INVESTIGATING USE OF BLUE, RED, AND FAR-RED LIGHT FROM LIGHT-EMITTING DIODES TO REGULATE FLOWERING OF PHOTOPERIODIC ORNAMENTAL CROPS

By

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ABSTRACT

INVESTIGATING USE OF BLUE, RED, AND FAR-RED LIGHT FROM LIGHT-EMITTING DIODES TO REGULATE FLOWERING OF PHOTOPERIODIC ORNAMENTAL CROPS

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When the natural photoperiod is short, lighting during the middle of the night (night interruption, NI) can promote flowering of long-day plants (LDPs) and inhibit flowering of short-day plants (SDPs). Unlike some conventional lamps, light-emitting diodes (LEDs) are energy efficient, durable, and controllable. We coordinated a trial with five commercial greenhouses to compare the efficacy of 4-hour NI lighting from red (R; 600 to 700 nm)+white (W)+far-red (FR; 700 to 800 nm) LEDs and conventional lamps to regulate flowering of eight photoperiodic ornamental crops. In most instances, the R+W+FR LEDs were as effective at controlling flowering as conventional lamps. Therefore, these LEDs specifically developed for flowering applications emit an effective spectrum and can replace less energy-efficient conventional lamps. In another experiment, we investigated the role of low-intensity (1 to 2 $\mu mol \cdot m^{-2} \cdot s^{-1}$) blue (B; 400 to 500 nm) light in regulating flowering of four LDPs and five SDPs. Low-intensity B light, alone and when added to R and FR light, did not influence flowering or plant morphology. In a third experiment, we determined whether B light at higher intensities (15 and 30 $\mu mol \cdot m^{-2} \cdot s^{-1}$) controlled flowering of five LDPs and one SDP. B light at 30 $\mu mol \cdot m^{-2} \cdot s^{-1}$ created long days in all crops as effectively as low-intensity R+W+FR light. However, the addition of B light to R+W+FR light did not further accelerate flowering. Therefore, the effectiveness of B light in NI lighting apparently depends on some threshold intensity and does not modify the response to R+W+FR light. The promotion of flowering from a higher irradiance of B light could be mediated by cryptochromes, phytochromes, or both.

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Introduction

Floriculture is the cultivation and management of flowering and ornamental plants. The expanded wholesale value of floriculture crops estimated in 15 U.S. States has been consistently greater than 4 billion U.S. dollars over the past decade (United States Department of Agriculture National Agricultural Statistics Service, 2013). Commercial ornamental plants are typically produced in greenhouses, where environmental factors can be controlled to regulate flowering time and obtain desirable plant attributes. Accelerated crop production can reduce greenhouse operating costs in heating, supplemental lighting, irrigation, pest control, growing space, and labor (Cavins and Dole, 2001). Meanwhile, maintaining at least moderate crop quality is required for market acceptance. Although a variety of plant growth regulators are commercially available, manipulation of growth characteristics with non-chemical approaches is of interest to greenhouse growers. Ultimately, sustainable practices and adaptive strategies in the floriculture industry are encouraged as awareness of the ongoing climate change arises.

Photoperiodism is the physiological reaction of organisms to the length of the day or night. Photoperiod plays a critical role in regulation of flowering in a variety of plants (Thomas, 2006). Circadian behavior of plants has been developed to adapt to changing photoperiodic cycles (Thomas, 2006). Plant circadian rhythms can regulate physiological processes including organ movement, germination, stomatal aperature, enzyme activity, photosynthetic activity, intracellular signaling, and flowering, among others (Webb, 2003). Synchronization to constantly changing photoperiod helps assure the occurrence of developmental transitions, such as the onset of flowering, under the most appropriate environmental conditions (Searle and Coupland, 2004).

In many species, photoperiod is sensed by plants as a trigger to flower at an appropriate time for successful pollination and seed development and dispersal (Searle and Coupland, 2004). Furthermore, photoperiod is used by some plants as a developmental cue to control bud dormancy, tuberization, and bud break (Jackson, 2009).

The lengths of light and dark periods each day regulate flowering of a broad range of plants, including many economically important agronomic and ornamental crops (Erwin and Warner, 2002; Mattson and Erwin, 2005; Runkle and Heins, 2003). A photoperiodic response is determined primarily by the duration of the dark period, also known as the critical night length or skotoperiod (Thomas and Vince-Prue, 1997). Plants are commonly classified into different response groups based on their flowering characteristics in response to photoperiod (Thomas and Vince-Prue, 1997). Photoperiod-indifferent (day-neutral) plants form flowers irrespective of photoperiod. Short-day (SD) plants (SDPs) flower most rapidly when uninterrupted dark periods are longer than some species-specific critical night length in each 24-h period, whereas flowering of long-day (LD) plants (LDPs) is most rapid when dark periods are shorter than some species-specific critical duration. Within each category, plants can be subdivided into qualitative (obligate) or quantitative (facultative) groups, meaning that the photoperiod is required for or accelerates flowering, respectively. For example, a quantitative LDP will eventually flower under SDs but will flower earlier under LDs. Critical photoperiod not only varies among species and cultivars, it can also overlap between LDPs and SDPs (Thomas and Vince-Prue, 1996). For example, all photoperiodic response classes existed in the *Hibiscus* spp. studied by Warner and Erwin (2001). The natural photoperiod differs by latitude and for plants such as *Arabidopsis thaliana*, a facultative LDP, bolting time was later for ecotypes from northern latitudes than from southern latitudes (Stinchcombe et al., 2004).

Photoperiodic lighting

Plants perceive light before sunrise and after sunset, so the length of the "natural" photoperiod is approximately 30 to 40 min longer than from sunrise to sunset, depending on latitude, time of year, and cloud cover (Faust and Heins, 1995; Runkle, 2002). When the photoperiod is naturally short, low-intensity (photoperiodic) lighting is used by commercial crop producers to inhibit flowering of SDPs and promote flowering of LDPs. This manipulation of photoperiod can lower production costs by reducing production time and improving the overall quality of the crop (Runkle and Heins, 2006). When the ambient photoperiod is short, LDs can be created by operating lamps beginning at the end of the day until the desired photoperiod is attained, which is known as day-extension (DE) lighting, or during the middle of the night, which is known as night-interruption (NI) or night-break lighting. During a long night, 4 h of NI lighting is recommended for the most complete and rapid flowering of LDPs, although shorter durations are effective for some crops (Runkle et al., 1998). Although night interruption lighting can generally be applied anytime during the night, a 4-h NI during a night from 1700 HR to 0800 HR was most effective when starting at 2200 HR, rather than 1800 HR or 0200 HR, at promoting flowering of dianthus (*Dianthus chinensis*) or inhibiting flowering of zinnia (*Zinnia elegans*) (Park et al., 2013). Light intensity required for effective photoperiodic lighting is typically very low (e.g., ≤1 $\mu mol \cdot m^{-2} \cdot s^{-1}$) (Whitman et al., 1998). For a 7-h DE from various broad-spectrum conventional light sources following a 9-h SD, the saturation irradiance for flowering ranged from <0.05 to 0.4 $\mu mol \cdot m^{-2} \cdot s^{-1}$, depending on species (Whitman et al., 1998). Some plants exhibit a fluence-dosage response. For example, days to flower of rice (*Oryza sativa*) increased

by approximately 20 d as red (R; 600 to 700 nm) light intensity as an NI increased from 26 to 19,700 μmol·m^{-2} (Ishikawa et al., 2009).

Photoperiodic lighting is typically provided continuously during the lighting period, although intermittent, or cyclic, lighting is sometimes as effective. Cyclic lighting can reduce energy consumption by reducing the amount of time lamps operate or the number of lamps needed to light a crop. Cycling incandescent (INC) lamps on for six min every half hour, during a 4-h NI, was as effective as a continuous NI for some crops, but not for others (Runkle et al., 1998; Blanchard and Runkle, 2010). Cyclic lighting can also be delivered successfully by high-pressure sodium (HPS) lamps with rotating reflectors (Blanchard and Runkle, 2010). For example, the rotating reflector of a 600-W HPS lamp moves a beam of light across a relatively large area (e.g., 140 m^2) at regular intervals (e.g., once per minute) (Blanchard and Runkle, 2010). Another technique to deliver LD lighting is placing lights on irrigation booms programmed to run (with lights on and water off) during the night. There is limited research-based information on "boom lighting" (Blom and Zheng, 2006), but some commercial growers have developed their own successful strategies, generally delivering at least 15,000 μmol·m^{-2} each night and ensuring plants are lighted at least once every 20 to 30 min for at least a 4-h period (M. Blanchard and E. Runkle, unpublished).

Electric lighting

Traditional light sources

INC and HPS lamps are commonly used as light sources for photoperiodic lighting. INC lamps emit a spectrum rich in R and far-red (FR; 700 to 800 nm) light, which are both required for rapid flowering of LDPs; however, extension growth can also be promoted (Runkle and

Heins, 2006). Although INC lamps are effective, they are inefficient at converting electrical energy into light (Narendran, 2011); approximately 14% of the total radiation output emitted from a 60-W INC lamp is between 400 and 850 nm (Thimijan and Heins, 1983). Many governments around the world have passed laws to reduce electricity consumption by phasing out INC bulbs and replacing them with energy-efficient alternatives, such as compact fluorescent (FL) lamps and light-emitting diodes (LEDs) (Narendran, 2011). HPS lamps provide light with considerably greater photosynthetic photon efficiency, ranging from 0.9 to 1.7 $\mu mol \cdot J^{-1}$ (Nelson and Bugbee, 2014); however, a large amount of shortwave radiation is also emitted by the HPS lamps. This energy can increase plant canopy temperature when delivered at a high irradiance, which can be desirable in some circumstances and undesirable in others, and consequently there must be sufficient distance between the lamps and plants to prevent tissue damage. In addition, since low-intensity lighting is sufficient to regulate flowering of a wide range of plants, the high radiation output from HPS lamps is unnecessary and can be energy intensive. Some greenhouse growers also use other high-intensity electric lamps, such as metal halide and mercury vapor lamps, which use electric arcs to produce photons through metal halides and/or vaporized mercury. Metal-halide lamps have similar efficiency to HPS lamps at converting electrical energy into photons (20 to 25%) (Fisher and Donnelly, 2001). In particular, ceramic metal-halide lamps have a photosynthetic photon efficiency of 1.3 to 1.5 $\mu mol \cdot J^{-1}$ (Nelson and Bugbee, 2014). Metal-halide lamps emit a higher proportion of blue (B; 400 to 500 nm) than R light than HPS lamps (Fisher and Donnelly, 2001).

Light-emitting diodes

An LED is a solid-state semiconductor device that permits current to move in one direction and converts electrical energy into light. Various materials are blended in an LED to

form a p-n semiconductor junction, where extra electrons from the atoms in the n-type material fall into the electron holes of the atoms in the p-type material to create photons. Various colors can be obtained in LEDs using different elements (e.g., AlInGaP and InGaN) to produce photons at different specific wavelengths. In contrast, conventional broad-spectrum light sources, such as INC, FL, and HPS lamps, are restricted in the controllability of spectral composition. Using LEDs allows the selection of the most efficacious spectral composition for desirable growth and development responses (Heo et al., 2002; Schubert and Kim, 2005). Moreover, some (but not all) LEDs as low-voltage devices are considerably more energy efficient than traditional light sources (Pimputkar et al., 2009). The photosynthetic photon efficiency of commercially available LEDs in 2014 range from 0.9 to 1.7 $\mu mol \cdot J^{-1}$ (Nelson and Bugbee, 2014), which indicates that the best LEDs are as efficient as the best HPS lamps, while the worst LEDs are as efficient than the worst HPS lamps. The power of LEDs is mainly used to generate light and conductive heat, but not radiated heat. On the contrary, conventional light sources generate a significant amount of infrared radiation that is not effective for photosynthesis. An LED lamp has a significantly long useful life time, ranging between 20,000 and 55,000 h (Morrow, 2008; Tähkämö et al., 2012). In comparison, the longevity of a traditional INC bulb is 1,000 h in most cases, while that of a compact FL lamp is 8,000 to 10,000 h (Tähkämö et al., 2012).

The effectiveness of LEDs in photoperiodic lighting can depend on their spectral composition. For example, FR LEDs were less effective at promoting flowering of the LDP cyclamen (*Cyclamen persicum*) than FL lamps, but LEDs emitting both B and R light were more effective than FL lamps (Shin et al., 2010). Appropriate combinations of LEDs can be equally or more effective, yet substantially more energy efficient, than traditional light sources. For example, LEDs with an R to FR light ratio (R:FR) of 0.66 ($P_{FR}/P_{R+FR} = 0.63$) or 1.07 (P_{FR}/P_{R+FR}

= 0.72) promoted flowering of LDPs as effectively as INC lamps with an R:FR of 0.59 (P_{FR}/P_{R+FR} = 0.64) (Figure I-2; Craig, 2012). The spectral characteristics of several newly developed LEDs are compared with those of traditional light sources, such as INC, HPS, and compact FL lamps, in Table I-1 and Figure I-1. Philips Lighting currently produces three types of screw-in LED lamps that emit FR (13 W, useful lifetime = 15,000 h), R+white (15 W, useful lifetime = 20,000 h), and R+white+FR (14 W, useful lifetime = 20,000 h) light for potential photoperiodic applications. The R+white lamp (R:FR = 53.4; P_{FR}/P_{R+FR} = 0.88) was developed for plants that do not require FR light for regulation of flowering, such as short-day plants. However, because flowering of some plants is regulated by both R and FR light, the R+white+FR lamp with an R:FR of 0.82 (P_{FR}/P_{R+FR} = 0.67; Table I-1, Figure I-1) was developed for a wide range of photoperiodic plants.

Light quality

Plants perceive the light environment through multiple families of photoreceptors, including R and FR light-absorbing phytochromes, ultraviolet-A and B light-absorbing cryptochromes, and B light-absorbing phototropins. Phytochromes are the primary photoreceptors that regulate flowering of photoperiodic crops, although at least in some species, such as in the Brassicaceae, phytochromes and cryptochromes interact and overlap in function (Cashmore et al., 1999). Green (G, 500 to 600 nm) light was reported to influence flowering of some plants in a few studies (Hamamoto et al., 2003; Hamamoto and Yamazaki, 2009; Jeong et al., 2012), although its mode of action has not been determined. Extensive studies have made valuable progress in understanding photoregulation of flowering and identifying the genetic basis in the model plant, *Arabidopsis thaliana*. In *Arabidopsis*, an NI from B, R, or FR light promoted

flowering, although R light was the least effective (Goto et al., 1991; Eskins, 1992; Carré, 1998). A DE rich in FR light also promoted flowering of *Arabidopsis* (Goto et al., 1991). However, flowering responses to photoperiodic lighting in *Arabidopsis* are not necessarily similar with that in other plants and thus, continued research on the effects of light quality on growth and flowering is merited.

Red and far-red light

The R/FR photoreversibility refers to phytochrome-mediated responses that can be reversed to regulate seed germination, the shade-avoidance response, and flowering. For example, R light triggers a response by converting phytochromes into their biologically active form, the FR-absorbing form (P_{FR}). In some instances, immediate exposure to FR light can counteract the response by reversing P_{FR} back to their inactive, R-absorbing form (P_R). The two forms of phytochromes, P_{FR} and P_R, can exist in plant cells as homodimers and heterodimers (Sharrock and Clack, 2004). The proportions of P_{FR} and P_R depend on the R:FR, which creates a P_{FR}/P_{R+FR} that mediates extension growth and flowering responses in plants (Sager et al., 1988). Although both P_R and P_{FR} absorb photons between approximately 300 and 800 nm, their spectral absorption curves differ (Sage, 1992). For example, the absorption peak wavelengths of extracted oat phytochromes are 665 nm for P_R and 725 nm for P_{FR} (Butler et al., 1965). Therefore, the conversion of P_R to P_{FR} is promoted most effectively by R light (Butler et al., 1964; Sager et al., 1988). In angiosperms, there are multiple phytochrome proteins, which have been named phyA, phyB, phyC, phyD, and phyE (Clack et al., 1994; Sharrock and Quail, 1989).

Different mechanisms and pathways of flowering may exist in SDPs and LDPs in response to the R:FR. Studying the use of LEDs that emit R and/or FR light can increase the understanding of how R and FR light in photoperiodic lighting regulate flowering without other,

potentially confounding spectra. An NI with a moderate to high R:FR effectively inhibits flowering of SDPs (Runkle and Heins, 2006; Vince, 1969). For example, a 4-h NI with an R:FR of 0.66 or higher inhibited flowering of chrysanthemum (*Dendranthema* × *grandiflorum*), whereas a 4-h NI with an R:FR of 0.28 or lower was not perceived as an LD (Craig and Runkle, 2013). Similarly, flowering of the SDP perilla (*Perilla ocymoides*) was strongly suppressed under a 10-h SD with a 10-min NI provided by R LEDs compared to no NI or a 10-min NI provided by FR LEDs (Choi, 2003). The efficacy of NI lighting also depends on its intensity. For example, flowering of chrysanthemum was completely inhibited when the intensity of R light, delivered as a DE, was above 1.4 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Hong et al., 2013). Similarly, as the light intensity of an effective 4-h NI (e.g., from R or white LEDs) increased, flowering time of chrysanthemum increased (Ho et al., 2012). Therefore, R or white LEDs and fluorescent (FL) lamps can create LDs that delay flowering of SDPs (Padhye and Runkle, 2011).

Some LDPs flower most rapidly when DE or NI lighting contains both R and FR light. For example, an NI with an R:FR of 0.66 or 1.07 most effectively promoted flowering of petunia (*Petunia ×hybrida*) 'Easy Wave White' and snapdragon (*Antirrhinum majus*) (Craig and Runkle, 2012), which confirms previous studies performed with broad-spectrum conventional lamps (Thomas and Vince-Prue, 1997). Replacement of conventional INC lamps with FR-deficient FL lamps can delay flowering of these and additional LDPs (Lane et al., 1965; Runkle et al., 2012).

Many commercial greenhouse growers in the U.S. produce a wide range of crops in the same greenhouse environment. Therefore, an effective photoperiodic lighting strategy must regulate flowering of all photoperiodic species. A 7-h DE (to create a 16-h LD) and a 4-h NI were almost always equally effective at promoting flowering of LDPs (Craig, 2012). An NI provided by B, R, or FR LEDs did not stimulate complete, rapid flowering of a variety of LDPs

(Craig and Runkle, 2012; 2013; Hamamoto et al., 2003). Therefore, a combination of different spectral wavebands (specifically, R and FR light) is essentially required to regulate flowering.

Blue light

The effects of B light on flowering responses, presumably mediated by cryptochromes and potentially phytochromes, are variable and less understood. Delivering an NI with B light can promote flowering of some LDPs and inhibit flowering of some SDPs, but have no effect on others. A 1-h NI from B light was more effective at promoting flowering of *Arabidopsis* than an NI from R light under SDs (Goto et al., 1991). In addition, the LDP lisianthus (*Eustoma grandiflorum*) flowered earlier under a 5-h NI provided by B LEDs at a photosynthetic photon flux (*PPF*) of 5 $\mu mol \cdot m^{-2} \cdot s^{-1}$ compared with under ambient SDs (11 to 12.5 h) without an NI (Yamada et al., 2011). Flowering of perilla was also strongly inhibited by a 3-h NI provided by B LEDs at a *PPF* of 8 to 10 $\mu mol \cdot m^{-2} \cdot s^{-1}$ during natural SDs (Hamamoto et al., 2003). Similarly, perilla flowered 13 d later under a 10-h SD with a 10-min NI from B LEDs than under the same SD without an NI (Choi, 2003). In the SDP rice, flowering is regulated by the *Heading date 1* (*Hd1*) and *Heading date 3a* (*Hd3a*) genes (Yano et al., 2000; Kojima et al., 2002). Under SDs, *Hd3a* expression is activated by *Hd1* to induce flowering, whereas under LDs, *Hd3a* expression is repressed by *Hd1*, and flowering is inhibited (Yano et al., 2000; Kojima et al., 2002). An NI with B or R light downregulated *Hd3a* expression through phytochrome B to delay flowering of rice, while an NI with FR light did not (Ishikawa et al., 2009). However, B light in photoperiodic lighting did not control flowering of some other crops. A 4-h NI provided by B LEDs at a *PPF* of 3.3 $\mu mol \cdot m^{-2} \cdot s^{-1}$ was not perceived as an LD by the LDPs petunia 'Wave Purple Classic', rudbeckia (*Rudbeckia hirta*), and tickseed (*Coreopsis verticillata*) (Craig, 2012). Similarly, a 4-h NI provided by B LEDs at a *PPF* of 0.8 or 3.3 $\mu mol \cdot m^{-2} \cdot s^{-1}$ was not perceived as an LD by

chrysanthemum (Ho et al., 2012). Even at a greater *PPF* of 70 $\mu mol \cdot m^{-2} \cdot s^{-1}$, a 4-h DE provided by B LEDs did not inhibit flowering of chrysanthemum (Jeong et al., 2012). Flowering responses can depend on the quantity of light at various wavelengths for photoperiodic lighting. A high intensity may be required for an effective NI from B light, whereas a low intensity is sufficient for R light to elicit and even saturate the same response. For example, to inhibit flowering of the SDP duckweed (*Lemna paucicostata*) grown under a 8-h SD using a 10-min NI from B (peak wavelength = 450 nm), G (peak wavelength = 550 nm), R (peak wavelength = 650 nm), and FR (peak wavelength = 750 nm) light, the fluence rate required for a 50% inhibitory effect was 10, 0.5, 0.1, and 3 $\mu mol \cdot m^{-2} \cdot s^{-1}$, respectively (Saji et al., 1982).

The spectral composition of the main photoperiod can influence the effectiveness of an NI from B light. For example, flowering of chrysanthemum was inhibited by an NI provided by B or FR LEDs when the main photoperiod was comprised of B light, but was not when the main photoperiod was comprised of white light or a combination of B and R light (Higuchi et al., 2012b). Delivering B light as a DE or NI may lead to different flowering responses in some species. For example, B LEDs delayed flowering of the SDP okra (*Abelmoschus esculentus*) when delivered as a DE but did not when delivered as an NI (Hamamoto and Yamazaki, 2009).

Mixing B and R light in NI lighting can accelerate flowering of some LDPs. Although a 4-h NI provided by B, R, or FR LEDs at a *PPF* of 4 $\mu mol \cdot m^{-2} \cdot s^{-1}$ promoted flowering of the LDP cyclamen compared with the 9-h SD, an NI provided by a mixture of B and R LEDs was most effective (Shin et al., 2010). In at least some SDP, the R to B light ratio or absolute light intensities of R and B light during an NI can influence flowering time. At a *PPF* of 0.4 $\mu mol \cdot m^{-2} \cdot s^{-1}$, a high R to B light ratio (3R:1B) was more inhibitory to flowering of chrysanthemum than a low R to B light ratio (1R:3B), but both mixtures of R and B light were

not as effective as R light alone at a *PPF* of 1.6 μmol·m^{-2}·s^{-1} (Ho et al., 2012). Since flowering of chrysanthemum is strongly inhibited by R light and typically is not affected by B light, it may be the absolute R light intensity, rather than the R to B ratio, that led to the observed effects. Additional flowering research on B light in photoperiodic lighting and the interactions between B, R, and FR light are merited.

Green light

Early studies on a limited number of plants indicated that G light was a relatively ineffective LD signal (Thomas and Vince-Prue, 1997). However, G light can be at least somewhat effective at regulating flowering of some SDPs and LDPs outside of the Brassicaceae. For example, a 2-h NI provided by G LEDs (peak wavelength = 530 nm) at a *PPF* of 8 to 10 μmol·m^{-2}·s^{-1} was as effective as that provided by yellow or R LEDs at inhibiting flowering of cosmos (*Cosmos bipinnatus*) and perilla and promoting flowering of spinach (*Spinacia oleracea*) grown during an SD season (Hamamoto et al., 2003). In addition, a 4-h NI provided by G LEDs (peak wavelength = 520 nm) delayed flowering of the SDP okra grown under an 8-h SD more effectively than that provided by B LEDs but less effectively than that provided by R LEDs (Hamamoto and Yamazaki, 2009). Following a 12-h photoperiod provided by FL lamps, a 4-h DE provided by G LEDs (peak wavelength = 518 nm) at a *PPF* of 70 μmol·m^{-2}·s^{-1} was as effective as that provided by R (peak wavelength = 632 nm) or white LEDs at inhibiting flowering of chrysanthemum (Jeong et al., 2012). Appearance of visible inflorescences of chrysanthemum grown under natural SDs with a 1-h NI provided by G FL lamps was delayed by 17 d compared with those grown without an NI or with an NI provided by ultraviolet-A or B FL lamps; and a 15-min NI provided by R LEDs (peak wavelength = 596 nm) was more effective at

inhibiting flowering than those with peak wavelengths of 530 nm, 639 nm, or 660 nm (Sumitomo et al., 2012).

Growth-response parameters

In many ornamental crop production situations, a grower's goal is to produce plants that are uniform with respect to stage of development (e.g., all vegetative or all reproductive) and morphology (e.g., of a desirable shape and height). Common metrics used to judge horticultural crops are flowering percentage, flower or inflorescence number, and plant height. A crop can have reduced value if standards set by the buyer are not met. Therefore, effects of electric lighting on growth, in addition to flowering, must be considered for commercial applications.

An FR-rich (i.e., low R:FR) environment triggers the shade-avoidance response, which typically includes changes in plant morphology and physiology (Cerdán and Chory, 2003). Manipulating the R:FR in photoperiodic lighting can influence extension growth responses without exogenous application of plant hormones. Extension growth is related to gibberellin biosynthesis, a hormone that promotes various physiological responses, especially stem elongation, and photoregulation of gibberellins has been investigated (Hirose et al., 2012; Reid et al., 2002; Zhao et al., 2007). A low R:FR increases biosynthesis of gibberellins, which can promote stem elongation (Kurepin et al., 2012), and a high R:FR can inhibit extension growth of many plants. For example, chrysanthemum plants grown under a 9-h natural SD with a subsequent 30-min DE provided by R and FR LEDs were taller when the R:FR was ≤0.7 than at 2.4 (Lund et al., 2007). Similarly, in a study with lisianthus, internode length on the main stem was shorter under an NI with an R:FR of 5 or 10 than under an NI with an R:FR of 0.5 to 3 (Yamada et al., 2011). Results from studies using LEDs are in accordance with earlier work using spectral filters, which indicated that stem extension was promoted as the R:FR (or

P_{FR}/P_{R+FR}) decreased (Runkle and Heins, 2001). Therefore, the use of LEDs in photoperiodic lighting at low intensities is a feasible way to inhibit or promote extension growth, irrespective of flowering. For example, a 30-min DE provided by R LEDs at 5 $\mu mol \cdot m^{-2} \cdot s^{-1}$ suppressed stem elongation of poinsettia (*Euphorbia pulcherrima*) grown under a 10-h SD (Islam et al., 2012).

In *Arabidopsis*, B light can induce the suppression of gibberellin biosynthesis genes and promote the expression of gibberellin inactivation genes, and the transcriptional regulation of these genes was mediated by both cryptochromes (cry1 and cry2) and phytochrome (phyA) (Zhao et al., 2007). In rice, B light caused a reduction in active gibberellin concentration, and the suppression of gibberellin biosynthesis and promotion of gibberellin inactivation was mediated by phytochromes (phyA, phyB, and phyC) and cryptochrome (cry1), respectively (Hirose et al., 2012). Therefore, although low-intensity B light may not regulate flowering of a wide range of plants in greenhouse production, it could potentially have an inhibitory effect on stem elongation. For example, internode elongation of chrysanthemum was suppressed by 60% under a 4-h NI provided by B LEDs at a *PPF* of 1.7 $\mu mol \cdot m^{-2} \cdot s^{-1}$ compared with FL lamps at a *PPF* of 150 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Shimizu et al., 2005); however, different light intensities under B LEDs and FL lamps in this study might have confounded the results. In high-intensity sole-source lighting, B light generally inhibits extension growth when added to R light. For example, B light and a combination of B and R light resulted in a shorter peduncle length of cyclamen than R light or FL light (Heo et al., 2003).

In contrast, other studies suggest B light can promote stem elongation of some plants. For example, chrysanthemum grown under an 11-h SD provided by R and B LEDs for 42 d flowered similarly but were 18 cm taller under an 11-SD with a 4-h DE provided by B LEDs at a *PPF* of 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Jeong et al., 2014). Furthermore, as the duration of B light was prolonged,

stem length increased as a result of increased internode length (Jeong et al., 2014). In a separate study with marigold, stem length was three times greater under only B LEDs than only under FL lamps or FL lamps plus R LEDs (Heo et al., 2002). Stem elongation in response to B light may vary among species, since stem length of eggplant (*Solanum melongena*) increased as B light intensity increased from 20 to 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$, whereas internode length of lettuce (*Lactuca sativa*) was suppressed by B light (Hirai et al., 2005). Therefore, the effects of B light on stem elongation are not fully understood because they depend on light intensity, other wavelengths, species, and possibly other factors.

APPENDIX

Table I-1. Spectral distribution characteristics of incandescent (INC), high-pressure sodium (HPS), and compact fluorescent (CFL) lamps, and red (R)+white (W)+far-red (FR), cool-white (CW), and warm-white (WW) light-emitting diodes (LEDs) between 400 and 800 nm. Data are based on measurements made at Michigan State University and the estimated phytochrome photoequilibria values (P_{FR}/P_{R+FR}) are estimated according to Sager et al. (1988).

				LEDs		
Parameter	**INC**	**HPS**	**CFL**	R+W+FR	CW	WW
Percentage (%) of photon flux (400−800 nm)						
Blue (B; 400−500 nm)	3	5	14	6	20	12
Green (500−600 nm)	14	51	37	13	46	39
Red (R; 600−700 nm)	30	38	42	36	30	43
Far red (FR; 700−800 nm)	54	6	7	44	4	6
Light ratio						
R:FR	0.56	5.90	6.19	0.82	7.47	7.18
B:R	0.09	0.12	0.32	0.18	0.67	0.27
P_{FR}/P_{R+FR}	0.64	0.86	0.83	0.67	0.84	0.84

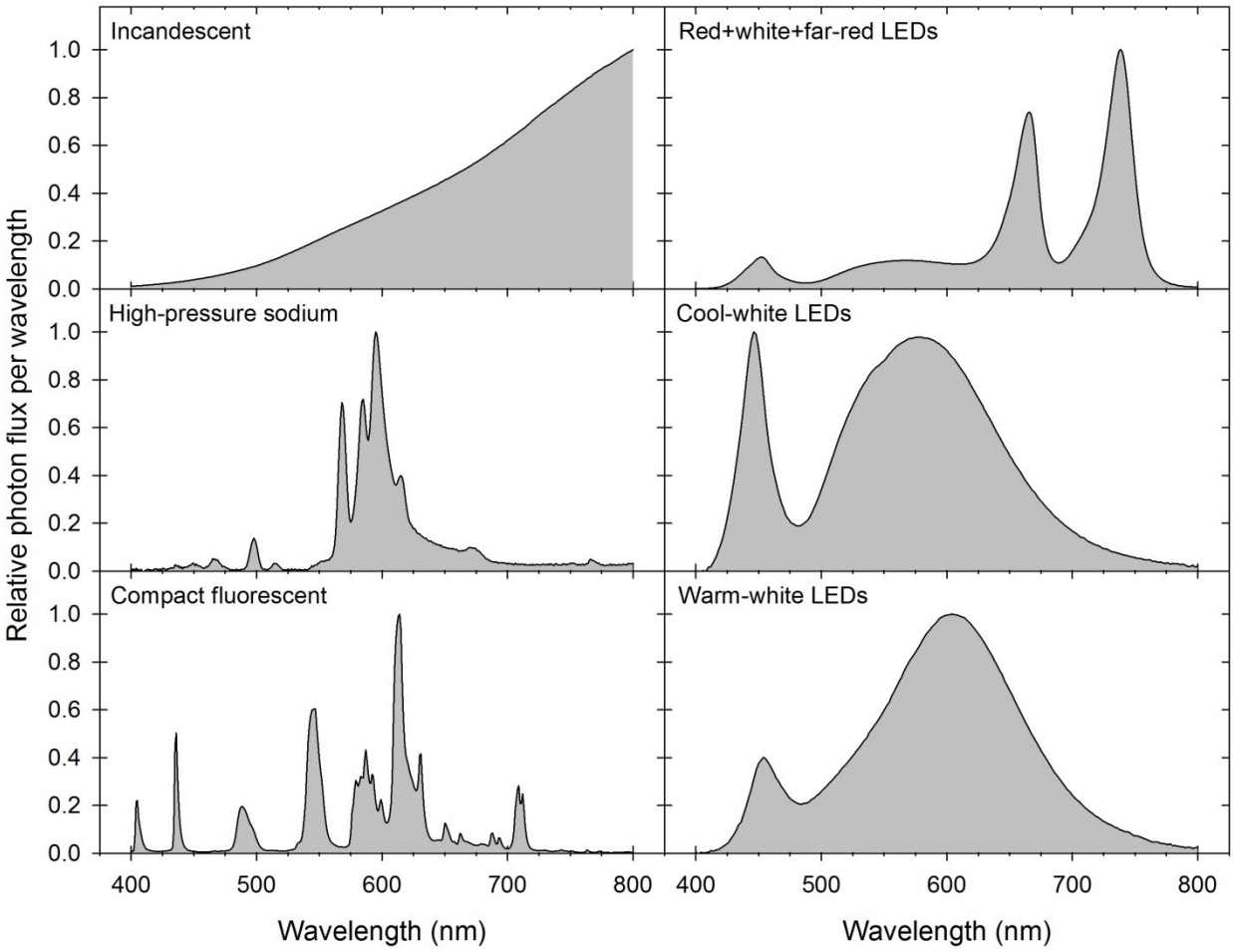

Figure I-1. Spectral distributions of several lamps and light-emitting diodes (LEDs) between 400 and 800 nm from measurements made at Michigan State University.

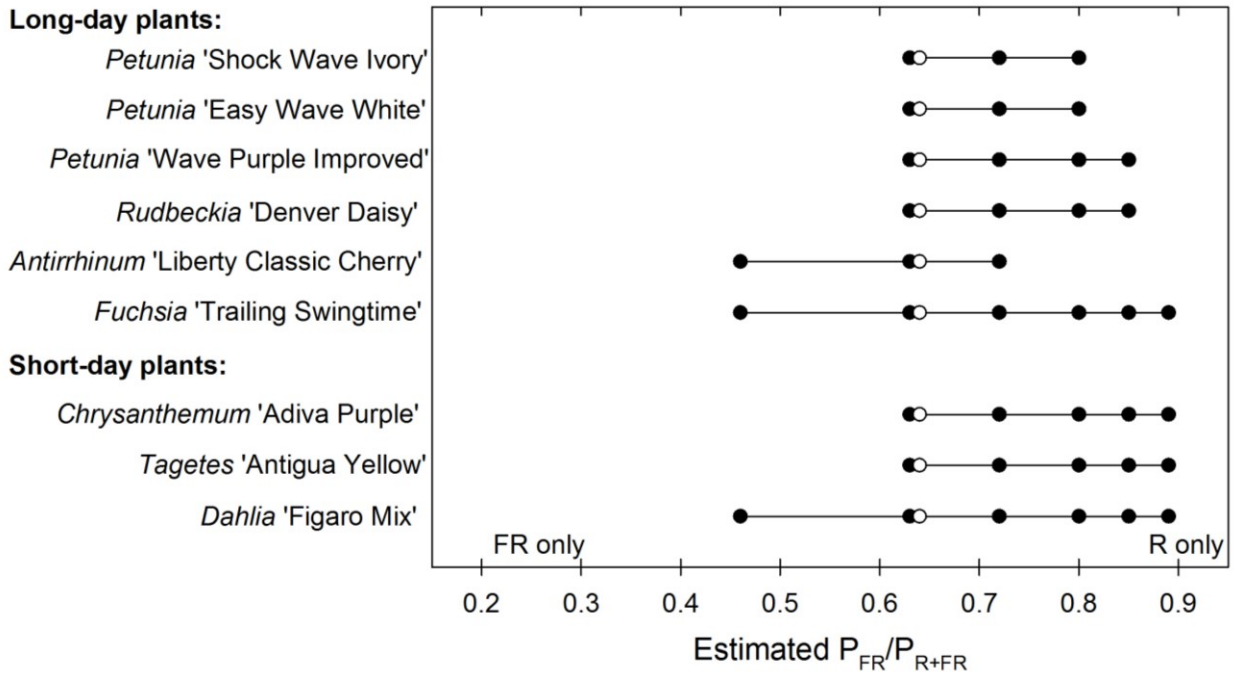

Figure I-2. Summary of the efficacy of 4-h night-interruption lighting treatments that promoted flowering of long-day plants and inhibited flowering of short-day plants (adapted from Craig, 2012). Light-emitting diodes (solid symbols) or incandescent lamps (open symbols) emitted different ratios of red (R; 600 to 700 nm) and far-red (FR; 700 to 800 nm) light. The phytochrome photoequilibria (P_{FR}/P_{R+FR}) values were estimated using the spectral distributions of the treatments and the model described by Sager et al. (1988). A lamp was considered effective for each species if flowering percentage was ≥90% for long-day plants and if time to flower was statistically similar to plants that flowered most rapidly (for long-day plants) or most slowly (for short-day plants).

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SECTION II

CONTROLLING FLOWERING OF PHOTOPERIODIC ORNAMENTAL CROPS WITH LIGHT-EMITTING DIODE LAMPS: A COORDINATED GROWER TRIAL

Controlling Flowering of Photoperiodic Ornamental Crops with Light-emitting Diode Lamps: A Coordinated Grower Trial

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Additional index words. Flowering lamp, LEDs, long days

Abstract.

Photoperiodic lighting from lamps with a moderate ratio of red (R; 600 to 700 nm) to far-red (FR; 700 to 800 nm) light effectively promotes flowering of long-day plants. Because of spectral controllability, long life span, and energy efficiency, light-emitting diodes (LEDs) have emerged as an alternative to conventional light sources, such as incandescent (INC) and high-pressure sodium (HPS) lamps. However, the efficacy of newly developed LEDs on flowering applications has not been published. We conducted a coordinated trial with five commercial greenhouse growers to investigate the efficacy of R+white (W)+FR LEDs, with an R:FR of 0.82, to regulate flowering of daylength-sensitive ornamental crops. The trial was also performed in two replicate greenhouses at Michigan State University (MSU). Ageratum (*Ageratum houstonianum*), calibrachoa (*Calibrachoa ×hybrida*), dahlia (*Dahlia ×hybrida*), dianthus (*Dianthus chinensis*), two petunia (*Petunia ×hybrida*) cultivars, snapdragon (*Antirrhinum majus*), and verbena (*Verbena ×hybrida*) were grown under natural short days (SDs) with 4-hour night-interruption (NI) lighting provided by the R+W+FR LEDs or conventional lamps typically used by each grower. Two companies used HPS lamps, whereas the other sites used INC lamps. In addition, a natural SD treatment, a truncated 9-hour SD treatment, and a compact fluorescent lamp NI treatment were provided at three different sites. With few exceptions, time to flower and flowering percentage of the bedding plant crops tested were similar under the R+W+FR LEDs to that under the conventional lamps at all sites. At MSU, ageratum, dianthus, petunia, snapdragon, and verbena flowered earlier under NI lighting treatments than under 9-hour SDs. In addition, plant height and visible flower bud or inflorescence number at flowering were similar under the R+W+FR LEDs and INC lamps for most crops. Therefore, we conclude that the R+W+FR LEDs

are as effective as lamps traditionally used in greenhouses at controlling flowering of photoperiodic plants.

Introduction

Most plants can be classified into one of three categories according to their photoperiodic responses: long-day plants (LDPs), short-day (SD) plants (SDPs), and day-neutral plants (Thomas and Vince-Prue, 1997). Flowering of LDPs is promoted when the night length is shorter than a species- or cultivar-specific critical skotoperiod, whereas flowering of SDPs is inhibited or delayed when the uninterrupted dark period is shorter than a critical skotoperiod (Thomas and Vince-Prue, 1997). When the ambient photoperiod is short, low-intensity photoperiodic lighting can be used to control flowering of LDPs and SDPs. This can be achieved by delivering light beginning at the end of the day until the desired photoperiod is met (day extension) or during the middle of the night (night interruption, NI). Although the minimum duration of effective NI lighting can vary among species, 4 h of NI lighting is typically sufficient to regulate flowering of photoperiodic crops (Runkle and Heins, 2003; Runkle et al., 1998). Generally, NI lighting is most effective when delivered during the middle of the long night. For example, to promote flowering of dianthus (*Dianthus chinensis*) or inhibit flowering of 'Dream Land' zinnia (*Zinnia elegans*), 4-h NI lighting during a night lasting from 1700 HR to 0800 HR was most effective starting at 2200 HR, rather than 1800 HR or 0200 HR (Park et al., 2013).

Conventional light sources, such as incandescent (INC), fluorescent (FL), and high-pressure sodium (HPS) lamps typically are used by commercial growers to deliver photoperiodic lighting. Incandescent lamps emit both red (R) and far-red (FR) light and are effective for a wide range of crops (Thomas and Vince-Prue, 1997). Because FL lamps emit little FR light, direct

replacement of INC lamps with FL lamps delays flowering of some FR-sensitive crops such as 'Wave Purple Classic' ('WPC') petunia (*Petunia ×hybrida*) (Runkle et al., 2012). High-pressure sodium lamps, either fixed or with a rotating reflector, also promote flowering of LDPs and inhibit flowering of SDPs (Blanchard and Runkle, 2009, 2010; Whitman et al., 1998). High-pressure sodium lamps used for day-extension lighting to provide a 16-h long day and INC lamps used for 4-h NI lighting following a 9-h SD were similarly effective at promoting flowering of four *Petunia* spp. (Warner, 2010).

Light-emitting diodes (LEDs) have several technical advantages over conventional lamps. Conventional lamps emit a broad spectrum of light, and their spectral distribution cannot be easily modified. In contrast, LEDs emit photons of specific colors of light by blending different proportions of different elements. Therefore, LED lighting allows selection of the most efficacious spectral composition for specific plant responses (Heo et al., 2002; Schubert and Kim, 2005). Many conventional lamps generate a significant amount of undesired infrared radiation, but LEDs emit little radiated heat and can be more energy efficient (Pimputkar et al., 2009). The expected lifetime of a traditional INC lamp is 1,000 h, whereas that of a compact FL (CFL) lamp is between 8,000 and 10,000 h (Tähkämö et al., 2012). In comparison, an LED lamp can last between 20,000 and 55,000 h when operated at favorable temperatures (Morrow, 2008; Tähkämö et al., 2012).

The capability to use narrow-band light from LEDs or to combine multiple wavebands has enabled researchers to determine the effects of light quality on flowering of a variety of crops without potentially confounding spectra. Light-emitting diodes with effective spectral composition can therefore replace conventional light sources. For example, LEDs emitting controlled amounts of blue (B; 400 to 500 nm), R, and FR light were a comparable alternative to

HPS lamps at inducing flowering of Ghent azalea (*Rhododendron simsii*), although the peak wavelengths of B, R, and FR light were not reported (Schamp et al., 2012). Flowering of the LDP cyclamen (*Cyclamen persicum*) was earlier under a mixture of R and B LEDs than FL lamps when used as NI lighting (Shin et al., 2010). In addition, LEDs with an R (peak wavelength = 660 nm) to FR (peak wavelength = 735 nm) light ratio (R:FR) of 0.66 or greater were as effective as INC lamps at inhibiting flowering of SDPs (Craig and Runkle, 2013). However, to our knowledge, studies on the efficacy of newly developed LEDs as an alternative to conventional lamp types on flowering applications have not been published.

Three commercial LED fixtures for photoperiodic lighting have been recently developed and marketed for potential flowering applications, emitting only FR, R + white (W), or R+W+FR. The 14-W R+W+FR LED lamp was developed as a commercial replacement for 100- to 150-W INC lamps to regulate flowering of ornamental crops. A small amount of W light was incorporated mainly for human vision. We coordinated a commercial greenhouse grower trial to investigate the efficacy of the R+W+FR LED lamp to control flowering of daylength-sensitive plants compared with conventional lamps. Photoperiodic lighting with a mixture of R and FR light was most effective at promoting flowering of LDPs (Thomas and Vince-Prue, 1997), and LEDs with an R:FR of 0.66 or 1.07 were as effective as INC lamps at promoting flowering of LDPs and inhibiting flowering of SDPs (Craig and Runkle, 2012). Therefore, we postulated that the R+W+FR LED lamps with an R:FR of 0.82 would be as effective as conventional lamps at regulating flowering of photoperiodic crops.

Materials and Methods

Plant material

All young plants were produced by a commercial plant producer (C. Raker & Sons, Litchfield, MI). Seeds of 'Hawaii Blue' ageratum (*Ageratum houstonianum*), 'Telstar Crimson' dianthus, 'Easy Wave Burgundy Star' ('EWBS') and 'WPC' petunia, 'Liberty Classic Yellow' snapdragon (*Antirrhinum majus*), and 'Obsession' verbena (*Verbena ×hybrida*) were sown into 288-cell (6-mL) plug trays on 5 Jan. 2013, 4 Jan. 2013, 29 Dec. 2012, 28 Dec. 2012, 26 Dec. 2012, and 5 Jan. 2013, respectively. Cuttings of 'Callie Deep Yellow' calibrachoa (*Calibrachoa ×hybrida*) and 'Dahlinova Texas' dahlia (*Dahlia ×hybrida*) were stuck into 51-cell (27-mL) strip trays on 5 Jan. 2013 and 9 Jan. 2013, respectively. These eight crops were chosen according to their photoperiodic flowering responses. The typical commercial production period for these propagules was shortened by 1 week to ship plants before they could be induced to flower. The young plants were express shipped in late January to Michigan State University (MSU; East Lansing, MI) and to the five commercial growers cooperating in this experiment: C. Raker & Sons, the Center for Applied Horticultural Research (CfAHR) at Altman Plants (Vista, CA), Henry Mast Greenhouse (Byron Center, MI), Krueger-Maddux Greenhouses (Sunman, IN), and Kube Pak (Allentown, NJ).

Upon receipt of the young plants, each site transplanted them into 18-cell (304-mL) trays (L-1801; Landmark Plastic Corporation, Akron, OH) filled with their typical peat-based growing medium for bedding-plant production, and four trays of each cultivar were placed under each lighting treatment described below. The dates of transplant and onset of treatments at C. Raker & Sons, CfAHR, Krueger-Maddux Greenhouses, Kube Pak, and MSU were 1 Feb. 2013, 2 Feb. 2013, 28 Jan. 2013, 18 Feb. 2013, and 5 Feb. 2013, respectively. Before transplant, all plants at Kube Pak were grown under natural SDs (≤10.8 h). At Henry Mast Greenhouse, plants were transplanted and transferred to an LED treatment on 1 Feb. 2013 and to an HPS treatment on 2

Feb. 2013 (see below). All plants were grown following the growers' standard production practices of watering, fertilization, and pest management. Application of plant-growth retardants was also at the discretion of the grower, and if an application was made, it was the same for all treatments. At C. Raker & Sons, daminozide (B-Nine WSG; OHP, Inc., Mainland, PA) at 2,500 ppm was applied as a foliar spray to dahlia, dianthus, and snapdragon on 13 Feb. 2013. At CfAHR, paclobutrazol (Bonzi; Syngenta, Greensboro, NC) was applied as a foliar spray at 14 ppm to 'EWBS' and 'WPC' petunia and at 7 ppm to snapdragon; daminozide at 3,200 ppm was applied as a foliar spray to calibrachoa, dianthus, verbena, and dahlia on 27 Feb. 2013. At Henry Mast Greenhouse, paclobutrazol at 1 ppm was applied as a substrate drench with a volume delivering 118 mL per pot to all plants on 22 Feb. 2013. No plant growth retardants were used at Krueger-Maddux Greenhouses, Kube Pak, and MSU.

Lighting treatments

At each site, 4-h NI lighting treatments were delivered by the R+W+FR LED lamps (GreenPower LED flowering DR/W/FR 120 V, E26; Philips, Eindhoven, the Netherlands) and one or two conventional lamp types at the discretion of the grower (Table II-1). All lamps operated from 2200 HR to 0200 HR every night to provide NI lighting, as controlled by an environmental control computer or a timer. At all sites except MSU, plants received the natural photoperiod. At MSU, opaque black cloth enclosing greenhouse benches was closed at 1700 HR and opened at 0800 HR to provide a truncated 9-h SD for all treatments. In addition to the LED and conventional lamp treatments, CfAHR, MSU, and Kube Pak provided control treatments, including an unlighted natural SD treatment at CfAHR, a truncated 9-h SD treatment at MSU, and a CFL treatment at Kube Pak. At all sites, if any two treatments were close together, a light barrier, such as a blackout fabric or black plastic sheet, was manually positioned between the

treatments at night to block all direct light from adjacent treatment(s). To avoid shade cast by the black screens during the day, they were pulled closed between 1600 HR and 2000 HR and retracted before 0900 HR. At C. Raker & Sons and Kube Pak, the treatments were far enough apart to avoid light contamination. At C. Raker & Sons, CfAHR, Henry Mast Greenhouse, Krueger-Maddux Greenhouses, Kube Pak, and MSU, the LED lamps were installed 3.5, 3.0, 7.0, 5.5, 7.0, and 3.1 feet, respectively, above plants and 3 to 10 feet apart. The conventional lamps were installed as per each grower's lighting standards. At C. Raker & Sons, two HPS lamps (400 W, PL2000; P.L. Light Systems Inc., Beamsville, ON, Canada) were hung 3.5 feet above the bench surface and 12 feet apart. At CfAHR, four INC lamps were placed 3 feet above benches and 3 feet apart. At Henry Mast Greenhouse, one HPS lamp (400 W, PL2000; P.L. Light Systems Inc.) was hung 7 feet above plants. At Krueger-Maddux Greenhouses, five INC lamps with metallic pie plates acting as reflectors were hung 4 feet above plants and 5 feet apart. At Kube Pak, three INC or CFL lamps were hung 10 feet above plants and 10 feet apart. At MSU, two INC lamps were hung 2.5 feet above plants and 2.5 feet apart and, along with the LEDs, were covered with multiple layers of aluminum mesh to achieve an average photon flux density of 2 $\mu mol \cdot m^{-2} \cdot s^{-1}$ between 400 nm and 800 nm (and was always between 1 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and 3 $\mu mol \cdot m^{-2} \cdot s^{-1}$). The spectral distribution of the LED and INC lamps was measured by a spectroradiometer (PS-200; StellarNet, Inc., Tampa, FL), and the phytochrome photoequilibrium was estimated according to Sager et al. (1988) (Figure II-1). Supplemental lighting provided by HPS lamps was used for all plants from 0800 to 1700 HR, delivering a photosynthetic photon flux (*PPF*) of 60 to 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at plant canopy. Controlled by an environmental control computer, the HPS lamps were automatically switched on when the ambient *PPF* was lower than 185 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and off when the ambient *PPF* was greater than 370 $\mu mol \cdot m^{-2} \cdot s^{-1}$.

Data collection and analysis

At all sites, date of first open flower was recorded for 12 plants in each treatment that were randomly selected at the beginning of the trial. Additional data were recorded at MSU, such as date of first visible flower bud or inflorescence (VB), number of VB, and main stem length at flowering. For 'EWBS' and 'WPC' petunia, the stem with the first open flower was measured for stem length. All plants were checked every 1 to 2 d for first flowering except at Kube Pak, where flowering was checked once or twice a week. Days to flower from the start of lighting treatments (and at Kube Pak from when plants were transplanted) and flowering percentage were subsequently calculated for each cultivar in each treatment. The trials ended on 10 Apr. 2013, 4 Apr. 2013, 8 Apr. 2013, 20 Apr. 2013, 4 Apr. 2013, and 24 June 2013, at C. Raker & Sons, CfAHR, Henry Mast Greenhouse, Krueger-Maddux Greenhouses, Kube Pak, and MSU, respectively. The photoperiod from sunrise to sunset, actual average daily temperature (ADT), and photosynthetic daily light integral (DLI) for each site are provided in Table II-1. At C. Raker & Sons, CfAHR, and Henry Mast Greenhouse, a weather station (WatchDog 2400; Spectrum Technologies, Aurora, IL) measured temperature and photosynthetically active radiation. At Krueger-Maddux Greenhouses, a light meter (Lightscout DLI 100 Light Meter; Spectrum Technologies) estimated the DLI, and the grower read instantaneous temperatures with a thermostat and thermometers but did not record actual data. At Kube Pak, a weather tracker (WatchDog 305; Spectrum Technologies) measured temperature and photosynthetically active radiation. At MSU, line quantum sensors (Apogee Instruments, Inc., Logan, UT) positioned horizontally at plant height measured photosynthetically active radiation every 10 s, and a data logger (CR10; Campbell Scientific, Logan, UT) recorded hourly averages. An aspirated thermocouple [36-gauge (0.127-mm diameter) type E] on each bench measured air temperature

every 10 s, and the same data logger recorded hourly averages. Data were analyzed with the SAS version 9.3 (SAS Institute, Inc., Cary, NC) mixed-model (PROC MIXED) and glimmix-model (PROC GLIMMIX) procedures, and pairwise comparisons between treatments were performed with Tukey's honest significant difference test ($P = 0.05$).

Calculation of operating costs

We estimated the initial investment and operating costs (in U.S. dollars) to uniformly deliver 4-h NI lighting with 150-W INC, 250-W HPS, and the 14-W R+W+FR LED lamps. Photoperiodic lighting was designed for a 4,320-square-foot (30×144 feet) greenhouse with 7-foot clearance above the bench. Data for INC and HPS lamps were adapted from Fisher and Both (2004). The expected useful lifetime for the R+W+FR LED lamp was 20,000 hours (Philips, 2014), and the purchase cost was $40 (E. Jansen, personal communication). Electrical costs were calculated according to the average retail price of electricity to the commercial sector in the United Sstates in 2013, which was $0.1029 per kilowatt-hour (Energy Information Administration, 2014).

Results

C. Raker & Sons

All plants flowered under NI lighting treatments delivered by either the HPS lamps or LEDs (data not shown). There was no significant effect of lamp type on flowering time for any crop except verbena, which flowered approximately 8 d earlier under the HPS lamps (Figure II-2). Although no data were recorded, the grower noted that plants under the HPS lamps were of higher visual quality than those under the LEDs: all cultivars appeared darker green and shorter under the HPS lamps.

CfAHR

All plants under the INC lamps and LEDs flowered at approximately the same time, whereas some of the LDPs did not flower under the natural SDs (Figure II-3 or data not shown). Only 8% of 'WPC' petunia flowered under SDs before the trial ended. For ageratum, dahlia, dianthus, 'EWBS' petunia, and verbena, there were no significant differences in flowering time among treatments (Figure II-4). In contrast, calibrachoa and snapdragon flowered 28 d and 8 d earlier, respectively, under the NI lighting treatments than under SDs. The grower observed that calibrachoa and snapdragon under the NI lighting treatments were more elongated than plants under SDs, and plants under the LEDs were more compact than those under the INC lamps. Verbena under the LEDs appeared taller than plants under the INC lamps, but no data were recorded.

Henry Mast Greenhouse

All plants flowered similarly under the NI lighting treatments delivered by HPS lamps or LEDs (Figure II-2), except only 8% of snapdragon under the HPS lamps had flowered before the trial ended. Although complete data of snapdragon under the HPS lamps were not collected, the grower estimated that flowering was delayed by ≈5 d under the HPS lamps compared with the LEDs.

Krueger-Maddux Greenhouses

All plants flowered similarly under the NI lighting treatments delivered by INC lamps or LEDs except snapdragon, which flowered approximately 8 d earlier under the INC lamps (Figure II-2). According to the grower, plants under the INC lamps appeared more elongated than those under the LEDs.

Kube Pak

'WPC' petunia did not flower under the NI lighting treatment delivered by CFL lamps before the trial ended. For ageratum, dahlia, dianthus, and snapdragon, flowering time was similar among the three NI lighting treatments (Figure II-2). 'EWBS' petunia and verbena flowered 10 d and 9 d earlier, respectively, under the LEDs than under the INC lamps, and calibrachoa flowered 10 to 17 d earlier under the LEDs than under the INC or CFL lamps. Flowering percentage under the CFL or INC lamps was lower than that under the LEDs for calibrachoa, dahlia, dianthus, 'EWBS' and 'WPC' petunia, and snapdragon (data not shown). For example, flowering percentage of 'WPC' petunia under the CFL lamps, INC lamps, and LEDs was 0%, 17%, and 50%, respectively, at the end of the trial.

MSU

All plants flowered under either the INC lamps or LEDs. Calibrachoa did not flower under SDs before the trial ended (Figure II-3). Two-thirds of 'WPC' petunia under SDs flowered in houses 10E and 13B. Ageratum, dianthus, 'EWBS' and 'WPC' petunia, and snapdragon flowered similarly under NI lighting treatments delivered by INC lamps or LEDs, and earlier than under SDs (Figure II-4). The flowering responses of calibrachoa and dahlia were inconsistent in houses 10E and 13B. Verbena flowered earlier under the INC lamps and LEDs than under SDs, but flowering was most rapid under the INC lamps in house 10E. The trends for days to VB were similar to those of days to flower (Table II-2). Except for dahlia and 'WPC' petunia, plant height at flowering was similar under the INC lamps and LEDs. The stem with the first flower of 'WPC' petunia was approximately 5 cm longer under the LEDs than under the INC lamps. Except for dianthus and 'EWBS' petunia in house 10E, VB number at flowering was similar under the INC lamps and LEDs.

Operating costs

The initial fixture and bulb costs per square foot were $0.06, $0.46, and $0.41 for 150-W INC, 250-W HPS, and the 14-W R+W+FR LED lamps, respectively (Table II-3). The electricity used per square foot per week was highest for INC lamps, followed by HPS lamps and the R+W+FR LED lamps. Considering electricity and bulb costs, bulb lifetime, energy consumption, and lamp spacing, the total operating costs per greenhouse per week were estimated to be $19.41, $9.19, and $3.76 for INC, HPS, and the R+W+FR LED lamps, respectively.

Discussion

In most cases, flowering time of the bedding plants tested was similar under NI lighting provided by INC or HPS lamps and the R+W+FR LEDs. The exceptions included verbena at C. Raker & Sons (delayed under the LEDs compared with HPS lamps), snapdragon at Krueger-Maddux Greenhouses (delayed under the LEDs compared with INC lamps), calibrachoa, 'EWBS' petunia and verbena at Kube Pak (delayed under INC lamps compared with the LEDs), and calibrachoa and verbena in house 10E at MSU (delayed under the LEDs compared with INC lamps). At MSU, stem length and VB number at flowering were generally similar under the NI lighting treatments. Therefore, we conclude that in most instances, the R+W+FR LEDs are as effective as lamps traditionally used in greenhouses, such as INC and HPS, when delivered as 4-h NI lighting.

Night-interruption lighting promotes flowering of LDPs when the natural days are short (Devlin, 2008). Generally, 4 h of NI lighting is effective for most LDPs. For example, more than 80% of the LDPs that received 4-h NI lighting treatments from INC or HPS lamps formed VB within 16 weeks, whereas most LDPs remained vegetative under a 9-h SD (Blanchard and Runkle, 2010). In the trials performed at MSU, the NI lighting treatments promoted flowering of

most LDPs compared with the 9-h SD treatment. The promoting effects of NI lighting treatments at CfAHR were somewhat less compared with that of the natural SD treatment. The natural daylength from sunrise to sunset at CfAHR increased from 10 h 37 m on 2 Feb. 2013 to 12 h 38 m on 4 Apr. 2013. Therefore, compared with the 9-h SD at MSU, plants at CfAHR were exposed to a longer natural photoperiod, which could have been sufficient to promote flowering of some crops. However, NI lighting accelerated flowering of calibrachoa, 'WPC' petunia, and snapdragon at CfAHR compared with the SD treatment, indicating these crops have a longer photoperiod for flowering than the other crops. The same strong photoperiodic responses of these crops occurred at MSU.

Phytochrome is primarily an R and FR light-absorbing photoreceptor that regulates flowering of LDPs. The radiation distribution determines the amounts of induced R-absorbing (P_R) and FR-absorbing (P_{FR}) forms of phytochrome in photoperiodic plants, resulting in a steady-state phytochrome photoquilibrium (defined as P_{FR}/P_{R+FR}) (Sager et al., 1988). Night-interruption lighting provided by R and FR FL lamps with an R:FR of 0.5 or 1.0 was most effective at promoting flowering of the LDP lisianthus (*Eustoma grandiflorum*; Yamada et al., 2009). Similarly, day-extension lighting provided by a mixture of R and FR LEDs with an R:FR between 0.23 and 0.71 promoted flowering of the LDP baby's breath (*Gypsophila paniculata*; Nishidate et al., 2012). Another study demonstrated that NI lighting provided by experimental LED fixtures with an estimated P_{FR}/P_{R+FR} of 0.63 (R:FR = 0.66) or 0.72 (R:FR = 1.07) most effectively promoted flowering of LDPs (Craig and Runkle, 2012). The flowering responses under these LEDs were also similar to those under the INC lamps with a P_{FR}/P_{R+FR} of 0.64 (R:FR = 0.59), indicating LEDs that emit an intermediate P_{FR}/P_{R+FR} are a feasible replacement for INC lamps. In this study, the P_{FR}/P_{R+FR} of the INC lamps and R+W+FR LEDs was 0.64 (R:FR = 0.56)

and 0.67 (R:FR = 0.82), respectively. Therefore, the similar proportions of the active form of phytochrome, P_{FR}, could account for similar flowering responses under these two NI lighting treatments.

Standard HPS lamps with a considerably higher R:FR (>4.0; P_{FR}/P_{R+FR} >0.8) could be less effective at promoting flowering of some LDPs than lamps with a lower R:FR (Blanchard and Runkle, 2009, 2010; Runkle and Heins, 2001). For example, coreopsis (*Coreopsis grandiflora*) and rudbeckia (*Rudbeckia hirta*) flowered 8 to 31 d earlier under 4-h NI lighting provided by INC lamps than rotating HPS lamps (Blanchard and Runkle, 2010). At Henry Mast Greenhouse, only 8% of snapdragon plants under the HPS lamps had flowered before the trial ended, whereas all plants had flowered under the LEDs. However, at C. Raker & Sons, verbena under the HPS lamps flowered earlier than plants under the LEDs. The earlier flowering of verbena could be attributed to a higher ADT (by 3.9 °F) under the HPS lamps (Table II-1). Similarly, the earlier flowering at CfAHR compared with that at the other sites could at least partially be explained by the higher ADT at CfAHR. A previous study showed that flowering time of 15 ornamental annual crops was shortened as the ADT increased (Vaid and Runkle, 2013). With the linear equation correlating the ADT and the flowering rate of petunia in this study, differences in flowering time of 'EWBS' petunia and snapdragon among our trial sites can be explained. Specifically, the models predict that 'EWBS' petunia and snapdragon under the LEDs would flower 7 and 9 d earlier, respectively, at CfAHR than at C. Raker & Sons, and the actual flowering time was accelerated by 10 and 13 d, respectively. The slight discrepancies between the estimated and actual flowering time could be from different genetics of cultivars, seedling maturity at transplant time, photoperiod, and DLI.

An increase in the DLI can also accelerate flowering (Currey and Erwin, 2011; Oh et al., 2009). For example, days to flower decreased for 'Apple Blossom' petunia, salvia (*Salvia coccinea*), and 'Dreamland Rose' zinnia as the DLI increased 12 to 19 $mol \cdot m^{-2} \cdot d^{-1}$ (Faust et al., 2005). Similarly, flowering time of 'Pocket Rose' snapdragon grown at 20 °C was shortened by 13 d when the DLI increased from 10.5 to 17.5 $mol \cdot m^{-2} \cdot d^{-1}$ (Warner and Erwin, 2005). Therefore, at C. Raker & Sons, a higher DLI (by 5.3 $mol \cdot m^{-2} \cdot d^{-1}$) could also account for the earlier flowering of verbena under the HPS lamps than under the LEDs. Average days to flower for all crops under the LEDs at C. Raker & Sons, Henry Mast Greenhouse, and Krueger-Maddux Greenhouses was 29%, 36%, and 53% longer, respectively, than at CfAHR. The DLI in California is typically higher than that in the other trial sites (Korczynski et al., 2002) and, in our trial, was greater than at the other sites. Therefore, the earlier flowering at CfAHR could at least partly be attributed to a higher DLI. The ADT and DLI can also interact to influence flowering time of various ornamental crops. According to a nonlinear ADT and DLI model developed to predict flowering time of 'Dreams Neon Rose' petunia grown under long days (Blanchard et al., 2011), this crop would flower 6 d earlier under the LEDs with the actual ADT and DLI at CfAHR than at C. Raker & Sons. In our trial, 'EWBS' and 'WPC' petunia flowered 10 and 16 d earlier, respectively, under the LEDs at CfAHR than at C. Raker & Sons, confirming that a high ADT and DLI can together accelerate flowering.

Delayed flowering under the CFL lamps at Kube Pak is in agreement with a previous report (Runkle et al., 2012) that 'WPC' petunia flowered 2 to 3 weeks later under 4-h NI lighting provided by CFL lamps than INC lamps, which indicates that a complete replacement of INC lamps with CFL lamps can delay flowering of some LDPs. The R:FR of CFL lamps, which emit little FR light, is higher than that of INC lamps (B. Bugbee, unpublished data; Padhye and

Runkle, 2009; Runkle et al., 2012). Night-interruption lighting with a high R:FR was less effective at promoting flowering of LDPs such as petunia, snapdragon, lisianthus, and viola compared with a moderate R:FR (Craig and Runkle, 2012; Kim et al., 2002; Runkle and Heins, 2001; Sato et al., 2009; Yamada et al., 2009). Therefore, CFL lamps or LEDs with little or no FR light are generally not as effective at controlling flowering of some LDPs.

Given the comparable effectiveness of the R+W+FR LEDs and conventional light sources, factors such as energy availability and cost, lighting use per year, lamp cost and longevity, and availability of energy rebates from utility companies are among the factors that should be considered when choosing a light source for photoperiodic lighting. The R+W+FR LEDs consume only 14 W per lamp, making them more efficient than most conventional lamp types. The useful lifetime of these LEDs at 77 °F and 90% intensity is at least 20,000 h (Philips, 2014), whereas that of INC bulbs is usually approximately 1,000 h (Lim et al., 2012). The greater energy efficiency and much longer lifetime should be weighed against the higher purchase price of the LEDs. For example, to provide similar photoperiodic lighting in a greenhouse, the total operating cost for the R+W+FR LEDs was calculated to be lower than that for INC and HPS lamps when various factors, such as initial purchase prices and bulb lifetime, were considered. Potential adopters of these LEDs for photoperiodic lighting should perform a similar economic analysis considering their specific lighting needs and costs. Given our research findings, the efficacy of these LEDs on flowering should not be a factor.

APPENDIX

Table II-1. Trial period, lamp type, lamp power, number of lamps per treatment, average daily temperature (ADT), and daily light integral (DLI) at different trial sites, including C. Raker & Sons, the Center for Applied Horticultural Research (CfAHR), Henry Mast Greenhouse, Krueger-Maddux Greenhouses, Kube Pak, and two separate greenhouses at Michigan State University (MSU), in a coordinated trial. Plants were grown under short days with or without 4-h night-interruption lighting from high-pressure sodium (HPS), incandescent (INC), compact fluorescent (CFL), or red+white+far-red light-emitting diode (LED) lamps. The short-day (SD) treatment at CfAHR was a natural day, whereas that at MSU was truncated to 9 h. –, No data.

Trial site	Trial period (2013)	Lamp type	Lamp power (W)	No. of lamps per treatment	Photoperiod[z] (h)	ADT (°F)	DLI ($mol \cdot m^{-2} \cdot d^{-1}$)
C. Raker & Sons	1 Feb.–10 Apr.	HPS	400	2	10.02–13.12	68.0	17.4
		LED	14	8		64.1	12.1
CfAHR	2 Feb.–4 Apr.	SD	–	–	10.62–12.63	70.6	20.5
		INC	150	2		71.1	20.8
		LED	14	2		70.8	19.4
Henry Mast Greenhouse	1 Feb.–8 Apr.	HPS	400	1	9.95–13.03		
		LED	14	6		63.1	8.9
Krueger-Maddux Greenhouses	28 Jan.–20 Apr.	INC	100	5	10.08–13.42		
		LED	14	6		62.0	13.3
Kube Pak	18 Feb.–4 Apr.	CFL	15	3	10.82–12.78		
		INC	150	3			
		LED	14	6		65.7	9.0
MSU house 10E	5 Feb.–24 June	SD	–	–	9.00	69.3	–
		INC	60	2		67.1	–
		LED	14	2		67.3	–
MSU house 13B	5 Feb.–24 June	SD	–	–	9.00	69.1	11.3
		INC	60	2		69.3	11.3
		LED	14	2		69.1	11.3

[z]The photoperiod was from sunrise to sunset at each trial site except at MSU, which was truncated with black cloth.

Table II-2. Flowering characteristics of eight bedding plant crops grown in two separate greenhouses (houses 10E and 13B) at Michigan State University in a coordinated trial. Plants were grown under a 9-h short day (SD) or an SD with 4-h night-interruption (NI) lighting from incandescent (INC) or red+white+far-red light-emitting diode (LED) lamps. 'EWBS', 'Easy Wave Burgundy Star'. 'WPC', 'Wave Purple Classic'. VB, visible bud. −, No data.

Photoperiod	Days to VB		Days to flower		Stem length (cm)		VB number	
treatment	10E	13B	10E	13B	10E	13B	10E	13B
				Ageratum				
SD	27 a[z]		52 a[z]		9.7 b	11.2 a	13.8 a[z]	
INC NI	22 b		40 b		12.4 a	9.9 a	14.8 a	
LED NI	21 b		41 b		12.0 a	11.1 a	15.0 a	
Treatment	***		***		*	NS	NS	
House	NS		NS		NS		*	
Treatment×house	NS		NS		*		NS	
				Calibrachoa				
SD	–	–	–	–	–		–	
INC NI	27 b	28 a	34 b	35 a	10.2 a[z]		3.5 a[z]	
LED NI	37 a	28 a	46 a	35 a	10.8 a		4.3 a	
Treatment	*	NS	*	NS	NS		NS	
House	NS		*		NS		*	
Treatment×house	*		*		NS		NS	
				Dahlia				
SD	23 a	17 b	41 a	30 b	13.5 c[z]		3.1 b[z]	
INC NI	22 a	21 a	37 b	35 a	20.2 a		8.0 a	
LED NI	23 a	22 a	37 b	35 a	18.9 b		8.0 a	
Treatment	NS	***	*	***	***		***	
House	***		***		*		***	
Treatment×house	***		***		***		***	
				Dianthus				
SD	46 a[z]		63 a[z]		5.5 b[z]		1.1 c	5.0 a
INC NI	38 b		53 b		6.9 a		6.1 a	6.6 a
LED NI	38 b		53 b		6.5 a		3.8 b	6.6 a
Treatment	***		***		***		***	NS
House	***		***		*		***	
Treatment×house	*		***		NS		*	
				'EWBS' petunia				
SD	59 a[z]		73 a[z]		22.0 a	18.4 a	14.1 b	10.9 b
INC NI	38 b		49 b		14.4 b	16.9 ab	19.8 a	16.3 a
LED NI	35 b		49 b		13.2 b	15.4 b	14.3 b	16.0 a
Treatment	***		***		***	*	*	*
House	***		***		NS		NS	
Treatment×house	***		***		***		*	
				'WPC' petunia				
SD	109 a[z]		116 a[z]		43.9 a[z]		11.5 a[z]	
INC NI	45 b		54 b		22.2 c		7.5 ab	
LED NI	45 b		54 b		27.3 b		7.0 b	

Table II-2 (cont'd)

Photoperiod treatment	Days to VB 10E	Days to VB 13B	Days to flower 10E	Days to flower 13B	Stem length (cm) 10E	Stem length (cm) 13B	VB number 10E	VB number 13B
Treatment	***		***		***		*	
House	*		*		*		*	
Treatment×house	NS		NS		NS		NS	
			Snapdragon					
SD	48 a[z]		71 a[z]		24.7 a[z]		19.1 a[z]	
INC NI	31 b		53 b		25.1 a		15.1 b	
LED NI	30 b		52 b		24.0 a		14.8 b	
Treatment	***		***		NS		***	
House	***		***		NS		*	
Treatment×house	NS		*		NS		NS	
			Verbena					
SD	29 a	26 a	58 a	43 a	10.7 b[z]		13.0 a[z]	
INC NI	22 b	21 b	40 c	36 b	15.3 a		6.1 b	
LED NI	26 a	21 b	44 b	38 b	15.0 a		6.3 b	
Treatment	***	***	***	***	***		***	
House	*		***		*		NS	
Treatment×house	*		***		NS		***	

NS, nonsignificant; *, ***, significant at $P \leq 0.05$ or 0.001, respectively. Means within columns followed by different letters are significantly different by Tukey's honest significant difference test at $P \leq 0.05$. [z], data pooled for analysis.

Table II-3. Estimation of initial investment and operating costs (in U.S. dollars) using incandescent (INC), high-pressure sodium (HPS), or red+white+far-red light-emitting diode (LED) lamps for 4-h night-interruption lighting in a 4,320-square-foot (30×144 feet) greenhouse with 7-foot clearance above the growing surface. Data for INC and HPS lamps are adapted from Fisher and Both (2004).

	INC (150 W)	HPS (250 W)	LED (14 W)
Number of fixtures per greenhouse	39	10	39
Area per fixture (square feet)	111	432	111
Fixture cost	$5.31	$168	$5.31
Bulb cost	$1.77	$32	$40
Bulb lifetime (h)	750	12,000	20,000
Initial fixture and bulb cost per square foot	$0.06	$0.46	$0.41
Electricity costs (including ballast)			
Electricity used per square foot per week (kWh)	0.0379	0.0190	0.0035
Electrical cost per square foot per week (at $0.1029/kWh)	$0.0039	$0.0020	$0.0004
Bulb costs			
Time operated per week (h)	28	28	28
Bulb life (wk.)	27	429	714
Bulb cost per square foot per week	$0.0006	$0.0002	$0.0005
Bulb cost per greenhouse per week	$2.56	$0.75	$2.18
Total operating cost			
Total operating cost per square foot per week	$0.0045	$0.0021	$0.0009
Total operating cost per greenhouse per week	$19.41	$9.19	$3.76

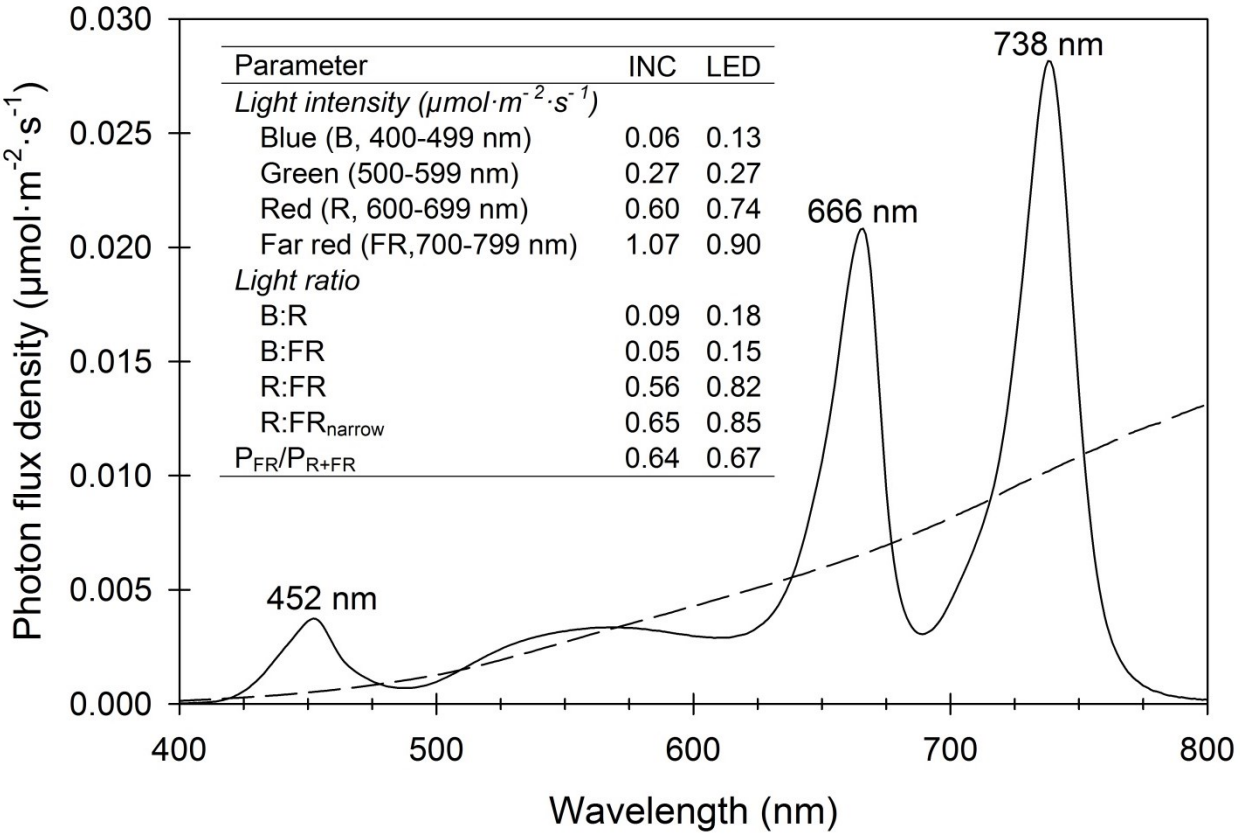

Figure II-1. Spectral distribution between 400 nm and 800 nm, lighting characteristics, and estimated phytochrome photoequilibria (P_{FR}/P_{R+FR}; Sager et al., 1988) of incandescent (INC, dashed line) and red+white+far-red light-emitting diode (LED, solid line) lamps used in a coordinated trial. The $R:FR_{narrow}$ was calculated as 655 to 665 nm:725 to 735 nm.

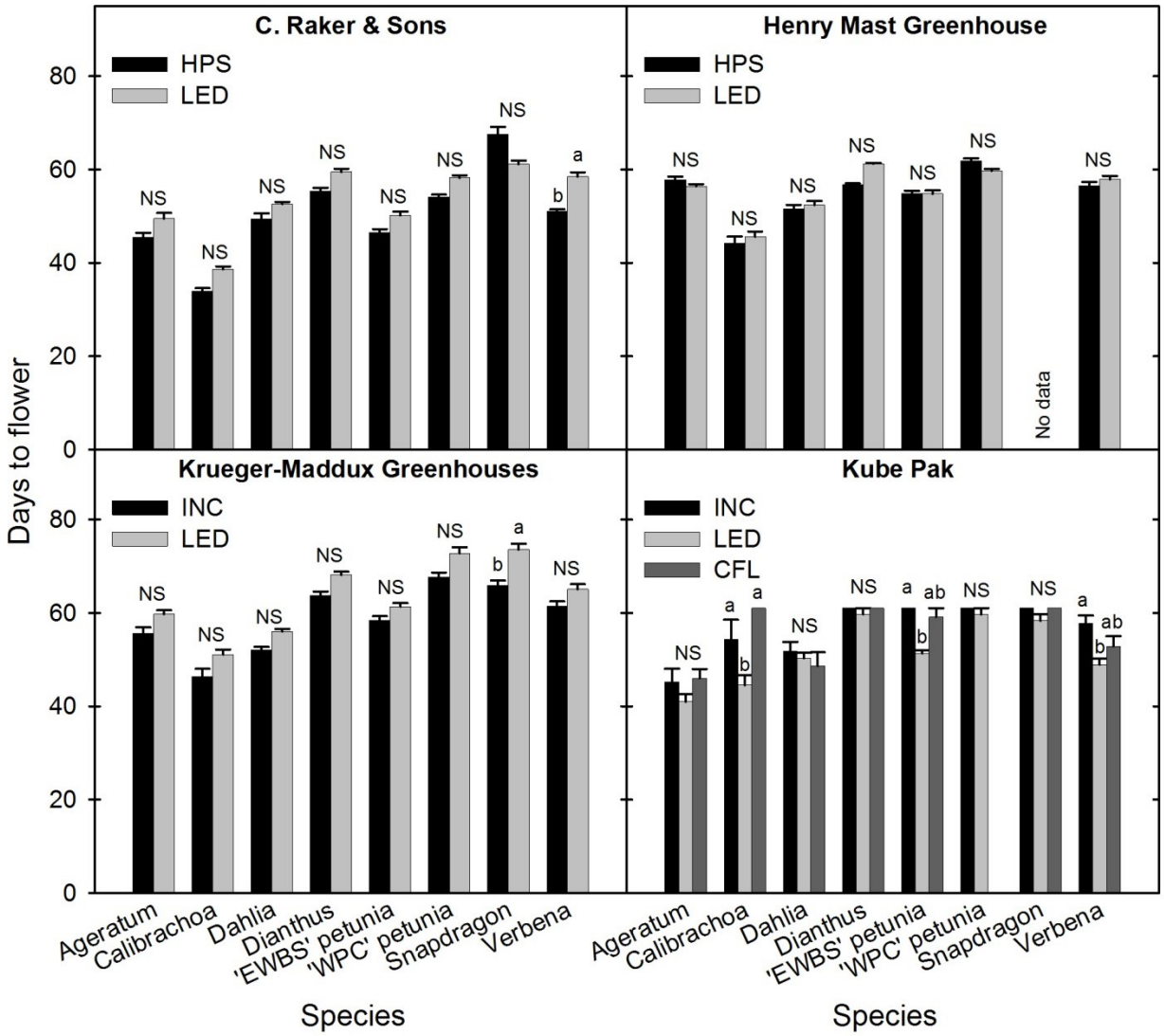

Figure II-2. Days to flower for eight bedding plant crops grown at four commercial greenhouses in a coordinated trial. Plants were grown under short days with 4-h night-interruption lighting from high-pressure sodium (HPS), incandescent (INC), compact fluorescent (CFL), or red+white+far-red light-emitting diode (LED) lamps. Values followed by different letters within species are significantly different by Tukey's honest significant difference test at $P \leq 0.05$; NS, nonsignificant. Error bars indicate standard errors. 'EWBS', 'Easy Wave Burgundy Star'. 'WPC', 'Wave Purple Classic'.

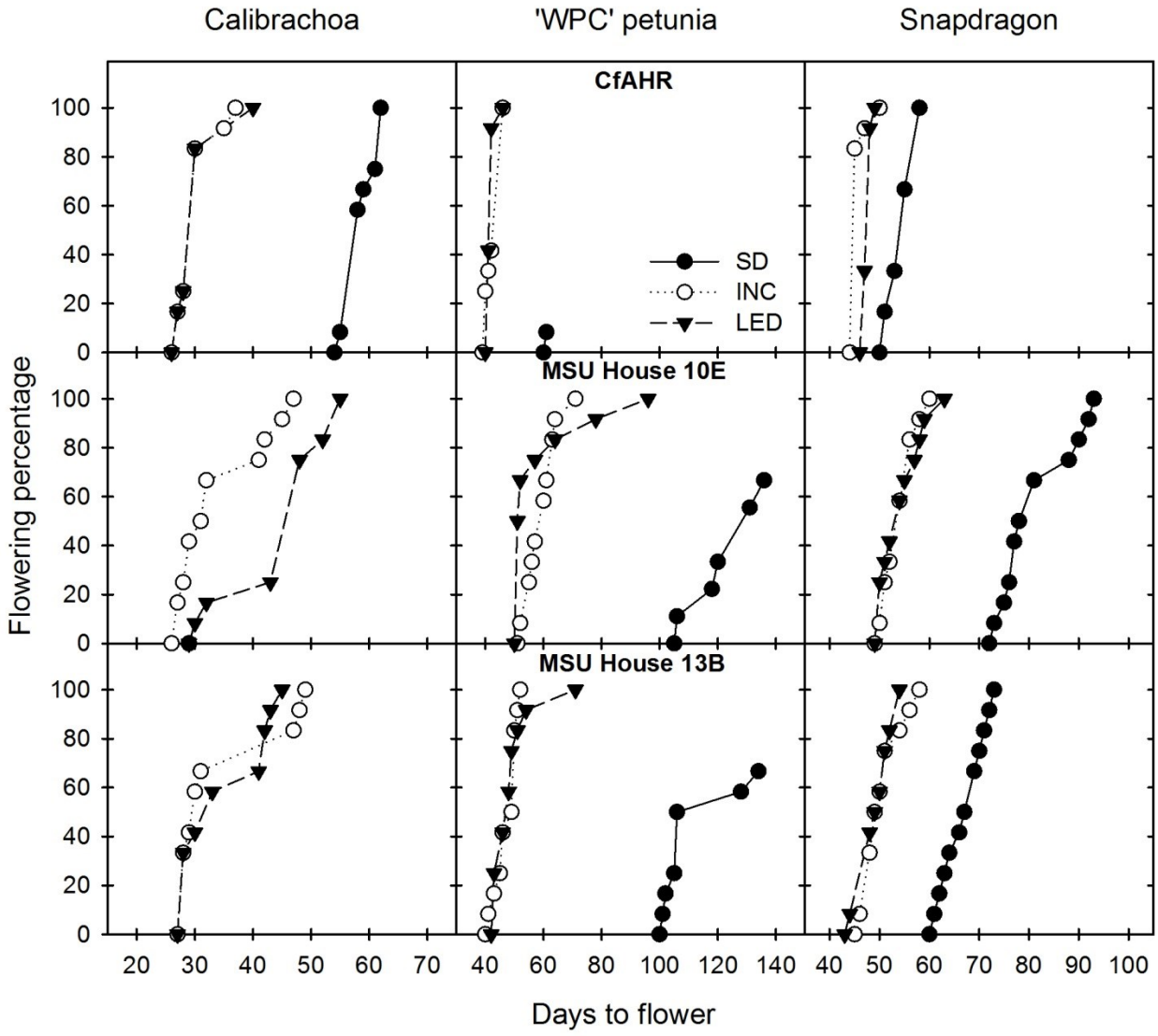

Figure II-3. Flowering percentage of 'Callie Deep Yellow' calibrachoa, 'Wave Purple Classic' ('WPC') petunia, and 'Liberty Classic Yellow' snapdragon at the Center for Applied Horticultural Research (CfAHR) and two separate greenhouses (houses 10E and 13B) at Michigan State University (MSU) in a coordinated trial. Plants were grown under a short-day (SD) treatment with or without 4-h night-interruption lighting from incandescent (INC) or red+white+far-red light-emitting diode (LED) lamps. The SD treatment at CfAHR had a natural photoperiod, whereas the photoperiod at MSU was truncated to 9 h.

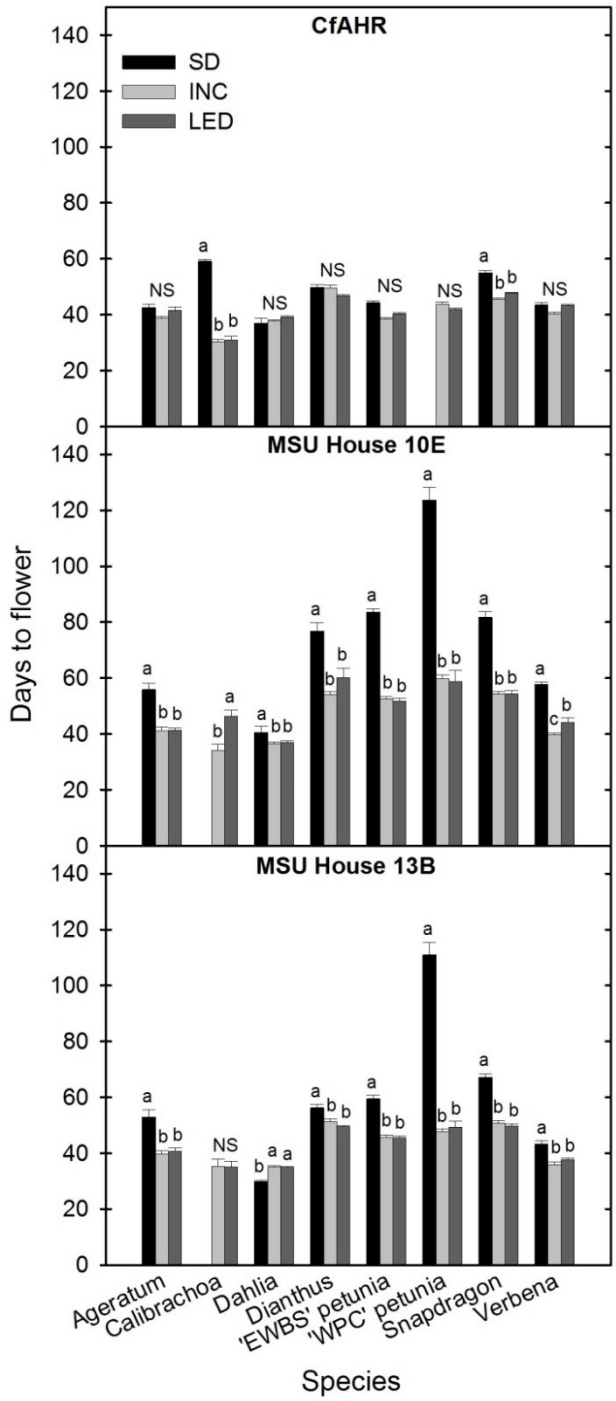

Figure II-4. Days to flower of eight bedding plant crops grown at the Center for Applied Horticultural Research (CfAHR) and two separate greenhouses (houses 10E and 13B) at Michigan State University (MSU) in a coordinated trial. Plants were grown under a short-day (SD) treatment with or without a 4-h night interruption from incandescent (INC) or red+white+far-red light-emitting diode (LED) lamps. The SD treatment at CfAHR had a natural photoperiod, whereas the photoperiod at MSU was truncated to 9 h. Values followed by different letters within species are significantly different by Tukey's honest significant difference test at $P \leq 0.05$; NS, nonsignificant. 'EWBS', 'Easy Wave Burgundy Star'. 'WPC', 'Wave Purple Classic'.

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SECTION III

LOW-INTENSITY BLUE LIGHT IN NIGHT-INTERRUPTION LIGHTING DOES NOT INFLUENCE FLOWERING OF ORNAMENTAL CROPS

Low-intensity Blue Light in Night-interruption Lighting does not Influence Flowering of Ornamental Crops

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Additional index words. Far-red light, LEDs, light-emitting diodes, red light, white light

Abstract.

The spectral quality of photoperiodic lighting can affect flowering of short-day plants (SDPs) and long-day plants (LDPs) differently. When delivered during the middle of the night (night interruption, NI), red (R; 600 to 700 nm) light alone can inhibit flowering of SDPs, whereas a combination of R and far-red (FR; 700 to 800 nm) light promotes flowering of some LDPs. However, the influence of low-intensity (≈1–2 $\mu mol \cdot m^{-2} \cdot s^{-1}$) blue (B; 400 to 500 nm) light, in addition to R and/or FR light, on regulating flowering, if any, has not been established. We investigated the effects of mixed B, R, and FR light on flowering of five SDPs: chrysanthemum (*Dendranthema* × *grandiflorum*), cosmos (*Cosmos sulfureus*), two cultivars of dahlia (*Dahlia pinnata*), and marigold (*Tagetes erecta*), and four LDPs: dianthus (*Dianthus chinensis*), two cultivars of petunia (*Petunia* ×*hybrida*), and rudbeckia (*Rudbeckia hirta*). Plants were grown in a greenhouse at constant 20 °C, receiving a truncated 9-hour short day (SD) with or without 4-hour NI lighting from incandescent (INC) lamps or white, B, B+R, B+FR, B+R+FR, or R+FR light-emitting diodes (LEDs). Each lighting treatment delivered a photon flux of 1.5 $\mu mol \cdot m^{-2} \cdot s^{-1}$ between 400 and 800 nm at plant height. Blue light alone was not perceived as a long day by all SDPs and LDPs tested. For all SDPs, white LEDs inhibited flowering most effectively. The B+R NI was as effective as the white NI at creating a long day for all SDPs except chrysanthemum. The B+FR NI inhibited flowering of marigold and dahlia 'Leanne', but not chrysanthemum or dahlia 'Gallery Pablo'. For marigold, the B+FR NI was less effective than other lighting treatments with R light. The B+R+FR and R+FR NI similarly delayed flowering of all SDPs except dahlia 'Gallery Pablo'. For all LDPs, an NI with R and FR light were most effective at promoting flowering. For example, flowering of petunia 'Wave Purple Classic' was

delayed under the W, B+R, and B+FR NI compared with the INC, B+R+FR and R+FR NI, and flowering responses under B+FR NI were variable. In contrast, the B+R and B+FR NI were as effective as the INC NI for petunia 'Wave Purple Improved'. We conclude that in at least the crops studied, low-intensity B light does not influence flowering. In addition, white LEDs that emit little FR light are effective at creating long days for SDPs but only for some LDPs.

Introduction

Flowering is influenced by various internal and external factors, including developmental competence, circadian rhythms, photoperiod, and vernalization (Hayama et al., 2007; Lee and Amasino, 1995; Thomas and Vince-Prue, 1997). Many different responses, such as flowering, dormancy, and tuberization, are controlled by photoperiod in a wide range of plants (Jackson, 2009). Seasonal changes in daylength can be sensed by plants to regulate the flowering process. With respect to flower initiation in response to daylength, most plants can be categorized into short-day (SDPs), long-day (LDPs), and day-neutral plants (Thomas and Vince-Prue, 1997). Flowering of SDPs and LDPs is induced when the skotoperiod is longer or shorter than some critical duration, respectively. When the natural daylength is short, artificial lighting delivered during the middle of the night (night interruption, NI) can inhibit flowering of SDPs and promote flowering of LDPs. Night-interruption light intensity of 1 to 2 $\mu mol \cdot m^{-2} \cdot s^{-1}$ from broad-spectrum conventional light sources is typically sufficient to regulate flowering (Whitman et al., 1998).

Phytochrome, a primarily red (R; 600 to 700 nm) and far-red (FR; 700 to 800 nm) light-absorbing photoreceptor, and cryptochrome, a primarily blue (B; 400 to 500 nm) and ultraviolet-A light-absorbing photoreceptor, are involved in regulation of flowering, and their functions are mediated by *CONSTANS* (*CO*), a transcription factor (Guo et al., 1998). In *Arabidopsis*, the

expression of the *CO* gene oscillates in a circadian rhythm and must coincide with irradiance. Under inductive photoperiodic conditions, the CO protein induces the expression of a signal, *FLOWERING LOCUS T* (*FT*) protein, which is produced in leaves and serves as a long-distance stimulus to induce flowering at the apical meristem (Corbesier et al., 2007; Imaizumi and Kay, 2006). Depending on species, multiple phytochromes (phyA, phyB, phyC, phyD, and phyE) and cryptochromes (cry1 and cry2) can exist (Clack et al., 1994; Sharrock and Quail, 1989). In at least some species of the Brassicaceae, phytochromes and cryptochromes can interact and overlap in function (Cashmore et al., 1999). The R/FR reversibility refers to the paradigm that phytochrome-mediated responses, such as flowering and seed germination, can be at least partially reversed by converting phytochromes between their inactive R light-absorbing form, P_R, and active FR light-absorbing form, P_{FR}. Irradiance and the R to FR light ratio (R:FR) elicit formation of P_R and P_{FR}, the proportions of which determine an estimated phytochrome photoequilibrium (P_{FR}/P_{R+FR}) (Sager et al., 1988).

The effectiveness of spectral wavebands in NI lighting to control flowering is somewhat different for SDPs and LDPs. In SDPs, R light is the most effective waveband to inhibit flowering (Thomas and Vince-Prue, 1997). The effect can be at least somewhat reversed by subsequent exposure to FR light, indicating involvement of phytochromes. A particular intensity threshold is required for specific wavelengths to interrupt the night effectively. For example, monochromatic light of 450, 550, 650, or 750 nm all inhibited flowering of the SDP duckweed (*Lemna paucicostata*), but the light intensity required for 50% flowering inhibition was 10, 0.5, 0.1, and 3 $\mu mol \cdot m^{-2} \cdot s^{-1}$, respectively (Saji et al., 1982). In some LDPs such as *Arabidopsis*, R light was effective at promoting flowering, but B and FR light were both more effective than R light at a similar intensity of 0.8 to 1.0 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Goto et al., 1991). However, B light at 3.3

μmol·m^{-2}·s^{-1} and FR light at 1.3 to 1.6 μmol·m^{-2}·s^{-1} were not perceived as a long day for a variety of photoperiodic ornamental crops (Craig, 2012; Craig and Runkle; 2012). Therefore, the efficacy of one or more wavebands of light at regulating flowering varies among species. Different combinations of wavebands can be more effective than monochromatic light. For example, a mixture of R and FR light was more effective at promoting flowering of LDPs than either alone (Craig and Runkle, 2012; Thomas and Vince-Prue, 1997).

Light-emitting diodes (LEDs) emitting similar intensities of R and FR light effectively regulated flowering of both SDPs and LDPs (Craig and Runkle, 2012; 2013). However, the effects of additional B light to R and/or FR light in NI lighting have been inconclusive. For example, flowering was earlier in chrysanthemum (*Dendranthema* × *grandiflorum*) 'Huang-Hsiu-Feng' and later in chrysanthemum 'Lung-Feng-Tzu' under a B+R (B:R = 1:3) NI than an R NI (Ho et al., 2012a). Moreover, a combination of B and R light (B:R = 1:1) promoted flowering of the LDP cyclamen (*Cyclamen persicum*) more effectively than B, R, or FR light alone (Shin et al., 2010). However, the B+R (B:R = 1:1) NI and the R NI were similarly effective at inhibiting flowering of chrysanthemum (Ho et al., 2012b). The objective of this study was to investigate the effects of NI lighting from different combinations of B, R, and/or FR light provided by LEDs on flowering characteristics of a range of daylength-sensitive ornamental crops. We postulated that low-intensity B light would have no positive or negative effect on flowering when added to R and FR light for NI lighting. In addition, we anticipated that W LED lamps would be less effective than INC lamps for some crops, since W LED lamps emit little FR light.

Materials and Methods

Plant material

The experiment was performed twice in time with the same growing practices and similar greenhouse environmental conditions. The experiment was first performed from 25 Jan. to 25 May 2013, and was replicated from 9 Apr. to 14 Oct. 2013. The plant species examined included five SDPs: chrysanthemum 'Golden Cheryl', cosmos (*Cosmos sulfureus*) 'Cosmic Yellow', dahlia (*Dahlia pinnata*) 'Leanne' and 'Gallery Pablo', and marigold (*Tagetes erecta*) 'American Antigua Yellow', and four LDPs: dianthus (*Dianthus chinensis*) 'Super Parfait Raspberry', petunia (*Petunia ×hybrida*) 'Wave Purple Classic' (WPC) and 'Wave Purple Improved' (WPI), and rudbeckia (*Rudbeckia hirta*) 'Indian Summer'. Rooted cuttings of dahlia 'Leanne' and 'Gallery Pablo' were received from a commercial grower (Bosgraaf Greenhouses, Inc., Hudsonville, MI) on 15 Jan. 2013 and 8 Apr. 2013. Plugs of all the other young plants, grown from either seeds or cuttings by a commercial young-plant producer (C. Raker & Sons, Inc., Litchfield, MI), were received on 15 Jan. 2013 for the first replication, within one week of seed sow, or after liners were rooted. For the second replication, most young plants were received on 25 Apr. 2013, whereas rooted cuttings of chrysanthemum and seedlings of petunia WPC were received on 10 May 2013. To avoid flower induction, all SDPs were grown under a 16-h photoperiod [consisting of natural days supplemented with light from high-pressure sodium (HPS) lamps] and all LDPs were grown under a truncated 9-h short-day (SD) photoperiod at constant 20 °C in a research greenhouse until the start of treatments. Once the plants were ready for transplant, ten randomly selected plants per treatment and cultivar were potted using a commercial peat-perlite medium (Suremix; Michigan Grower Products, Inc., Galesburg, MI) and transferred to different treatments in another research greenhouse maintained at constant 20 °C. Chrysanthemum, cosmos, dahlia 'Leanne' and 'Gallery Pablo', and marigold were transplanted on 7 Feb., 24 Jan., 24 Jan., 24 Jan., and 24 Jan. 2013, respectively, for the first replication, and

on 10 May, 2 May, 9 Apr., 9 Apr., and 2 May 2013, respectively, for the second replication. Dianthus, petunia WPC and WPI, and rudbeckia were transplanted on 6 Feb., 7 Feb., 7 Feb., and 7 Feb. 2013, respectively, for the first replication, and on 2 May, 20 May, 2 May, and 8 May 2013, respectively, for the second replication.

Lighting treatments

A truncated 9-h natural SD photoperiod was achieved by closing opaque black cloth at 1700 HR and opening it at 0800 HR for all treatments. In addition to a 9-h SD control, 4-h NI lighting treatments were delivered from 2230 HR to 0230 HR by INC lamps (60 W; Philips, Amsterdam, Netherlands) or white (10.5 W, peak wavelength = 606 nm; model 9290002204, Philips Lighting, Somerset, NJ), B (18 W, peak wavelength = 462 nm; model 121109-125040-7779, LEDwholesalers, Hayward, CA), B+R (peak wavelength = 659 nm), B+FR (peak wavelength = 737 nm), B+R+FR, or R+FR LEDs. Red and FR light were delivered by customized LED fixtures containing three R and/or FR LEDs per fixture (5 W; CCS, Inc., Kyoto, Japan). Photon flux at plant height was averaged from measurements using a portable spectroradiometer (PS200, StellarNet, Inc., Tampa, FL) at four different locations within the treatment area and was adjusted to 1.3 to 1.7 $\mu mol \cdot m^{-2} \cdot s^{-1}$ between 400 and 800 nm for all NI lighting treatments by lamp positioning and use of aluminum mesh. Spectral distribution characteristics of NI lighting treatments were provided in Table III-1 and Figure III-1. Plants were placed on the bench area only where light intensity at plant height was between 1 and 3 $\mu mol \cdot m^{-2} \cdot s^{-1}$. The NI lighting treatments using multiple combinations of LEDs delivered equal intensities of different colors. For each NI lighting treatment, the R:FR was calculated using 10-nm and 100-nm wavebands, and the phytochrome photoequilibrium was estimated using the spectra in Figure III-1, as described by Sager et al. (1988).

Greenhouse environment

The experiment was conducted in a glass-glazed greenhouse at Michigan State University (East Lansing, MI) maintained at a constant air temperature of 20 °C as controlled by a greenhouse environmental control system (Integro 725; Priva North America, Vineland, Ontario, Canada). Roof and side vents, cellulose evaporative-cooling pads, and exhaust fans in the greenhouse were used for cooling and ventilation when needed. An aspirated thermocouple [36-gauge (0.127-mm diameter) type E] located in the middle of each bench measured air temperature at plant height every 10 s, and a data logger (CR10; Campbell Scientific, Logan, UT) recorded hourly averages. The data logger controlled a 1500-W electric heater underneath each bench to automatically switch on to provide supplemental heat when the nighttime air temperature at plant height was <18.9 °C. The average daily air temperature of each treatment during the two replications of the experiment is provided in Table III-2.

Supplemental lighting provided by 400-W HPS lamps (PL2000; P.L. Light Systems Inc., Beamsville, ON, Canada) was delivered from 0800 to 1700 HR at a photosynthetic photon flux (*PPF*) of 60 to 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at plant height. Controlled by the environmental control computer, the HPS lamps automatically switched on when the ambient solar *PPF* was <185 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and off when it was >370 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Line quantum sensors (Apogee Instruments, Inc., Logan, UT) positioned horizontally at plant height measured *PPF* every 10 s, and the same data logger recorded hourly averages. The average daily light integral was 11.5 $mol \cdot m^{-2} \cdot d^{-1}$ and 13.3 $mol \cdot m^{-2} \cdot d^{-1}$ during the first and second replications of the experiment, respectively.

Data collection and analysis

Leaf number on the primary stem was recorded at the onset of treatments, and the most recently mature leaf was marked. Dates of first visible bud or inflorescence (VB) and first open

flower were recorded. For plants in the Asteraceae, flowering was considered to occur when the outermost row of ray flowers of an inflorescence were open. At flowering, VB number, leaf number on the stem with the first open flower, and plant height (from media surface to the apex of an inflorescence) were also recorded. For petunia, length of the stem with the first open flower was measured, and leaf number at flowering was counted. Leaf number was not recorded for chrysanthemum grown under NI lighting treatments emitting R light due to the lack of a primary stem and inconsistent branching patterns. Data were analyzed using the SAS v.9.3 (SAS Institute, Inc., Cary, NC) mixed-model (PROC MIXED) and glimmix-model (PROC GLIMMIX) procedures, and pairwise comparisons between treatments were performed using Tukey's honest significant difference test ($P = 0.05$).

Results

Short-day plants

All chrysanthemum plants flowered under all treatments (data not shown). However, compared with plants grown under the SD, all NI lighting treatments emitting R light substantially delayed VB appearance; the B and B+FR NI did not delay VB appearance (Table III-3). The B and B+FR NI had no or minimal effect on flowering time, respectively, whereas the B+R, INC, R+FR, B+R+FR, and W NI delayed flowering by 52, 64, 74, 76, and 96 d, respectively (Figure III-2). At flowering, chrysanthemum grown under the B+R+FR, R+FR, and INC NI were approximately 19 cm taller than those under the B NI and SD. Stem length was approximately 15 cm greater under the W and B+R NI than under the B NI and SD. At flowering, there were >200 VBs per plant under all NI lighting treatments except the B and B+FR NI, which had a similar VB number as chrysanthemum under the SD (26 to 32 VBs).

All cosmos plants flowered under all treatments. Plants grown under all NI lighting treatments formed the first VB and flowered similarly as those grown under the SD, indicating this cultivar is day neutral (Table III-3). Extension growth under all NI lighting treatments was similar to that under the SD, but cosmos plants grown under W, B+R, B+FR, and R+FR NI were approximately 4 cm taller than those grown under the B NI. There was no effect of photoperiod treatment on VB number or leaf number.

All dahlia 'Leanne' plants flowered under all NI lighting treatments, but flowering percentage under the SD was 100% and 20% in the first and second replications, respectively (data not shown). Compared with the SD, all NI lighting treatments except the B NI delayed VB appearance by 6 to 12 d and flowering by 7 to 13 d (Table III-3). 'Leanne' plants grown under the B+R and B+FR NI flowered 5 and 6 d later, respectively, than those grown under the B+R+FR NI. At flowering, plants were tallest under treatments emitting FR light (i.e., the INC, B+FR, B+R+FR, and R+FR NI), and those under the B NI and SD were shortest. Plants grown under all NI lighting treatments except the B NI had approximately two more VBs than those grown under the SD. The increase in leaf number of 'Leanne' at flowering showed a similar treatment response as flowering time, developing the most and fewest leaves under the B+FR NI and SD, respectively.

No dahlia 'Gallery Pablo' plants flowered under the SD, and all plants flowered under all NI lighting treatments except the B and B+FR NI (data not shown). Flowering percentage was 0% and 11% under the B NI and 11% and 67% under the B+FR NI in the first and second replication, respectively. The B+R+FR NI slightly delayed VB appearance compared to the other treatments emitting R light. 'Gallery Pablo' plants grown under the B+R+FR NI flowered 5 d later than those grown under the R+FR NI. Plants were approximately 5 cm taller under treatments

emitting R and FR light (i.e., the INC, B+R+FR, and R+FR NI) than the treatments emitting R but not FR (i.e., the W and B+R NI).

All marigold plants flowered under all treatments (data not shown). Plants flowered similarly under the B NI and SD. Compared with plants grown under the B NI and SD, the B+FR NI delayed flowering by 4 d while all the other NI lighting treatments, which all emitted R light, delayed flowering by 11 d. At flowering, plants were approximately 4 cm taller under the INC, W, B+R+FR, and R+FR NI than under the B NI and SD. There were more VBs under the B NI compared with the INC, W, B+R+FR, and R+FR NI. The increase in leaf number was 9 under the B NI and SD, 11 under the B+FR NI, and 13 under all the other NI lighting treatments, which all emitted R light.

Long-day plants

All dianthus plants flowered (data not shown), but compared with plants grown under the SD, the R+FR and B+R+FR NI accelerated flowering by 5 or 6 d, while flowering time was similar to the SD under all the other NI lighting treatments (Figure III-2). At flowering, plants were approximately 4 cm taller under the INC, W, B+FR, B+R+FR, and R+FR than under the SD (Table III-4). Plants grown under the B+R+FR and R+FR NI were approximately 4 cm taller than those grown under the B and B+R NI. Plants grown under the B+R NI and SD formed approximately four more VBs than those grown under the R+FR NI.

Petunia WPC plants did not flower under the B NI or SD, whereas all plants flowered under all the other NI lighting treatments except the B+R NI in the first replication (30% flowering) and the B+FR NI in the second replication (60% flowering). Plants flowered similarly under NI lighting treatments emitting both R and FR light (i.e., the INC, B+R+FR, and R+FR NI). Compared with plants grown under the INC NI, the W, B+R, and B+FR NI delayed

flowering by 8, 14, and 24 d, respectively. At flowering, the main stem of plants was approximately 14 cm longer under the B+FR NI than under the INC and B+R+FR NI. Plants grown under the B+FR NI had approximately eight fewer VBs than those grown under NI lighting treatments emitting R light (i.e., the INC, W, B+R, B+R+FR, and R+FR NI). The increase in leaf number showed a similar trend as that for days to flower.

All petunia WPI plants flowered under all treatments except the B NI, where flowering percentage was 70% in the second replication. Otherwise, plants flowered similarly under the B NI and SD. Compared with plants grown under the SD, all NI lighting treatments emitting R and/or FR light promoted flowering by 16 to 21 d. Compared with plants grown under the INC NI, flowering was similar under NI lighting treatments emitting R and/or FR light except the W NI. Plants flowered 4 or 5 d earlier under the B+R+FR NI than under NI lighting treatments emitting B light with either R or FR light (i.e., the W, B+R, and B+FR NI). At flowering, extension growth was greatest under the B NI and SD and similar under all the other NI lighting treatments. Plants grown under the W and B+R NI had similar VB number compared with those grown under the INC NI. Plants developed at least twice the number of leaves before flowering under the B NI and SD than the other NI lighting treatments.

All rudbeckia plants flowered and at the same time under all NI lighting treatments emitting R light. No plants flowered under the SD or NI lighting emitting B or B+FR light. Compared with plants grown under the INC NI, plant height at flowering was similar under the W and B+R NI and was approximately 10 cm greater under the B+R+FR and R+FR NI. Plants grown under the B+R NI had approximately three more VBs than those grown under the R+FR NI.

Discussion

Blue light at 0.6 to 1.6 μmol·m^{-2}·s^{-1}, alone or when added to R and/or FR light as a 4-h NI, generally did not influence flowering in the SDP or LDP studied. The integrated cumulative irradiance of B light delivered in these treatments ranged from 8,900 to 22,600 μmol·m^{-2}·d^{-1}. Recent studies also have shown that 4-h NI lighting provided by B light alone at a low intensity (1 to 3 μmol·m^{-2}·s^{-1}) did not affect flowering of several SDPs and LDPs (Craig, 2012; Ho et al., 2012a). However, other studies using light sources that emitted a greater intensity of B light for NI lighting did regulate flowering. For example, in the LDP henbane (*Hyoscyamus niger*) grown under 10-h SDs, 2-h NI lighting from B light at 13 μmol·m^{-2}·s^{-1} (cumulative irradiance of 93,600 μmol·m^{-2}·d^{-1}) promoted flowering, but 10 min at 13 μmol·m^{-2}·s^{-1} (7,800 μmol·m^{-2}·d^{-1}) or 2 h at 3 μmol·m^{-2}·s^{-1} (21,600 μmol·m^{-2}·d^{-1}) did not (El Hattab, 1968). Similarly, 2-h NI lighting provided by B LEDs at 8 to 10 μmol·m^{-2}·s^{-1} (57,600 to 72,000 μmol·m^{-2}·d^{-1}) strongly inhibited flowering of the SDP beefsteak mint (*Perilla ocymoides*) (Hamamoto et al., 2003). In addition, 4-h NI lighting provided by B LEDs at 4 μmol·m^{-2}·s^{-1} (57,600 μmol·m^{-2}·d^{-1}) promoted flowering of the LDP cyclamen (Shin et al., 2010). The threshold intensity, duration, or cumulative irradiance for an effective B-light flowering response could vary among species. For example, 10 min of B light at >10 μmol·m^{-2}·s^{-1} (>6,000 μmol·m^{-2}·d^{-1}) inhibited flowering of duckweed (Saji et al., 1982), but 2 h of B light at 13 μmol·m^{-2}·s^{-1} (93,600 μmol·m^{-2}·d^{-1}) was required to promote flowering of henbane (El Hattab, 1968).

An NI using R light is generally most effective at inhibiting flowering of SDPs (Choi, 2003; Thomas and Vince-Prue, 1997). For example, flowering was delayed as the R:FR increased from 0.66 to 147.29, reinforcing that a moderate-to-high R:FR controls flowering of SDPs (Craig and Runkle, 2013). White, FR-deficient light at 0.1 or 81 μmol·m^{-2}·s^{-1} used for 30

min as an NI was as effective as R light at 0.07 μmol·m^{-2}·s^{-1} at inhibiting flowering of the SDP minute duckweed (*Lemna perpusilla*) when the base photoperiod was 10 h (Takimoto, 1973). Flowering of chrysanthemum 'Huang-Hsiu-Feng' and 'Lung-Feng-Tzu' was also delayed under 4-h NI lighting from R light at 1.6 μmol·m^{-2}·s^{-1} or W light at 0.5 to 0.8 μmol·m^{-2}·s^{-1} (Ho et al., 2012). Similarly in our study, a W NI strongly inhibited flowering of nearly all SDPs studied, and the B+R NI was comparably effective for SDPs except chrysanthemum. Surprisingly, the B+FR NI delayed flowering of dahlia 'Leanne' and to a lesser extent, marigold. For the SDPs rice and beefsteak mint, a B or R NI, but not an FR NI, delayed flowering (Choi, 2003; Ishikawa et al., 2009). However, an FR NI inhibited flowering of chrysanthemum and Japanese morning glory (*Pharbitis nil*), suggesting a low P_{FR}/P_{R+FR} could regulate flowering (Thomas and Vince-Prue, 1997). In addition, flowering of dahlia 'Carolina Burgundy' under an FR NI was similarly delayed as under an R NI (Craig and Runkle, 2013). Therefore, since B light did not influence flowering in our study, FR light alone or B+FR light reduced the P_{FR}/P_{R+FR} to 0.12 and inhibited flowering of some SDPs such as dahlia 'Leanne' and marigold.

The B+R and B+FR NI both promoted flowering of petunia WPC and WPI, but flowering was even earlier under the B+R+FR NI. These results confirm that a mixture of R and FR light is often more effective at promoting flowering of LDPs than R or FR light alone (Thomas and Vince-Prue, 1997). Since an R:FR of 0.66 or 1.07 was generally more effective at promoting flowering of LDPs than higher or lower ratios (Craig and Runkle, 2012), the efficacy of the B+R+FR NI in our study may be explained by its effective R:FR of 1.05. Flowering time of most crops studied was similar under the B+R+FR, R+FR (R:FR = 0.98), and INC NI (R:FR = 0.61), indicating that LEDs with a moderate R:FR have the potential to replace INC lamps in flowering applications, and there is no benefit of including low-intensity B light to R and FR

light in photoperiodic lighting. However, not all LDPs require FR light for early flowering, such as rudbeckia in our study, which flowered similarly with or without FR light, and fuchsia (*Fuchsia ×hybrida*) 'Trailing Swingtime', which flowered most rapidly under an R NI, respectively (Craig, 2012).

In our study, the B+FR NI was perceived as a long day by petunia WPC and WPI, but not by rudbeckia, indicating sensitivity to B+FR light is variable among species. Similarly, petunia WPI flowered earlier under the FR NI than under the SD, but flowering of many other LDPs was not promoted under an FR NI (Craig, 2012; Craig and Runkle, 2012). Therefore, the promotive effects of the B+FR NI for petunia could be attributed to FR light, but the possibility of the interaction between B and FR light cannot be excluded. Since FR light converts P_{FR} to P_R and thus reduces P_{FR}/P_{R+FR}, early flowering under the B+FR or FR NI may be triggered at a very low P_{FR}/P_{R+FR} under low-intensity lighting for certain species, or may be regulated by mechanisms that involve photoreceptors besides phytochromes.

For each LDP, a flowering promotion index was calculated for each NI lighting treatment by multiplying flowering percentage, reciprocal of flowering time, and minimum flowering time within cultivar (Runkle and Heins, 2003). The flowering promotion indices were plotted according to the P_{FR}/P_{R+FR} values in the NI lighting treatments (Figure III-3). A P_{FR}/P_{R+FR} of 0.71 corresponded with the most rapid and complete flowering of all LDPs, in agreement with Craig and Runkle (2012). However, flowering responses were variable among LDPs under a very high P_{FR}/P_{R+FR} of 0.88 or a very low P_{FR}/P_{R+FR} of 0.12. In addition, a P_{FR}/P_{R+FR} of 0.53 under the B NI resulted in a flowering promotion index ranging from 0 to 0.9. The addition of B light to R and FR light had a negligible effect on the estimated P_{FR}/P_{R+FR} and accordingly did not influence the

flowering promotion index. Therefore, for NI lighting from low-intensity B, R or FR light, the estimated P_{FR}/P_{R+FR} is apparently not a consistent indicator of flowering responses of LDPs.

When plants are competing for light, such as under a canopy, the R:FR is decreased, triggering shade-avoidance responses such as increased stem elongation, hyponastic leaf growth, early flowering, and reduced branching (Cerdán and Chory, 2003). Plants grown under closed canopies with an R:FR of 0.05 were taller than those grown under full sunlight with an R:FR of 1.2 (Vandenbussche et al., 2005). Since stem length was recorded at flowering, it is crucial to consider flowering time and leaf number at flowering when evaluating extension growth. Compared with the B+R NI, the B+R+FR NI promoted extension growth by 16 to 20% in dahlia 'Gallery Pablo', dianthus, and rudbeckia, all of which flowered simultaneously under these two NI lighting treatments. In our study, dahlia 'Leanne' was 5 cm taller under the B+FR NI than under the B+R NI and flowered simultaneously under these two NI lighting treatments. Similarly, stem elongation of Italian bellflower (*Campanula isophylla*) was promoted under a 3-h FR NI compared with a 3-h R NI (Moe et al., 1991). Alternatively, NI lighting with a high R:FR can inhibit extension growth. For example, internode length of lisianthus (*Eustoma grandiflorum*) was shorter under an NI with an R:FR of 5 to 10 than 0.5 to 1 (Yamada et al., 2011). Similarly in our study, extension growth of chrysanthemum, dahlia 'Leanne' and 'Gallery Pablo', and rudbeckia under NI lighting treatments with a high R:FR, such as the W and B+R NI, was less than that under NI lighting treatments emitting both R and FR light.

Apart from the R:FR, low-intensity B light can influence the shade-avoidance response through crytochromes and phototropins (Vandenbussche et al., 2005). Although our results show that extension growth of all crops was not affected by low-intensity B light when added to R and FR light, other studies that delivered higher intensities reported that B light suppressed stem

elongation (Folta and Childers, 2008; Shimizu et al., 2006) or promoted stem elongation (Jeong et al., 2014). The discrepancies could be at least partially explained by differences in light intensity, delivery time, and duration, as well as variation among species. For example, a 4-h NI from B light at 1.7 $\mu mol \cdot m^{-2} \cdot s^{-1}$ inhibited extension growth of chrysanthemum 'Reagan' compared with a 4-h NI provided by fluorescent lamps (Shimizu et al., 2006), whereas an 11-h base photoperiod with 4-h DE from B light at 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ promoted extension growth of chrysanthemum 'Zembla' compared to no DE lighting (Jeong et al., 2014). In addition, when the *PPF* ranged from 20 to 150 $\mu mol \cdot m^{-2} \cdot s^{-1}$, B light promoted stem length of eggplant (*Solanum melongena*) but suppressed that of lettuce (*Lactuca sativa*) compared with green, R, or green+B light (Hirai et al., 2006). The effects of high-intensity B light in NI lighting on extension growth have not yet been elucidated.

Based on our results and those of other studies, the most effective spectral composition for NI lighting differs somewhat between SDPs and LDPs. For SDPs, W and usually R+FR light were most effective at inhibiting flowering. In contrast, R+FR light most promoted flowering of LDPs, and W light was sometimes less effective. Low-intensity (0.6 to 1.6 $\mu mol \cdot m^{-2} \cdot s^{-1}$) B light did not affect flowering characteristics or growth attributes alone or when added to R and FR light. Although a combination of B and FR light was perceived as a long day in some crops, such as dahlia 'Leanne' and petunia WPC and WPI, it was not effective at interrupting the night for the other crops studied. Our study also corroborates that LEDs can be a viable replacement for INC or compact fluorescent lamps when used for photoperiodic lighting of daylength-sensitive ornamental crops (Craig and Runkle, 2012).

APPENDIX

Table III-1. Night-interruption lighting characteristics and estimated phytochrome photoequilibria (P_{FR}/P_{R+FR}; Sager et al., 1988) of incandescent (INC) lamps and white (W), blue (B), B + red (R), B + far red (FR), B+R+FR, and R+FR light-emitting diodes. The $R:FR_{narrow}$ was calculated as 655 to 665 nm:725 to 735 nm.

Parameter	INC	W	B	B+R	B+FR	B+R+FR	R+FR
Light intensity ($\mu mol \cdot m^{-2} \cdot s^{-1}$)							
B (400−499 nm)	0.05	0.18	1.57	0.70	0.79	0.62	0.00
Green (500−599 nm)	0.19	0.72	0.01	0.00	0.00	0.01	0.00
R (600−699 nm)	0.41	0.76	0.00	0.77	0.00	0.51	0.71
FR (700−799 nm)	0.66	0.03	0.00	0.00	0.77	0.49	0.72
Light ratio							
R:FR	0.61	26.5	–	–	0.00	1.05	0.98
$R:FR_{narrow}$	0.68	17.5	–	–	0.00	1.84	1.61
B:R	0.12	0.25	–	0.91	–	1.20	–
B:FR	0.08	7.10	–	–	1.03	1.26	–
B:R:FR	–	–	–	–	–	1:1.2:1.3	–
P_{FR}/P_{R+FR}	0.65	0.87	0.53	0.88	0.12	0.71	0.71

–, not applicable.

Table III-2. Number of incandescent (INC) lamps and white (W), blue (B), B + red (R), B + far red (FR), B+R+FR, and R+FR light-emitting diode (LED) lamps used in each night-interruption lighting treatment and average daily air temperature (ADT) in each treatment during two replications (rep.) of the experiment.

	No. of lamps	ADT (°C)	
Treatment	used	Rep. 1	Rep. 2
Short day	0	20.5	22.3
INC	4	20.0	21.2
W	4	20.4	21.4
B	4	20.4	21.4
B+R[z]	4+4	20.8	21.9
B+FR	4+14	20.5	21.2
B+R+FR	4+14	20.1	21.1
R+FR	16	20.5	21.5

[z]R and/or FR light was provided by customized LED fixtures containing three R and/or FR diodes per lamp.

Table III-3. Days to first visible bud or inflorescence (VB) and main stem length at flowering, VB number per plant at flowering, and increase in leaf number from transplant at flowering for five short-day plants. Plants were grown at a constant 20 °C under a truncated 9-h short-day (SD) with or without 4-h night-interruption lighting from incandescent (INC) lamps or white (W), blue (B), B + red (R), B + far red (FR), B+R+FR, or R+FR light-emitting diodes. All data within each cultivar are pooled across experimental replications.

Photoperiod treatment	Days to VB	Stem length (cm)	VB number	Increase in leaf number
		Chrysanthemum 'Golden Cheryl'		
SD	19 c[z]	11.3 e	32 d	11.2 a
INC	42 b	28.6 bc	219 c	ND
W	49 a	27.8 c	429 a	ND
B	20 c	11.7 e	30 de	11.5 a
B+R	42 b	26.0 c	240 bc	ND
B+FR	20 c	15.8 d	26 e	12.3 a
B+R+FR	49 a	33.3 a	305 b	ND
R+FR	48 a	30.8 ab	281 bc	ND
Treatment	***[y]	***	***	NS
Replication	***	NS	***	NS
Treatment×replication	***	***	***	NS
		Cosmos 'Cosmic Yellow'		
SD	25 ab	22.4 ab	14.0 a	9.1 a
INC	25 ab	23.9 ab	14.9 a	9.5 a
W	28 a	24.3 a	18.3 a	9.9 a
B	24 b	20.6 b	13.1 a	8.9 a
B+R	27 ab	24.1 a	16.6 a	9.3 a
B+FR	25 ab	24.6 a	13.7 a	8.6 a
B+R+FR	25 ab	23.4 ab	15.2 a	9.5 a
R+FR	25 ab	24.1 a	16.5 a	8.8 a
Treatment	*	***	NS	NS
Replication	***	NS	*	NS
Treatment×replication	*	NS	*	*
		Dahlia 'Leanne'		
SD	25 c	15.6 c	2.3 b	8.5 c
INC	34 ab	23.3 a	4.4 a	12.9 ab
W	34 ab	19.4 b	3.7 a	12.8 b
B	25 c	16.4 c	3.3 ab	11.3 bc
B+R	34 ab	19.4 b	4.4 a	12.6 b
B+FR	37 a	24.1 a	4.4 a	14.7 a
B+R+FR	31 b	23.3 a	4.2 a	11.2 bc
R+FR	33 b	23.5 a	4.5 a	12.9 b
Treatment	***	***	*	***
Replication	***	*	***	***
Treatment×replication	*	***	NS	NS
		Dahlia 'Gallery Pablo'		
SD	–	–	–	–

Table III-3 (cont'd)

Photoperiod treatment	Days to VB	Stem length (cm)	VB number	Increase in leaf number
INC	43 b	29.9 a	3.6 a	15.7 a
W	43 b	25.9 b	3.6 a	15.2 a
B	–	–	–	–
B+R	43 b	25.3 b	3.9 a	15.3 a
B+FR	–	–	–	–
B+R+FR	46 a	29.7 a	3.6 a	15.2 a
R+FR	42 b	31.1 a	3.0 a	14.3 a
Treatment	*	***	NS	NS
Replication	NS	***	*	*
Treatment×replication	*	*	*	NS
	Marigold 'American Antigua Yellow'			
SD	19 c	13.3 c	9.2 abc	9.1 c
INC	26 a	17.9 ab	8.9 bc	13.2 a
W	26 a	17.0 ab	9.0 b	12.8 a
B	19 c	14.7 c	11.3 a	9.4 c
B+R	24 a	16.8 b	9.3 ab	12.3 ab
B+FR	21 b	16.1 bc	10.8 ab	10.9 b
B+R+FR	25 a	18.5 ab	8.8 bc	13.5 a
R+FR	25 a	18.7 a	7.5 c	12.8 a
Treatment	***	***	***	***
Replication	***	***	*	***
Treatment×replication	***	***	***	NS

[z] Means within columns followed by different letters are significantly different by Tukey's honest significant difference test at $P \leq 0.05$. ND, no data. −, did not flower.
[y] NS, non-significant; *, ***, significant at $P \leq 0.05$ or 0.001, respectively.

Table III-4. Days to first visible bud or inflorescence (VB) and main stem length at flowering, VB number per plant at flowering, and increase in leaf number from transplant to flowering for four long-day plants. Plants were grown at a constant 20 °C under a truncated 9-h short-day (SD) with or without 4-h night-interruption lighting from incandescent (INC) lamps or white (W), blue (B), B + red (R), B + far red (FR), B+R+FR, or R+FR light-emitting diodes. All data within each cultivar are pooled across experimental replications.

Photoperiod treatment	Days to VB	Stem length (cm)	VB number	Increase in leaf number
	Dianthus 'Super Parfait Raspberry'			
SD	31 a[z]	14.0 d	14.1 a	16.4 a
INC	29 a	17.3 abc	11.5 ab	16.1 a
W	30 ab	17.1 abc	11.8 ab	16.3 a
B	31 a	14.4 cd	12.5 ab	16.1 a
B+R	28 ab	16.1 bcd	14.5 a	15.4 a
B+FR	27 ab	18.0 ab	11.4 ab	15.2 a
B+R+FR	27 ab	18.7 a	10.8 ab	14.6 a
R+FR	26 b	19.0 a	10.1 b	15.2 a
Treatment	*[y]	***	*	NS
Replication	*	*	NS	***
Treatment×replication	NS	NS	NS	NS
	Petunia 'Wave Purple Classic'			
SD	–	–	–	–
INC	37 bc	35.1 b	15.7 a	19.3 b
W	44 a	40.9 ab	20.5 a	25.3 a
B	–	–	–	–
B+R	42 ab	38.7 ab	18.6 a	26.6 a
B+FR	52 a	50.4 a	9.3 b	34.9 a
B+R+FR	34 c	37.1 b	17.6 a	16.6 c
R+FR	35 c	39.6 ab	16.4 a	18.3 bc
Treatment	***	*	***	***
Replication	NS	*	***	NS
Treatment×replication	NS	NS	*	NS
	Petunia 'Wave Purple Improved'			
SD	43 a	36.5 ab	16.4 d	31.2 a
INC	24 cd	27.7 c	25.6 a	12.1 c
W	27 b	27.5 c	23.0 abc	13.4 bc
B	50 a	42.4 a	15.8 cd	36.2 a
B+R	27 bc	29.8 bc	26.2 ab	14.4 bc
B+FR	27 bc	34.6 abc	20.3 bcd	15.7 b
B+R+FR	24 d	30.8 c	20.7 bcd	13.0 c
R+FR	26 bcd	30.8 bc	20.1 cd	13.0 bc
Treatment	***	***	***	***
Replication	***	NS	***	*
Treatment×replication	***	***	*	*
	Rudbeckia 'Indian Summer'			
SD	–	–	–	–

Table III-4 (cont'd)

Photoperiod treatment	Days to VB	Stem length (cm)	VB number	Increase in leaf number
INC	48 a	60.4 c	9.6 ab	9.1 a
W	47 a	62.6 bc	9.9 ab	8.8 a
B	–	–	–	–
B+R	47 a	59.4 c	11.6 a	8.8 a
B+FR	–	–	–	–
B+R+FR	46 a	71.5 a	8.9 ab	9.1 a
R+FR	47 a	68.4 ab	8.3 b	8.9 a
Treatment	NS	***	*	NS
Replication	***	NS	***	*
Treatment×replication	NS	NS	*	NS

[z] Means within columns followed by different letters are significantly different by Tukey's honest significant difference test at $P \leq 0.05$. −, did not flower.
[y] NS, non-significant; *, ***, significant at $P \leq 0.05$ or 0.001, respectively.

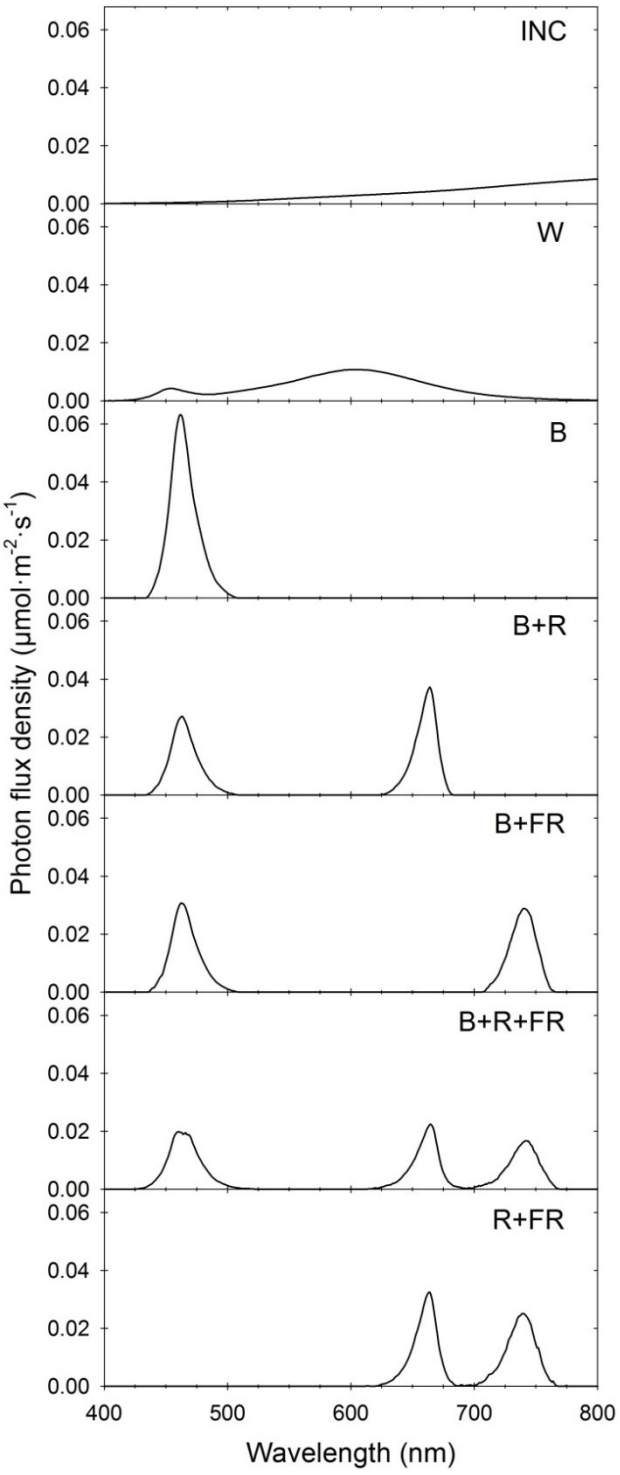

Figure III-1. Spectral distribution of night-interruption lighting treatments between 400 and 800 nm from incandescent (INC) lamps or white (W), blue (B), B + red (R), B + far red (FR), B+R+FR, and R+FR light-emitting diodes.

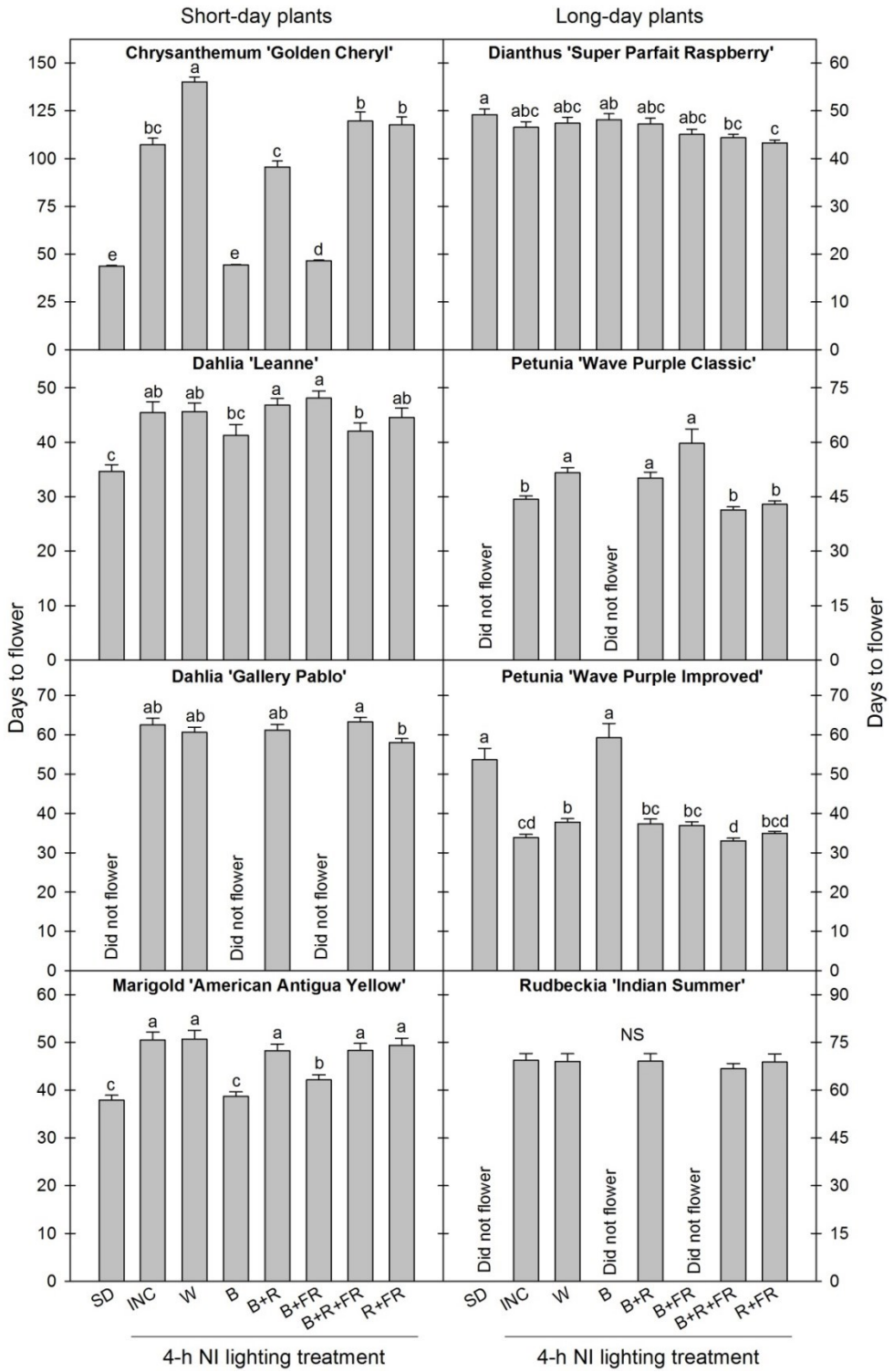

Figure III-2. Days to flower of four short-day and four long-day plants under a truncated 9-h short-day (SD) treatment with or without 4-h night-interruption (NI) lighting from incandescent (INC) lamps or white (W), blue (B), B + red (R), B + far red (FR), B+R+FR, or R+FR light-emitting diodes. All data are pooled from two replications. Values followed by different letters within species are significantly different by Tukey's honest significant difference test at $P \leq 0.05$; NS, non-significant. Error bars indicate standard errors.

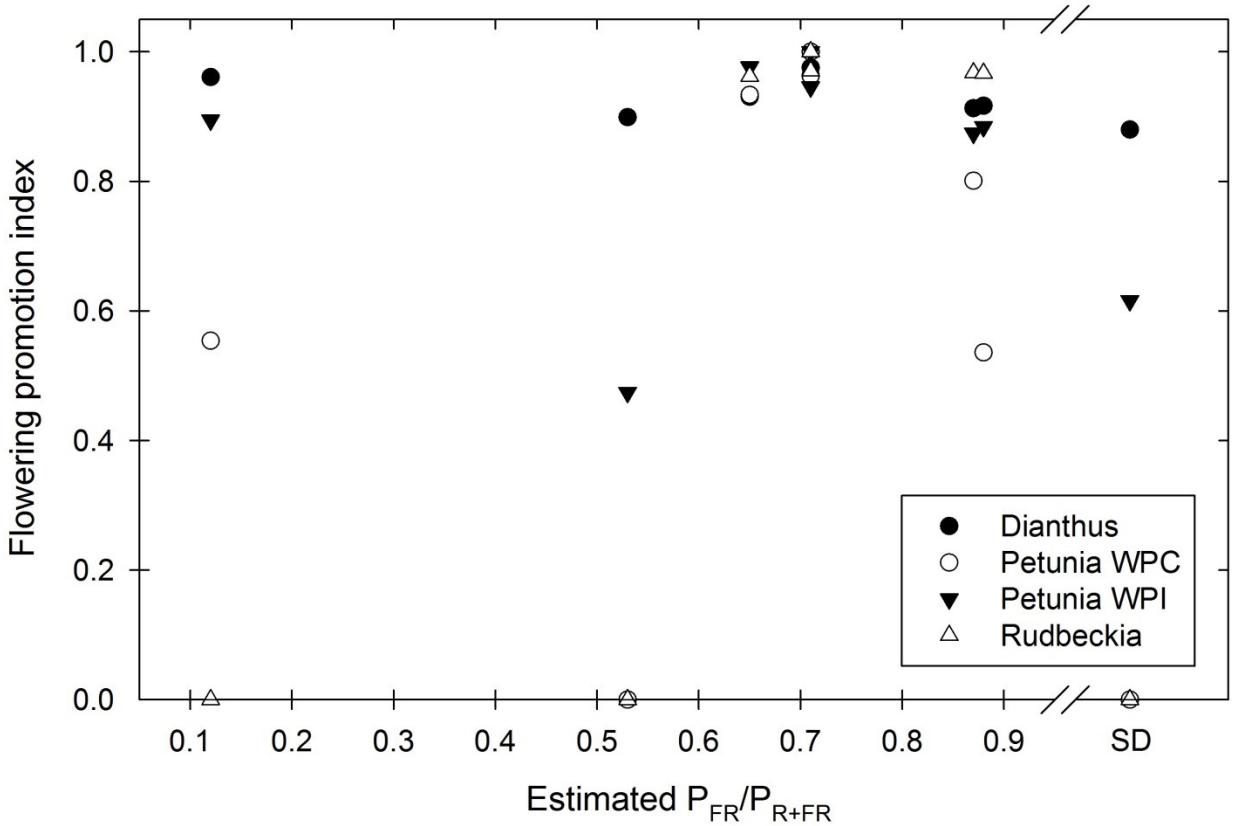

Figure III-3. The influence of estimated phytochrome photoequilibrium (P_{FR}/P_{R+FR}) of night-interruption lighting on the flowering promotion index of four long-day plants under a truncated 9-h short-day (SD) treatment with 4-h night-interruption lighting from incandescent lamps or white, blue, red, and/or far-red light-emitting diodes. The P_{FR}/P_{R+FR} values were calculated for each treatment according to Sager et al. (1988). The flowering promotion index was calculated as $FP \times FT_{min} \times FT_t^{-1}$, where FP= flowering percentage, FT_{min}= flowering time (d) of the treatment that induced the most rapid flowering, and FT_t= flowering time (d) of treatment (Runkle and Heins, 2003). All data are means from two replications with ten observations per treatment and replication. WPC, 'Wave Purple Classic'. WPI, 'Wave Purple Improved'.

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SECTION IV

HIGH-INTENSITY BLUE LIGHT AS A NIGHT INTERRUPTION CAN REGULATE FLOWERING OF PHOTOPERIODIC CROPS

High-intensity Blue Light as a Night Interruption Can Regulate Flowering of Photoperiodic Crops

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Abstract.

Under a short photoperiod, lighting at the end of a day (day extension, DE) or during the middle of a night (night interruption, NI) can regulate flowering of photoperiodic crops. Low-intensity red (R; 600 to 700 nm) and far-red (FR; 700 to 800 nm) light controls flowering of a wide range of plants, whereas low-intensity blue (B; 400 to 500 nm) light generally does not. However, the effects of high-intensity B light alone or added to R and FR light on flowering and photomorphogenesis have not been fully elucidated. We grew plants of calibrachoa (*Calibrachoa ×hybrida*), coreopsis (*Coreopsis grandiflora*), petunia (*Petunia ×hybrida*), rudbeckia (*Rudbeckia hirta*), snapdragon (*Antirrhinum majus*), and marigold (*Tagetes erecta*) in a greenhouse at 20 °C under a 9-h natural short day (SD) with or without 5.5-h DE and/or 4-h NI lighting from light-emitting diodes. Blue light was delivered at 0, 1, 15, or 30 $\mu mol \cdot m^{-2} \cdot s^{-1}$, in some cases with R+white (W)+FR light at 2 $\mu mol \cdot m^{-2} \cdot s^{-1}$ between 400 and 800 nm. Peak wavelengths of B, R, and FR light were 450 nm, 666 nm, and 738 nm, respectively. Blue light at 30 $\mu mol \cdot m^{-2} \cdot s^{-1}$ created long days (LDs) in all crops as effectively as R+W+FR light. Flowering of calibrachoa and petunia, but not other crops, was 2 to 4 days earlier when B light at 30 $\mu mol \cdot m^{-2} \cdot s^{-1}$ was added to R+W+FR light. For all crops tested except rudbeckia and marigold, NI lighting was more effective than DE lighting. Rudbeckia was 14 to 19% shorter at flowering under B light at 30 $\mu mol \cdot m^{-2} \cdot s^{-1}$ than under a combination of B and R+W+FR light, but there were few or no height differences among treatments in other crops. Chlorophyll content, only measured in marigold, was promoted under high-intensity B light. We conclude that NI lighting with high-intensity B light, alone and when added to R and FR light, can regulate flowering of a wide range of crops.

Introduction

Through adaptation and evolution, plants have developed sophisticated circadian behavior to synchronize to constantly changing photoperiodic cycles in the natural environment. Among many physiological processes, flowering of some plants is regulated by photoperiod (Thomas, 2006). Most plants can be categorized into one of three response groups: long-day plants (LDPs), short-day plants (SDPs), and day-neutral plants. Flowering of LDPs occurs or is accelerated when the night length is less than a critical duration, and flowering of SDPs occurs or is accelerated when the night length is sufficiently long (Thomas and Vince-Prue, 1997). The critical photoperiod differs among species and cultivars and can overlap between LDPs and SDPs (Taiz and Zeiger, 2010).

A large number of photoperiodic specialty crops are produced in northern climates during winter and early spring, when daylength is relatively short (e.g., <12 h). Photoperiodic lighting at a low intensity (1 to 2 $\mu mol \cdot m^{-2} \cdot s^{-1}$) hastens flowering of LDPs and inhibits flowering of SDPs. LDs can be created by electric lights to extend the natural photoperiod (day extension, DE) or to interrupt the long night (night interruption, NI) (Thomas and Vince-Prue, 1997). Generally, DE lighting that creates a day ≥16 h or 4-h NI lighting in the middle of the dark period are effective at controlling flowering of most photoperiodic plants (Craig, 2012; Runkle and Fisher, 2004; Runkle et al., 1998). Cyclic lighting, such as operating incandescent (INC) lamps intermittently during a 4-h NI or using stationary high-pressure sodium (HPS) lamps with rotating reflectors, is another technique to deliver photoperiodic lighting while reducing energy inputs, but flowering of some LDPs is not as rapid as under a continual 4-h NI (Blanchard and Runkle, 2010; Runkle et al., 1998).

Light is perceived through different classes of photoreceptors in higher plants, including five red (R; 600 to 700 nm) and far-red (FR; 700 to 800 nm) light-absorbing phytochromes, ultraviolet-A/blue (B; 400 to 500 nm) light-absorbing cryptochromes, and B light-absorbing phototropins, as identified in the LDP *Arabidopsis thaliana* (Casal, 2000). These photoreceptors interact to mediate flowering and photomorphogenesis (Cashmore et al., 1999). There are similarities as well as differences in how SDPs and LDPs respond to the spectral distribution of photoperiodic lighting. R light is the most effective waveband at inhibiting flowering of SDPs; a moderate to high R to FR light ratio (R:FR; ≥0.66) was generally effective during an NI (Craig and Runkle, 2013). In contrast, a combination of R and FR light is more effective at promoting flowering of LDPs than either R or FR light alone (Thomas and Vince-Prue, 1997); the optimum R:FR was between 0.66 and 1.07 (Craig and Runkle, 2012). Phytochromes are primarily R and FR light-absorbing photoreceptors that regulate flowering by establishing their active and inactive forms primarily in response to R and FR light (Sager et al., 1988). The most effective 10-nm wavebands of R and FR light are 655 to 665 nm and 725 to 735 nm, respectively, which correspond to the absorption peak wavelengths of extracted oat phytochromes (Butler et al., 1965; Sager et al., 1988). In addition, both active and inactive forms of phytochromes also absorb B light approximately equally, but to a lesser extent than R and FR light, although absorption peak wavelengths shift slightly from each other (Butler et al., 1965; Sager et al., 1988).

Specific functions of B light in flowering-time regulation are not as well understood. Previous studies showed that B light (peak wavelength = 455 nm) at 3 $\mu mol \cdot m^{-2} \cdot s^{-1}$ did not "create" (i.e., mimic) LDs when delivered as 4-h NI lighting for a range of photoperiodic ornamental plants (Craig, 2012; Ho et al., 2012). Similarly, chrysanthemum (*Dendranthema* × *grandiflorum*) 'Zembla' flowered similarly under an 11-h photoperiod with or without 4-h DE

lighting with B light (peak wavelength = 455 nm) at 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Singh et al., 2013). However, B light at low and high intensities was perceived as an LD signal by LDPs and SDPs in other studies (Hamamoto et al., 2003; Saji et al., 1982; Shin et al., 2010). Whether photoperiodic B light mediates flowering may depend on light intensity, light duration, specific B light wavelengths, and species and cultivars. Although we concluded that B light at 1 to 2 $\mu mol \cdot m^{-2} \cdot s^{-1}$ was not effective at interrupting the night, the effectiveness of a higher intensity of B light cannot be eliminated for two reasons: B light-absorbing cryptochromes mediate flowering in at least some plants, and phytochromes have low secondary absorption peaks in the B region (Butler et al., 1965; Vierstra and Quail; 1983), so a higher irradiance may be required to elicit a phytochrome-mediated response.

Conventional broad-spectrum light sources, such as compact fluorescent (Runkle et al., 2012), HPS (Blanchard and Runkle, 2010), and INC (Craig and Runkle, 2012) lamps, can effectively create LDs for most photoperiodic crops, but much of the light emitted – and therefore energy consumed – is not necessary for photoperiodic lighting. In contrast, light-emitting diode (LED) technology is typically at least as energy efficient as conventional lamps (Nelson and Bugbee, 2014; Pimputkar et al., 2009), enables specification of spectral composition and structural design, and increases the useful life span of the lamp (Schubert and Kim, 2005). If the optimal spectrum that effectively regulates flowering is clearly understood, LEDs can be used to enhance the productivity and sustainability of specialty crop production. This study investigated the effects of B light, with and without R+W+FR light, from LEDs to control flowering of photoperiodic ornamental crops. We postulated that high-intensity B light would create effective LDs when delivered alone.

Materials and Methods

Plant material

Young plants were obtained from a commercial young-plant producer (C. Raker & Sons, Litchfield, MI) within one week of seed sow or for calibrachoa, as newly rooted liners. Tested crops included five LDPs: calibrachoa (*Calibrachoa ×hybrida*) 'Callie Yellow Improved', coreopsis (*Coreopsis grandiflora*) 'Early Sunrise', petunia (*Petunia ×hybrida*) 'Wave Purple Improved', rudbeckia (*Rudbeckia hirta*) 'Indian Summer', and snapdragon (*Antirrhinum majus*) 'Liberty Classic Yellow', and one SDP: marigold (*Tagetes erecta*) 'American Antigua Yellow'. This experiment was performed twice in time in a research greenhouse. All plants were received on 22 Nov. 2013 for the first replication and on 13 Feb. 2014 for the second replication. Calibrachoa, coreopsis, petunia, rudbeckia, snapdragon, and marigold were transplanted on 12 Dec., 13 Dec., 13 Dec., 12 Dec., 12 Dec., and 10 Dec. 2013, respectively, for the first replication, and on 14 Feb., 18 Feb., 18 Feb., 18 Feb., 18 Feb., and 16 Feb. 2014, respectively, for the second replication. Before the onset of treatments, all LDPs were grown under a truncated 9-h short day (SD) created by opaque black cloth from 0800 to 1700 HR, whereas marigold was grown under a 16-h LD. The natural photoperiod was supplemented by 400-W HPS lamps (PL2000; P.L. Light Systems Inc., Beamsville, ON, Canada) that delivered a photosynthetic photon flux (*PPF*) of 60 to 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at plant canopy from 0600 to 2200 HR. The HPS lamps switched on when the ambient solar *PPF* was <185 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at plant canopy and turned off when the ambient *PPF* was >370 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Because calibrachoa were reproductive upon receipt in the second replication, all plants were pinched to eight nodes on 27 Feb. 2014 and treated with ethephon (Florel; Southern Agricultural Insecticides, Inc., Palmetto, FL) as a 500 $mg \cdot L^{-1}$ foliar spray at a volume of 0.2 $L \cdot m^{-2}$ on 5 May 2014, and these applications effectively made them vegetative.

When the plants were ready for transplant based on production standards, ten plants of each species were transplanted into plastic pots filled with a commercial peat-perlite medium (Suremix; Michigan Grower Products, Inc., Galesburg, MI) and placed randomly on each of eight benches in a glass-glazed research greenhouse maintained at constant 20 °C as controlled by a greenhouse environmental control system (Integro 725; Priva, De Lier, Netherlands). An aspirated thermocouple [36-gauge (0.127-mm diameter) type E] located in the middle of each bench measured air temperature at plant canopy every 10 s. Line quantum sensors (Apogee Instruments, Inc., Logan, UT) positioned horizontally at plant canopy measured photosynthetic photon flux (*PPF*) in three of the treatments every 10 s. A data logger (CR10; Campbell Scientific, Logan, UT) recorded hourly averages of air temperature and *PPF*. When the nighttime air temperature at plant canopy was <18.9 °C, a 1500-W electric heater underneath each bench provided supplemental heating. The average daily air temperature in each treatment is provided in Table IV-1. The average photosynthetic daily light integral (DLI) was 9.0 and 14.7 $mol \cdot m^{-2} \cdot d^{-1}$ during the first and second replications of the experiment, respectively. Watering and fertility were applied to all plants alike according to established experimental protocols as described by Vaid et al. (2014).

Lighting treatments

All plants were subjected to a truncated 9-h natural photoperiod from 0800 to 1700 HR, achieved by opening and closing opaque black cloth. Each bench was randomly assigned with a 9-h SD control or one of the seven photoperiodic lighting treatments: B_0* DE, B_0* NI, B_1* NI, B_{15}* NI, B_{30}* NI, B_{30} NI, and B_0* DE+B_{30} NI, where each number following B represents its intensity (in $\mu mol \cdot m^{-2} \cdot s^{-1}$) provided by B LEDs (14 W, GreenPower LED research module blue; Philips, Eindhoven, the Netherlands), and * indicates delivery of R+W+FR light (14 W,

GreenPower LED flowering DR/W/FR 120V, E26; Philips) at 2 μmol·m^{-2}·s^{-1} between 400 and 800 nm (Figure IV-1). The B LEDs had a peak wavelength of 450 nm, and the R+W+FR LEDs had peak wavelengths of 666 nm and 738 nm. The NI lighting treatments were delivered from 2230 to 0230 HR, and the DE lighting treatments were delivered from 1700 to 2230 HR. Spectral characteristics of the lighting treatments were measured by a portable spectroradiometer (LI-1800, LI-COR, Inc., Lincoln, NE) (Table IV-2). For each lighting treatment, the R:FR was described using 100-nm or 10-nm wavebands, and phytochrome photoequilibrium (P_{FR}/P_{R+FR}) was calculated according to Sager et al. (1988). Light intensity was adjusted as needed by layering mesh screen under the light sources, moving light sources vertically, and/or using a dimming program that regulates B light intensity. All plants under the photoperiodic lighting treatments were placed on benches only where 1 to 3 μmol·m^{-2}·s^{-1} of R+FR light and/or 70 to 130% of the target B light intensity was achieved as measured by the spectroradiometer.

Data collection and analysis

On the day of transplant, leaf number on the primary stem was recorded, and the edge of the most recently developed leaf was marked with white correction liquid. For all plants, date of the first visible bud or inflorescence (VB) was recorded. For plants in the Asteraceae, when the outermost row of ray flowers of the first inflorescence were perpendicular to the stem, and for other plants when the first flower opened, date of flowering, plant height (from the media surface to the tallest flowering inflorescence or stem), VB number of the whole plant, and leaf number above the marked leaf on the primary stem were recorded. For petunia, the stem with the first open flower was selected for measurements of stem length and leaf number. Additionally, marigold appeared darker green under some of the treatments, so relative leaf chlorophyll content of marigold was measured using an instant chlorophyll meter (SPAD-502, Spectrum

Technologies, Inc., Aurora, IL). The second to seventh fully expanded true leaves below the first inflorescence of a plant were selected for chlorophyll content measurement, and the average of the six measurements were recorded. Days to VB from transplant, days to flower from transplant (and for calibrachoa in the second replication, from when ethephon was applied), increase in leaf number, and flowering percentage were subsequently calculated.

Data were analyzed with the SAS (Version 9.3; SAS Institute, Cary, NC) mixed-model (PROC MIXED) and glimmix-model (PROC GLIMMX) procedures, and pairwise comparisons between treatments were performed using Tukey's honest significant difference test ($P = 0.05$). Data were pooled from two replications when there was no interaction between main effects and replication, or response trends were similar between replications.

Results

Calibrachoa 'Callie Yellow Improved'

In our study, lighting treatments indicate treatments using NI and/or DE lighting. All plants flowered under all lighting treatments within 30 d after transplant, whereas plants under the SD did not flower within 60 d after transplant (data not shown). Thus, no data were collected for plants under the SD. Compared with that under the B_0* NI, flowering under the B_1* NI and B_{15}* NI was similar, but flowering under the B_{30}* NI was accelerated by 4 d (Figure IV-2). The B_{30} NI promoted flowering similarly to the other NI lighting treatments. Plants flowered 4 d earlier under the B_0* NI than the B_0* DE. Flowering was similar under the B_0* DE and B_0* DE+B_{30} NI. Plants under the B_{30}* NI formed VB 4 d earlier than those under the B_0* DE (Table IV-3). The main stem of plants under the B_0* DE+B_{30} NI was 28 to 39% longer than that under the B_{30}* and B_{30} NI. Visible bud number was similar under all lighting treatments.

Coreopsis 'Early Sunrise'

Most plants (≥80%) flowered under all lighting treatments, whereas no plants flowered under the SD (data not shown). Flowering time was similar under R+W+FR NI lighting treatments irrespective of additional low- or high-intensity B light (Figure IV-2). The B_{30} NI was as effective at promoting flowering as the B_0* NI. Plants under the B_0* DE flowered 7 d later than those under the B_0* NI and formed VB 7 or 8 d later and developed 40 to 58% more VBs at flowering than those under the B_1* NI and B_{30}* NI (Table IV-3). Plants were 13 to 18% shorter under the B_{30} NI than under all other lighting treatments except the B_0* NI and B_{15}* NI. Plants developed two more leaves before flowering under the B_0* DE than under the B_1* NI.

Petunia 'Wave Purple Improved'

All plants under all lighting treatments formed VB and flowered 24 to 31 d earlier than those under the SD (Table IV-3, Figure IV-2). Flowering percentage under the SD was 100% and 40% in the first and second replications, respectively (data not shown). The B_{30} NI was as effective at promoting flowering as all the other NI lighting treatments delivering R+W+FR light. Plants under the B_0* DE flowered 5 d later than those under the B_0* NI. Formation of the first VB was 4 to 5 d earlier under the B_{15}* NI and B_{30}* NI than under the B_0* DE. The main stem length of plants at flowering under the SD was 33 to 41% greater than that under all the other treatments delivering only NI lighting. Visible bud number was similar under all lighting treatments. Plants under the B_0* DE, B_0* NI, and B_{30} NI had 45 to 55% more VBs than those under the SD. Leaf number was 24 to 27 greater under the SD than under all lighting treatments. Plants under the B_0* DE and B_0* DE+B_{30} NI had 2 or 3 more leaves than those under the B_{30}* NI.

Rudbeckia 'Indian Summer'

All plants formed the first VB and flowered simultaneously under all lighting treatments (data of flowering percentage not shown; Table IV-3, Figure IV-2), whereas no plants flowered under the SD. Plants were 8 to 13 cm shorter under the B_{30} NI than under all other lighting treatments except the B_0* DE and B_0* NI (Table IV-3). Plants had 38 to 46% more VBs under the B_0* DE+B_{30} NI than under the B_0* NI, B_1* NI, and B_{30} NI. Leaf number at flowering was similar under all lighting treatments.

Snapdragon 'Liberty Classic Yellow'

All plants flowered under all treatments (data not shown), but plants under the lighting treatments developed VB and flowered 7 to 15 d earlier than those under the SD (Table IV-3, Figure IV-2). Plants flowered 5 d later under the B_0* DE than under the B_0* NI. The B_{30} NI was as effective at promoting flowering as the B_0* NI and B_1* NI, but less effective than the B_{15}* NI and B_{30}* NI. Plants under the B_{30}* NI and B_0* DE+ B_{30} NI had the first VB 3 to 7 d earlier than those under all the other lighting treatments except the B_{15}* NI. When measured 46 and 42 d after transplant, plants under the B_{30} NI were shorter than those under the B_{15}* NI, B_{30}* NI, and B_0* DE+B_{30} NI (Figure IV-3). However, plant height at flowering was similar under all lighting treatments. Plants formed 2 to 4 more VBs under the SD and B_{30} NI than under the B_1* NI, B_{15}* NI, and B_0* DE+B_{30} NI. Plants developed the most and fewest leaves before flowering under the SD and B_0* DE+B_{30} NI, respectively.

Marigold 'American Antigua Yellow'

All plants flowered under all treatments (data not shown). Compared with the SD, all lighting treatments delayed VB appearance by 7 to 8 d and flowering by 13 to 15 d. Plants under the SD were 31 to 37% shorter than those under all lighting treatments (Table IV-3, Figure IV-2). Plants were 1.1 to 1.5 cm taller under the B_{30}* NI than under the B_0* DE and B_0* NI. Plants

under the B_{30} NI and B_{30}* NI formed 2 to 6 more VBs than those under the B_0* NI and B_1* NI. Plants had 6 or 7 more leaves under all lighting treatments than under the SD. The SPAD value generally increased with B light intensity and was greatest under lighting treatments with B light at 30 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Figure IV-4).

Discussion

For a variety of LDPs and SDPs, low-intensity B light (<5 $\mu mol \cdot m^{-2} \cdot s^{-1}$) is generally ineffective at extending natural SDs (Thomas and Vince-Prue, 1997). In Chapter 3 of this thesis, we concluded that B light (peak wavelength = 462 nm) at 1 to 2 $\mu mol \cdot m^{-2} \cdot s^{-1}$, alone and when added to R+FR light, did not influence flowering. Similarly, a 4-h NI with B light (peak wavelength = 455 nm) at 3 $\mu mol \cdot m^{-2} \cdot s^{-1}$ did not promote flowering of several obligate LDPs (Craig, 2012). In addition, a 4-h NI with B light (peak wavelength = 450 nm) at 0.8 $\mu mol \cdot m^{-2} \cdot s^{-1}$ or B light (peak wavelength = 470 nm) at 3.3 $\mu mol \cdot m^{-2} \cdot s^{-1}$ did not affect flowering of chrysanthemum 'Huang-Hsiu-Feng' or 'Lung-Feng-Tzu' (Ho et al., 2012).

For at least some plants in the Brassicaceae, B light alone is effective for photoperiodic lighting (Thomas and Vince-Prue, 1997). For example, 1-h NI lighting at 250 $mW \cdot m^{-2}$ (probably <2 $\mu mol \cdot m^{-2} \cdot s^{-1}$) from B fluorescent tubes (peak wavelength = 460 nm, but also weakly emitted FR light) promoted flowering of *Arabidopsis* (Goto et al., 1991). Additional plants outside of the Brassicaceae perceived B light as an LD signal. For example, a 1-h NI with B light (peak wavelength = 436 nm, intensity not reported) inhibited flowering of the SDP rice (*Oryza sativa*) (Ishikawa et al., 2009). A 10-min B NI (peak wavelength = 450 nm) inhibited flowering of the SDP duckweed (*Lemna paucicostata*); however, B light needed to be 20, 100, and 3 times higher in intensity, respectively, than green, R, and FR light to have the same inhibitory effect (Saji et

al., 1982). Similarly, the absolute amount of energy for B light to elicit the same flowering inhibition or promotion response as caused by R light was 20, 150, and 250 times higher, respectively, for the SDPs soybean (*Glycine max*) and cocklebur (*Xanthium strumarium*) and the LDP barley (*Hordeum vulgare*) (Thomas and Vince-Prue, 1997). Therefore, the effectiveness of B light in photoperiodic lighting is apparently dependent on a threshold intensity that can vary among species.

The promotion of flowering from at least a minimum threshold of B light could be mediated by cryptochromes, phytochromes, or both. As mentioned previously, phytochromes absorb blue light, but to a lesser extent than R and FR light (Vierstra and Quail; 1983). Therefore, a higher intensity of B light than R+FR light would logically be required to induce a phytochrome-mediated flowering response. However, the effectiveness of high-intensity B light can depend on light quality in the main photoperiod, at least for some crops. For example, a 4-h NI with B light (peak wavelength = 456 nm) at 39 $\mu mol \cdot m^{-2} \cdot s^{-1}$ did not inhibit flowering of chrysanthemum 'Reagan' when the base 12-h photoperiod was provided by white fluorescent lamps at 150 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Higuchi et al., 2012). In contrast, a 4-h NI with B light at 20 $\mu mol \cdot m^{-2} \cdot s^{-1}$ inhibited flowering when the main photoperiod consisted of solely B light at 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$. In our study, a 4-h NI with B light at 30 $\mu mol \cdot m^{-2} \cdot s^{-1}$ promoted flowering of all LDPs and inhibited flowering of all SDPs. To our knowledge, using a B NI to regulate flowering of popular photoperiodic ornamental crops has not been previously published.

Flowering of calibrachoa and petunia, both of the Solanaceae, was slightly earlier under the B_{30}* NI than under the B_0* NI. The average DLI throughout the experiment was approximately 12 $mol \cdot m^{-2} \cdot d^{-1}$, and a 4-h NI with B light at 15 and 30 $\mu mol \cdot m^{-2} \cdot s^{-1}$ increased the DLI by 0.2 and 0.4 $mol \cdot m^{-2} \cdot d^{-1}$ (or 1.7% and 3.3%), respectively, which is relatively

insignificant. Although increasing the average DLI can accelerate flowering of many crops (Fausey et al., 2005; Oh et al., 2009), flowering time of ageratum (*Ageratum houstonianum*), begonia (*Begonia ×semperflorens-cultorum*), impatiens (*Impatiens walleriana*), petunia 'Apple Blossom', and salvia (*Salvia coccinea*) was similar under an average DLI of 5 and 12 $mol \cdot m^{-2} \cdot d^{-1}$ (Faust et al., 2005). The intensity of the R+W+FR light already exceeded the threshold to regulate flowering (Whitman et al., 1998). Furthermore, a previous study showed that when the *PPF* of a 4-h NI intermittently provided by HPS lamps ranged from 0.8 to 25.4 $\mu mol \cdot m^{-2} \cdot s^{-1}$, flowering of campanula 'Pearl Deep Blue', coreopsis 'Early Sunrise', and petunia 'East Wave Coral Reef' was similar (Blanchard and Runkle, 2010). Therefore, this promotion of flowering from additional B to R+W+FR light was probably not from greater photosynthesis. Earlier flowering under B_{30}* NI cannot be readily explained by the estimated P_{FR}/P_{R+FR} of the lighting treatments, since their values (Table IV-2) are within the moderate range that regulates flowering of LDPs through phytochromes (Craig and Runkle, 2012). A cryptochrome-mediated response or the coaction of activated phytochromes and cryptochromes offers a reasonable explanation, because sensitivity of flowering to photoperiod can be mediated by both families of photoreceptors (Cashmore et al., 1999).

The B_0* DE+B_{30} NI (which created an 18.5-h day) was as effective as the B_0* DE (which created a 14.5-h day) and B_{30} NI at controlling flowering of all crops except petunia and snapdragon. In agreement with these results, time to flower of petunia 'Express Blush Pink' decreased linearly as the photoperiod increased up to 14.4 h, and a longer photoperiod did not further promote flowering (Adams et al., 1998). However, the B_0* DE+B_{30} NI was more promotive than the B_0*DE and B_{30} NI for snapdragon. For snapdragon, an increase in photoperiod decreased flowering time, and flowering was most rapid under a 24-h photoperiod

(Cremer et al., 1998; Flint, 1960; Langhans and Maginnes, 1962). Some other facultative LDPs, such as *Arabidopsis* (Corbesier et al., 1996) and annual baby's breath (*Gypsophila elegans*) (Takeda, 1996), also flowered most rapidly under continuous light. Therefore, the earlier flowering of snapdragon under the 18.5-h day could simply be from a longer photoperiod.

All lighting treatments with R+W+FR light promoted flowering of all LDPs. The efficacy of R+W+FR light could at least partially be attributed to its effective R:FR of 0.81, since an R:FR of 0.59 to 1.07 promoted flowering of LDPs the most (Craig and Runkle, 2012). Similarly, the LDP lisianthus (*Eustoma grandiflorum*) 'Nail Peach Neo' flowered earlier as the R:FR decreased from 10 to 0.5 (Yamada et al., 2009). In addition, an R:FR of 0.23 to 0.71 promoted flowering of the LDP baby's breath (*Gypsophila paniculata*) 'Bristol Fairy' (Nishidate et al., 2012). These studies reinforce the paradigm that a somewhat equal mixture of R and FR light is more effective than R or FR light alone at promoting flowering of LDPs (Thomas and Vince-Prue, 1997).

DE and NI lighting are used to create LDs for regulation of flowering of photoperiodic plants, especially ornamentals and other specialty crops (Thomas and Vince-Prue, 1997). Flowering of rudbeckia 'Denver Daisy', tickseed (*Coreopsis verticillata*) 'Moonbeam', and spinach (*Spinacia oleracea*) 'Bloomsdale Longstanding' was similarly promoted under a 9-h day with a 7-h DE or 4-h NI (Craig, 2012). In addition, flowering of campanula (*Campanula carpatica*) 'Deep Blue Clips' and coreopsis 'Early Sunrise' was similar under a 9-h day with a 6-h DE or 4-h NI provided by INC, CFL, or both lamps (Padhye and Runkle, 2011). In our study, rudbeckia and marigold flowered similarly when an LD was created by a 5.5-h DE or 4-h NI provided by R+W+FR LEDs, but flowering of calibrachoa, coreopsis, petunia, and snapdragon was 14%, 10%, 11%, and 8% earlier, respectively, under the 4-h NI. Other studies have reported

earlier flowering from NI lighting than from DE lighting. For example, a 4-h NI promoted flowering of baby's breath 'Bristol Fairy' more effectively than a 4-h DE (Shillo and Halevy, 1982). In addition, a 4-h NI inhibited flowering of chrysanthemum 'Bianca' more effectively than a 6-h DE (Runkle et al., 2012).

In addition to the R:FR, extension growth of many crops is mediated by B light. For example, a 4-h NI provided by B LEDs (peak wavelength = 450 nm) at 1.7 $\mu mol \cdot m^{-2} \cdot s^{-1}$ inhibited internode length of chrysanthemum 'Reagan' compared with fluorescent lamps at 150 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Shimizu et al., 2006), although dramatic differences in light intensity were potentially confounding. Moreover, lettuce (*Lactuca sativa*) and radish (*Raphanus sativus*) were shorter under 12% B light+2% green+86% R light than under 2% green+98% R light (Cope et al., 2014). In our study, the intent of including the B_0* DE+B_{30} NI was to determine if an NI with B light would inhibit extension growth of plants under LDs (9-h SDs+5.5-h DE); however, B light did not influence stem length of most crops at flowering, and plant height of rudbeckia was 19% greater with the B NI. Since high-intensity B light was perceived as an LD in our study, a prolonged photoperiod might have promoted stem elongation of rudbeckia due to an increase in gibberellin biosynthesis or sensitivity (Xu et al., 1997). Other studies show the promotive effects of B light on extension growth. For example, chrysanthemum 'Zembla' grown for 42 d was 1.3 times taller but flowered similarly under a 4-h DE with B light (peak wavelength not reported) at 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ following an 11-h photoperiod compared with no DE lighting (Jeong et al., 2014). In addition, stem length of eggplant (*Solanum melongena*), but not lettuce, was greater under B light (peak wavelength = 470 nm) than under green (peak wavelength = 525 nm) or R light (peak wavelength = 660 nm), and it increased with B light intensity up to 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Hirai et al., 2006). Therefore, the role of B light in mediating extension growth is species and

cultivar specific (Hirai et al., 2006; Mizuno et al., 2009) and depends on delivery method, light intensity, and light duration, among other factors.

Compared with the SD, chlorophyll content per unit leaf area of marigold increased under high-intensity B light, but was similar under low-intensity NI lighting, confirming that increased chlorophyll content under a prolonged photoperiod occurred only with high-intensity lighting (Friend, 1961). Similarly, chlorophyll content per unit leaf area of cucumber (Hogewoning et al., 2010) and strawberry (Nhut et al., 2003) grown under sole-source lighting increased as B light intensity increased under a constant *PPF*. In the second replication of our study, chlorophyll content under the B_{30} NI was higher than that under the B_{30}* NI. In chrysanthemum, chlorophyll content of plants grown under sole-source lighting was reduced when FR light, rather than R light, was added to B light (Kim et al., 2004). Additionally, photoselective films intercepting FR light enhanced chlorophyll content of cucumber, tomato, and bell pepper seedlings compared with neutral-density films (Rajapakse and Li, 2004). Therefore, the inclusion of FR in photoperiodic lighting could potentially decrease chlorophyll content.

In conclusion, 4-h NI lighting with B light (peak wavelength = 450 nm) at 30 $\mu mol \cdot m^{-2} \cdot s^{-1}$ alone controlled flowering of all LDPs and SDPs studied; and it was as effective as 4-h NI lighting from R+W+FR light at 2 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Adding B light at 30 $\mu mol \cdot m^{-2} \cdot s^{-1}$ to R+W+FR light further promoted flowering of calibrachoa and petunia, but not other crops. Extension growth of most crops was not suppressed by additional B light at up to 30 $\mu mol \cdot m^{-2} \cdot s^{-1}$ while maintaining low-intensity R+W+FR light. The efficacy of high-intensity B light indicates possible involvement of cryptochromes, perhaps together with phytochromes, for regulating flowering. In all LDPs except rudbeckia, NI lighting was more promotive than DE lighting.

APPENDIX

Table IV-1. Average daily temperature (ADT) for each treatment during two replications (rep.) of the experiment. Plants were grown under a truncated 9-h short-day (SD) treatment with or without 4-h night-interruption (NI) and/or 5.5-h day-extension (DE) lighting from light-emitting diodes (LEDs). Numbers that follow blue (B) light represent their intensities in $\mu mol \cdot m^{-2} \cdot s^{-1}$. The asterisk (*) indicates low-intensity lighting provided by red+white+far-red LEDs.

Photoperiod treatment	ADT (°C) rep. 1	ADT (°C) rep. 2
SD	19.8	20.5
B_0* DE	19.8	21.2
B_0* NI	19.8	21.1
B_1* NI	19.8	19.7
B_{15}* NI	19.7	20.1
B_{30}* NI	20.1	20.2
B_{30} NI	20.0	19.9
B_0* DE+B_{30} NI	19.8	21.2

Table IV-2. Spectral characteristics and estimated phytochrome photoequilibria (P_{FR}/P_{R+FR}; Sager et al., 1988) of night-interruption lighting treatments. Numbers that follow blue (B) light represent their intensities in $\mu mol \cdot m^{-2} \cdot s^{-1}$. The asterisk (*) indicates low-intensity lighting provided by red+white+far-red LEDs. The $R:FR_{narrow}$ was calculated as 655 to 665 nm:725 to 735 nm. −, no data.

	Lighting treatment				
Parameter	B_0*	B_1*	B_{15}*	B_{30}*	B_{30}
Light intensity ($\mu mol \cdot m^{-2} \cdot s^{-1}$)					
Blue (B, 400−500 nm)	0.14	1.64	14.65	29.57	29.69
Green (500−600 nm)	0.30	0.30	0.34	0.41	0.13
Red (R, 600−700 nm)	0.81	0.84	0.78	0.82	0.00
Far red (FR, 700−800 nm)	1.00	1.08	0.99	1.15	0.00
Light ratio					
R:FR	0.81	0.78	0.78	0.71	0.57
$R:FR_{narrow}$	0.89	0.77	0.86	0.70	0.65
B:R	0.17	1.94	18.76	36.01	27932
P_{FR}/P_{R+FR}	0.67	0.64	0.57	0.54	0.48

Table IV-3. Days to first visible bud or inflorescence (VB), main stem length at flowering, VB number per plant at flowering, and increase in leaf number from transplant at flowering for five long-day plants and one short-day plant, marigold. Plants were grown under a truncated 9-h short-day (SD) treatment with or without 4-h night-interruption (NI) and/or 5.5-h day-extension (DE) lighting from light-emitting diodes (LEDs). Numbers that follow blue (B) light represent their intensities in $\mu mol \cdot m^{-2} \cdot s^{-1}$. The asterisk (*) indicates low-intensity lighting provided by red+white+far-red LEDs. All data within each species were pooled across experimental replications.

Photoperiod treatment	Days to VB	Stem length (cm)	VB number	Increase in leaf number
	Calibrachoa 'Callie Yellow Improved'			
SD	–	–	–	–
B_0* DE	17.5 a	14.9 ab	8.5 a	–
B_0* NI	15.7 ab	14.0 ab	7.1 a	–
B_1* NI	14.7 ab	14.1 ab	7.2 a	–
B_{15}* NI	13.8 ab	14.9 ab	5.9 a	–
B_{30}* NI	13.1 b	13.3 b	5.6 a	–
B_{30} NI	14.3 ab	12.2 b	7.8 a	–
B_0* DE+B_{30} NI	15.1 ab	17.0 a	7.1 a	–
Treatment	*	*	NS	–
Replication	***	***	***	–
Treatment×replication	NS	NS	*	–
	Coreopsis 'Early Sunrise'			
SD	–	–	–	–
B_0* DE	50.0 a	32.3 a	19.8 a	17.9 a
B_0* NI	43.5 abc	30.4 ab	15.1 abc	16.1 ab
B_1* NI	41.9 c	33.8 a	12.5 c	15.6 b
B_{15}* NI	46.0 abc	31.7 ab	15.6 abc	17.2 ab
B_{30}* NI	42.8 bc	33.7 a	14.1 bc	16.4 ab
B_{30} NI	47.4 abc	28.1 b	16.5 abc	17.1 ab
B_0* DE+B_{30} NI	47.7 ab	34.2 a	17.9 ab	17.5 ab
Treatment	*	***	*	*
Replication	***	***	NS	NS
Treatment×replication	*	NS	*	NS
	Petunia 'Wave Purple Improved'			
SD	56.6 a	35.7 a	14.3 b	46.5 a
B_0* DE	31.6 b	28.2 ab	22.1 a	22.2 b
B_0* NI	28.2 bc	25.3 b	20.9 a	21.3 bc
B_1* NI	27.9 bc	26.3 b	19.5 ab	20.6 bc
B_{15}* NI	27.3 c	26.2 b	19.4 ab	20.1 bc
B_{30}* NI	27.0 c	25.4 b	19.2 ab	19.2 c
B_{30} NI	27.6 bc	26.8 b	20.8 a	20.8 bc
B_0* DE+B_{30} NI	30.1 bc	29.0 ab	18.8 ab	21.6 b
Treatment	***	*	*	***
Replication	***	*	NS	*
Treatment×replication	***	*	NS	*

Table IV-3 (cont'd)

Photoperiod treatment	Days to VB	Stem length (cm)	VB number	Increase in leaf number
		Rudbeckia 'Indian Summer'		
SD	–	–	–	–
B_0* DE	55.3 a	53.6 cd	14.4 ab	11.9 a
B_0* NI	52.7 a	56.6 bcd	12.6 b	10.9 a
B_1* NI	52.2 a	61.1 abc	12.4 b	12.2 a
B_{15}* NI	54.0 a	65.3 a	15.9 ab	12.2 a
B_{30}* NI	51.1 a	63.2 ab	15.1 ab	11.8 a
B_{30} NI	50.7 a	52.8 d	13.1 b	11.4 a
B_0* DE+B_{30} NI	53.2 a	64.0 ab	18.1 a	12.0 a
Treatment	NS	***	*	NS
Replication	***	***	*	NS
Treatment×replication	NS	NS	NS	NS
		Snapdragon 'Liberty Classic Yellow'		
SD	46.2 a	42.7 b	17.0 a	35.9 a
B_0* DE	39.1 b	49.5 a	15.5 abc	25.4 b
B_0* NI	35.6 c	46.8 a	14.4 bcd	23.2 bc
B_1* NI	35.4 cd	46.0 ab	13.6 cd	22.3 cd
B_{15}* NI	33.6 de	47.3 a	13.3 d	21.1 d
B_{30}* NI	32.8 e	47.6 a	14.2 bcd	20.8 d
B_{30} NI	35.8 c	47.2 ab	16.2 ab	24.8 b
B_0* DE+B_{30} NI	32.0 e	47.2 a	13.9 cd	18.9 e
Treatment	***	*	***	***
Replication	***	***	NS	***
Treatment×replication	*	NS	NS	NS
		Marigold 'American Antigua Yellow'		
SD	18.3 b	10.6 d	12.4 d	11.0 b
B_0* DE	24.9 a	15.3 c	16.6 abc	17.0 a
B_0* NI	25.8 a	15.7 bc	15.2 c	17.4 a
B_1* NI	26.4 a	16.0 abc	13.8 cd	17.7 a
B_{15}* NI	25.3 a	16.4 ab	14.8 bcd	17.2 a
B_{30}* NI	25.5 a	16.8 a	17.3 ab	17.5 a
B_{30} NI	25.0 a	15.9 abc	19.8 a	17.1 a
B_0* DE+B_{30} NI	26.2 a	16.0 abc	15.1 abcd	17.2 a
Treatment	***	***	***	***
Replication	***	NS	*	***
Treatment×replication	NS	NS	*	NS

NS, nonsignificant; *, ***, significant at $P \leq 0.05$ or 0.001, respectively. Means within columns followed by different letters are significantly different by Tukey's honest significant difference test at $P \leq 0.05$. −, no data.

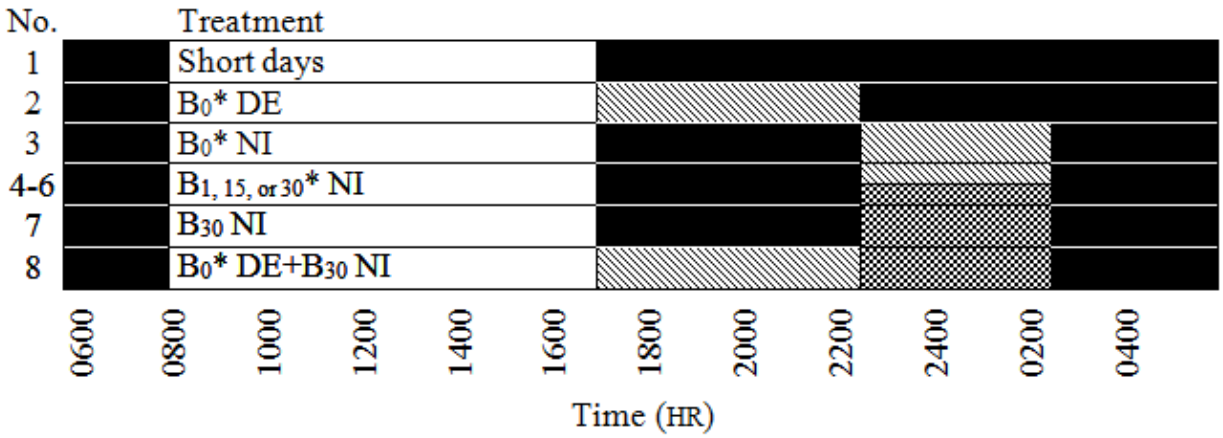

Figure IV-1. Diagram of photoperiodic lighting treatments indicating the truncated natural photoperiod (white bars; 0800 to 1700 HR), darkness (black bars), low-intensity red+white+far-red light (diagonal bar fill), and blue light (grid fill). Treatments consist of a truncated 9-h short-day treatment with or without 4-h night-interruption (NI) and/or 5.5-h day-extension (DE) lighting from light-emitting diodes (LEDs). Numbers that follow blue (B) light represent their intensities in $\mu mol \cdot m^{-2} \cdot s^{-1}$. The asterisk (*) indicates low-intensity lighting provided by red+white+far-red LEDs.

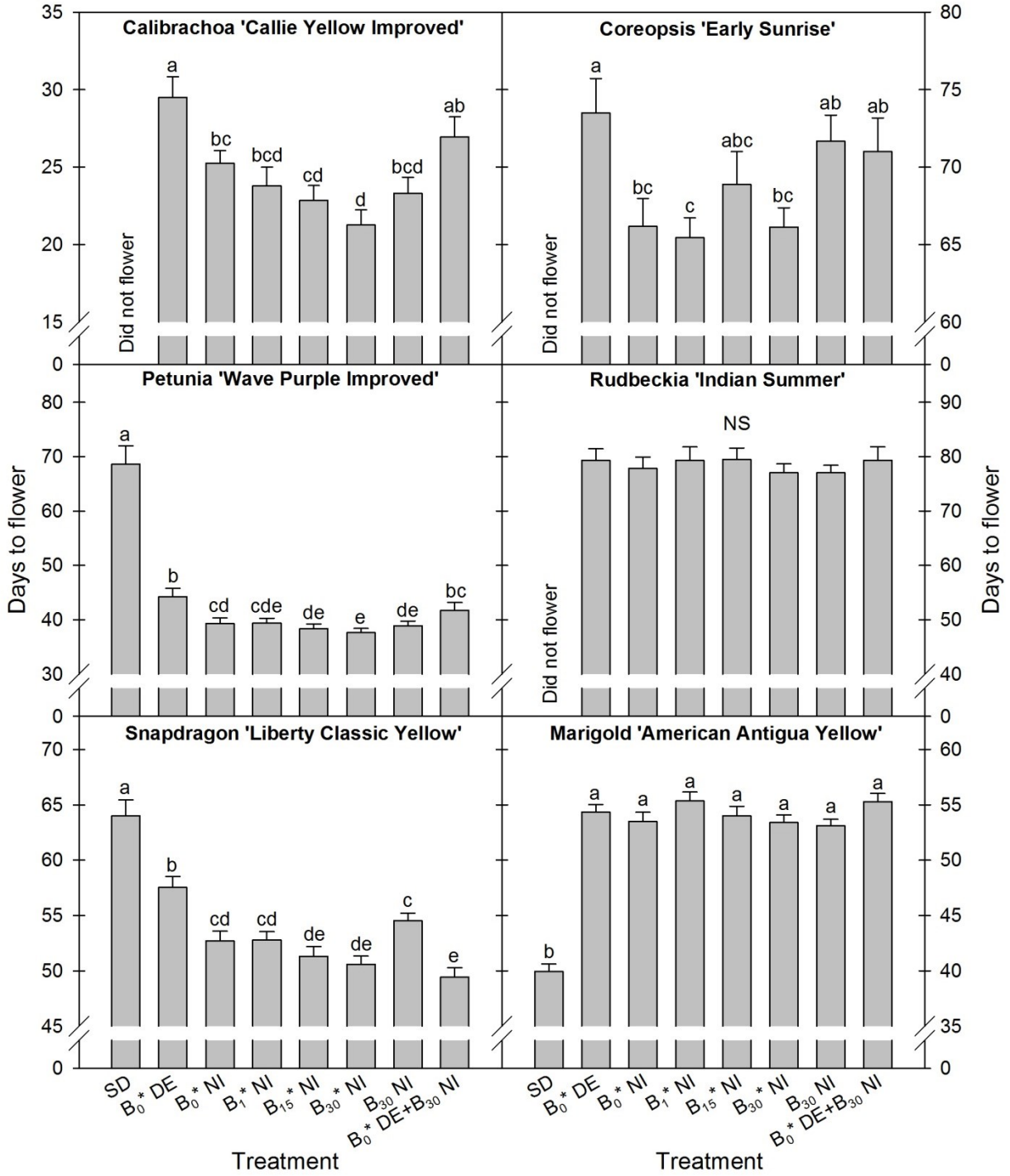

Figure IV-2. Days to flower of five long-day plants and one short-day plant (marigold) grown under a truncated 9-h short-day (SD) treatment with or without 4-h night-interruption (NI) and/or 5.5-h day-extension (DE) lighting from light-emitting diodes (LEDs). Numbers that follow blue (B) light represent their intensities in $\mu mol \cdot m^{-2} \cdot s^{-1}$. The asterisk (*) indicates low-intensity lighting provided by red+white+far-red LEDs. All data were pooled from two replications. Values followed by different letters within species are significantly different by Tukey's honest significant difference test at $P \leq 0.05$; NS, nonsignificant. Error bars indicate standard errors (n = 20). No data were collected from plants that did not flower before the experiment ended.

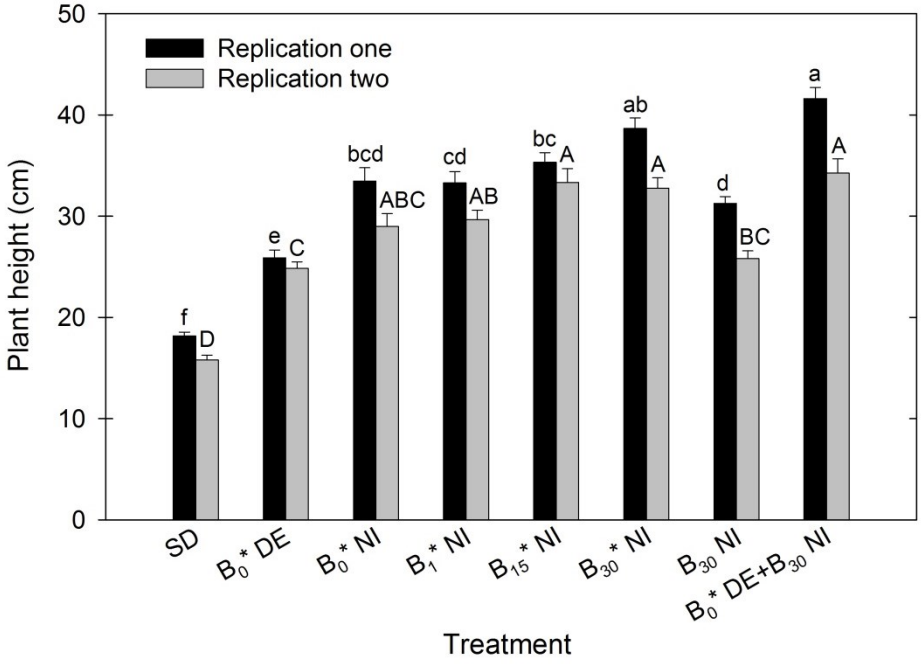

Figure IV-3. Plant height of snapdragon 46 and 42 days after transplant in replication one and two, respectively. Plants were grown under a truncated 9-h short-day (SD) treatment with or without 4-h night-interruption (NI) and/or 5.5-h day-extension (DE) lighting from light-emitting diodes (LEDs). Numbers that follow blue (B) light represent their intensities in $\mu mol \cdot m^{-2} \cdot s^{-1}$. The asterisk (*) indicates low-intensity lighting provided by red+white+far-red LEDs. Values followed by different letters within replication are significantly different by Tukey's honest significant difference test at $P \leq 0.05$. Error bars indicate standard errors (n = 10).

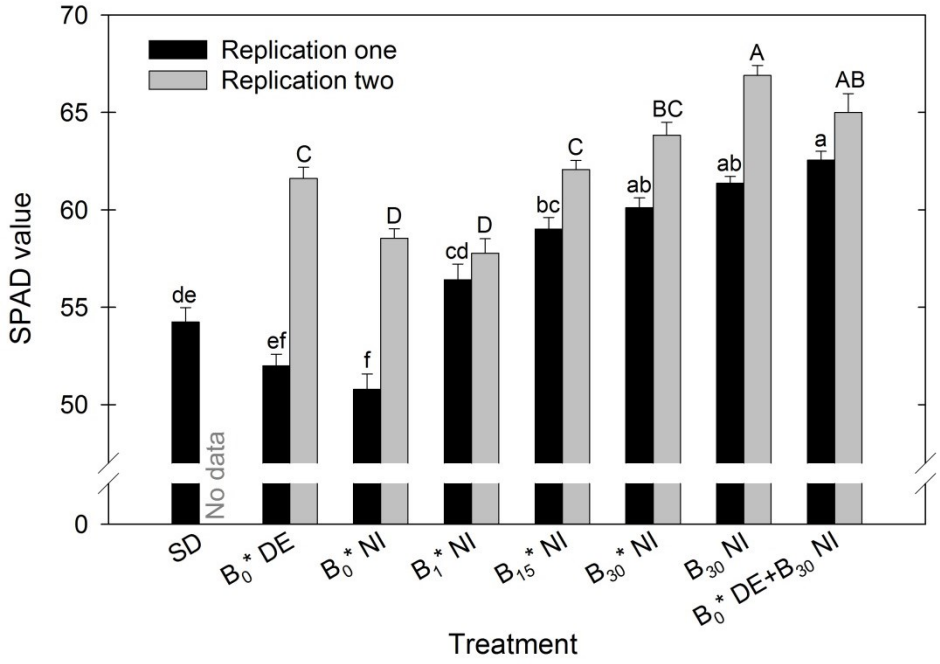

Figure IV-4. SPAD value (chlorophyll content per unit leaf area) of marigold 63 and 65 days after transplant in replication one and replication two, respectively. Plants were grown under a truncated 9-h short-day (SD) treatment with or without 4-h night-interruption (NI) and/or 5.5-h day-extension (DE) lighting from light-emitting diodes (LEDs). Numbers that follow blue (B) light represent their intensities in $\mu mol \cdot m^{-2} \cdot s^{-1}$. The asterisk (*) indicates low-intensity lighting provided by red+white+far-red LEDs. Values followed by different letters within replication are significantly different by Tukey's honest significant difference test at $P \leq 0.05$. Error bars indicate standard errors (n = 10).

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