequilibrium. The ratio between Pfr and the total phytochrome pool (Pfr/Ptotal) can be an indicator of phytochrome states, which can be estimated by the light spectrum (Sager, 1988).

By definition, FR is outside of the PAR waveband, and it promotes stem elongation and leaf expansion independently from photosynthesis. Unlike R, which is mostly absorbed by leaves, most FR is reflected or transmitted, creating an FR-enriched (low R:FR) environment under a plant canopy, especially under high plant density. Once a plant perceives a shade signal, stems elongate and leaves expand to compete with nearby plants in an attempt to capture more light. This phenomenon is called the shade-avoidance response and is mediated by phytochrome. Thus, the inclusion of FR light in electrical lights can indirectly promote plant growth. For example, the stem dry mass of pepper was 70% greater under R+FR (peaks at 660+735 nm) compared to R alone, both at a *PPFD* of 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Brown et al., 1995). In addition, pepper under R+FR was 55% taller than under R. In a separate study, geranium, petunia, snapdragon, and impatiens were grown under different sole-source lighting treatments from LEDs in a growth chamber (Park and Runkle, 2017). LED lighting provided 32 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of B light (peak at 447 nm) either with a total photon flux of 128 $\mu mol \cdot m^{-2} \cdot s^{-1}$ from R (peak at 660 nm) and FR (peak at 731 nm), or 128 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of R with additional intensities of FR light. The stem length of geranium, petunia, snapdragon, and impatiens decreased by 41%, 95%, 41%, and 24%, respectively, as the estimated phytochrome photoequilibria increased from 0.69 to 0.88. The addition of FR to the same *PPFD* increased total leaf area of geranium and snapdragon by 7% and shoot dry weight by 28-50%. The promotion of extension growth from FR is often undesirable in ornamental production, but it can be beneficial in cases where stem extension is often desired, such as in cut flower production.

Although plant growth regulators are widely used in commercial floriculture production, manipulating light quality, especially R and FR, can be an alternative way to regulate extension growth. Generally, the more FR light the plant receives (lower R:FR), the taller the plant. For

example, five LDP species [bellflower, coreopsis, pea (*Pisum sativum*), lobelia (*Lobelia ×speciosa*), and pansy] were studied under natural, R-light deficient (R_d) or FR-light deficient (FR_d) environments with a similar DLI (Runkle and Heins, 2001). R_d had a low R:FR while FR_d had a high R:FR. The R_d environment increased plant height from the onset of the experiment to visible bud (VB) by 65% in bellflower and 23% in pea compared to plants in the natural light environment. The FR_d environment suppressed stem extension in pea and pansy by 20% and 14%, respectively, compared to natural light. In addition, stem extension in bellflower, coreopsis, pea, and pansy showed a negative linear relationship with the R:FR.

In addition to the influence on stem elongation, a lack of FR can delay flower initiation and development in some LDPs. In the same experiment that Runkle and Heins (2001) conducted, FR_d filters delayed time to VB by 2 d in bellflower and 14 d in coreopsis, as well as delayed flower development of pansy by 21 d compared to natural light. Similarly, petunia grown under FR-absorbing films (R:FR=1.51) delayed flowering by 11 d compared to plants under clear films (R:FR=1.05) (Ilias and Rajapakse, 2005). In addition, there were 42% fewer petunia flowers under FR-absorbing films compared to the clear films, respectively.

Blue light

The effects of B light on stem elongation, which are mediated by cryptochrome, are not fully understood. Contradictory results have been reported under B light with or without the presence of R light. Generally, with the presence of R light, the addition of blue inhibits extension growth as its intensity (or proportion) increases. For example, in a study with lettuce, spinach (*Spinacia oleracea*) and mustard (*Sinapis alba*), plants were grown under MH, HPS, MH+tungsten halogen lamps, and HPS+MH at the same *PPFD* of either 320 or 700 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Tibbitts et al., 1983). There was a strong negative relationship between B photon flux density

and hypocotyl length under both *PPFD*s. Similarly, stem length (from the cotyledon to the center of the apical bud) of lettuce seedlings grown under a *PPFD* of 80 µmol·m^{-2}·s^{-1} significantly decreased (from 14 cm to 6 cm) as the B light proportion increased from 10% to 40% (Okamoto et al., 1996). In another study with five LDP, a blue deficient (B_d) environment increased stem length from the onset of the experiment to VB by 100%, 72%, 17%, and 16% in bellflower, coreopsis, lobelia, and pea respectively, compared to natural light (Runkle and Heins, 2001). In addition, a B_d environment increased stem elongation in coreopsis, lobelia, and pansy by 31%, 11%, and 10% respectively, from VB to flowering.

However, cryptochrome-mediated responses cannot occur without the presence of active phytochrome, which is activated by R light (Ahmad and Cashmore, 1997). Therefore, B light cannot trigger photomorphogenic responses alone. For example, marigold and salvia grown under 90 µmol·m^{-2}·s^{-1} of monochromatic B LEDs with a 16-h photoperiod were both taller than plants grown under FL providing the same *PPFD* (Heo et al., 2002). In a study with tomato seedlings, the hypocotyl length linearly decreased as the B light proportion increased from 10% to 75% (Hernández et al., 2016). However, under 100% B light, hypocotyl length was 34-56% greater than seedlings grown under 20-75% B treatments.

Plant growth responses under monochromatic R compared to R+B are species specific. When added to R light, B light typically promotes plant growth and increases biomass. For example, when lettuce, radish (*Raphanus sativus*), and spinach were grown under 300 µmol·m^{-2}·s^{-1} from R LEDs with B FL lamps (peaks at 660+450 nm, 10% B light), additional light 30 µmol·m^{-2}·s^{-1} from B LEDs increased dry mass by 70%, 200%, and 150%, respectively, compared to additional light from R LEDs at the same *PPFD* (Yorio et al., 2001). In ornamental plants, the leaf area of both dumbcane (*Dieffenbachia amoena*) and rubber fig (*Ficus elastic*)

under 30 μmol·m^{-2}·s^{-1} monochromatic R or B for 50 days was similar compared to natural light, but increased by 23% and 26% respectively, under R+B with the same *PPFD* (Heo et al., 2010). However, in a separate study, impatiens, salvia, and petunia seedlings were grown under only R LEDs or R+B LEDs at a *PPFD* of 160 μmol·m^{-2}·s^{-1} and an 18-h photoperiod. Fresh shoot weight of impatiens was 53%-78% greater under R compared to R+B (≥ 50% B) and salvia was 65-98% greater under R compared to R+B (≥ 25% B). In addition, salvia had a 70-133% greater dry weight under R compared to R+B (≥ 25% B) and petunia had 33-91% greater dry weight under R compared to R+B (≥ 13% B). These findings indicate that sole-source lighting with a mixture of R and B is generally effective at promoting growth for some, but not all crops, and responses could depend on the total *PPFD* delivered, the photon flux densities of B and R, or the B:R.

Anthocyanins are one of the most abundant pigments in higher plants and its synthesis is highly dependent on light quality. These compounds can add color to petals, leaves, and fruits, and have benefits for human health when consumed. Activation of the anthocyanin pathway along with the accumulation of pigmentation involves the regulation of light signals, including B light. The anthocyanin concentration of lettuce increased by 31% when grown under white LEDs (W) supplemented with B compared to W alone, both at a *PPFD* of 300 μmol·m^{-2}·s^{-1} in the growth chamber (Li and Kubota, 2009). In a separate study, red-leaf lettuce was grown under HPS lamps with or without two different B peak wavebands (455 nm and 470 nm) at 200 μmol·m^{-2}·s^{-1} with a 16-h photoperiod in the greenhouse (Samuolienė et al., 2012). The total anthocyanin concentration increased by 35-106% under the two HPS+B treatments compared to plants grown under HPS alone. These responses could be attributed to the activation of the *chs*

gene, which is a flavonoid biosynthetic gene, under UV-A/blue light and thus promotes anthocyanin accumulation in plant tissues (Christie and Jenkins, 1996).

Green light

For a long time, green light (G) has been believed to be less effective at driving photosynthesis than R or B radiation, for two reasons: it has a relatively higher leaf reflectance and canopy penetration rate, and in vitro chlorophyll absorbs much more B and R than G radiation (Klein, 1992). However, G has different impacts on plant growth, depending in part on the photon flux density delivered. In some plants, G light can promote leaf expansion and shoot biomass at a lower intensity but inhibit it at a higher intensity. For example, lettuce grown under R+B LEDs with or without 7 $\mu mol \cdot m^{-2} \cdot s^{-1}$ supplemental G LEDs at a similar *PPFD* had no significant differences in leaf area and shoot fresh and dry weight (Kim et al., 2004). In a separate study, lettuce was grown under an 18-h photoperiod in a growth chamber with R+B, R+B with green FL lamps, green FL lamps, and cool-white FL lamps (Kim et al., 2004). The fraction of G in those four lighting treatments was 0%, 24%, 51%, and 86% respectively, with a total *PPFD* of 150 $\mu mol \cdot m^{-2} \cdot s^{-1}$. As the photon flux density of G increased from 0 to 36 or 77 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (the G fraction increased from 0% to 24% or 51%), lettuce developed 31% or 13% larger leaves and had 47% or 14% greater shoot dry weight, respectively. However, as the G light intensity continued to increase to 129 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (the G fraction increased to 86%), there was a 30% and 46% decrease in leaf area and shoot dry weight, respectively, compared to plants under no G.

In addition to affecting plant growth, including G in the spectrum has several potential benefits. The addition of G to R+B light allows plants to appear their typical green color rather than a purplish color, which makes it easier to visually detect nutritional or physiological

disorders, diseases, and/or pest issues (Wollaeger and Runkle, 2014). G light also penetrates deeper into a plant canopy, which could lead to less loss of lower leaves under the canopy.

Considerations for Lighting Fixtures

Fixture efficacy (i.e., electrical efficiency) is among the most important factors to consider when selecting lamp types for indoor or greenhouse production of plants. LEDs can convert up to 45% of electrical energy into photosynthetic light, depending on the color, while traditional single-ended (module) HPS and INC convert about 30% and 6%, respectively, into light (Michigan State University, 2011). Among LED types, the most electrically efficient ones emit B and R, as well as B LEDs coated with phosphors to create a cool-white spectrum (Nelson and Bugbee, 2014). Photosynthetic photon efficacy (PPE) is the appropriate metric to describe the PAR photon output divided by the energy input, with the unit of $\mu mol \cdot J^{-1}$ (Runkle and Bugbee, 2017). In 2014, the PPE of the most efficient LED arrays, double-ended HPS, ceramic MH, and FL were 1.70, 1.70, 1.46, and 0.95 $\mu mol \cdot J^{-1}$, respectively (Nelson and Bugbee, 2014), but the PPE of LEDs continues to increase because of technology improvements.

In addition to PPE, canopy photon capture efficiency can also influence fixture efficacy. As the plant growth area under the lighting fixture decreases, the amount of radiation that strikes areas without plants increases (Nelson and Bugbee, 2014), leading to a decreased canopy photon capture efficiency. Therefore, greenhouse characteristics need to be considered when selecting appropriate lamp types and their distribution of light. Precision luminaires or LEDs with adjustable angles can be used to deliver more directional lighting to plants, especially in small-scale greenhouses with widely spaced benches (Nelson and Bugbee, 2014).

In addition to lamp efficacy and the distribution of light, several other factors merit consideration when selecting lamps including cost, spectrum, longevity and durability, light uniformity, tolerance to damp conditions, supply and cost of electricity, and shading from the lighting fixtures (Runkle, 2017). Non-uniform lighting can potentially cause uneven plant growth and flowering, creating non-uniform plants with varying watering demands (Fisher et al., 2001). FL lamps generally have a large shadow considering its low photon output (Nelson and Bugbee, 2014) and thus, are not commonly used in greenhouses. In contrast, LEDs (and to a lesser extent, HPS and MH lamps) can be mounted on the greenhouse structure and provide light with less shading.

Maintenance cost for a lighting system is highly dependent on the life expectancy of the fixture. The estimated life of conventional lamps is around 10,000 h [for example, 10,000 h for double-ended HPS lamps (Nelson and Bugbee, 2014) and 8,000-10,000 for CFL (Tähkämö et al., 2012)], but LEDs have a life expectancy of as much as 55,000 h if used in an appropriate environment (Nelson and Bugbee, 2014). However, the purchase and replacement cost of LEDs is usually substantially more expensive than conventional lamps.

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SECTION II

REGULATING FLOWERING AND EXTENSION GROWTH OF POINSETTIA USING RED AND FAR-RED LEDS FOR END-OF-DAY LIGHTING

Regulating Flowering and Extension Growth of Poinsettia Using Red and Far-red LEDs for End-of-day Lighting

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Abstract

Manipulating light quality is a potential alternative method of regulating plant height in the commercial production of ornamental crops. In particular, end-of-day (EOD) lighting with a high red (R, 600-700 nm) to far-red (FR, 700–800 nm) ratio (R:FR) can suppress extension growth while a low R:FR can promote it. We investigated the impacts of the R:FR and duration of EOD lighting in regulating extension growth and flowering of two poinsettia cultivars, 'White Glitter' and 'Marble Star'. Plants were grown at 20 °C under 9-h short days with or without EOD lighting provided by two types of light-emitting diode (LED) bulbs: R+white+FR (subsequently referred to as R+FR) and FR only. The R:FR ratios were 0.73 and 0.04 respectively, and the photon flux density between 400 to 800 nm was adjusted to 2-3 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at plant canopy. The six end-of-day lighting treatments were R+FR or FR for 2 or 4 h, 2h R+FR followed by 2 h FR, and 4 h R+FR followed by 2 h FR. We also investigated the impact of a 4-h high-intensity (13 $\mu mol \cdot m^{-2} \cdot s^{-1}$) EOD FR treatment in the second replication. EOD lighting generally increased poinsettia extension growth, with the greatest promotion under the longest lighting periods. There were no differences in days to first bract color and days to anthesis when the 9-h day was extended by 2 h, but they were delayed under 4- or 6-h EOD treatments except 2-h R+FR + 2-h FR and 4-h FR. Four hours of high-intensity EOD FR greatly promoted extension growth and delayed or prevented bract coloration in both cultivars. We conclude that EOD lighting promotes extension growth of poinsettia and specifically, EOD FR at a low intensity is not perceived as long-day signal whereas a higher intensity of FR is perceived and delays flowering.

Keywords: *Euphorbia pulcherrima*, light quality, morphogenesis, photoperiod, photoreversibility, phytochrome

Introduction

Poinsettia (*Euphorbia pulcherrima*) is a popular potted-flowering crop, especially for the Christmas holiday, because of its colorful and showy bracts. Approximately one-third of the global poinsettia market is in the U.S., while the remaining market is mostly in Europe (Taylor et al., 2011). Poinsettia was the second most valuable potted flowering plant after orchids in 2015, accounting for $140 million in wholesale sales and representing 17% of the total value of potted flowering plants sold in the U.S. (USDA, 2016). Coordinated control of flowering of poinsettia is crucial so that commercial crops are marketable for pre-determined dates for the Christmas holiday. It is a short-day (SD) plant with a critical photoperiod of around 12 hours and 20 minutes (night length of 11 hours and 40 minutes) and thus, is naturally induced to flower in the northern hemisphere beginning in late September (Ecke et al., 2004).

Height control is one of the major challenges in commercial greenhouse production of poinsettia. High-quality poinsettia requires the plants to be marketed at specific target heights, which is typically 36 to 41 cm for plants grown in 15-cm containers (Taylor et al., 2011). Excessively tall poinsettia can develop branches that are more susceptible to breakage and increase transportation cost (Clifford et al., 2004). Therefore, plant growth retardants (PGRs) are commonly used to suppress stem extension to produce more compact plants. Chlormequat chloride, daminozide, uniconazole, paclobutrazol, and flurprimidol, used either as foliar spray or drench, are effective at inhibiting stem elongation (Currey and Lopez, 2011; Latimer and Whipker, 2013; Lopez and Runkle, 2007).

For ornamentals, although the promotion of stem growth is usually not desired in commercial production, it can be beneficial in some situations, such as in cut flower production or when plants are shorter than desired. Gibberellic acid is commonly applied by commercial

growers to increase plant height and promote leaf expansion of poinsettia when an excessive concentration of a PGR was previously applied (Lopez and Runkle, 2007). However, the use of PGRs is restricted to various degrees by different governments (Rajapakse et al., 1999). Different strategies can be used as an alternative way to manipulate extension growth, such as cooler night than day temperatures, less crop spacing, and avoiding phosphorus deficiency (Ecke et al., 2004; Runkle, 2005).

Light quality manipulation is an alternative strategy to manage plant height, especially the ratio of red (R, 600-700 nm) and far-red (FR, 700-800 nm) radiation. R and FR radiation are perceived by phytochrome photoreceptors, which have two forms: a R light-absorbing (Pr) form and a FR light-absorbing (Pfr) form (Butler et al., 1959). The interconversion between these two forms of each phytochrome in plants is known as photoreversibility, and can at least partially regulate seed germination, extension growth, and flowering (Borthwick, 1952; Schopfer et al., 1982; Borthwick and Downs, 1964). Spectral filters have been used experimentally to determine the effects of different light qualities on plant height. For example, poinsettia were grown under cladding materials of neutral density (control) (R:FR = 1.07) or FR, R, and blue (B, 400-500 nm) plastic filters creating an FR deficient, R deficient, and B deficient environment with an R:FR of 1.74, 0.04, and 1.05, respectively, under sunlight (Clifford et al., 2004). The internode lengths were increased by 71% and 9% under R and B deficient filters, respectively, and decreased by 20% under the FR deficient filter compared to the control.

End-of-day (EOD) lighting can also be used to regulate extension growth by manipulating the R:FR ratio. Generally, plants elongate under a low R:FR ratio. For example, chrysanthemum (*Chrysanthemum*×*morifolium*) was grown under a 9-h short day (SD) with EOD lighting for 30 min at a photosynthetic photon flux density (*PPFD*) of 1-3 $\mu mol \cdot m^{-2} \cdot s^{-1}$ with

either a high (2.4) or low (0.4) R:FR (Lund et al., 2007). Plant height after 3 weeks increased by 50-75% with EOD lighting at the low R:FR compared to the high ratio. In a separate study, impatiens (*Impatiens walleriana*), geranium (*Pelargonium ×hortorum*), and petunia (*Petunia ×hybrida*) were grown under an 8.5-h day with 30 min of EOD lighting at 20 $\mu mol \cdot m^{-2} \cdot s^{-1}$ with an R:FR of 0.9 or 8.4 (Randall, 2014). Stem length of impatiens, geranium, and petunia was promoted by 29%, 20%, and 44%, respectively, after 21 d under the lower R:FR compared to the higher ratio.

End-of-day lighting can also be used to extend the natural photoperiod and create long days to regulate flowering of photoperiodic crops. The threshold irradiance to regulate flowering of several herbaceous perennials ranged from 0.05 to 0.4 $\mu mol \cdot m^{-2} \cdot s^{-1}$, while the saturation irradiance ranged from 0.2-1.0 $\mu mol \cdot m^{-2} \cdot s^{-1}$, depending on the species (Whitman et al., 1998). Generally, an intensity of 1-3 $\mu mol \cdot m^{-2} \cdot s^{-1}$ is recommended to accelerate flowering of long-day plants (LDPs) and inhibit flowering of short-day plants (SDPs) (Runkle, 2015).

Red light is typically effective at inhibiting flowering of SDPs. For example, the flowering of chrysanthemum, dahlia (*Dahlia hortensis*), and marigold (*Tagetes erecta*) was delayed by 42, 11, and 10-20 d when grown under 4-h night interruption (NI) provided by LEDs with an R:FR ≥0.66 at a photon flux density of 1.3-1.6 $\mu mol \cdot m^{-2} \cdot s^{-1}$ compared to SD control (Craig and Runkle, 2013). The inclusion of FR with R radiation, delivered as EOD or NI lighting, had little to no effect on regulating flowering of SDPs, but did promote flowering of some LDPs. However, a low-intensity of FR alone as an NI is generally not perceived as a long-day (LD) signal by LDPs and SDPs. For example, the SDP marigold flowered 10-19 d earlier under SDs or NI with only FR compared to NI with a combination of R and FR (Craig and Runkle, 2013).

R/FR photoreversibility is one of the characteristic features for phytochrome responses and was first discovered in a lettuce (*Lactuca sativa*) seed germination experiment (Borthwick et al., 1952). R light promoted lettuce seed germination, whereas subsequent FR inhibited it. This kind of photoreaction response was also established on flower initiation of some model plants. For example, a short period of R light as an NI prevented the flower initiation of the SDP soybean (*Glycine max*) and pigweed (*Amaranthus caudatus*) and induced the flowering of the LDP henbane (*Hyoscyamus niger*), while subsequent FR irradiation reversed the effects of R light (Downs, 1956). Although there are three action modes for phytochrome responses, photoreversibility is a characteristic of low-fluence response (Li et al., 2011). This suggests that phytochrome-mediated flowering responses could be affected by the last NI lighting treatment and potentially show photoreversibility in at least some light-sensitive plants.

The objective of this study was to investigate whether EOD FR would promote extension growth without influencing flowering of poinsettia. We also wondered whether flowering could be inhibited by delivering FR after R given the phytochrome photoreversibility response. We postulated that a low intensity of FR as EOD lighting would promote extension growth but not regulate flowering and thus, could be used to increase plant height without influencing crop scheduling. We also anticipated that ending EOD lighting with FR would at least partly reverse the effects of R light at inhibiting flowering.

Materials and Methods

Plant materials

Unrooted cuttings of two cultivars of poinsettia, ‘White Glitter’ and ‘Marble Star’, were obtained from C. Raker & Sons (Litchfield, MI) for replication 1 and Syngenta Flowers (Gilroy,

CA) for replication 2. They were rooted at 23 °C under a 16-h long day in a propagation greenhouse at Michigan State University (MSU, East Lansing, MI). Rooted cuttings were transplanted into 15-cm pots containing 70% peatmoss, 21% perlite, and 9% vermiculite potting media (SUREMIX; Michigan Grower Products, Inc., Galesburg, MI) and grown in a glass-glazed greenhouse. All plants were grown under a 16-h photoperiod consisting of natural daylengths with supplemental lighting at a *PPFD* of 70 μmol·m^{-2}·s^{-1} provided from 400-W high-pressure sodium fixtures (LR48877; P.L. Light System, Beamsville, ON, Canada) for replication 1 or red+white LEDs (210 W, peak wavelength = 660 nm; GreenPower LED top lighting DR/W/MB; Philips, Eindhoven, The Netherlands) for replication 2, from transplanting until the start of treatments. Supplemental lighting was automatically switched on when the outside ambient solar *PPFD* was <437 μmol·m^{-2}·s^{-1}, as controlled by a greenhouse environmental control system (Integro 725; Priva North America, Vineland, Ontario, Canada). Plants were pinched back to six nodes from the soil surface about three weeks after transplanting. About four weeks after pinching, 70 (replication 1) or 80 (replication 2) pots of the most uniform poinsettias of each cultivar were selected and randomly assigned to seven (replication 1) or eight (replication 2) benches with different lighting treatments in the same greenhouse. Plants were irrigated as necessary with reverse osmosis water supplemented with a water-soluble fertilizer containing (mg·L^{-1}) 250 N, 25 P, 239 K, 154 Ca, 38 Mg, 3.4 Fe, 0.8 Cu, 0.8 Zn, 1.7 Mn, 0.4 B, and 0.4 Mo (EC = 2.0).

Lighting treatments

Ten plants of each cultivar were grown under a 9-h truncated natural day created by pulling the black cloth over each bench daily at 1700 HR and opening it at 0800 HR. They received six (replication 1) or seven (replication 2) EOD lighting treatments or no EOD

treatment (control). The EOD lighting treatments were delivered by R+white+FR LEDs (GreenPower DR/W/FR flowering lamps; Philips) (subsequently referred to as R+FR) with an R:FR of 0.73, and FR LEDs (GreenPower FR flowering lamps; Philips) with an R:FR of 0.04 (Fig. 1). The EOD lighting treatments were: 2 h of R+FR or FR (1700 HR to 1900 HR), 2 h of R+FR followed by 2 h of FR (1700 HR to 1900 HR + 1900 HR to 2100 HR), 4 h of R+FR or FR (1700 HR to 2100 HR), and 4 h of R+FR followed by 2 h of FR (1700 HR to 2100 HR + 2100 HR to 2300 HR) (Table 1). Layers of wire mesh were placed over the lamps so that the average photon flux density (from 400 to 800 nm) at plant canopy was between 2 and 3 $\mu mol \cdot m^{-2} \cdot s^{-1}$. In addition, 4 h of FR (1700 HR to 2100 HR) (subsequently referred to as H-FR) at 10-15 $\mu mol \cdot m^{-2} \cdot s^{-1}$ was provided as an additional treatment in replication 2. Photon flux measurements were made with a spectroradiometer (PS-200; StellerNet, Inc. Tampa, FL) at four representative positions 18 cm above the bench. The average photon flux density of the R+FR, FR, and H-FR lighting treatments were 2.6, 2.5, and 13.4 $\mu mol \cdot m^{-2} \cdot s^{-1}$, respectively.

Environmental conditions

Plants were grown at a constant temperature setpoint of 20 °C. Whitewash (Kool Ray Classic; Continental Products Co., Euclid, OH) was applied to the greenhouse glazing to deliver a more similar daily light integral (DLI) between the two replications. The *PPFD* at bench height was recorded by a quantum sensor (LI-190SA; LI-COR, Lincoln, NE). Air temperature was recorded on benches by aspirated thermocouples (Type E; Omega Engineering, Stamford, CT) near canopy height. Air temperature and the *PPFD* were collected by a data logger (CR-10; Campbell Scientific, Logan, UT) every ten seconds and average values were recorded hourly. Daily temperatures were checked routinely and averages are reported in Table 1. The average DLI during the study was 7.4 and 10.5 $mol \cdot m^{-2} \cdot d^{-1}$ for replication 1 and 2, respectively.

Plant measurements

Plant height (from the substrate surface to the tallest meristem) was measured at the initiation of the lighting treatments. Height (from the substrate surface to the bottom of the flower bud) was measured at anthesis for flowering plants, and for non-flowering plants, height was recorded after 15 weeks of treatments. Date of first bract color (when the first leaf on each plant showed partial color), date of first anthesis (when the first flower showed pollen tubes), and node number were also recorded. Average internode length was calculated by final plant height divided by node number only in replication 2.

Experimental design and data analysis

The experiment was performed twice, with treatments initiated in October 2016 and April 2017. The experiment was a randomized complete block design with subsamples. Two replications were considered two blocks to account for seasonal changes in environmental conditions. Each bench was regarded as the experimental unit for the EOD lighting treatment. Within the experimental unit, ten individual plants per cultivar were the subsamples. Data were pooled from two replications and were analyzed with the SAS (SAS Institute, Inc., Cary, NC) mixed-model (PROC MIXED) and glimmix-model (PROC GLIMMIX) procedures. Pairwise comparisons between treatments were performed using Tukey's honest significant difference test at $P \leq 0.05$.

Results

All plants of both cultivars showed bract coloration and reached anthesis except for some plants under the 4-h R+FR, 4-h R+FR + 2-h FR, and 4-h H-FR treatments (Table 2). The general trends for bract coloration and anthesis were similar in both cultivars (Fig. 2). When the day was

extended for ≤4 h of lighting, days to first bract coloration and anthesis were similar to plants grown under the 9-h SD (control), except for plants under the 4-h R+FR treatment. The 4-h R+FR delayed bract coloration and anthesis by 34 and 29 d in 'Marble Star' and 28 and 23 d in 'White Glitter', respectively, compared to the SD control, whereas the 4-h FR EOD did not delay flowering. In addition, the 4-h R+FR + 2-h FR and 4-h H-FR treatments delayed first bract coloration of 'Marble Star' by 45 and 55 d and anthesis by 34 and 38 d, respectively, compared to the SD control. Similarly, in 'White Glitter', bract coloration and anthesis were delayed by 17 and 34 d, respectively, under 4-h R+FR + 2-h FR EOD lighting. The days to bract coloration and anthesis are statistically similar under 4-h R+FR and 4-h R+FR + 2-h FR, therefore, no phytochrome photoreversibility was observed. Under the 4-h R+FR + 2-h FR and 4-h H-FR lighting treatments, 'Marble Star' reached anthesis shortly after first bract coloration, and the interval was much shorter than for plants under the other lighting treatments.

Among the plants under treatments that fully flowered, stem length generally increased as the duration of light increased in both cultivars (Fig. 3). Plants of both cultivars were tallest under the longest EOD lighting treatment with a low-light intensity (4-h R+FR + 2-h FR). The increase in stem length at the end of the experiment for 'Marble Star' and 'White Glitter' was 161% and 207% greater, respectively, under the longest EOD lighting compared to plants grown under the SD control. In addition, extension growth at anthesis of 'Marble Star' under the 4-h R+FR was 125% greater than that of the control. Stem elongation of 4-h H-FR for 15 weeks was statistically similar with those under 4-h R+FR followed by 2-h FR. Therefore, 4-h of high-intensity FR was as effective as the 6-h EOD lighting treatment in increasing plant height, and thus plants were also the tallest among all the lighting treatments.

‘Marble Star’ had an average of 14 or 15 nodes under all treatments 15 weeks after the initiation of the treatments except for the 4-h R+FR, 4-h R+FR + 2-h FR, and 4-h H-FR treatments, which developed 20, 20, and 27 nodes, respectively, before anthesis (Fig. 3). Similarly, ‘White Glitter’ had an average of 15 to 19 nodes overall but developed 6 and 9 more nodes under the 4-h R+FR + 2-h FR and 4-h H-FR treatments, respectively, compared to the SD control. Average internode length of most EOD lighting treatments was significantly greater than plants grown under the 9-h day. ‘Marble Star’ and ‘White Glitter’ grown under 2-h R+FR + 2-h FR developed a 22% and 19% longer internode, respectively, compared to those under 2-h R+FR. Similarly, ‘White Glitter’ developed a 21% greater internode length, respectively, when grown under 4-h R+FR + 2-h FR compared to 4-h R+FR. In addition, the average internode length for both cultivars was significantly greater for plants under 4-h H-FR compared to 4-h FR, with a promotion of 13% in ‘Marble Star’ and 30% in ‘White Glitter’.

Discussion

We tested the hypothesis that flowering of the SDP poinsettia would not be influenced by delivering FR light during an otherwise long night. Several LDPs including black-eyed susan (*Rudbeckia hirta*) and fuchsia (*Fuchsia hybrida*) were reportedly insensitive to 4-h NI with FR alone at 1.3-1.6 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for accelerating flowering compared to NI with R+FR at the same photon flux density (Craig and Runkle, 2016). In SDPs, the flowering time of chrysanthemum, dahlia, and marigold exposed to a 4-h NI with 1.3 to 1.6 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of FR alone were similar to that of the SD control treatment (Craig and Runkle, 2013). Consistent with these responses, this study showed that both cultivars of poinsettia grown under a 9-h day with 2- or 4-h EOD lighting of low-intensity FR alone showed bract color and reached anthesis at a similar time as

the SD control. In addition, the previous study showed that a moderate to high R:FR (≥ 0.66) was the most effective NI for the SDPs for delaying the flowering (Craig and Runkle, 2013). In this study, 4-h EOD lighting with a R:FR of 0.73 delayed the poinsettia bract color and anthesis development. Therefore, a low-intensity of FR alone as EOD lighting was not perceived as an LD signal in poinsettia whereas a mixture of R and FR inhibited flowering.

Interestingly, the flowering percentage decreased in both cultivars when grown under 4-h EOD lighting of 13 $\mu mol \cdot m^{-2} \cdot s^{-1}$ FR compared to the SD control. Days to first bract color and anthesis of 'Marble Star' were significantly delayed and 'White Glitter' still remained vegetative when the experiment ended. In contrast, Higuchi et al. (2012) grew the SDP chrysanthemum under cool white fluorescent tubes at 150 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for 12 hours per day with or without a 4-h NI provided by either R or FR monochromatic LEDs. A 62 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of FR NI did not inhibit the flowering of chrysanthemum. These results suggest that the reproductive process of poinsettia is relatively sensitive to FR radiation and even a moderate dose of FR is sufficient to inhibit the flowering of poinsettia but not in other SDPs such as chrysanthemum.

The critical photoperiod of poinsettia is around 12 hours and 20 minutes (Ecke et al., 2004). As expected, plants grown with 2 h of R+FR EOD lighting, creating an 11-h photoperiod, flowered similar to those under the SD control. We also expected that the 2-h R+FR + 2-h FR EOD lighting treatment would create an SD because the low-intensity FR would not be perceived as an LD signal, and indeed, that occurred. Surprisingly, plants under the 4-h R+FR and 4-h R+FR + 2-h FR treatments (creating a 13-h or 15-h photoperiod, respectively) flowered, although some plants did not flower in Rep. 2 and flowering was delayed. However, unlike plants under SD conditions, we noticed that the primary stems of some plants grown under ≥ 4-h EOD lighting remained vegetative, while bract color and anthesis occurred on lower branches

that were at least partly shaded by the primary stems (data not collected). We postulate that the leaves on the primary stem prevented R light from reaching lower branches and thus, those branches were induced to flower.

The flowering of plants grown under 4-h R+FR EOD lighting was delayed, and we did not observe a reversing effect of subsequent 2-h FR EOD lighting that one might expect with phytochrome photoreversibility. Phytochrome photoreversibility responses are reportedly low-fluence responses with saturating photon fluxes of around 1 to 1,000 μmol·m^{-2} (Li et al., 2011). In this study, the total photon fluence of R light during one night was 11,500 to 17,500 μmol·m^{-2}, which exceeded the response saturation range. In addition, once receiving the R light, phytochrome would change from the biologically inactive Pr form to biologically active Pfr form. The Pfr transition action can vary from slow to fast in responses such as stem elongation, seed germination, and flower induction (Kendrick and Kronenberg, 2012). For example, the transition action can vary from 9 h of darkness between R and FR required for a 50% loss of photoreversibility in germination of lettuce seeds, to 30-60 min before Pfr drops and induces flowering of the SDP cocklebur (*Xanthium stunarium*) (Borthwick et al., 1954; Kendrick and Kronenberg, 2012; Salisbury, 1981). Therefore, 2 h of FR at a low fluence immediately following R may not be a sufficient dose to reverse the flowering inhibition by 4-h of R light.

Generally, plant height increased as the lighting duration increased, with the greatest promotion under the longest photoperiod or under a higher intensity of EOD FR lighting. Longer stems can result from longer internodes, more nodes because of the delay in the development and flower initiation, or both. Craig and Runkle (2013) reported that SDPs grown under NI with a moderate R:FR were taller than those grown under NI with FR alone because plants under FR-only NI entered the reproduction stage earlier in development. Similarly, chrysanthemum and

marigold under 4-h NI that delayed the flowering resulted in significantly taller plants compared to the SD treatment (Meng and Runkle, 2015). In this study, both cultivars of poinsettia grown under 4-h FR initiated the flowering process similar to that of plants under the SD control, whereas flowering under 4-h R+FR, 4-h R+FR + 2-h FR, and 4-h H-FR was delayed and plants developed more nodes before flowering. Therefore, the flower initiation was later in the development and the overall extension of plants under those treatments was greater than the others.

Delivering low-intensity EOD FR successfully promoted poinsettia extension growth without delaying flowering. Promotion of stem length can be achieved by providing EOD lighting, and a low R:FR is typically more effective than a high R:FR. For example, the hypocotyl length of tomato seedlings under 12-min EOD lighting treatment, regardless of light quality, was 20-44% greater than that without an EOD treatment (Chia and Kubota, 2010). In addition, the hypocotyl length under EOD lighting with a R:FR of 0.05 was 20% greater than under EOD lighting with a R:FR of 0.47. In another poinsettia study, two cultivars ('Christmas Spirit' and 'Christmas Eve') were exposed to R or FR EOD lighting for 30 min at 10 μmol·m^{-2}·s^{-1} following a 10-h SD (Islam et al., 2014). The internode length after 11 weeks was 55-107% greater under EOD-FR compared to EOD-R. In our study, plant height in 'Marble Star' under the 2-h EOD lighting treatments (regardless of light quality) was statistically similar to the SD control, while in 'White Glitter', plants were significantly taller. In addition, no differences in height and internode length were observed for both cultivars grown under 2- and 4-h EOD-FR compared to R+FR. Therefore, the sensitivity of response to R/FR in stem elongation might be cultivar specific. This is supported by Rajapakse et al. (1993), who reported that a 15 min EOD-

FR treatment did not influence plant height of one cultivar of chrysanthemum but increased height by ~50% in another cultivar.

APPENDIX

Table II-1. Means (±SD) of greenhouse air temperature during the two experimental replications (Rep.) as measured by aspirated thermocouples. Plants were grown under a 9-h short day (15-h dark period; black bar) without or with end-of-day lighting from red+white+far-red (R+FR; white bar) or far-red (FR; grey bar) light-emitting diodes at 2 to 3 μmol·m^{-2}·s^{-1} for 2 or 4 h. In Rep. 2, an additional treatment of a high-intensity far-red (H-FR) at 13 μmol·m^{-2}·s^{-1} was included.

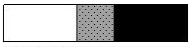
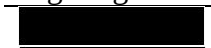
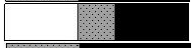
		Average air temperature (°C)	
Lighting treatment		Rep. 1	Rep. 2
9-h control		20.0 ± 1.5	23.7 ± 4.2
2-h R+FR		20.0 ± 1.9	21.5 ± 3.1
2-h FR		19.8 ± 2.2	21.9 ± 3.2
2-h R+FR + 2-h FR		19.4 ± 1.3	21.7 ± 3.2
4-h R+FR		19.9 ± 1.4	22.0 ± 3.1
4-h FR		19.8 ± 1.3	22.0 ± 3.1
4-h R+FR + 2-h FR		19.4 ± 1.4	21.9 ± 3.3
4-h H-FR		--	23.6 ± 4.1

Table II-2. Effect of end-of-day (EOD) lighting treatments on the percentage of plants with bract color and reaching anthesis of two cultivars of poinsettia (‘Marble Star’ and ‘White Glitter’). See Table 1 for descriptions of lighting treatments.

	Bract color				Anthesis			
	Rep 1		Rep 2		Rep 1		Rep 2	
Lighting treatment	‘Marble Star’	‘White Glitter’	‘Marble Star’	‘White Glitter’	‘Marble Star’	‘White Glitter’	‘Marble Star’	‘White Glitter’
	100	100	100	100	100	100	100	100
	100	100	100	100	100	100	100	100
	100	100	100	100	100	100	100	100
	100	100	100	100	100	100	100	100
	100	100	40	90	100	100	30	30
	100	100	100	100	90	100	100	100
	80	100	30	40	50	80	20	20
 *	--	--	40	20	--	--	30	0

*Only performed in Rep 2.

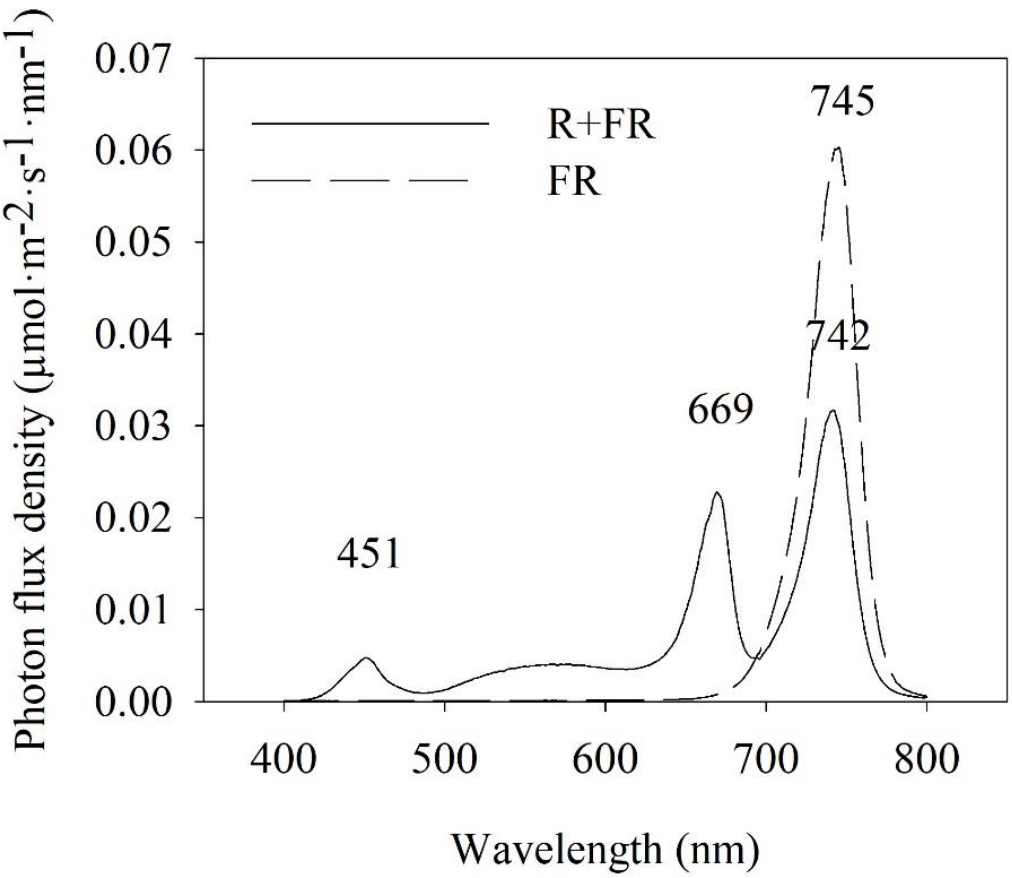


Figure II-1. Spectral distribution of two types of end-of-day (EOD) lighting treatments delivering red (R, 600 to 700 nm), and/or far-red (FR, 700 to 800 nm) radiation. The photon flux density of the two EOD lighting treatments was 2 to 3 μmol·m^{-2}·s^{-1}.

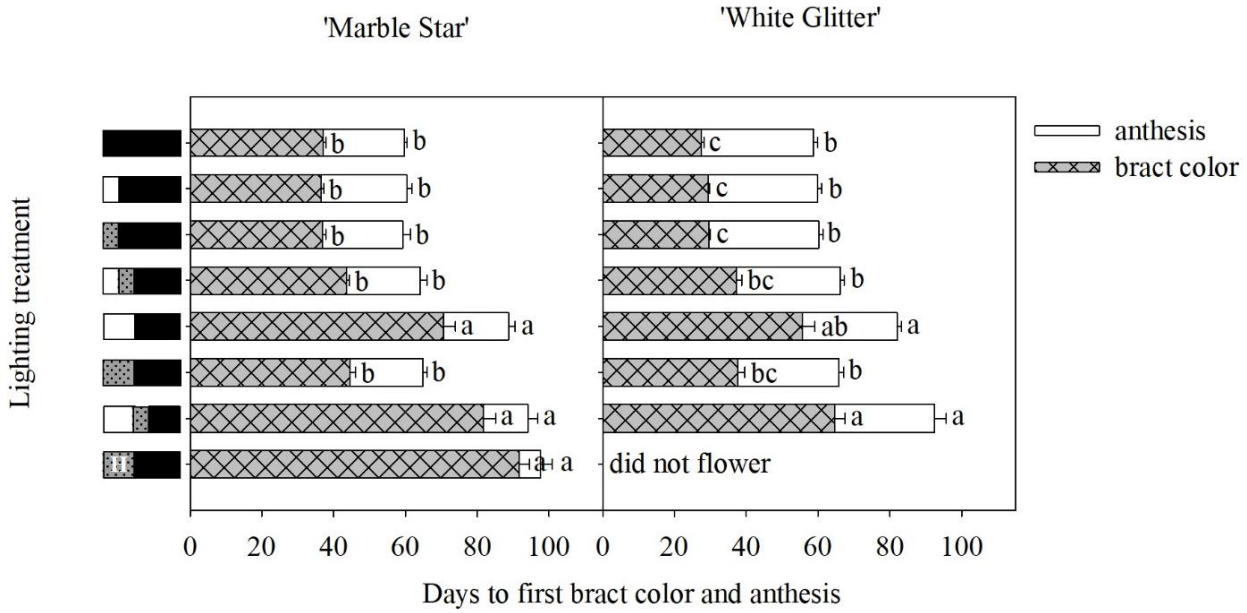


Figure II-2. Days to first bract color and anthesis of two cultivars of poinsettia grown under a 9-h short-day (control) and seven red and/or far-red end-of-day lighting treatments (see Table 1 for treatment descriptions). All treatments were delivered at a photon flux density (400 to 800 nm) of 2 to 3 µmol·m^{-2}·s^{-1}, except 4-h H-FR, which was delivered at 13 µmol·m^{-2}·s^{-1}. All data were pooled from two replications, except 4-h H-FR, which was only conducted in the second replication. Pairwise comparison was made within each cultivar. Means sharing a letter are not statistically different by Tukey's honest significant difference test at $P \leq 0.05$. Error bars indicate standard error.

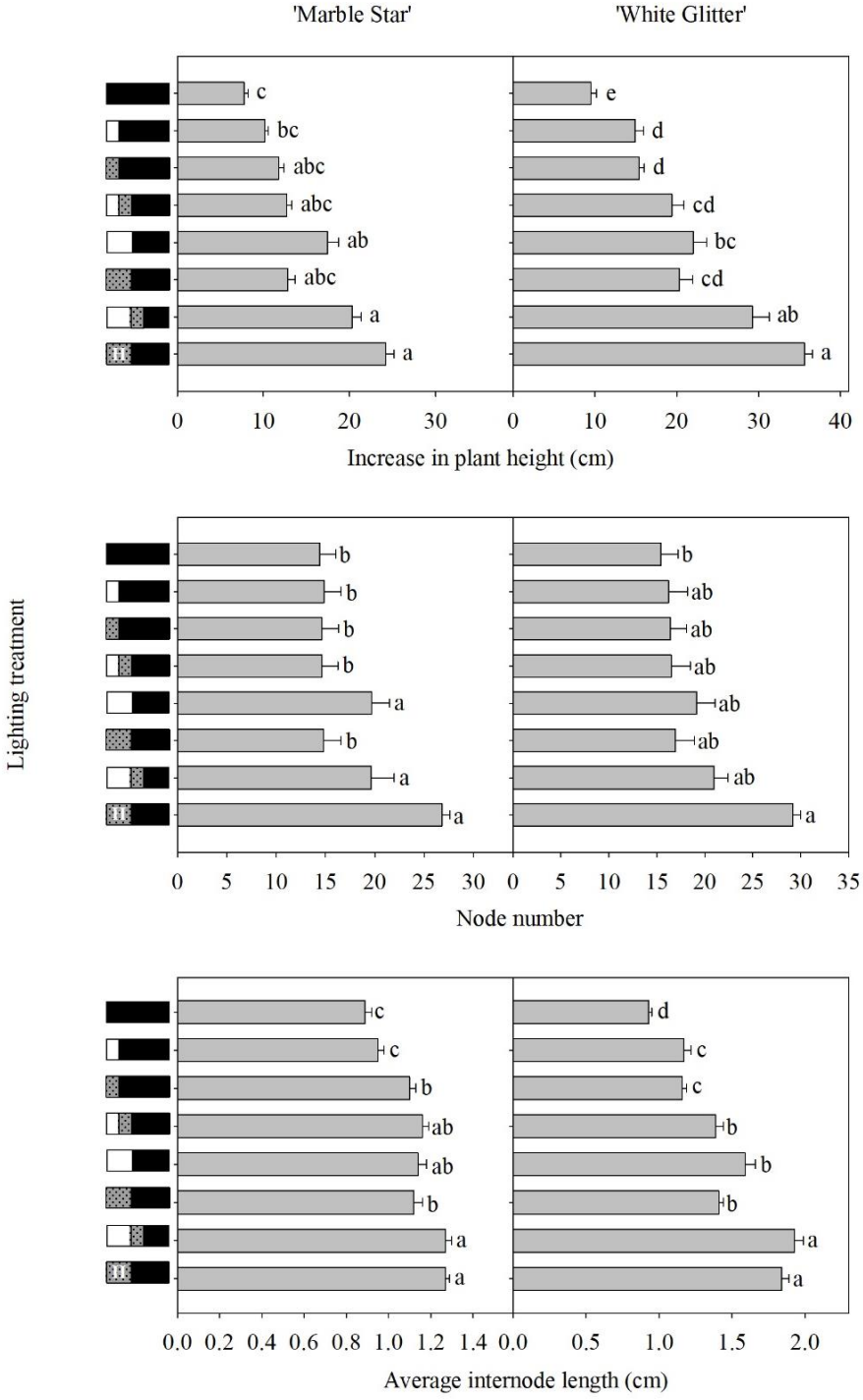


Figure II-3. Increase in plant height, node number, and average internode length of two cultivars of poinsettia grown under a 9-h short-day (control) and seven end-of-day red and/or far-red lighting treatments (see Table 1 for treatment descriptions). All treatments were delivered at a photon flux density (400 to 800 nm) of 2 to 3 $\mu mol \cdot m^{-2} \cdot s^{-1}$, except 4-h H-FR, which was delivered at 13 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Pairwise comparisons were made within each cultivar. Means sharing a letter are not statistically different by Tukey's honest significant difference test at $P \leq 0.05$. Error bars indicate standard error.

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SECTION III

MANIPULATING GROWTH, COLOR, AND TASTE ATTRIBUTES OF FRESH CUT LETTUCE BY GREENHOUSE SUPPLEMENTAL LIGHTING

Manipulating Growth, Color, and Taste Attributes of Fresh Cut Lettuce by Greenhouse Supplemental Lighting

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Abstract

Supplemental lighting (SL) is often used in greenhouse lettuce production to increase yield when the solar daily light integral (DLI) is low. High-pressure sodium (HPS) fixtures are traditionally used to deliver SL, but light-emitting diodes (LEDs) have become a viable, more energy-efficient replacement. Red (R, 600-700 nm) and blue (B, 400-500 nm) light are especially effective in promoting photosynthesis and increasing crop growth, while far-red (FR, 700-800 nm) light has the potential to increase yield by promoting leaf expansion. We performed three greenhouse experiments with HPS or LED fixtures to determine the impacts of SL on lettuce growth, coloration, and sensory attributes. We grew lettuce at 20 °C without or with supplemental lighting from HPS or R+B LEDs with a 16-h photoperiod (Expts. 1 and 2). In Expt. 3, we grew plants without or with HPS SL without or with R+FR photoperiodic lighting at the end of the day during the growing (first) stage, and/or SL from R+B or B LEDs during the finishing (second) stage. SL enhanced lettuce growth and yield by 32-104% regardless of light quality. Four hours of 2 to 5 $\mu mol \cdot m^{-2} \cdot s^{-1}$ end-of-day R+FR lighting had few effects on lettuce growth or quality attributes. Compared to no SL, lettuce provided with R+B LED SL for 7 d before harvest was 27% darker, 76-82% redder, and 39-55% less yellowish. Consumers tended to prefer lettuce grown under natural daylight more than plants grown with SL, and had a less bitter, sweeter, and a more likable aftertaste. We conclude that providing different types of greenhouse SL at different growing stages can improve lettuce growth and coloration but could be less preferred by consumers.

Keywords: Blue light, end-of-day lighting, far-red light, *Lactuca sativa*, light quality, red light

Introduction

Lettuce (*Lactuca sativa*) is the second most consumed vegetable (only to potato) in the American diet (Produce for Better Health Foundation, 2015), of which 45% is leaf and romaine lettuce (USDA and Economic Research Service, 2018). Most lettuce is commercially produced outdoors in desert regions of CA and AZ, but an increasing amount is grown in controlled environments. Lettuce growth can be slow when the daily light integral (DLI) is low, such as in greenhouses during the winter in northern latitudes. Therefore, supplemental lighting (SL) is often used to increase the DLI for greenhouse lettuce production. Typically, 12 to 16 h of SL at 50-75 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for lettuce seedlings is recommended (Dorais and Gosselin, 2002). The recommended DLI for finished plant production in greenhouses is somewhat cultivar specific, with 17 $mol \cdot m^{-2} \cdot d^{-1}$ for Boston bibb lettuce, but a maximum of 15 $mol \cdot m^{-2} \cdot d^{-1}$ for other cultivars to prevent a calcium deficiency that results in tipburn (Brechner and Both, 1996).

High-pressure sodium (HPS) fixtures are widely used for SL in greenhouses while arrays of light-emitting diodes (LEDs) are increasingly being used because of their technological advantages. LEDs have a significantly longer lifetime than conventional fixtures, ranging from 20,000 to 55,000 h compared with the lifetime for HPS bulbs of 10,000 h (Nelson and Bugbee, 2014). The photosynthetic photon efficacy of the most efficient LED and double-ended HPS fixture in 2014 was similar (1.7 $\mu mol \cdot J^{-1}$), but the photosynthetic photon efficacy of LEDs continues to increase because of technology improvements (Fisher et al., 2017). For example, in 2018, the two LEDs tested with the greatest efficacy were approximately 50% greater than a 1,000-W double-ended HPS fixture (Radetsky, 2018). In addition, LEDs can provide a crop-specific spectrum to elicit desirable photomorphogenic and quality attributes. However, the relatively high investment cost for LEDs is the greatest obstacle to expanding implementation by

the commercial greenhouse industry. A hybrid lighting system that combines some of the features of LEDs with conventional HPS fixtures could be an economically efficient option (Olle and Viršilė, 2013).

Far-red (FR, 700 to 800 nm) light regulates leaf morphology and promotes leaf expansion. Lettuce grown under white fluorescent lamps with supplemental FR developed a 44% longer and 15% wider leaf, resulting in a 65% larger leaf compared to without FR, both at a photosynthetic photon flux density (*PPFD*) of 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Li and Kubota, 2009). Providing a low dose and a short period of FR as end-of-day (EOD) lighting can also increase leaf area in some species. For example, a 5 min EOD-FR pulse for 18 d elongated tobacco (*Nicotiana tabacum*) leaves by 11% (Kasperbauer and Peaslee, 1973). In Easter lily (*Lilium longiflorum*), leaf area of 'Nellie White' increased by 17% when exposed to 1-h EOD-FR at a photon flux density of 0.2 to 6.5 $\mu mol \cdot m^{-2} \cdot s^{-1}$ compared to those without EOD-FR (Blom et al., 1995). Therefore, we postulated that low-fluence EOD-FR to increase leaf expansion early in development, followed by high-intensity SL to increase biomass and coloration, could be an economic strategy to improve crop quality in greenhouse lettuce production.

The biomass or harvestable yield of many horticultural crops is related to the average DLI. For example, the biomass of Boston-type lettuce increased up to 270%, along with a greater head firmness and a ~30% reduction of production cycle length, under continuous greenhouse SL at a *PPFD* of 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ from HPS fixtures compared to without SL (Gaudreau et al., 1994). In another study, the fresh mass of kale (*Brassica oleracea*) grown indoors increased from 8 to 93 grams per plant as the DLI increased from 10.8 to 43.2 $mol \cdot m^{-2} \cdot d^{-1}$ (Lefsrud et al., 2006). Similarly in romaine lettuce, shoot fresh weight was enhanced by 14%, 24%, and 27% as the

DLI increased from 5 to 10, 20, and 30 mol·m^{-2}·d^{-1}, respectively, when grown indoors (Fu et al., 2012).

Anthocyanins are one of the most abundant pigments in higher plants, and they contribute to leaf coloration as well as antioxidant concentration. Their biological synthesis is highly dependent on light quality, especially blue (B; 400-500 nm) and ultraviolet (UV; 280- 400 nm) radiation through cryptochrome responses (Mancinelli, 1985). For example, the total anthocyanin concentration in red-leaf lettuce grown under HPS fixtures increased by 35-106% with supplemental B LEDs at 200 µmol·m^{-2}·s^{-1}, depending on the peak wavelengths (455, 470, 505, 535 nm), compared to without supplemental B (Samuolienė et al., 2012). Similarly in grapes (*Vitis labrusca* × *V. vinifera*), the total anthocyanin concentration of the skin increased by 46% when measured 77 d after full bloom and when treated with 6-h day extension lighting at 13-17 µmol·m^{-2}·s^{-1} from B LEDs (peak = 450 nm) compared with red (R; 600-700 nm) LEDs (peak = 660 nm) (Kondo et al., 2014). However, other studies indicate a combination of R and B are more effective than monochromatic B in increasing anthocyanin concentration. For example, red-leaf lettuce 'Ruby Sky' was grown under monochromatic R, B, or R+B LEDs at a supplemental *PPFD* of 100 µmol·m^{-2}·s^{-1} under a 16-h photoperiod in a greenhouse (Owen and Lopez, 2015). Maximum leaf coloration during the finishing stage occurred 7 d earlier under R+B than R or B alone. In addition, the relative redness (a* value) of 'Ruby Sky' under R+B was 12-151% higher than R or B LEDs alone at the end of the experiment.

The objectives of this study were to 1) assess the increase in growth of lettuce from SL provided by HPS or LED fixtures, 2) determine if SL influences consumer sensory properties of lettuce during greenhouse production, and 3) quantify and compare the impacts of different types of greenhouse SL during the different growth phases on the quality and quantity of cut lettuce

production.

Materials and Methods

Expt.1: Supplemental greenhouse lighting

Plant materials

Seeds of five lettuces (‘Salanova Red Incised’, ‘Salanova Red Sweet Crisp’, ‘Salanova Green Incised’, ‘Salanova Green Sweet Crisp’, and ‘Salanova Green Butter’) were obtained from Johnny’s Selected Seeds (Winslow, ME). They were sown in 128-cell plug trays and grown in a research greenhouse at 20 °C under a 16-h photoperiod (from 6:00 to 22:00 HR) until ready for transplant. The most uniform 30 seedlings of each cultivar were selected and then transplanted into 11-cm pots containing 70% peatmoss, 21% perlite, and 9% vermiculite potting media (SUREMIX; Michigan Grower Products, Inc., Galesburg, MI) and placed on greenhouse benches and under lighting treatments (Table 1). Plants were irrigated as necessary with reverse osmosis water supplemented with a water-soluble fertilizer containing ($mg \cdot L^{-1}$) 125 N, 12 P, 100 K, 65 Ca, 12 Mg, 1 Fe and Cu, 0.5 Mn and Zn, 0.3 B, and 0.1 Mo (MSU RO Water Special; GreenCare Fertilizers, Inc., Kankakee, IL).

Environmental conditions

The experiment was performed at 20 °C in three nearly identical compartments of the Michigan State University (MSU) Plant Science Research Greenhouses and light fixtures were installed in two of the compartments. Roof vents and fans were controlled by a greenhouse environmental control system (Integro 725; Priva North America, Vineland, Ontario, Canada). One heavy whitewash (Kool Ray Classic; Continental Products Co., Euclid, OH) was applied in late March to the exterior of the greenhouse to reduce the ambient light intensity. The *PPFD* at

plant canopy height was measured in each treatment and recorded by a quantum sensor (LI-190SA; LI-COR, Lincoln, NE). Air temperatures were recorded on benches in each treatment by aspirated thermocouples (Type E; Omega Engineering, Stamford, CT) near canopy height. Temperature and the *PPFD* were collected by a data logger (CR-10; Campbell Scientific, Logan, UT) every ten seconds and average values were recorded hourly. Average daily temperature and DLI are reported in Table 1.

Lighting treatments

After transplanting, plants were randomly placed under ambient daylight (no SL), supplemental HPS, or supplemental R+B LEDs until harvest (for 34 and 38 d in the two experimental replications). Four HPS fixtures (400W; LR48877; P.L. Light System, Beamsville, ON, Canada) and six R+B LED research fixtures (Light Speed USA; Grand Rapids, MI) were placed ~ 1.4 m and ~ 1.2 m, respectively, above the benches in each of two compartments. Fixture heights were adjusted to provide a similar *PPFD* in the two SL treatments. SL was turned on automatically when the outside ambient solar light level fell below 223 $W \cdot m^{-2}$ (a *PPFD* of 437 $\mu mol \cdot m^{-2} \cdot s^{-1}$). The average *PPFD* (± SD) from the SL treatments was 84 ± 8 $\mu mol \cdot m^{-2} \cdot s^{-1}$ under the HPS fixtures and 78 ± 6 $\mu mol \cdot m^{-2} \cdot s^{-1}$ under the LEDs. Photon flux measurements of the lighting fixtures were made on the greenhouse benches with a spectroradiometer (PS-200; Apogee Instruments Inc., Logan, UT; Fig. 1).

Plant measurements and experimental design. The experiment was performed twice, with the treatments initiated in Mar. and Apr. 2016. The experiment was a randomized complete block design with subsamples. Two replications were considered two blocks to account for seasonal changes in environmental conditions. After harvest, leaf number (leaves ≥ 7 or 3.5 cm for 'Salanova Green Butter' in replication 1 and 2, respectively, and leaves ≥ 3 cm for other cultivars

in both replications) and shoot fresh weight (using an A&D Weighing GR-1000 balance, San Jose, CA) were recorded. In addition, the leaf area of the ten largest leaves was measured by a leaf area meter (LI-3000; LI-COR) and leaf color was measured using a colorimeter (CR-400/410; Konica Minolta Sensing Americas Inc., Ramsey, NJ) after calibration to a standard white plate (L* = 97.9, a* = –0.56, b* = 2.88). L* indicates the lightness and darkness (white: L* = 100; black: L* = 0). Chromametric a* and b* are the ratio of greenness to redness (green: a* = –60; red: a* = +60) and blueness to yellowness (blue: b* = –60; yellow: b* = +60), respectively. The average leaf size was that measured for the ten largest leaves and the average leaf fresh weight was calculated by shoot fresh weight divided by leaf number. Data were analyzed for two replications separately with the SAS (SAS Institute, Inc., Cary, NC) mixed-model (PROC MIXED) procedure. Pairwise comparisons between treatments were performed using Tukey's honest significant difference test at $P \leq 0.05$ within each replication.

Expt. 2: Sensory evaluation

Plant materials and growth conditions

Seeds of 'Salanova Green Incised' and 'Salanova Green Sweet Crisp' were obtained from Johnny's Selected Seeds and sown into 128-cell trays on 25 Aug. 2016. Growth conditions, lighting treatments, and environmental monitoring were as described in Expt. 1 unless otherwise noted. To improve crop uniformity, plants were cut back on 20 Oct. and again on 10 Nov. From 11 Nov. to the harvest day, the average DLIs were 3.8 $mol \cdot m^{-2} \cdot d^{-1}$ in the non-supplemented daylight treatment and 9.1 $mol \cdot m^{-2} \cdot d^{-1}$ in the SL treatments. On average, SL contributed ~58% of the DLI in the HPS and R+B LED treatments. Average daily air temperature was 19.6 °C and varied by < 0.3°C among the greenhouse compartments.

Sample preparation and consumer sensory evaluation

Immediately after harvest on 01 Dec. 2016, lettuce was rinsed in reverse-osmosis water, dried in a salad spinner, cut into bite-size pieces, stored at 4 °C in plastic bins, and remained refrigerated overnight. Consumer acceptance testing was conducted the following day at the Sensory Evaluation Laboratory in the Department of Food Science and Human Nutrition at MSU. Eighty-four panelists recruited by E-mail and flyers were all product consumers. Portions of lettuce were equivalent to approximately 4 to 6 cm^2 and were served to panelists in random order with 3-digit blinding codes following the protocol described by Szczygiel et al. (2017). A 9-point hedonic scale (1= dislike extremely; 9= like extremely) was used to measure overall acceptability, appearance, flavor, and aftertaste, while a 5-point hedonic scale (1= not at all bitter/sweet; 5= extremely bitter/sweet) was used to measure bitterness and sweetness. The taste test was performed once and consumer sensory data were collected using SIMS (vs. 6.0) sensory software (SIMS, Berkeley Heights, NJ, USA) as Szczygiel et al. (2017). Data were analyzed as in Expt. 1.

Expt. 3: Supplemental greenhouse lighting at different growing stages

Plant material

Seeds of three lettuces (‘Salanova Red Incised’, ‘Salanova Red Sweet Crisp’ and ‘Salanova Green Incised’) were obtained from Johnny’s Selected Seeds and sown in 98-cell plug trays and grown as previously described for 21 d after seed sow. The most uniform 70 seedlings of each cultivar were transplanted and assigned to different lighting treatments (Table 1), which consisted of a growing stage for three weeks and a finishing stage for ten days before harvest, with ten plants for each treatment.

Environmental conditions

The experiment was performed in five nearly identical compartments of the MSU Plant Science Research Greenhouses and light fixtures were installed in four of the compartments. Environmental conditions and monitoring were as described in Expt. 1 unless otherwise noted. Two greenhouse compartments contained HPS fixtures, one contained R+B LEDs, and another contained only B LEDs (peak wavelength = 450 nm; GreenPower LED research module blue; Philips, Eindhoven, The Netherlands). The average daily temperature and DLI in each treatment and replication are reported in Table 1.

Lighting treatments

During the growing stage, plants were grown under ambient light (control) or ambient light with SL from HPS fixtures at a *PPFD* of 98 $\mu mol \cdot m^{-2} \cdot s^{-1}$ with or without a 4-h EOD lighting treatment (from 22:00 to 02:00 HR). The EOD treatment was delivered by red+white+far-red LEDs (GreenPower DR/W/FR flowering lamps; Philips) with an R:FR of 0.73 (Fig. 1) and a *PPFD* of 2-5 $\mu mol \cdot m^{-2} \cdot s^{-1}$. After three weeks, ten plants of each cultivar grown under SL were then provided with one of two finishing stage lighting treatments: the R+B LED arrays at a *PPFD* of 89 $\mu mol \cdot m^{-2} \cdot s^{-1}$ or B LED arrays at a *PPFD* of 95 $\mu mol \cdot m^{-2} \cdot s^{-1}$.

Plant measurements and experimental design

The experiment was performed twice, with the treatments initiated in Jan. and Apr. 2017, and data collection and analysis were as in Expt. 1 unless otherwise noted. At harvest, leaf number (leaves $\geq$ 4 cm), shoot fresh weight, leaf area of the three largest leaves, leaf color, and shoot dry weight (after plants were dried in an oven at 80 °C for 5 d) of each cultivar were measured and recorded. The average leaf size was that for the three largest leaves.

Results

Expt. 1: Supplemental greenhouse lighting

Plant growth

Generally, plants developed more leaves under SL treatments than without, but the type of SL had little to no impact (Fig. 2). SL increased leaf number by 8 to 12 in 'Salanova Red Incised', 9 to 14 in 'Salanova Red Sweet Crisp', ~8 in 'Salanova Green Incised', ~7 in 'Salanova Green Sweet Crisp', and 24 to 36 in 'Salanova Green Butter' in the two replications. In replication 2, the average leaf size of 'Salanova Green Incised' and 'Salanova Green Sweet Crisp' increased by 23-30% and 10-21%, respectively, under SL compared to no SL.

In most instances, shoot fresh weight of all five cultivars was significantly greater under SL (Fig. 2). In 'Salanova Green Incised' and 'Salanova Green Butter', plants grown under SL treatments were 43-84% and 30-46% heavier, respectively, compared to those grown without SL. 'Salanova Green Sweet Crisp' had the greatest fresh weight among the lettuce varieties tested. In 'Salanova Red Sweet Crisp', plants grown under LEDs were 33% heavier than no SL in replication 1, while HPS or LED SL increased the fresh weight by 54% in replication 2. In addition, the average leaf fresh weight of 'Salanova Green Incised' and 'Salanova Green Sweet Crisp' increased by 38% and 32-50%, respectively, under SL treatments compared to no SL in replication 2.

Leaf coloration

Both red-leaf cultivars developed a darker leaf color under SL, with the lightness (L*) value reduced by 9-14% and 13-25%, in 'Salanova Red Sweet Crisp' and 'Salanova Red Incised' respectively, compared to those grown under ambient light (Fig. 3). The R+B LED SL increased the degree of redness (a* value) in both red-leaf cultivars, by 59% in 'Salanova Red Sweet Crisp' and 90% in 'Salanova Red Incised', compared to the control in replication 2. In addition, SL

treatments decreased the degree of yellowness (b* value) in both cultivars, with the greatest reduction under the R+B LED treatment.

Expt. 2: Sensory evaluation

In 'Salanova Green Incised', the overall consumer acceptability was slightly higher for lettuce from the no SL treatment than from the R+B LED treatment, and lettuce under HPS lamps was rated in between (Table 2). There were no statistical differences in appearance, but the overall flavor of lettuce grown without SL was preferred to plants grown under the SL treatments. Lettuce grown without SL was less bitter, sweeter, and had a more likable aftertaste compared to plants grown under the SL treatments. There were no flavor differences between lettuce grown under the HPS and LED treatments. In 'Salanova Green Sweet Crisp', bitterness was the only attribute for which panelists detected differences between the lighting treatments. Plants grown with R+B LED lighting were perceived as more bitter than plants grown without SL, and plants grown with HPS lighting were rated between the other treatments.

Expt. 3: Supplemental greenhouse lighting at different growing stages

Plant growth

In the three cultivars tested, SL increased leaf number (by 5 to 10) only in 'Salanova Green Incised' (Fig. 4). 'Salanova Red Incised' and 'Salanova Green Incised' had 20-35% and 41-62% greater average leaf size under SL, respectively, while 'Salanova Red Sweet Crisp' maintained a similar leaf size under all treatments.

Generally, fresh shoot weight of 'Salanova Red Sweet Crisp' was statistically similar under the treatments. However, plants grown under HPS lamps during both the growing and

finishing stages, and HPS+EOD lighting followed by R+B LED lighting, developed a 55% and 59% greater fresh shoot weight, respectively, than no SL (Fig. 4). In ‘Salanova Green Incised’, most SL treatments significantly increased the shoot and the average leaf fresh weights, but there were no differences among SL treatments. In addition, SL promoted shoot dry weight by 66-102%, 68-100%, and 125-180% of ‘Salanova Red Incised’, ‘Salanova Red Sweet Crisp’, and ‘Salanova Green Incised’, respectively, but again, there were no differences among SL treatments (data not shown).

Leaf coloration

All SL treatments significantly decreased the lightness (L* value) for ‘Salanova Red Sweet Crisp’ compared to no SL (L* = 41.3), with the greatest reduction for plants grown under HPS lamps during the growing stage followed by R+B for the finishing stage (Fig. 5). Similarly, ‘Salanova Red Incised’ developed significantly darker leaves when grown under R+B during the finishing stage. All SL treatments increased the degree of redness (a* value) by 29-89% and 40-83% for ‘Salanova Red Sweet Crisp’ and ‘Salanova Red Incised’, respectively. The greatest promotion for leaf redness was under R+B for the finishing stage in both red leaf cultivars. The average degree of yellowness (b* value) for ‘Salanova Red Sweet Crisp’ and ‘Salanova Red Incised’ under ambient light was 20.4 and 27.4 CIELAB units, respectively, and b* values were significantly decreased by 19-40% and 29-60%, respectively, under the SL treatments. In ‘Salanova Red Sweet Crisp’, plants were 50-60% less yellow when grown under R+B LEDs during the finishing stage. SL generally did not have effects on the lightness (L* value), degree of redness (a* value) and degree of yellowness (b* value) for ‘Salanova Green Incised’ regardless of light quality (data not shown).

Discussion

In Expt. 1, we determined the impacts of SL on greenhouse lettuce growth and postulated that SL will increase crop yield compared with no SL. Previous research has shown that Boston lettuce hydroponically grown under SL HPS or LEDs for four weeks developed a 15-39% and 22-29% greater fresh and dry mass, respectively, compared to plants without SL (Martineau et al., 2012). In a separate study, lamb's lettuce (*Valerianella locusta*) were grown under ambient solar light with or without white or R+B LED SL at a *PPFD* of 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ in the greenhouse (Wojciechowska et al., 2013). Both SL treatments greatly increased fresh weight, by 25-120% under white LEDs and 46-144% under R+B LEDs, respectively, compared to those without SL. Gaudreau et al. (1994) also indicated that day-extension lighting from 16 to 24 h at a *PPFD* of 50-100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ increased lettuce biomass by 20 %. Consistent with these responses, this study showed that SL generally increased lettuce leaf number (by up to 60%), average leaf size (by up to 51%), and fresh weight (by up to 104%).

We anticipated that SL would increase crop yield similarly if the *PPFD* is similar among treatments, regardless of the photon flux distribution within the photosynthetically active radiation waveband. Consistent with our hypothesis, we did not observe any growth differences under HPS and R+B LEDs among all cultivars in Expts. 1 and 3 except 'Salanova Red Incised' in replication 1 of Expt. 1. This was supported by Brazaitytė et al. (2006) that the fresh mass and photosynthetic productivity of lettuce 'Grand Rapids' was similar under HPS and R+B LEDs when grown indoors. In contrast, previous studies have also shown that crop growth and biomass can be influenced by the quality of SL. For example, lettuce 'Frillice' grown under R+B LED SL in the greenhouse had a 53% greater fresh weight compared to that under HPS, both at a *PPFD* of 120-140 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Pinho et al., 2007). Similarly, the yield of lamb's lettuce under

monochromatic R or R+B SL LEDs increased by 18-26% and 18-41%, respectively, in two consecutive winters compared to that under HPS, both at a *PPFD* of 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Wojciechowska et al., 2015). Therefore, lettuce sensitivity to the quality of SL may be cultivar-specific, and more studies are merited. In addition, SL from HPS and LEDs contributed 23-26% and 16-23% of DLI, respectively, in Expt. 1, and 40-61% and 18-49%, respectively, in Expt. 3. Therefore, the majority of the light which came from the sunlight may diminish the impacts on growth differences from SL with different light qualities.

Among the five cultivars we tested, 'Salanova Green Butter' had the greatest leaf number and developed 52 to 61 more leaves than the other four cultivars. However, its average leaf size and average leaf fresh weight were significantly lower than the others and therefore, did not result in the greatest yield. 'Salanova Green Sweet Crisp' had the greatest harvestable yield, and the fresh shoot weight was 33-79% and 34-71% greater than the other four cultivars under natural daylight and SL, respectively. Within the red-leaf cultivars, 'Salanova Red Sweet Crisp' had a 25-35% greater yield than 'Salanova Red Incised' in both experiments.

In Expt. 3, we tested the effects of EOD lighting (R:FR = 0.73) on lettuce growth, with the expectation that R+FR will promote leaf expansion and therefore increase fresh and dry weight of lettuce. However, we did not observe any differences in leaf size and yield between plants provided with or without 4-h of EOD lighting. Similar results were reported by Kubota et al. (2011) that fresh and dry weight of baby leaf lettuce 'Red Salad' was similar without or with EOD-FR with a dose of 1.2 to 9.2 $mol \cdot m^{-2} \cdot d^{-1}$ in the greenhouse. In a separate study, lettuce 'Cherokee' and 'Waldmann's Green' were grown under natural daylight with or without 50 $\mu mol \cdot m^{-2} \cdot s^{-1}$ EOD lighting provided by B, R, and white (Chinchilla et al., 2018). None of the EOD lighting treatments influenced leaf area, leaf number, fresh weight, or dry weight,

regardless of light quality, except EOD-B increased fresh weight by 18% compared to the natural daylight control. Together, these studies indicate that lettuce growth is relatively insensitive to EOD low-intensity lighting.

Anthocyanins, which are antioxidant compounds that influence red pigmentation, are higher in concentration in red-leaf cultivars than in green (Samuolienė et al., 2012). Providing SL is one of the ways to increase lettuce quality including its appearance and nutritional value, especially when the DLI is low. As in previous studies (Giliberto et al., 2005; Owen and Lopez, 2015), this study demonstrates that SL improves lettuce leaf coloration. This was also supported by Mancinelli (1985) that the production of small concentration of anthocyanins can be induced by single short irradiance, while the accumulation of larger concentrations of anthocyanins requires a prolonged period at a high *PPFD*, such as SL.

Anthocyanin concentration can also be increased by delivering B SL (Giliberto et al., 2005; Samuolienė et al., 2012) and therefore, we postulated that lettuce leaf pigmentation would be greatest under B SL during the finishing stage. However, this study indicates that a mixture of R and B is more effective at increasing leaf coloration than monochromatic B or HPS fixtures. This is in agreement with Owen and Lopez (2015), who reported that the relative redness (a* value) was 45-370% greater in four cultivars of lettuce with 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ R+B SL (R:B = 1:1) compared to plants under monochromatic R or B. Similarly, the anthocyanin concentration of red-leaf lettuce 'Banchu Red Fire' seedlings under 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ R+B was 350% and 80% higher than monochromatic R and B, respectively, at a similar *PPFD* in a growth chamber (Johkan et al., 2010). In a separate study, lettuce grown indoors under 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of R+B had a 265% higher anthocyanin concentration than when grown under R alone at a similar *PPFD* (Stutte et al., 2009). Mancinelli (1985) suggested that the spectral sensitivity of anthocyanin

production was species-specific and categorized crops into three groups based on action peaks for anthocyanin production: UV/B, R, and FR (group I); UV/B and R (group II); and UV/B only (group III), respectively. Based on all of these results, and that anthocyanin concentration significantly decreased under FR SL (Li and Kubota, 2009; Stutte et al., 2009), we postulate that lettuce belongs to group I, where UV/B, R, and FR all regulate anthocyanin biosynthesis and degradation.

Consumer taste preference is one of the most important aspects to assess the quality of edible crops and appearance, flavor, bitterness, sweetness, and aftertaste to ensure marketability. However, very few studies have been published on the sensory evaluation of lettuce grown under SL with different light qualities. Eskins et al. (1995) reported that the bitterness of lettuce grown under 170 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of R was significantly less than under B at a similar *PPFD*. In addition, they suggested that lettuce grown under 550 $\mu mol \cdot m^{-2} \cdot s^{-1}$ white had intermediate bitterness at a younger stage (25 d), but became the most bitter with maturity (41 d), compared to monochromatic R or B. In a separate study, green-leaf Boston type lettuce grown under 210 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of R+B SL was evaluated as the least preferred by consumers and the shape, crispness, and sweetness was rated lower than plants grown under R+B+white LEDs or fluorescent lamps (Lin et al., 2013). Our study indicated that consumers prefer lettuce grown under natural daylight compared to with SL, although there was a trade-off with lower yield. In addition, we did not observe any consumer preference differences between HPS or R+B LEDs SL. However, we only tested two green-leaf cultivars, and consumer perception for red-leaf cultivars may be different and additional research is needed. These findings collectively show that lettuce sensory properties can be influenced by light quality, and consumer preference should be considered when installing SL fixtures.

APPENDIX

Table III-1. Means (± SD) of greenhouse air temperature and daily light integral (DLI) during the two experimental replications (rep) in Expt. 1 and 3 as measured by aspirated thermocouples and quantum sensors. The supplemental lighting treatments were none, high-pressure sodium (HPS) and red+blue (R+B) light-emitting diodes (LEDs), and blue (B) LEDs. The 4-h end-of-day lighting provided by red+white+far-red flowering lamps at 2 to 5 μmol·m^{-2}·s^{-1} in Expt. 2.

Lighting treatment	Average air temp (°C)		Average DLI (mol·m^{-2}·d^{-1})	
	Rep 1	Rep 2	Rep 1	Rep 2
		Expt. 1		
None (control)	20.8 ± 1.1	21.0 ± 1.5	7.5 ± 3.3	8.2 ± 3.4
HPS	21.1 ± 1.1	20.8 ± 1.2	10.2 ± 2.4	10.6 ± 2.4
R+B LEDs	20.8 ± 1.2	20.9 ± 1.5	9.7 ± 2.3	9.8 ± 2.7
		Expt. 3		
None (control)	19.7 ± 0.5	21.1 ± 2.0	7.6 ± 3.5	11.9 ± 4.4
HPS	20.2 ± 0.7	20.9 ± 1.9	16.3 ± 7.3	17.7 ± 4.0
HPS+EOD	19.6 ± 0.5	20.9 ± 1.9	20.1 ± 8.8	19.8 ± 4.4
R+B LEDs	19.4 ± 0.5	20.7 ± 2.0	14.3 ± 5.5	14.1 ± 2.7
B LEDs	21.0 ± 0.6	21.8 ± 1.8	14.8 ± 2.3	—[z]

[z]Data missing.

Table III-2. Sensory attributes and mean scores of lettuce grown under three different greenhouse light conditions in Expt. 2. Samples with different letters within each cultivar and the attribute column are significantly different at the 95% confidence level. For 'Green Incised', n=45 (12 male and 33 female). For 'Green Sweet Crisp', n=39 (12 male and 27 female).

Lighting treatment	Overall acceptability[z]	Appearance[z]	Overall flavor[z]	Bitterness[y]	Sweetness[y]	Aftertaste[x]
			'Salanova Green Incised'			
None	6.51 a	7.13	6.53 a	1.62 b	1.58 a	5.49 a
HPS	5.87 ab	7.69	5.22 b	2.82 a	1.31 b	4.56 b
LED	5.67 b	7.29	5.07 b	3.11 a	1.29 b	4.38 b
Significance	***	NS	***	***	*	***
			'Salanova Green Sweet Crisp'			
None	6.49	7.18	6.4	1.90 b	1.31	5.46
HPS	5.69	6.49	5.56	2.44 ab	1.51	4.90
LED	5.97	6.77	5.56	2.51 a	1.36	4.82
Significance	NS	NS	NS	*	NS	NS

NS, *, or *** Nonsignificant or significant at $P < 0.05$, or 0.001, respectively.
[z]Evaluated with a 9-point scale: 1= dislike extremely; 9= like extremely.
[y]Evaluated with a 5-point scale: 1= not at all bitter or sweet; 5= extremely bitter or sweet.
[x]Evaluated with a 9-point scale: 1= dislike extremely; 9= like extremely with 5= none detected.

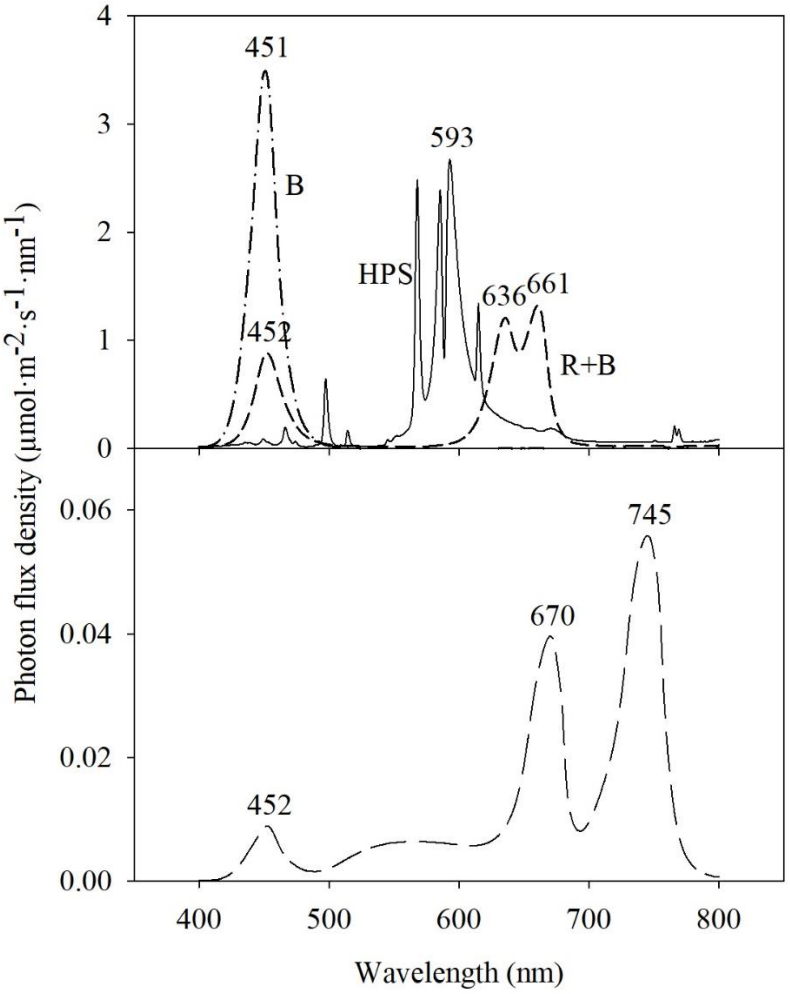

Figure III-1. The spectral distribution of supplemental lighting treatments (top) delivered by high-pressure sodium (HPS) fixtures, red+blue (R+B) light-emitting diodes (LEDs) (in Expt. 1 and 2), and B LEDs (in Expt. 2), and end-of-day lighting (bottom) provided by red+white+far-red LEDs. The peak wavelengths (in nm) are provided for each fixture type.

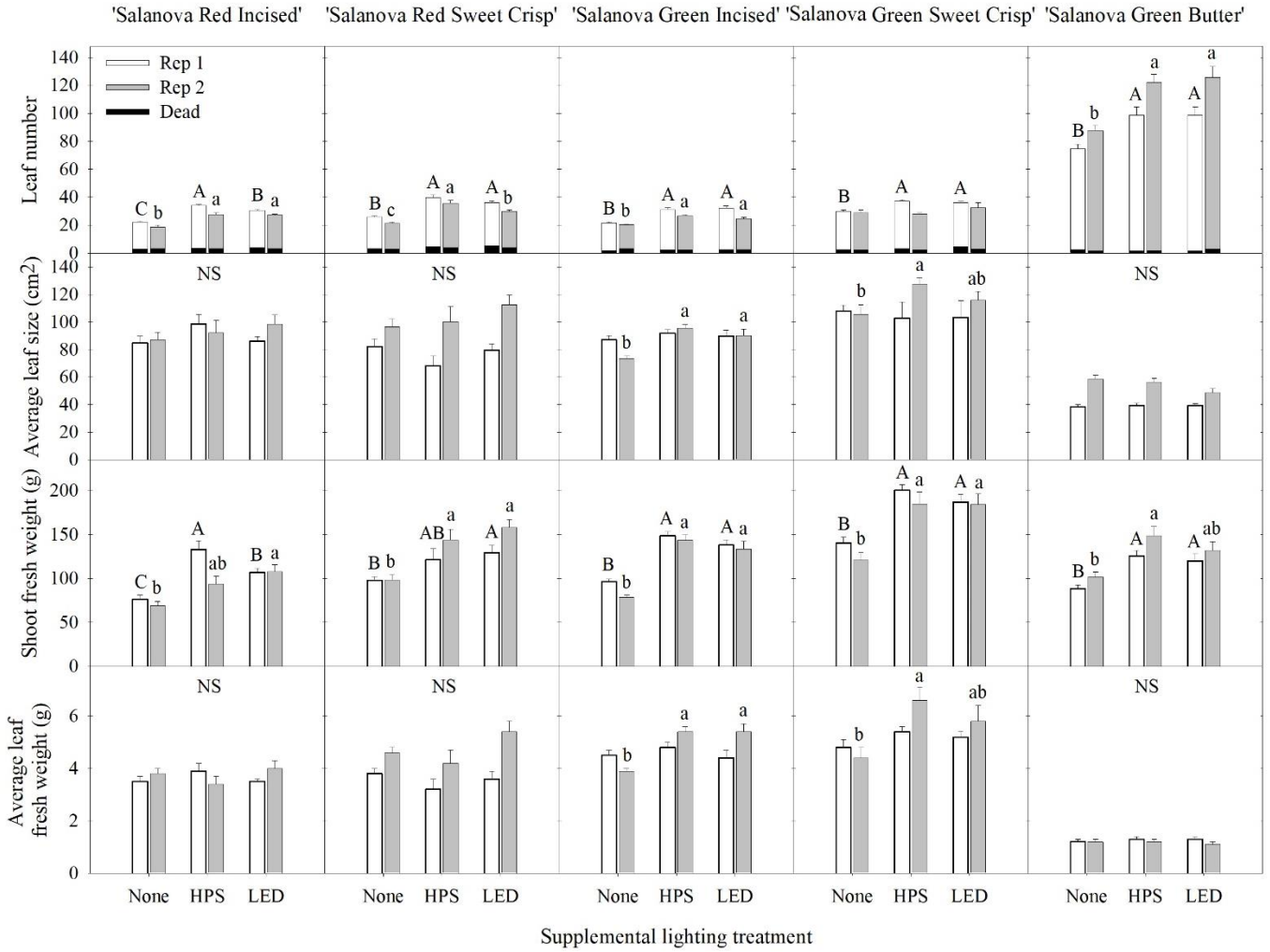

Figure III-2. Growth characteristics of five cultivars of lettuce grown without supplemental lighting (none) or with supplemental lighting from high-pressure sodium (HPS) or light-emitting diodes (LED) in Expt. 1. Leaf number of 'Salanova Green Butter' included leaves ≥ 7 or 3.5 cm in length for replication 1 (Rep 1) or replication 2 (Rep 2), respectively, while leaf number for the other four cultivars included leaves ≥ 3 cm in both replications. Within the same replication, means with the same letter are not statistically different by Tukey's honest significant difference test at $P \leq 0.05$. Error bars indicate standard error.

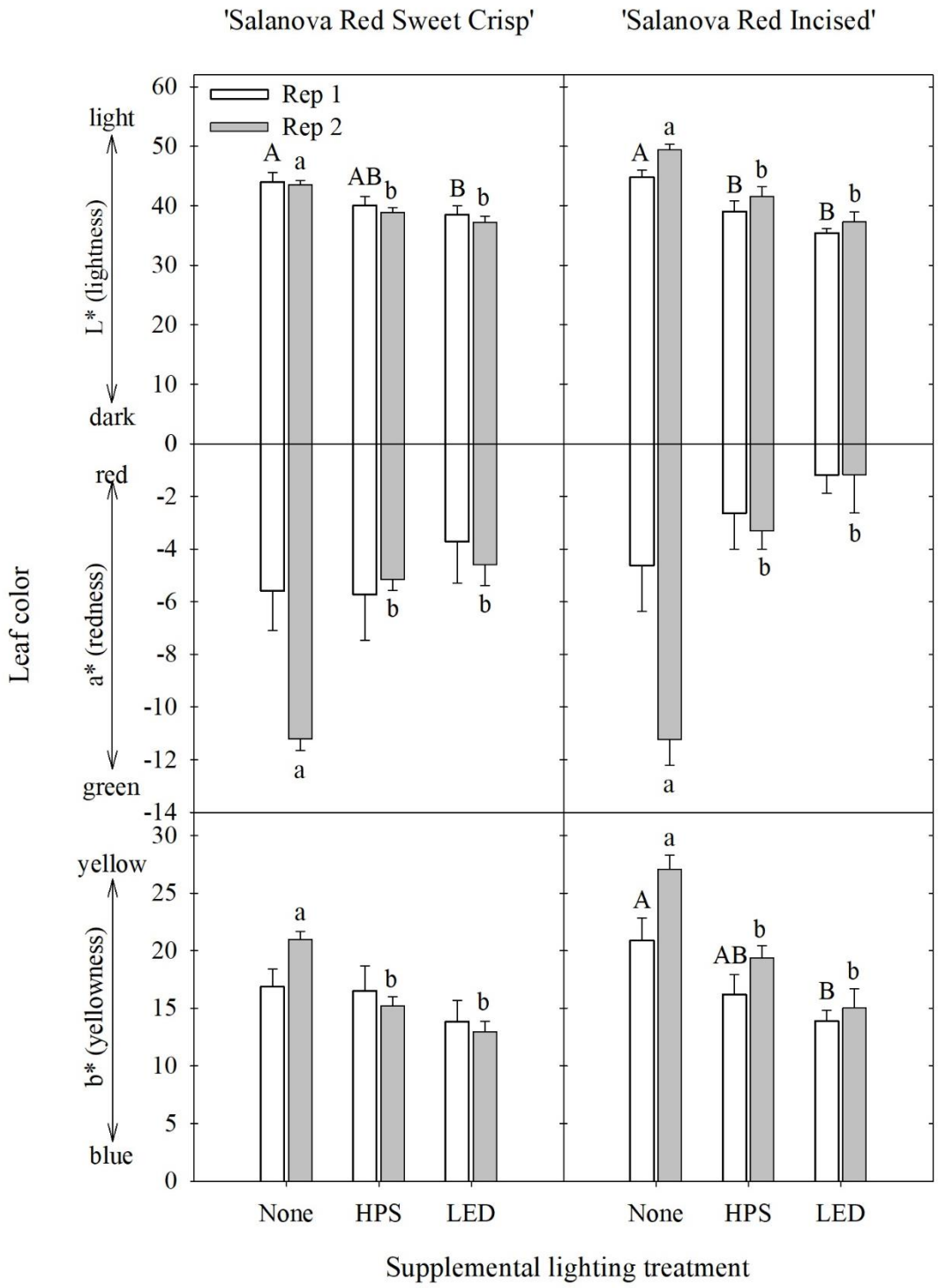

Figure III-3. Leaf coloration characteristics of two cultivars of lettuce grown without supplemental lighting (none) or with supplemental lighting from high-pressure sodium (HPS) or light-emitting diodes (LED) in Expt. 1. In replication (Rep) 1, a single measurement was taken on one outer leaf per plant while in Rep 2, measurements were taken on three outer leaves per plant. Within the same replication, means with the same letter are not statistically different by Tukey's honest significant difference test at $P \leq 0.05$. Error bars indicate standard error.

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SECTION IV

INVESTIGATING THE INTERACTION OF BLUE AND FAR-RED RADIATION ON GROWTH AND SUBSEQUENT FLOWERING OF FLORICULTURE CROPS

Investigating the Interactions of Blue and Far-red Radiation on Growth and Subsequent Flowering of Floriculture Crops

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Abstract

Manipulating the radiation spectrum of sole-source lighting (SSL) with light-emitting diodes (LEDs) enables the regulation of plant growth, development, and quality attributes of high-value ornamental transplants. Blue (B, 400-500 nm) radiation generally inhibits extension growth while far-red (FR, 700-800 nm) radiation promotes it, and FR can accelerate subsequent flowering of some long-day plants. We quantified growth responses and subsequent flowering of a variety of ornamental seedlings to the addition of FR radiation to two combinations of B+red (R, 600-700 nm) SSL, and compared responses to plants under white SSL or greenhouse conditions. Seedlings were grown at 20 °C under an 18-h photoperiod either in the greenhouse or indoors under nine SSL treatments (subscript values indicate the photon flux density of each waveband, in $\mu mol \cdot m^{-2} \cdot s^{-1}$): $B_{20}R_{160}$, $B_{20}R_{160}FR_{10}$, $B_{20}R_{160}FR_{20}$, $B_{20}R_{160}FR_{40}$, $B_{60}R_{120}$, $B_{60}R_{120}FR_{10}$, $B_{60}R_{120}FR_{20}$, $B_{60}R_{120}FR_{40}$, and warm white (WW_{180}) LEDs. Among all the species tested, the addition of 40 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of FR only increased the seedling height of snapdragon (*Antirrhinum majus*) and zinnia (*Zinnia elegans*) by 64-134% and 52-96%, respectively, regardless of the proportion of B, compared to SSL treatments without FR or in the greenhouse. Similarly, WW_{180} promoted seedling stem elongation by 75-139% in snapdragon compared to SSL without FR or the greenhouse control, but the promotive effect of WW_{180} was not significant in the other species. Relative chlorophyll content of zinnia and petunia (*Petunia ×hybrida*) generally decreased as the photon flux density of FR increased, and in both species was 13-14% greater under 60 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of B compared to under 20 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of B. However, radiation treatments did not influence leaf area and dry shoot weight in any species. The subsequent flowering of snapdragon was accelerated by 7-11 d with the additional 20 or 40 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of FR or WW_{180} compared to SSL without FR or the greenhouse control. We

conclude that when ≥20 µmol·m^{-2}·s^{-1} of B is delivered to crops, the addition of 20 or 40 µmol·m^{-2}·s^{-1} of FR can accelerating the flowering of at least some long-day plants with little to no effect on extension growth.

Keywords: Bedding plants, blue radiation, controlled-environment agriculture, floriculture, LEDs, light quality, phytochrome photoequilibrium, red radiation, red to far-red ratio

Introduction

Most floriculture crops including annuals, herbaceous perennials, potted flowering plants, and cut flowers, are produced in two distinct phases: the young plant stage and the finish plant stage (Lopez et al., 2017). The production of ornamental propagules (e.g., plugs and liners) is a significant segment of the floriculture crop industry in the U.S. In 2015, for the 15 States surveyed, its wholesale value accounted for $394 million, which was a 15% increase from 2014 (USDA, 2016). To meet the largest market period during the spring (February through May), most young floriculture plants are produced commercially in greenhouses during the late winter and early spring (December through April). However, during this time, low ambient temperature and photosynthetic daily light integral (DLI) in temperate climates are limiting factors to consistently produce high-quality plants on schedule (Lopez and Runkle, 2008). Commercially, sole-source lighting (SSL) was most commonly used in closed systems (e.g., plant factory) for the production of high-value specialty crops such as leafy greens, microgreens, and herbs at a high density (Mitchell and Stutte, 2017). However, there is an increasing interest in growing uniform and reliable high-value floriculture transplants indoors, where the environment can be controlled with SSL from light-emitting diodes (LEDs).

Sole-source lighting from LEDs enables control of the radiation spectrum that can regulate plant growth, development, and quality attributes. The vast majority of research with LED SSL has focused on investigating the effects of different mixtures of blue (B, 400-500 nm) and red (R, 600-700 nm) radiation on plant growth (Massa et al., 2008). R radiation promotes leaf expansion, stem elongation, and biomass accumulation (Mitchell and Stutte, 2017). For example, the stem length of chrysanthemum (*Dendranthema grandiflorum*) in vitro grown under 50 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of R LEDs (peak = 650 nm) for five weeks was 67% and 108% greater than under B (peak = 440 nm) and B+R LEDs (Kim et al., 2004). Similarly, leaf area of impatiens (*Impatiens walleriana*), tomato (*Solanum lycopersicum*), salvia (*Salvia splendens*), and petunia (*Petunia ×hybrida*) seedlings was 54-60%, 40-46%, 34-39% and 35-49% greater, respectively, under monochromatic R (peaks = 634 and 664 nm) than under B (peak = 446 nm) alone or B+R at a photosynthetic photon flux density (*PPFD*) of 160 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Wollaeger and Runkle, 2014). In addition, fresh and dry weight under R LED SSL increased by 52% and 55% in impatiens, 40% and 28% in tomato, 32% and 44% in salvia, and 38% and 60% in petunia, respectively, than under B SSL. Similarly, dry weight of spinach (*Spinacia oleracea*) was up to 47% greater under R than under B, depending on the cultivar, at a *PPFD* of 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Li et al., 2011).

Adding B radiation to an R-dominant spectrum inhibits extension growth and increases leaf chlorophyll concentration, eliciting phenotypes similar to plants grown under sunlight (Lobiuc et al., 2017; Mitchell et al., 2012; Wang, et al., 2016). Wollaeger and Runkle (2015) reported that substituting 50% of R (peaks = 634 and 664 nm) with B (peak = 446 nm) inhibited the stem length of impatiens, salvia, and tomato by 48 to 54% at a *PPFD* of 160 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Similarly, hypocotyl length of lettuce (*Lactuca sativa*) seedlings decreased by 93% when R

(peak = 660 nm) LEDs was substituted with 60 μmol·m^{-2}·s^{-1} of B (peaks = 435-470 nm) under a similar *PPFD* (Hoenecke et al., 1992). In cucumber (*Cucumis sativus*), leaf chlorophyll concentration increased by 38% as the proportion of B increased from 0 to 50% (Hogewoning et al., 2010). However, increasing B can inhibit leaf expansion and subsequent plant growth. For example, cucumber seedlings were grown under 54 μmol·m^{-2}·s^{-1} of supplemental lighting with different B:R ratios under a low DLI in the greenhouse (Hernández and Kubota, 2014). Leaf area of seedlings decreased by 7% and 13% as the B proportion increased from 0 to 4% and 16%, respectively. In a separate study, the leaf area of tomato, cucumber, and pepper (*Capsicum annum*) grown indoors decreased by 24-40% when the B proportion of SSL increased from 10 to 30%, and similarly the dry mass decreased by 14 to 26% (Snowden et al., 2016). In several ornamental seedlings, at least 10 μmol·m^{-2}·s^{-1} of B added to R radiation produced high-quality transplants (Wollaeger and Runkle, 2015).

In addition to B+R, recent studies have investigated the merits of including far-red (FR, 700-800 nm) radiation in SSL (Craver and Lopez, 2015; Lee et al., 2016; Meng and Runkle, 2017; Park and Runkle, 2017, 2018). Although the magnitude of plant responses varies among species, the inclusion of FR (peak = 731 nm) radiation to a B+R spectrum (peaks = 447 and 660 nm) stimulated stem elongation in petunia, geranium (*Pelagonium ×hortorum*), snapdragon (*Antirrhinum majus*), and impatiens, and leaf expansion and subsequent dry matter accumulation in geranium and snapdragon (Park and Runkle, 2017). Similarly, the addition of FR (peak = 735 nm) to B+R (peaks = 440 and 660 nm) increased leaf area and shoot fresh weight of lettuce by 25-60% and 21-52%, respectively (Lee et al., 2016). In addition, FR radiation can promote subsequent flowering of some long-day plants (LDPs). Craig and Runkle (2016) reported that the flowering of petunia, snapdragon, black-eyed susan (*Rudbeckia hirta*), and fuchsia (*Fuchsia*

×*hybrida*) was accelerated when FR was added to R light as night-interruption (NI) lighting in greenhouses. Similarly, the flowering of snapdragon was accelerated by 10-12 d when 160 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of B+R included 16-64 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of FR during indoor production of seedlings (Park and Runkle, 2017). However, considering the different sensitivities of plants to FR radiation and interactive effects of radiation wavebands, more information is needed on how FR interacts with B and R radiation to elicit desired quality attributes of ornamental crops.

Here we quantified the responses of a variety of floriculture crop seedlings to the addition of FR radiation to two combinations of B+R SSL lighting, and compared plants to those grown under white SSL, or under greenhouse conditions. We anticipated that the sensitivity of plants to FR radiation would be related to the shade tolerance and photoperiodic flowering response of crops. Specifically, we postulated that FR would promote stem elongation, leaf expansion, and subsequent seedling growth more in shade-avoiding species than in shade-tolerant species, and inclusion of FR in a radiation spectrum would accelerate subsequent flowering of at least some LDP, but minimally influence subsequent flowering in short-day plants (SDPs) and day-neutral plants (DNP). We also postulated that an increase in B radiation would diminish the effects of FR radiation on stem elongation and leaf expansion while increasing leaf chlorophyll concentration.

Materials and Methods

Plant material

LDPs dianthus (Dianthus *barbatus* ‘Jolt Cherry’), petunia (‘Wave Blue’), and snapdragon (‘Liberty Classic Yellow’), SDPs african marigold (*Tagetes erecta* ‘Antigua Orange’), coleus (*Plectranthus scutellarioides* ‘Wizard Golden’), and zinnia (*Zinnia elegans* ‘Magellan Pink’),

and DNPs geranium (‘Pinto Premium Orange Bicolor’), impatiens (‘Super Elfin XP Red’), and tomato (‘Micro Tom’) were selected for study based on commercial significance, photoperiodic flowering response, and shade tolerance. Impatiens and coleus are shade-tolerant plants while the others are shade-avoiding plants. Seeds of each species were sown in 128-cell plug trays by a commercial young plant producer (Raker-Roberta’s, Litchfield, MI). They were transferred to an environmentally controlled glass-glazed research greenhouse at Michigan State University (MSU) (East Lansing, MI) within 7 d of seed sow and grown at 20 °C until the appearance of the first true leaves. A 16-h photoperiod (from 0600 to 2200 HR) was delivered using ambient solar radiation with supplemental high-pressure sodium (HPS) fixtures (400W; LR48877; P.L. Light System, Beamsville, ON, Canada) that automatically turned on when the *PPFD* outdoors was <437 μmol·m^{-2}·s^{-1}. The *PPFD* at seedling height from the HPS fixtures was 67 μmol·m^{-2}·s^{-1}. For each replication (rep.), the days from seed sow to the start of the radiation treatments was (rep. 1, 2): african marigold (8, 10), coleus (12, 16), dianthus (9, 10), geranium (8, 10), impatiens (12, 14), petunia (12, 16), snapdragon (14, 16), tomato (12, 10), and zinnia (8, 10). Each plug tray was then divided into four sections, each with 32 seedlings, thinned to one seedling per cell, and placed under the SSL treatments.

Radiation treatments and environmental conditions during the seedling stage

The experiment was performed in one of the two compartments of the MSU Controlled Environment Lighting Laboratory (CELL), which had four racks in each compartment. Each rack (1.2 × 0.6 × 2.4 m) contained three vertically stacked shelves and the top of each shelf contained three LED panels (OSRAM Innovation, Beverly, MA) 0.5 m above the seedling trays. The panels contained B (peak = 449 nm), R (peak = 664 nm), FR (peak = 733 nm), and warm white (WW, peak = 639 nm) LEDs that faced down towards the plants. The photon flux density

of each LED type was independently adjusted by computer software customized by OSRAM Innovation. Radiation treatments were designed to determine the effects of the addition of FR radiation to typical B+R spectra with either a low or high B photon flux density. Three racks provided the following nine SSL radiation treatments with an 18-h photoperiod (subscript values indicate the photon flux density of each waveband, in $\mu mol \cdot m^{-2} \cdot s^{-1}$): $B_{20}R_{160}$, $B_{20}R_{160}FR_{10}$, $B_{20}R_{160}FR_{20}$, $B_{20}R_{160}FR_{40}$, $B_{60}R_{120}$, $B_{60}R_{120}FR_{10}$, $B_{60}R_{120}FR_{20}$, $B_{60}R_{120}FR_{40}$, and WW_{180} (Table 1). The WW_{180} treatment emitted a photon flux density for B, green (500-600 nm), R, and FR of 14, 54, 95, and 17 $\mu mol \cdot m^{-2} \cdot s^{-1}$, respectively. To serve as another comparison, seedlings were grown in a greenhouse under ambient sunlight with supplemental lighting from HPS fixtures at a *PPFD* of 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at plant height to achieve an 18-hour photoperiod and a similar DLI. For each radiation treatment, the R:FR ratio, which was calculated with 100-nm wavebands, phytochrome photoequilibrium (PPE) value, which was estimated as described by Sager et al. (1988), and the average DLI are reported in Table 1.

All seedlings were grown at a constant 20 °C. The *PPFD* at plant height in CELL or on the greenhouse bench was measured by a quantum sensor (LI-190SA; LI-COR, Lincoln, NE). Seedling trays within each radiation treatment (shelf) were rotated every day to prevent positional effects. Air temperature in CELL and the greenhouse were measured near plant height by bare thermocouples and an aspirated thermocouple (Type E; Omega Engineering, Stamford, CT), respectively. Temperature and the *PPFD* at both locations were collected by a data logger (CR-1000; Campbell Scientific, Logan, UT) every ten seconds and average values were recorded hourly. Average air temperatures (± standard error) in two replications were 20.1 ± 0.5 and 19.9 ± 1.3 °C in CELL and 19.9 ± 0.6 and 21.2 ± 1.1 °C in the greenhouse, respectively.

In CELL, the temperature was automatically controlled by an air conditioner (HBH030A3C20CRS; Heat Controller, Jackson, MI) and the air conditioner was controlled by a thermostat (TH8321R1001; Honeywell, Morris Plains, NJ) through a gateway and wireless sensor (THM6000R1002, C7189R1004; Honeywell, Morris Plains, NJ). Humidity was monitored by a transmitter (HMDW110; Vaisala, Helsinki, Finland) and in rep. 2, increased by a humidifier (LV600HH; Lĕvoit, Anaheim, CA) that ran continuously. The actual average relative humidity in the compartment was 29% and 41% in rep. 1 and 2, respectively. In the greenhouse, whitewash (Kool Ray Classic; Continental Products Co., Euclid, OH) was applied to the greenhouse glazing to reduce the ambient light intensity to deliver a similar DLI as in the SSL treatments. Roof vents and fans were controlled by a greenhouse environmental control system (Integro 725; Priva North America, Vineland, Ontario, Canada). In both locations, seedlings were irrigated as necessary with deionized water supplemented with a water-soluble fertilizer containing ($mg \cdot L^{-1}$) 50 N, 19 P, 50 K, 23 Ca, 4 Mg, 1 Fe, 0.5 Cu, 0.5 Zn, 0.5 Mn, 0.3 B, and 0.1 Mo (MSU Plug Special; GreenCare Fertilizers, Inc., Kankakee, IL).

Environmental conditions during the finish stage

At the end of seedling stage, when the seedlings had well–developed root systems, ten seedlings of each species from each radiation treatment and replication were selected and transplanted into 10-cm pots containing 70% peatmoss, 21% perlite, and 9% vermiculite potting media (SUREMIX; Michigan Grower Products, Inc., Galesburg, MI) and randomly placed on benches in the MSU research greenhouse. For each replication, the number of days under the radiation treatments before seedling data collection and transplanting was (rep. 1, 2): african marigold (27, 27), coleus (35, 32), dianthus (27, 26), geranium (27, 27), impatiens (23, 24), petunia (25, 24), snapdragon (29, 28), tomato (22, 24), and zinnia (21, 21). Plants were grown at

a constant 20 °C under a 16-h photoperiod provided by sunlight supplemented by 400-W HPS fixtures at a *PPFD* of 59 μmol·m^{-2}·s^{-1}. Photon flux density measurements were made during the finishing stage in the greenhouse with a spectroradiometer (PS-200; Apogee Instruments Inc., Logan, UT) above the benches at nine representative positions at plant height. HPS fixtures were automatically turned on from 0600 to 2200 HR when the *PPFD* was <437 μmol·m^{-2}·s^{-1}. Air temperature and *PPFD* were monitored and recorded as described above. The average air temperature and DLI during the finishing stage in the greenhouse for rep. 1/ 2 were 20.0/20.6 °C and 10.2/15.2 mol·m^{-2}·d^{-1}, respectively. Plants were irrigated as necessary with reverse osmosis water supplemented with a water-soluble fertilizer containing (mg·L^{-1}) 125 N, 12 P, 100 K, 65 Ca, 12 Mg, 1 Fe and Cu, 0.5 Mn and Zn, 0.3 B, and 0.1 Mo (MSU RO Water Special; GreenCare Fertilizers, Inc., Kankakee, IL).

Data collection and analysis

The experiment was performed twice in time. The most uniform 20 plants from each tray section of each species in each radiation treatment and replication were selected for data collection: ten for the seedling stage and ten for the finish stage. At the end of the seedling stage, stem length (from media level to apical meristem), leaf number, and leaf area [using a leaf area meter (LI-3000; LI-COR)] were measured for all nine species. Leaves with leaf length of ≥ 2 cm (or 3 cm for geranium, tomato and african marigold) were counted in leaf number and included in leaf area. The average leaf area was calculated by dividing total leaf area by leaf number. An index of relative chlorophyll concentration (SPAD value) was measured on the second (for geranium) or third (for coleus, petunia, and zinnia) leaf from the meristem using a SPAD meter (SPAD-502, Minolta corporation, Ltd., Osaka, Japan). Three readings per leaf were taken and the average was recorded. After drying in an oven at 80 °C for ≥ 5 d, shoot dry weight of all

species and root dry weight of petunia, tomato, and zinnia was measured using a balance (A&D Weighing GR-1000, San Jose, CA). During the finish stage, date of first open flower and visible bud or inflorescence number at first flowering were recorded on all species except coleus. Plant height at flowering (length of the primary stem from the substrate surface to the top of the inflorescence) was measured except on impatiens. Leaf number on the primary stem at flowering was recorded on snapdragon, tomato, and zinnia.

The experiment used a randomized complete block design. Two replications were considered as two blocks and each shelf in CELL or the bench in the greenhouse were regarded as the experimental unit for the radiation treatment. Within the experimental unit, ten individual seedlings and ten individual plants at the finish stage per species were the subsamples. Data were pooled from two replications and were analyzed with the SAS (version 9.4; SAS Institute, Inc., Cary, NC) mixed-model (PROC MIXED) and glimmix-model (PROC GLIMMIX) procedures. Pairwise comparisons between treatments were performed using Tukey's honest significant difference test at $P \leq 0.05$.

Results

Seedling stage

Seedling stem length of all species was similar among the ten radiation treatments except for snapdragon, petunia, and zinnia (Fig. 2). Stem length of snapdragon and zinnia generally increased as FR was added to either $B_{20}R_{160}$ or $B_{60}R_{120}$. Seedlings were 64-134% (for snapdragon) and 52-96% (for zinnia) taller with the addition of 40 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of FR compared to that in the greenhouse or indoor treatments without FR. In snapdragon, stem length under WW_{180} was similar to that under $B_{20}R_{160}$ FR_{20}, $B_{20}R_{160}$ FR_{40}, and $B_{60}R_{120}FR_{40}$. In contrast, zinnia

stem length under WW_{180} was statistically similar to that under the other treatments. In petunia, stem length was 92% and 108% taller in the greenhouse than the indoor treatments without FR (i.e., $B_{20}R_{160}$ and $B_{60}R_{120}$), respectively, while stem length under these three treatments was similar to that in the other radiation treatments.

Under $B_{60}R_{120}$, the SPAD value of zinnia decreased by 17% with the addition of 40 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of FR (Fig. 3). Similarly, in petunia, the SPAD value under $B_{60}R_{120}$ decreased by 16-23% with additional FR at $\geq$20 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Under $B_{20}R_{160}$, SPAD value in petunia decreased with the addition of 40 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of FR. SPAD value of zinnia and petunia was 14% or 13% higher, respectively, under $B_{60}R_{120}$ than $B_{20}R_{160}$, while SPAD value was similar under $B_{60}R_{120}$ and $B_{20}R_{160}$ when the same amount of FR was added. In geranium and coleus, there were no differences in SPAD value among treatments (data not shown).

Radiation treatment did not influence average leaf area or dry shoot weight in any species (Table 2). Similarly, dry root weight of zinnia and petunia were similar under the radiation treatments. In tomato, the dry root weight of seedlings under $B_{20}R_{160}FR_{10}$ was 40-47 % greater than that under WW_{180} indoors or in the GH, but dry root weight under these three treatments was similar to that in the other treatments (data not shown).

Finish stage

Radiation treatments during the seedling stage had little to no effect on days to subsequent visible bud or flower, inflorescence number, plant height at flowering, or leaf number in all the species tested except for snapdragon (Table 3). In snapdragon, subsequent flowering was accelerated by 7-11 d with 20 or 40 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of FR (with $B_{20}R_{160}$ or $B_{60}R_{120}$) or under WW_{180} compared to indoor treatments without FR or in the greenhouse (Fig. 4). Plant height of snapdragon at flowering was 17-32% shorter with the addition of 10 to 40 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of FR

(with $B_{20}R_{160}$ or $B_{60}R_{120}$) or under WW_{180} compared to seedling treatments without FR. Snapdragon developed 8-29% fewer visible flower buds with the addition of 20 or 40 μmol·m^{-2}·s^{-1} of FR with $B_{20}R_{160}$, 10 to 40 μmol·m^{-2}·s^{-1} of FR with $B_{60}R_{120}$, and WW_{180} compared to indoor treatments without FR or in the GH. In addition, snapdragon developed 9 or 10 fewer leaves before flowering with the additions of 20 or 40 μmol·m^{-2}·s^{-1} FR to $B_{20}R_{160}$ or 40 μmol·m^{-2}·s^{-1} of FR to $B_{60}R_{120}$ compared to indoor treatments without FR. In geranium, plants at first flowering had an average of one more inflorescence when seedlings were grown under $B_{60}R_{120}$ than under $B_{20}R_{160}FR_{20}$, and those had a similar inflorescence number to seedlings grown under the other treatments (data not shown).

Discussion

In a wide range of species, stem elongation increases linearly as the R:FR and estimated PPE decrease (Smith, 1994; Runkle and Heins, 2001). Under vegetative shade outdoors, the R:FR decreases and in response, shade-avoiding species elongate in an attempt to better capture photosynthetic light while shade-tolerant species show a reduced shade-avoidance response (Franklin, 2008; Gommers et al., 2013; Smith, 1994). We postulated the addition of FR in SSL would promote stem elongation and leaf expansion of seedlings in shade-avoiding species and have less of an effect in shade-tolerant species. In the shade-avoiding snapdragon and zinnia, the addition of 40 μmol·m^{-2}·s^{-1} of FR increased stem length by 64-71% and 93-96%, respectively, under both $B_{20}R_{160}$ and $B_{60}R_{120}$ (Fig. 2). In contrast, the addition of FR did not meaningfully increase extension growth in the other five shade-avoiding species and both shade-tolerant coleus and impatiens. Even among the shade-avoiding species, the sensitivity of extension growth to R:FR depends on species. For example, when the R:FR increased from 1:1 to 1:0 (the PPE

increased from 0.69 to 0.88), stem length of shade-avoiding geranium and snapdragon decreased by 41%, while that of shade-avoiding petunia decreased by 95% (Park and Runkle, 2017).

The R:FR and estimated PPE value have been used to predict the effects of the radiation spectrum on phytochrome-mediated extension growth. In this study, the PPE value was a more accurate predictor of extension growth than the R:FR. For example, WW_{180}, which had an R:FR of 5:1, had a similar PPE value as $B_{20}R_{160}FR_{40}$. Both treatments influenced seedling growth similarly in all species, including snapdragon and zinnia, under the same *PPFD*. In addition, $B_{60}R_{120}FR_{10}$ and $B_{60}R_{120}FR_{20}$, which had similar PPE values but different R:FRs (12:1 and 6:1, respectively), had similar effects on promoting stem elongation on snapdragon, zinnia, and petunia. Together, in the presence of B radiation, these findings suggest that the PPE value is a better indicator to assess crop extension growth responses compared to the R:FR.

FR radiation is involved in regulating photoperiodic flowering responses, especially in some LDPs. During a long night, R is the most effective at inhibiting flowering of SDPs, while the flowering of a wide range of LDPs is promoted most when the night is interrupted with R and FR (Craig and Runkle, 2013; Downs and Thomas, 1982; Oh and Runkle, 2016). For example, in LDPs including snapdragon, NI lighting with an intermediate PPE value between 0.63 and 0.80 was the most effective at promoting flowering (Craig and Runkle, 2016). In a separate study, the subsequent flowering of snapdragon was accelerated when SSL included ≥16 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of FR (creating a PPE ≤0.85), and the acceleration was saturated when the PPE was between 0.69 and 0.85 (Park and Runkle, 2017). Consistent with this response, the subsequent flowering of LDP snapdragon was hastened in this study when SSL included ≥20 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of FR (creating a PPE of 0.81 to 0.85) (Fig. 4). Therefore, delivering R+FR that creates a PPE value between 0.63 and 0.85 is effective at accelerating the flowering of LDPs. The inclusion of FR

radiation during the seedling stage had no effect on the subsequent flowering of SDP or DNP in this study. Similarly, a 4-h NI with different light qualities from LEDs had little or no effect on flowering percentage and days to visible bud on DNP such as geranium when grown indoors under white SSL at a *PPFD* of 180 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Park et al., 2017). Based on all these results, we recommend SSL that includes B, R, and FR radiation that creates a PPE value between 0.81 and 0.85 to promote subsequent flowering of ornamental seedlings without excessive extension growth.

FR and B radiation have antagonistic effects on chlorophyll concentration; increasing FR decreases chlorophyll concentration while B increases it. For example, lettuce grown indoors had 12% less chlorophyll concentration in leaves with supplemental lighting of 160 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of FR than without (Li and Kubota, 2009). In geranium, petunia, and snapdragon seedlings, SPAD value decreased linearly as the estimated PPE decreased (as the R:FR decreased) (Park and Runkle, 2017). In contrast, increasing B from 0 to 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at a total *PPFD* of 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ increased the chlorophyll concentration in cucumber seedlings by 50% (Hernández and Kubota, 2016). Similarly, the chlorophyll concentration in lettuce increased by 23% as B increased from 0 to 11% at a *PPFD* of 200 $mol \cdot m^{-2} \cdot s^{-1}$ (Wang et al., 2016). In this study, the addition of 40 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of FR decreased the SPAD value of zinnia and petunia (regardless of the B proportion) and $\geq$20 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of FR decreased the SPAD value of petunia under $B_{60}R_{120}$ (Fig. 3). Increasing B from 20 to 60 $\mu mol \cdot m^{-2} \cdot s^{-1}$ increased the SPAD value in petunia and zinnia by 13-14% only without FR. However, SPAD value of SSL treatments with the same FR photon flux density were all similar under 20 or 60 $\mu mol \cdot m^{-2} \cdot s^{-1}$of B radiation, suggesting that the inclusion of at least 10 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of FR can diminish the effect of increasing B by 40 $\mu mol \cdot m^{-2} \cdot s^{-1}$.

Increasing the B photon flux density inhibits plant height, leaf area, and shoot dry weight in many species (Hernández and Kubota, 2016; Nanya et al., 2012). However, in this study, increasing B from 20 to 60 μmol·m^{-2}·s^{-1} had little effect on plant height, leaf area, and shoot dry weight in any species tested. Similarly, in cucumber seedlings, the fresh and dry mass of cucumber seedlings were similar as the B proportion increased from 0 to 16% at a *PPFD* of 54 μmol·m^{-2}·s^{-1} (Hernández and Kubota, 2014). In addition, increasing B from 0 to 30% at a *PPFD* of 100 mol·m^{-2}·s^{-1} had no effect on shoot dry mass of snapdragon, impatiens, geranium, and petunia (Randall and Lopez, 2014). In a separate study, increasing B from 0 to 10 μmol·m^{-2}·s^{-1} inhibited plant height of impatiens, salvia, and tomato, but plants of each species under ≥ 10 μmol·m^{-2}·s^{-1} of B were generally of similar height (Wollaeger and Runkle, 2015). Considering that we tested 20 or 60 μmol·m^{-2}·s^{-1} of B photon flux densities, apparently 20 μmol·m^{-2}·s^{-1} of B was sufficient to saturate the suppressive effects of B on stem elongation, leaf area, and biomass accumulation.

Here, we showed that including a low photon flux density of FR (10 to 40 μmol·m^{-2}·s^{-1}) in R+B SSL generally had little effect on seedling growth of the ornamental species tested except for the extension growth of two shade-avoiding species with the addition of 40 μmol·m^{-2}·s^{-1} of FR (PPE ≤0.83). The inclusion of FR to create a PPE between 0.81 and 0.85 during the seedling stage accelerated flowering of the LDP snapdragon but did not influence the subsequent flowering of SDPs and DNP. The estimated PPE value for WW was similar to, or slightly higher than, the two B+R radiation spectra that included 40 μmol·m^{-2}·s^{-1} of FR, and they had similar promotive effects on extension growth and subsequent flowering. A B photon flux density of 60 μmol·m^{-2}·s^{-1} produced a greater chlorophyll concentration in zinnia and petunia than 20 μmol·m^{-2}·s^{-1} of B without FR, but generally seedling growth and subsequent flowering with or

without FR were similar under the two different B photon flux densities (20 or 60 μmol·m^{-2}·s^{-1}). Therefore, SSL that includes B and has a PPE between 0.81 and 0.85 is suggested to produce high-quality and relatively compact seedlings with greener leaves, while accelerating the subsequent flowering of at least some LDPs.

APPENDIX

Table IV-1. Spectral characteristics and average photosynthetic daily light integral (DLI) of nine sole-source radiation treatments in two replications (rep) delivered indoors by blue (B, 400-500 nm), red (R, 600-700 nm), far-red (FR, 700-800 nm), and warm white (WW) light-emitting diodes (LEDs) or one greenhouse treatment with sunlight supplemented by high-pressure sodium (HPS) fixtures. The subscript values that follow each LED type indicate their photon flux density in $\mu mol \cdot m^{-2} \cdot s^{-1}$.

				DLI ($mol \cdot m^{-2} \cdot d^{-1}$)	
Radiation treatment		R:FR[a]	PPE[b]	Rep 1	Rep 2
$B_{20}R_{160}$		1:0	0.88	12.0	11.7
$B_{20}R_{160}FR_{10}$		16:1	0.87	11.7	11.7
$B_{20}R_{160}FR_{20}$		8:1	0.85	11.7	11.4
$B_{20}R_{160}FR_{40}$		4:1	0.83	11.9	11.6
$B_{60}R_{120}$		1:0	0.87	11.7	11.8
$B_{60}R_{120}FR_{10}$		12:1	0.85	11.5	11.7
$B_{60}R_{120}FR_{20}$		6:1	0.84	11.9	11.5
$B_{60}R_{120}FR_{40}$		3:1	0.81	11.9	11.8
WW_{180}		5:1	0.83	11.6	11.6
Greenhouse	HPS	5:1	0.86	12.1	12.5
	Sunlight	1:1	0.72		

[a] R:FR: Ratio of the photon flux integral of red (R, 600-700 nm) and far-red (FR, 700-800 nm) radiation.
[b] PPE: Phytochrome photoequilibria estimated following Sager et al. (1988).

Table IV-2. Average leaf area, dry shoot weight, and dry root weight of nine species at the end of the seedling stage. Lighting treatments had no statistical differences on all nine species and data for each species was pooled from all lighting treatments. Data for each species represent the mean (±SE) of two replications with 10 subsamples (plants) per replication.

Species	Average leaf area (cm^2)	Dry shoot weight (g)	Dry root weight (g)
African marigold	5.96 ± 1.45	0.19 ± 0.06	– [a]
Coleus	4.39 ± 1.56	0.10 ± 0.03	–
Dianthus	3.99 ± 0.69	0.15 ± 0.03	–
Geranium	11.56 ± 2.04	0.23 ± 0.06	–
Impatiens	3.11 ± 0.84	0.08 ± 0.04	–
Petunia	2.37 ± 1.03	0.10 ± 0.03	0.042 ± 0.02
Snapdragon	3.46 ± 0.79	0.16 ± 0.04	–
Tomato	6.20 ± 1.50	0.15 ± 0.04	0.023 ± 0.01
Zinnia	8.02 ± 1.96	0.14 ± 0.03	0.062 ± 0.02

[a] Data not collected.

Table IV-3. Days to flower after transplant, visible bud or inflorescence number, plant height, and leaf number of eight species at the finishing stage. Lighting treatments had no statistical differences on eight of the species and data for each species was pooled from all lighting treatments. Data for each species represent the mean (±SE) of two replications with 10 subsamples (plants) per replication.

Species	Days to flower	Visible flower bud or inflorescence number	Plant height at flowering (cm)	Leaf number at flowering
African marigold	39 ± 3	13.8 ± 2.1	13.8 ± 1.5	–[a]
Coleus	–	–	11.6 ± 2.5	–
Dianthus	55 ± 4	15.7 ± 2.2	46.7 ± 5.3	–
Geranium	51 ± 4	3.0 ± 0.7	22.9 ± 2.2	–
Impatiens	19 ± 5	26.9 ± 12.3	–	–
Petunia	24 ± 4	18.9 ± 7.8	7.9 ± 1.8	–
Tomato	10 ± 3	6.1 ± 2.3	6.8 ± 1.2	4.2 ± 0.7
Zinnia	27 ± 2	4.2 ± 1.2	15.8 ± 3.0	8.2 ± 0.7

[a] Data not collected.

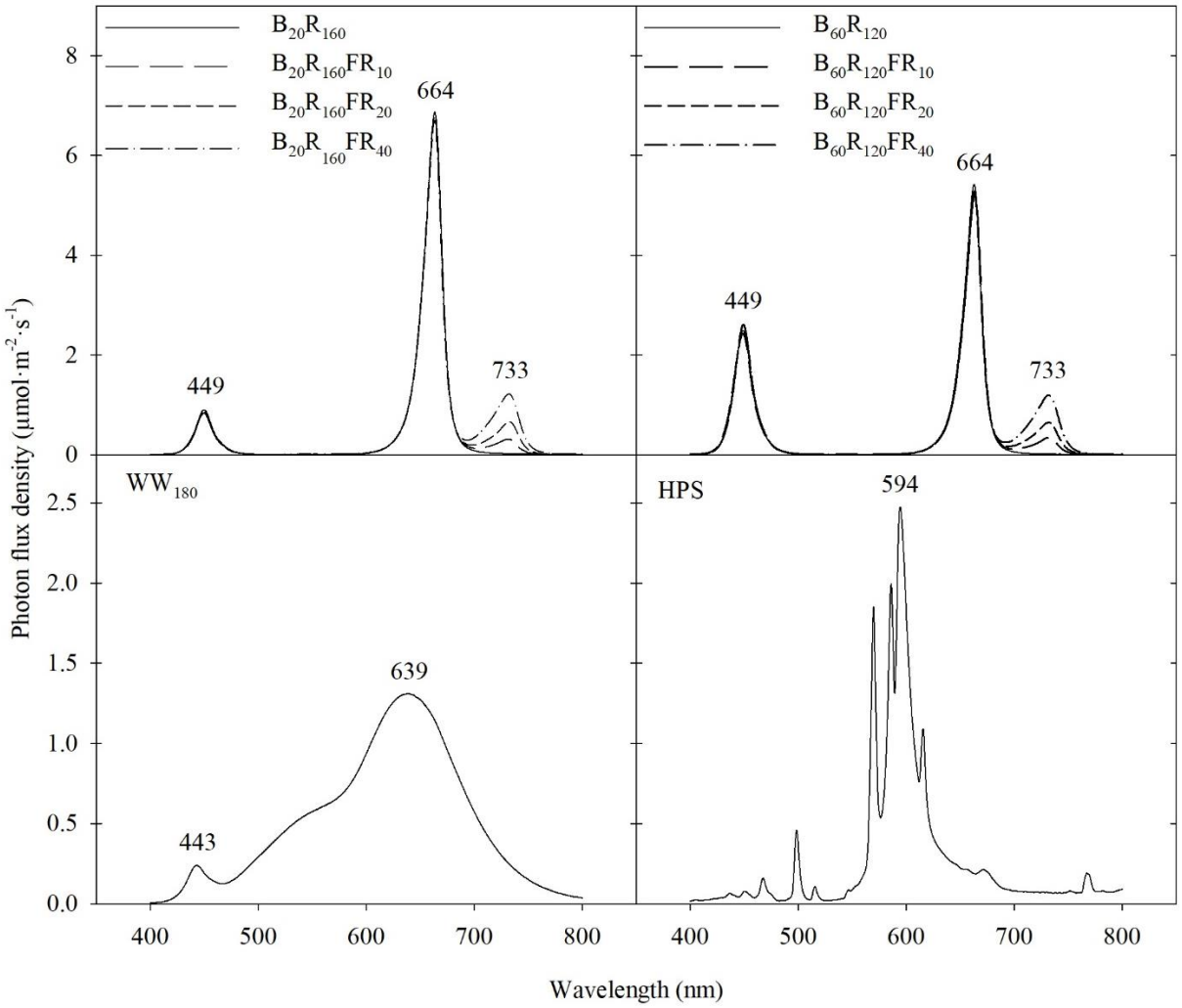

Figure IV-1. The spectral distribution of sole-source lighting treatments delivered from mint white (MW), red (R), blue (B), and green (G) light-emitting diodes (LEDs) at total photosynthetic photon flux density (*PPFD*) = 160 μmol·m^{-2}·s^{-1}. The subscript values after each LED type indicate the percentages of the total *PPFD* delivered from each LED type.

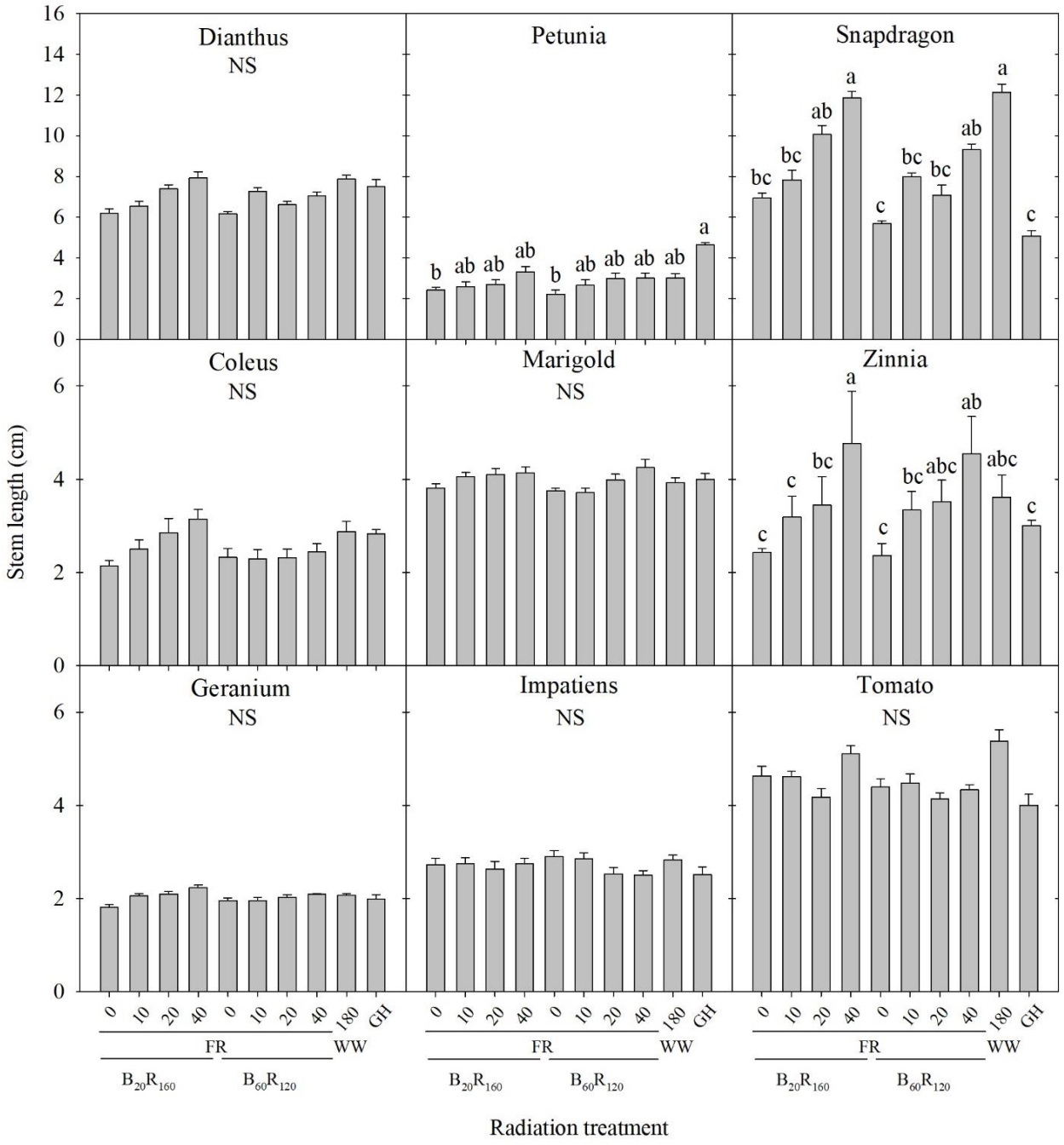

Figure IV-2. Stem length of seedlings grown under nine sole-source lighting treatments delivered by blue (B, 400-500 nm), red (R, 600-700 nm), far-red (FR, 700-800 nm), and warm white (WW) light-emitting diodes (LEDs) indoors and one greenhouse treatment (GH) with supplemental lighting from high-pressure sodium fixtures. The subscript values that follow each LED type indicate their intensity in $\mu mol \cdot m^{-2} \cdot s^{-1}$. The top, middle, bottom row represents long-day plants, short-day plants, and day-neutral plants, respectively. Data for each species represent the mean of two replications with 10 subsamples (plants) per replication. Means sharing a letter are not statistically different by Tukey's honest significant difference test at $P \leq 0.05$ and NS indicates nonsignificance. Error bars indicate the standard error and was calculated by 20 subsamples from two replications.

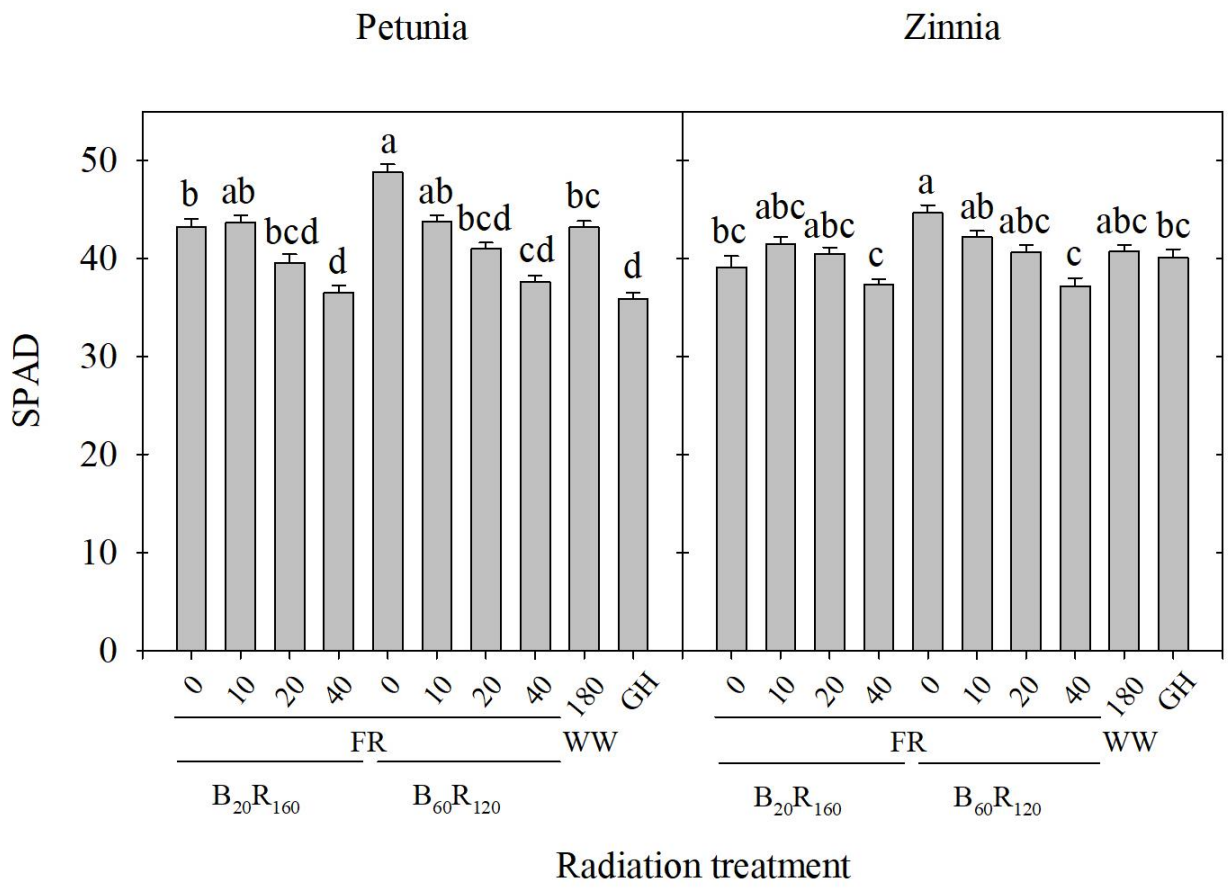

Figure IV-3. SPAD index value of petunia and zinnia seedlings grown under nine sole-source lighting treatments delivered by blue (B, 400-500 nm), red (R, 600-700 nm), far-red (FR, 700-800 nm), and warm white (WW) light-emitting diodes (LEDs) indoors and one greenhouse treatment (GH) with supplemental lighting from high-pressure sodium fixtures. The subscript values that follow each LED type indicate their intensity in $\mu mol \cdot m^{-2} \cdot s^{-1}$. Data for each species represent the mean of two replications with 10 subsamples (plants) per replication. Means sharing a letter are not statistically different by Tukey's honest significant difference test at $P \leq 0.05$ and NS indicates nonsignificance. Error bars indicate the standard error and was calculated by 20 subsamples from two replications.

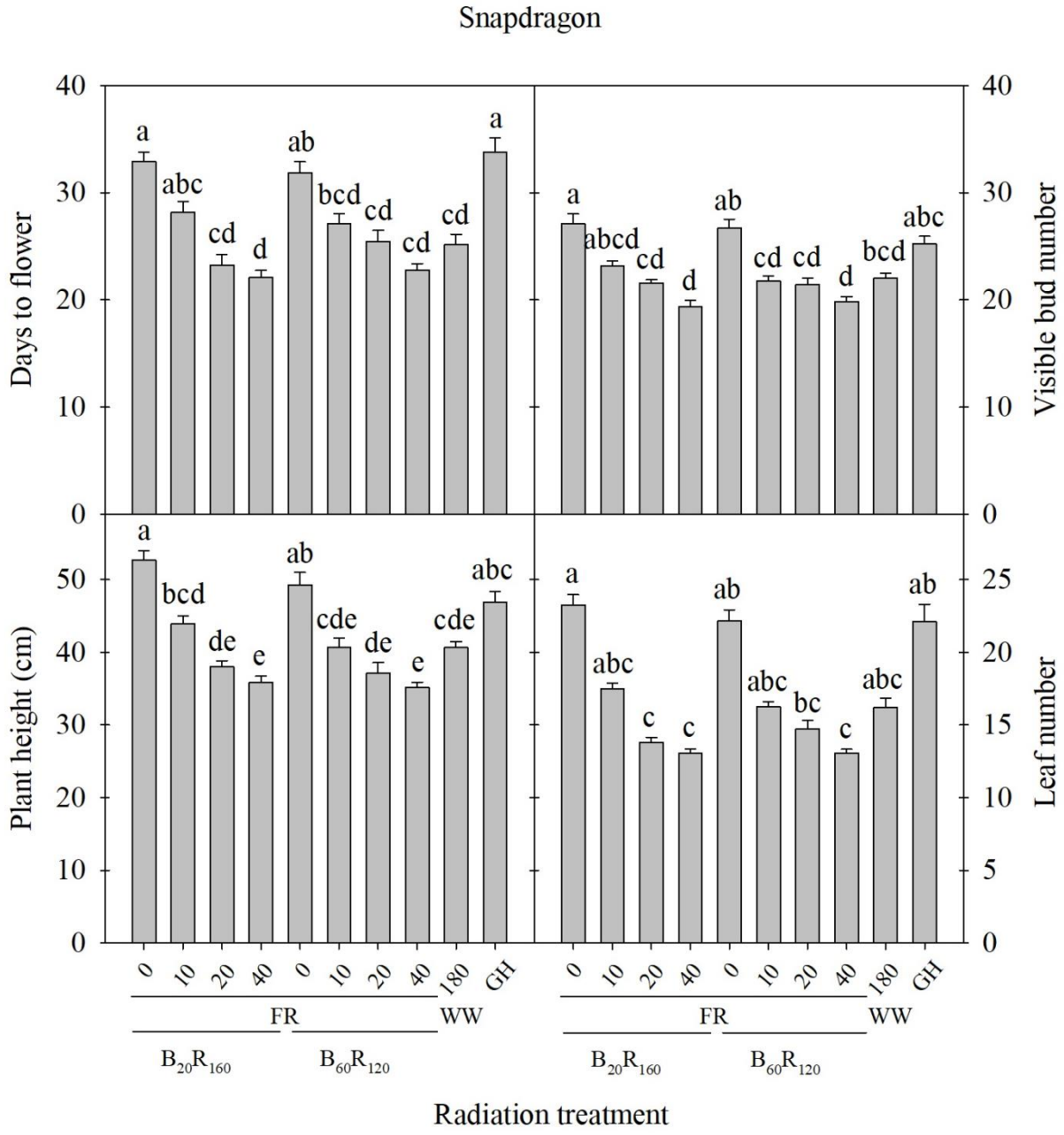

Figure IV-4. Flowering characteristics of snapdragon at finishing stage when seedlings were grown under nine sole-source lighting treatments delivered by blue (B, 400-500 nm), red (R, 600-700 nm), far-red (FR, 700-800 nm), and warm white (WW) light-emitting diodes (LEDs) indoors and one greenhouse treatment (GH) with supplemental lighting from high-pressure sodium fixtures. The subscript values that follow each LED type indicate their intensity in $\mu mol \cdot m^{-2} \cdot s^{-1}$. Data represent the mean of two replications with 10 subsamples (plants) per replication. Means sharing a letter are not statistically different by Tukey's honest significant difference test at $P \leq 0.05$ and NS indicates nonsignificance. Error bars indicate the standard error and was calculated by 20 subsamples from two replications.

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