Moderate-intensity blue radiation during the night can regulate flowering, but not extension growth, of several photoperiodic ornamental crops

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Abstract

When the natural photoperiod is short, lighting at the end of a day (day extension) or during the middle of a night (night interruption) can regulate flowering through intricate photoreceptive pathways. Phytochromes primarily absorb red (R; 600 to 700 nm) and far-red (FR; 700 to 800 nm) radiation and mediate flowering and photomorphogenesis. Although blue (B; 400 to 500 nm) radiation does not influence flowering at a low intensity, it can be well absorbed by photoreceptors such as cryptochromes and, to a lesser extent, phytochromes. Therefore, a relatively high dose of B radiation may be required to trigger these and other photoreceptors to elicit flowering responses. We grew five long-day plants and two short-day plants in a controlled-environment greenhouse under a 9-h short day with or without 5.5-h day-extension or 4-h night-interruption lighting from light-emitting diodes. B radiation was delivered at 0, 1 (low), 15, or 30 (moderate) $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, with or without low R+white+FR radiation. Moderate B radiation created long days in all crops as effectively as low R+white+FR radiation. Flowering of calibrachoa and petunia, but not other crops, was 2 to 4 d earlier when moderate B radiation was added to low R+white+FR radiation. At a sufficiently high intensity, B radiation possibly mediated these flowering responses through interactions of signaling molecules and multiple photoreceptors besides phytochromes. There were few or no photomorphogenic differences among flower-inducing treatments in most crops. We conclude that night-interruption lighting with moderate B radiation, alone and when added to low R and FR radiation, can regulate flowering, but does not inhibit extension growth, of a wide range of photoperiodic crops.

Keywords: Day-extension lighting, LEDs, Light-emitting diodes, Night-interruption lighting

Abbreviations: B, blue; DE, day extension; FR, far red; LD, long day; LED, light-emitting diode; NI, night interruption; PPE, phytochrome photoequilibrium; PPFD, photosynthetic photon flux density; R, red; SD, short day; VB, visible flower bud or inflorescence; W, white.

1. 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 (LD) plants, short-day (SD) plants, and day-neutral plants. Flowering of LD plants is promoted when the night length is less than a critical duration, and flowering of SD plants 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 in LD plants and SD plants (Thomas and Vince-Prue, 1997).

A large number of photoperiodic specialty crops are produced in protected environments in northern latitudes during winter and early spring, when daylength is relatively short (e.g., <12 h). Growers often deliver low-intensity (1 to $2 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) photoperiodic lighting at night to hasten flowering of LD plants to shorten production time and inhibit flowering of SD plants to stimulate vegetative growth. Therefore, photoperiodic lighting is crucial for scheduling crops so they are in flower on predetermined dates, can reduce production costs, and can elicit a stronger flowering response such as increase flower number. 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 during the middle of the night is similarly effective at controlling flowering of photoperiodic plants (Craig, 2012; Runkle and Fisher, 2004; Runkle et al., 1998).

Radiation is perceived through different classes of photoreceptors in higher plants, including phytochromes that primarily absorb red (R, 600 to 700 nm) and far-red (FR, 700 to 800 nm) radiation, cryptochromes that absorb blue (B, 400 to 500 nm) and ultraviolet-A radiation, and phototropins that absorb B radiation, as identified in the LD plant *Arabidopsis thaliana* (Casal, 2000). These photoreceptors interact to mediate flowering and photomorphogenesis (Cashmore et al., 1999; Demotes-Mainard et al., 2016; Huché-Thélier et al., 2016).

Phytochromes regulate flowering by establishing their active and inactive forms primarily in response to R and FR radiation (Sager et al., 1988). The most effective 10-nm wavebands of R and FR radiation 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 the active (P_{FR}) and inactive (P_R) forms of phytochromes weakly absorb B and ultraviolet-A radiation, with secondary P_R and P_{FR} absorption peaks at 380 and 408 nm, respectively (Butler et al., 1965; Sager et al., 1988). A phytochrome photoequilibrium (PPE), the fraction of P_{FR} in the total phytochrome pool, is established depending on the spectral distribution. There are similarities as well as differences in how SD plants and LD plants respond to the spectral distribution of photoperiodic lighting. R radiation with little or no FR, which elicited a moderate to high PPE (0.63 to 0.89), was effective at inhibiting flowering of SD plants (Craig and Runkle, 2013). Although R radiation alone can create an LD response in some LD plants, other LD plants require a combination of R and FR radiation for the most rapid flowering (Thomas and Vince-Prue, 1997); the most effective PPE to induce several herbaceous ornamentals was between 0.63 and 0.72 (Craig and Runkle, 2016).

For a variety of LD plants and SD plants, low-intensity B radiation ($<5 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) is generally not effective at extending natural SDs (Thomas and Vince-Prue, 1997). For example, B radiation (peak wavelength = 450, 455, 462, or 470 nm) at 0.8 to $3 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (PPE ≈ 0.52) was not perceived as LDs when delivered as a 4-h NI for a range of photoperiodic ornamental plants (Craig, 2012; Ho et al., 2012; Meng and Runkle, 2015). Likewise, chrysanthemum (*Chrysanthemum* $\times$ *morifolium*) ‘Zembla’ flowered similarly under an 11-h photoperiod with or without a 4-h DE with B radiation (peak wavelength = 455 nm) at $100 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (PPE not reported, but probably ≈ 0.5) (Singh et al., 2013).

However, in other studies, B radiation was perceived as LDs by LD plants and SD plants (Hamamoto et al., 2003; Saji et al., 1982; Shin et al., 2010). For at least some plants in the Brassicaceae, B radiation alone is reportedly effective for photoperiodic lighting (Thomas and Vince-Prue, 1997). For example, a 1-h NI at $250 \text{ mW}\cdot\text{m}^{-2}$ (probably $<2 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) from B fluorescent tubes (peak wavelength = 460 nm; PPE not reported, but probably ≈ 0.5), which also weakly emitted FR radiation, promoted flowering of *Arabidopsis* (Goto et al., 1991). Additional plants outside of the Brassicaceae perceived B radiation as LDs. For example, a 1-h NI with B radiation (peak wavelength = 436 nm; intensity and PPE not reported) inhibited flowering of the SD plant rice (*Oryza sativa*) (Ishikawa et al., 2009). A 10-min B NI (peak wavelength = 450 nm; PPE not reported, but probably ≈ 0.5) inhibited flowering of the SD plant duckweed (*Lemna paucicostata*); however, B radiation needed to be 100 and 3 times higher in intensity, respectively, than R and FR radiation to have the same inhibitory effect (Saji et al., 1982). Similarly, the absolute amount of energy for B radiation to elicit the same flowering inhibition or promotion response as caused by R radiation was 20, 150, and 250 times higher, respectively, for the SD plants soybean (*Glycine max*) and cocklebur (*Xanthium strumarium*) and the LD plant

barley (*Hordeum vulgare*) (Thomas and Vince-Prue, 1997). The photoperiodic pathway mediated by B radiation involves stabilization of *CONSTANS* proteins through interactions among photoreceptors and signaling molecules, such as cryptochrome 2, *SUPPRESSOR OF PHYA-105*, *FLAVIN-BINDING KELCH REPEAT F-BOX 1*, and *GIGANTEA* (Fornara et al., 2009; Huché-Thélier et al., 2016; Song et al., 2012; Valverde et al., 2004). The coincidence of the photoperiod and expression of the transcription factor *CONSTANS* and the floral promoter *FLOWERING LOCUS T* induces flowering (Abe et al., 2005; Corbesier et al., 2007).

Given the contrasting results from the studies above, whether photoperiodic B radiation mediates flowering could depend on radiation intensity, radiation duration, specific B radiation wavelengths, and species. It was still unclear if B radiation could control flowering of common ornamental crops grown in commercial greenhouses. Although B radiation at 1 to 2 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (PPE = 0.53) was not effective at interrupting the night for a wide range of ornamental crops (Meng and Runkle, 2015), the effectiveness of a higher intensity of B radiation cannot be eliminated for two reasons. First, B radiation-absorbing photoreceptors (e.g., cryptochromes) mediate flowering in at least some plants, and second, phytochromes have low secondary absorption peaks in the B region (Butler et al., 1965; Vierstra and Quail; 1983), so a higher irradiance of B radiation may be required to elicit a phytochrome-mediated response. However, even if high-intensity B radiation could regulate flowering, it would be impractical for photoperiodic lighting unless it was more effective than low-intensity R and FR radiation. It is the potential of using B radiation to regulate photomorphogenesis that may justify this application. B radiation may substitute for plant growth regulators to produce desirably compact ornamentals because of its inhibitory role on extension growth (Islam et al., 2012; Kim, 2004). High-intensity B radiation could also be useful if it did not interfere with flowering but inhibited

extension growth while contributing to photosynthesis. This study investigated whether B radiation at a moderate intensity (e.g., $30 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), with and without R+white (W)+FR radiation, could regulate flowering while controlling extension growth of a range of photoperiodic ornamental crops.

2. Materials and Methods

2.1. Plant materials

Several ornamental crops were chosen for study according to their economic importance and photoperiodic response, as well as our experience in working with the plants. 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 LD plants, calibrachoa (*Calibrachoa* $\times$ hybrida) ‘Callie Yellow Improved’, coreopsis (*Coreopsis grandiflora*) ‘Early Sunrise’, petunia (*Petunia* $\times$ hybrida) ‘Wave Purple Improved’, rudbeckia (*Rudbeckia hirta*) ‘Indian Summer’, and snapdragon (*Antirrhinum majus*) ‘Liberty Classic Yellow’; and two SD plants, chrysanthemum ‘Cheryl Golden Yellow’ and marigold (*Tagetes erecta*) ‘American Antigua Yellow’. This experiment was performed twice. Plants were received on 22 Nov. 2013 for the first replication (Rep. 1) and on 13 Feb. 2014 for the second replication (Rep. 2). Calibrachoa, coreopsis, petunia, rudbeckia, snapdragon, marigold, and chrysanthemum were transplanted on 12 Dec., 13 Dec., 13 Dec., 12 Dec., 12 Dec., 10 Dec. 2013, and 16 Feb. 2014, respectively, for Rep. 1, and on 14 Feb., 18 Feb., 18 Feb., 18 Feb., 18 Feb., 16 Feb., and 18 Apr. 2014, respectively, for Rep. 2. Before the onset of treatments, all LD plants were grown under a truncated 9-h 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 light from 400-W

high-pressure sodium lamps (PL2000; P.L. Light Systems Inc., Beamsville, ON, Canada) that delivered a photosynthetic photon flux density (PPFD) of 60 to 90 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at plant canopy from 0600 to 2200 HR. The high-pressure sodium lamps switched on when the ambient solar PPFD was $<185 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at plant canopy and turned off when the ambient PPFD was $>370 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Because calibrachoa were reproductive on receipt in Rep. 2, 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 $\text{mg}\cdot\text{L}^{-1}$ foliar spray at 0.2 $\text{L}\cdot\text{m}^{-2}$ on 5 May 2014, and these applications effectively made them vegetative (Dole and Wilkins, 1999).

When the plants were ready for transplant according to commercial production standards, 10 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, the 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 PPFD in three of the treatments every 10 s. A data logger (CR10; Campbell Scientific, Logan, UT) recorded hourly averages of air temperature and PPFD. When the nighttime air temperature at plant canopy was <18.9 °C, a 1500-W electric heater underneath each bench provided supplemental heating. The mean daily air temperature in each treatment is provided in Table 1. The mean photosynthetic daily light integral was 9.0 and 14.7 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ during Reps. 1 and 2, respectively. Watering and fertility were applied to all plants alike according to established experimental protocols as described by Vaid et al. (2014).

Table 1. Mean daily air temperature 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) or 5.5-h day-extension (DE) lighting from light-emitting diodes (LEDs). DE and NI indicate lighting at $2 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ provided by red+white+far-red LEDs. Blue (B) radiation was delivered only as an NI, and numbers that follow B radiation represent their intensities in $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. See Fig. 1 for descriptions of experimental treatments.

Photoperiod treatment	Air temperature [mean $\pm$ SD ($^{\circ}\text{C}$)]	
	Rep. 1	Rep. 2
SD	19.8 ± 2.0	20.5 ± 1.9
DE	19.8 ± 1.4	21.2 ± 2.0
NI	19.8 ± 0.9	21.1 ± 2.2
NI+B ₁	19.8 ± 0.7	19.7 ± 1.3
NI+B ₁₅	19.7 ± 0.8	20.1 ± 1.3
NI+B ₃₀	20.1 ± 1.1	20.2 ± 1.4
B ₃₀	20.0 ± 1.0	19.9 ± 1.3
DE+B ₃₀	19.8 ± 1.4	21.2 ± 2.0

Fig. 1. Diagram of photoperiodic lighting treatments indicating the truncated natural photoperiod (white bars; 0800 to 1700 HR), darkness (black bars), red+white+far-red radiation at $2 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (diagonal bar fill), and blue radiation (vertical dash fill). Treatments consisted of a truncated 9-h short-day treatment with or without 4-h night-interruption (NI) or 5.5-h day-

extension (DE) lighting. DE and NI indicate lighting at $2 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ provided by red+white+far-red light-emitting diodes. Blue (B) radiation was delivered only as an NI, and numbers that follow B radiation represent their intensities in $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$.

2.2. 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 as an unlighted control or to one of the seven photoperiodic lighting treatments: DE, NI, NI+B₁, NI+B₁₅, NI+B₃₀, B₃₀, and DE+B₃₀, where DE and NI indicate lighting from R+W+FR light-emitting diodes (LEDs) (14 W, GreenPower LED flowering DR/W/FR 120V, E26; Philips, Eindhoven, the Netherlands) at $2 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ between 400 and 800 nm and each number after B represents its intensity (in $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) provided by B LEDs (14 W, GreenPower LED research module blue; Philips) (Fig. 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. NI and DE lighting were compared because they are two common lighting strategies used to regulate flowering in greenhouse production, which are usually equally effective but sometimes their efficacy varies (Thomas and Vince-Prue, 1997). Because the sensitivity of multiple flowering-related transcription factors oscillates in circadian rhythms and often peaks near the middle of the night (Park et al., 1999), a shorter duration of lighting is usually sufficient to regulate flowering during the middle of the night (NI) than when delivered at the end of the day (DE). Spectral characteristics of the lighting treatments were measured by a portable spectroradiometer at the initial growing height of plants (LI-1800; LI-COR, Inc., Lincoln, NE) (Table 2). For each

lighting treatment, the R-to-FR radiation ratio (R:FR) was described using 100- or 10-nm wavebands, and the estimated PPE was calculated according to Sager et al. (1988). Radiation intensity was adjusted as needed by layering mesh screen under the radiation sources, moving radiation sources vertically, or using a dimming program that regulated B radiation intensity. All plants under the photoperiodic lighting treatments were placed on benches only where 1 to 3 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ of R+FR radiation or 90% to 110% of the target B radiation intensity was achieved as measured with the spectroradiometer.

Table 2. Spectral characteristics and estimated phytochrome photoequilibria (PPE; Sager et al., 1988) of lighting treatments. Day extension (DE) and night interruption (NI) indicate lighting at 2 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ provided by red+white+far-red LEDs. Blue (B) radiation was delivered only as an NI, and numbers that follow B radiation represent their intensities in $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. See Fig. 1 for descriptions of experimental treatments. The R:FR_{narrow} was calculated as 655 to 665 nm:725 to 735 nm.

Parameter	Lighting treatment				
	DE/NI	NI+B ₁	NI+B ₁₅	NI+B ₃₀	B ₃₀
<i>Radiation intensity ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)</i>					
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
<i>Radiation ratio</i>					
R:FR	0.81	0.78	0.78	0.71	NA ^z
R:FR _{narrow}	0.89	0.77	0.86	0.70	NA
B:R	0.17	1.94	18.76	36.01	NA
PPE	0.67	0.64	0.57	0.54	0.48

^zNA, not applicable.

2.3. 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. 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 was perpendicular to the stem, and for other plants when the first flower opened, date of flowering, plant height (from the medium 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. The VB number is a measure of the magnitude of a flowering response. For petunia, the stem with the first open flower was selected for measurements of stem length and leaf number. Days to VB from transplant, days to flower from transplant (and for calibrachoa in Rep. 2, from when ethephon was applied), increase in leaf number, and flowering percentage were subsequently calculated. In addition, plant height of snapdragon was measured 46 and 42 d after transplant for Reps. 1 and 2, respectively to evaluate extension growth without the influence of flowering time.

Data were analyzed with SAS (version 9.3; SAS Institute, Cary, NC) means (PROC MEANS), mixed-model (PROC MIXED), and glimmix-model (PROC GLIMMIX) procedures, and pairwise comparisons between treatments were performed with Tukey's honest significant difference test ($\alpha = 0.05$). Data from Reps. 1 and 2 were pooled when there was no interaction between main effects and replication or when response trends were similar between replications.

3. Results

Although there were a few treatment-by-replication interactions, all data from Reps. 1 and 2 were pooled because of similar response trends among treatments, which substantiated the reproducibility of the results. Since the experimental block was time, differences between the

two replications represented seasonal variations that applied to all treatments. The effects of multiple factors are presented in Table 3.

3.1. Long-day plants

All lighting treatments induced complete flowering of calibrachoa, petunia, rudbeckia, and snapdragon and $\geq 80\%$ of coreopsis plants (data not shown). Coreopsis and rudbeckia did not flower under the SD. The B₃₀ was as effective as the NI at promoting flowering of all LD plants. The addition of B₃₀ to the NI triggered a slightly stronger LD response in calibrachoa and petunia, which flowered 4 and 2 d earlier, respectively, than under the NI (Fig. 2). However, the additional B radiation did not influence flowering of the other crops. All LD plants grown under the NI flowered similarly with or without B₁ or B₁₅ (Fig. 2). For plants grown under the DE, the subsequent B₃₀ did not affect flowering of any LD plants except snapdragon, which flowered earlier under the DE+B₃₀ than under the DE and B₃₀ (Fig. 2).

With R+W+FR radiation at $2 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, the NI was more promotive of flowering than the DE for all LD plants except rudbeckia. Flowering of calibrachoa, coreopsis, petunia, and snapdragon was 4, 7, 5, and 5 d earlier, respectively, under the NI than under the DE (Fig. 2). For snapdragon, delayed flowering was associated with an increase in leaf number (correlation not shown). Similarly, petunia developed 29 to 32 more leaves when flowering was delayed by 29 to 36 d under the SD than under all lighting treatments (Table 3 and Fig. 2). Lighting treatments had no effect on flower development (time from first VB to open flower) for any species.

Table 3. Main stem length, visible bud or inflorescence (VB) number per plant, and increase in leaf number from transplant at flowering for five long-day plants and two short-day (SD) plants. Plants were grown under a truncated 9-h SD treatment with or without 4-h night-interruption (NI) or 5.5-h day-extension (DE) lighting from light-emitting diodes (LEDs). DE and NI indicate lighting at $2 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ provided by red+white+far-red LEDs. Blue (B) radiation was delivered only as an NI, and numbers that follow B radiation represent their intensities in $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. See Fig. 1 for descriptions of experimental treatments. All data within each species were pooled between replications (n = 20).

Photoperiod treatment	Stem length (cm)	VB (no.)	Increase in leaf (no.)
<i>Calibrachoa</i>			
SD	25.3 a ^z	9.4 a	— ^y
DE	14.9 bc	8.5 ab	—
NI	14.0 bc	7.1 ab	—
NI+B ₁	14.1 bc	7.2 ab	—
NI+B ₁₅	14.9 bc	5.9 ab	—
NI+B ₃₀	13.3 c	5.6 b	—
B ₃₀	12.2 c	7.8 ab	—
DE+B ₃₀	17.0 b	7.1 ab	—
Treatment	*** ^x	*	—
Replication (Rep.)	***	***	—
Treatment×Rep.	***	***	—
<i>Coreopsis</i>			
SD	—	—	—
DE	32.3 a	19.8 a	17.9 a
NI	30.4 ab	15.1 abc	16.1 ab
NI+B ₁	33.8 a	12.5 c	15.6 b
NI+B ₁₅	31.7 ab	15.6 abc	17.2 ab
NI+B ₃₀	33.7 a	14.1 bc	16.4 ab
B ₃₀	28.1 b	16.5 abc	17.1 ab
DE+B ₃₀	34.2 a	17.9 ab	17.5 ab
Treatment	***	*	*
Rep.	***	NS	NS
Treatment×Rep.	NS	*	NS
<i>Petunia</i>			
SD	35.9 a	12.9 b	51.2 a
DE	28.2 b	22.1 a	22.2 b
NI	25.3 b	20.9 a	21.3 b

Photoperiod treatment	Stem length (cm)	VB (no.)	Increase in leaf (no.)
NI+B ₁	26.3 b	19.5 ab	20.6 b
NI+B ₁₅	26.2 b	19.4 ab	20.1 b
NI+B ₃₀	25.4 b	19.2 ab	19.2 b
B ₃₀	26.8 b	20.8 a	20.8 b
DE+B ₃₀	29.0 b	18.8 ab	21.6 b
Treatment	***	*	***
Rep.	*	NS	NS
Treatment×Rep.	*	NS	NS
<i>Rudbeckia</i>			
SD	—	—	—
DE	53.6 cd	14.4 ab	11.9 a
NI	56.6 bcd	12.6 b	10.9 a
NI+B ₁	61.1 abc	12.4 b	12.2 a
NI+B ₁₅	65.3 a	15.9 ab	12.2 a
NI+B ₃₀	63.2 ab	15.1 ab	11.8 a
B ₃₀	52.8 d	13.1 b	11.4 a
DE+B ₃₀	64.0 ab	18.1 a	12.0 a
Treatment	***	*	NS
Rep.	***	*	NS
Treatment×Rep.	NS	NS	NS
<i>Snapdragon</i>			
SD	42.7 b	17.0 a	35.9 a
DE	49.5 a	15.5 abc	25.4 b
NI	46.8 a	14.4 bcd	23.2 bc
NI+B ₁	46.0 ab	13.6 cd	22.3 cd
NI+B ₁₅	47.3 a	13.3 d	21.1 d
NI+B ₃₀	47.6 a	14.2 bcd	20.8 d
B ₃₀	47.2 ab	16.2 ab	24.8 b
DE+B ₃₀	47.2 a	13.9 cd	18.9 e
Treatment	*	***	***
Rep.	***	NS	***
Treatment×Rep.	NS	NS	NS
<i>Chrysanthemum</i>			
SD	10.3 d	31.4 c	—
DE	16.3 c	75.4 b	—
NI	20.7 b	97.6 ab	—
NI+B ₁	23.9 ab	149.6 a	—
NI+B ₁₅	21.6 ab	132.3 a	—
NI+B ₃₀	26.4 a	147.0 a	—
B ₃₀	16.8 c	83.3 b	—
DE+B ₃₀	20.9 b	121.5 a	—
Treatment	***	***	—
Rep.	***	***	—
Treatment×Rep.	***	*	—

Photoperiod treatment	Stem length (cm)	VB (no.)	Increase in leaf (no.)
<i>Marigold</i>			
SD	10.6 d	12.4 d	11.0 b
DE	15.3 c	16.6 abc	17.0 a
NI	15.7 bc	15.2 c	17.4 a
NI+B ₁	16.0 abc	13.8 cd	17.7 a
NI+B ₁₅	16.4 ab	14.8 bcd	17.2 a
NI+B ₃₀	16.8 a	17.3 ab	17.5 a
B ₃₀	15.9 abc	19.8 a	17.1 a
DE+B ₃₀	16.0 abc	15.1 abcd	17.2 a
Treatment	***	***	***
Rep.	NS	*	***
Treatment×Rep.	NS	*	NS

^zMeans followed by different letters within columns for each species are significantly different

by Tukey's honest significant difference test at $P \leq 0.05$.

^yNo data.

^xNS, *, *** Nonsignificant or significant at $P \leq 0.05$ or 0.001, respectively.

Fig. 2. Time to first open flower and first visible bud or inflorescence (VB) of five long-day plants grown under a truncated 9-h short-day (SD) treatment with or without 4-h night-interruption (NI) or 5.5-h day-extension (DE) lighting from light-emitting diodes (LEDs). DE and NI indicate lighting at $2 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ provided by red+white+far-red LEDs. Blue (B) radiation was delivered only as an NI, and numbers that follow B radiation represent their intensities in $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. See Fig. 1 for descriptions of experimental treatments. 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. Letters outside and inside the bars are for time to first open flower and time to first VB, respectively. Error bars indicate standard errors ($n = 20$). No data were collected from plants that did not flower before the experiment ended.

The main stem length of all LD plants at flowering was generally similar among the lighting treatments (Table 3). However, coreopsis and rudbeckia were 13% to 19% shorter under the B₃₀ than under most other lighting treatments (Table 3). Calibrachoa under the DE+B₃₀ were 28% to 39% taller than those under the NI+B₃₀ and B₃₀ (Table 3). When measured 46 and 42 d after transplant for Reps. 1 and 2, respectively, snapdragon plants under the B₃₀ were shorter than those under the NI+B₁, NI+B₁₅, NI+B₃₀, and DE+B₃₀ (Fig. 3). However, at flowering, plant height of snapdragon was similar under all lighting treatments.

Fig. 3. Plant height of snapdragon 46 and 42 d after transplant in replications 1 and 2, respectively. Data were pooled from two replications. Plants were grown under a truncated 9-h short-day (SD) treatment with or without 4-h night-interruption (NI) or 5.5-h day-extension (DE) lighting. See Fig. 1 for descriptions of experimental treatments. 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 ($n = 20$).

VB number of calibrachoa and petunia was similar under all lighting treatments (Table 3). Coreopsis under the DE developed 40% to 58% more VBs at flowering than those under the NI+B₁ and NI+B₃₀ (Table 3). Rudbeckia formed 38% to 46% more VBs under the DE+B₃₀ than under the NI, NI+B₁, and B₃₀ (Table 3). The VB number of coreopsis and snapdragon was positively correlated with days to flower (correlations not shown).

3.2. Short-day plants

Flowering of chrysanthemum was incomplete under all treatments except the SD, DE, and B₃₀, whereas all marigold plants flowered under all treatments (data not shown). All lighting treatments delayed flowering of marigold by 13 to 15 d compared with the SD; however, the efficacy of the lighting treatments differed for chrysanthemum (Fig. 4). The B₃₀ was as inhibitory to flowering of chrysanthemum as the DE. Flowering of chrysanthemum under the NI was 11 d later when B₃₀ was added (Fig. 4). The NI delayed flowering of chrysanthemum by 11 d compared with the DE (Fig. 4).

Plant height and VB number of chrysanthemum at flowering had similar trends among treatments and were positively correlated with time to flower (Table 3) (correlations not shown). Marigold under the SD was 31% to 37% shorter than those under all lighting treatments (Table 3). Marigold developed 6 or 7 more leaves under all lighting treatments than under SD (Table 3).

Fig. 4. Time to first open flower and first inflorescence (VB) of two short-day (SD) plants grown under a truncated 9-h SD treatment with or without 4-h night-interruption (NI) or 5.5-h day-extension (DE) lighting. See Fig. 1 for descriptions of experimental treatments. 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 ($n = 20$).

4. Discussion

The similar trends of time to first VB and time to flower showed that the photoperiodic radiation treatments influenced floral induction and initiation, but not development from VB to flower. In this study, a 4-h NI with B₃₀ (with the lowest estimated PPE of all treatments, 0.48) promoted flowering of all LD plants and inhibited flowering of all SD plants at least as effectively as R+W+FR radiation (with the highest estimated PPE of all treatments, 0.67). The estimated PPE of a light source alone does not accurately predict its efficacy at controlling flowering because the moderate-intensity B NI (estimated PPE = 0.48) regulated flowering, whereas low-intensity B NIs with a similar estimated PPE of 0.51 (Craig, 2012) or 0.53 (Meng and Runkle, 2015) did not for crops such as petunia and rudbeckia that were also used in the current study. Therefore, a moderate estimated PPE (0.45 to 0.70) can be associated with effectiveness at regulation of flowering (Craig and Runkle, 2016) only when the spectrum reaches a sufficiently high intensity to saturate flowering responses. Earlier flowering under NI+B₃₀ (estimated PPE = 0.54) than under NI (estimated PPE = 0.67) cannot be readily explained by the estimated PPE because their values are both within the most effective range of PPE that regulates flowering of LD plants through phytochromes (Craig and Runkle, 2016).

Aside from phytochromes, other photoreceptors absorbing B radiation (e.g., cryptochrome 1 and 2 and FLAVIN-BINDING KELCH REPEAT F-BOX 1) may regulate the photoperiodic pathway mediated by B radiation (Cashmore et al., 1999; Folta and Carvalho, 2015; Huché-Thélier et al., 2016). In fact, B radiation can induce flowering of *Arabidopsis* by activating cryptochrome 2 against phytochrome B mediated by R radiation (Guo et al., 1998; Wang and Folta, 2013). In addition, B radiation enhances the interaction of FLAVIN-BINDING KELCH REPEAT F-BOX 1 with CONSTANS protein through the former's LOV domain and

ultimately facilitates the expression of *FLOWERING LOCUS T* (Song et al., 2012). Perhaps these and other photoreceptors are involved in the control of flowering mediated by moderate-intensity B radiation in the ornamental crops studied.

Flowering of calibrachoa and petunia, both of the Solanaceae, was slightly earlier under the NI+B₃₀ than under the NI. Although an increased light intensity can increase photosynthesis and thus influence flowering, the increased daily light integral here is relatively insignificant from a photosynthesis perspective; the average daily light integral during the experiment was >9 mol·m⁻²·d⁻¹, and the 4-h NI with B₁₅ and B₃₀ increased the daily light integral by merely 0.2 and 0.4 mol·m⁻²·d⁻¹. Flowering time of petunia was accelerated by 2% and 4% with additional B₁₅ and B₃₀, respectively, somewhat matching the increases in daily light integral, whereas that of calibrachoa was accelerated by much greater degrees, 10% and 16%, respectively. However, attributing this flowering promotion proportionally to the increased daily light integral (and hence photosynthesis) is problematic. Although increasing the average daily light integral 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 daily light integral of 5 and 12 mol·m⁻²·d⁻¹ (Faust et al., 2005). Furthermore, when the PPFD of a 4-h NI intermittently provided by high-pressure sodium lamps ranged from 0.8 to 25.4 μmol·m⁻²·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 radiation cannot be attributed to the increased daily light integral (or photosynthesis).

The DE+B₃₀ (which created an 18.5-h day) was as effective as the DE (which created a 14.5-h day) at controlling flowering of all LD plants except 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). The critical photoperiods in these cases were less than 14.5 h. Therefore, DE alone sufficiently saturated flowering responses of most LD plants, and extended lighting did not further promote flowering. However, snapdragon might have a longer critical photoperiod than the other LD plants so that a longer photoperiod was needed to achieve the most rapid promotion of flowering. 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 LD plants, such as *Arabidopsis* (Corbesier et al., 1996) and annual baby’s breath (*Gypsophila elegans*) (Takeda, 1996), also flowered most rapidly under continuous radiation. Therefore, the earlier flowering of snapdragon under the 18.5-h day could simply have been caused by a longer photoperiod.

All lighting treatments with R+W+FR radiation promoted flowering of all LD plants. The efficacy of R+W+FR radiation, which created an estimated PPE of 0.67, was expected because a PPE of 0.63 to 0.72 promoted flowering of LD plants the most (Craig and Runkle, 2016). Similarly, the LD plant lisianthus (*Eustoma grandiflorum*) ‘Nail Peach Neo’ flowered earlier as the R:FR decreased from 10 to 0.5 (PPE not reported, but probably decreased from 0.9 to 0.6) (Yamada et al., 2009). In addition, an R:FR of 0.23 to 0.71 (PPE not reported, but probably between 0.4 to 0.7) promoted flowering of the LD plant baby’s breath (*Gypsophila paniculata*) ‘Bristol Fairy’ (Nishidate et al., 2012). Additional FR radiation may accelerate flowering by reducing the active P_{FR} form of phytochrome B, which acts as an inhibitor of flowering in both

LD plants and SD plants (Reed et al., 1994; Taiz et al., 2015). In addition, phytochrome A and phytochrome C can exert crucial roles in upregulation of flowering (Chen et al., 2014; Taiz et al., 2015). However, FR radiation alone does not create a long day (Craig and Runkle, 2016). Collectively, these studies reinforce the paradigm that a somewhat equal mixture of R and FR radiation (which creates an intermediate PPE) is more effective than R or FR radiation alone at promoting flowering of LD plants (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 incandescent lamps, compact fluorescent ones, or both (Padhye and Runkle, 2011). In our study, rudbeckia and marigold flowered similarly when an LD was created by the 5.5-h DE or 4-h NI, 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).

Aside from the R:FR, B radiation mediates extension growth of many crops. In our study, we delivered combinations of R+W+FR and B radiation at various intensities to determine whether an NI with B radiation would inhibit extension growth of plants under LDs; however, B

radiation did not influence stem length of most crops at flowering. One exception is plant height of rudbeckia, which was 19% greater with the B NI following the DE. Because moderate-intensity B radiation was perceived as an LD in our study, a prolonged photoperiod might have promoted stem elongation of rudbeckia because of an increase in gibberellin biosynthesis or sensitivity (Xu et al., 1997). Other studies have shown the promotive effects of B radiation on extension growth. For example, chrysanthemum ‘Zembla’ grown for 42 d was 33% taller but flowered similarly under a 4-h DE with B radiation (peak wavelength not reported) at $100 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ after an 11-h photoperiod compared with no DE lighting (Jeong et al., 2014). In addition, stem length of eggplant (*Solanum melongena*), but not lettuce (*Lactuca sativa*), was greater under B radiation (peak wavelength = 470 nm) than under green (peak wavelength = 525 nm) or R radiation (peak wavelength = 660 nm), and it increased with B radiation intensity up to $100 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Hirai et al., 2006). Therefore, the role of B radiation in mediating extension growth is species and cultivar specific (Hirai et al., 2006; Mizuno et al., 2009) and depends on delivery method, radiation intensity, and radiation duration, among other factors. In contrast, B radiation in photoperiodic lighting is inhibitory to stem elongation in other studies. For example, a 4-h NI provided by B LEDs (peak wavelength = 450 nm) at $1.7 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ inhibited internode length of chrysanthemum ‘Reagan’ compared with fluorescent lamps at $150 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Shimizu et al., 2006), although significant differences in radiation intensity were potentially confounding. Lettuce and radish (*Raphanus sativus*) were shorter under 12% B radiation+2% green+86% R radiation than under 2% green+98% R radiation (Cope et al., 2014). In this study, B radiation neither promoted nor inhibited extension growth of most ornamental crops studied, possibly because the amount of B radiation delivered during the day (from sunlight) had already saturated B-absorbing photoreceptors.

In addition to flowering time, VB number and leaf number are important crop quality characteristics in floriculture production. Although VB number was not affected by lighting for calibrachoa and petunia, later flowering was associated with a greater VB number for coreopsis, snapdragon, and chrysanthemum, in accordance with Craig (2012). The increase in leaf number was generally proportional to time to flower, showing similar leaf developmental rates in various lighting treatments. Therefore, differences in flowering time were not caused by leaf developmental variations.

In conclusion, 4-h NI lighting with B₃₀ (peak wavelength = 450 nm) controlled flowering of all LD plants and SD plants studied, and it was as effective as 4-h NI lighting from R+W+FR radiation at 2 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Adding B₃₀ to R+W+FR radiation further promoted flowering of calibrachoa and petunia, but not other crops. In all LD plants except rudbeckia, the NI was more promotive than the DE. Extension growth of most crops was not suppressed by additional B radiation at up to 30 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ while delivering low-intensity R+W+FR radiation. The efficacy of moderate-intensity B radiation indicates possible involvement of signaling molecules and photoreceptors besides phytochromes in the regulation of flowering.

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