



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



Qingwu Meng, Erik S. Runkle\*

Department of Horticulture, 1066 Bogue Street, Michigan State University, East Lansing, MI 48824-1325, USA

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## ABSTRACT

Lighting that creates an effective phytochrome photoequilibrium at the end of the day (day extension) or during the middle of the night (night interruption) can regulate flowering of photoperiodic ornamentals grown under short days. In addition to phytochrome regulation, blue (B) radiation can elicit cryptochrome-mediated photoperiodic responses, such as flowering and stem growth. Although B radiation at a low intensity does not influence plant development, we postulated that it could regulate flowering at a higher intensity while acting as a plant growth regulator. We grew five long-day plants [calibrachoa (*Calibrachoa × hybrida*), coreopsis (*Coreopsis grandiflora*), petunia (*Petunia × hybrida*), rudbeckia (*Rudbeckia hirta*), and snapdragon (*Antirrhinum majus*)] and two short-day plants [chrysanthemum (*Chrysanthemum × morifolium*) and marigold (*Tagetes erecta*)] 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)  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , with or without low red (R)+white+far-red (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 2–4 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 morphological 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.

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## 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 ( $1\text{--}2 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) 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  $\geq 16$  h and 4-h NI lighting during the middle of the night are

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

\* Corresponding author.

E-mail address: [runkleer@msu.edu](mailto:runkleer@msu.edu) (E.S. Runkle).

similarly effective at controlling flowering of photoperiodic plants (Craig, 2012; Runkle and Fisher, 2004; Runkle et al., 1998).

Radiation is perceived through multiple classes of photoreceptors in higher plants, including phytochromes that primarily absorb red (R, 600–700 nm) and far-red (FR, 700–800 nm) radiation, cryptochromes that absorb blue (B, 400–500 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-Théliér 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 655–665 nm and 725–735 nm, respectively, which correspond to the absorption peak wavelengths of extracted oat phytochromes (Butler and Lane, 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 and Lane, 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 (0.63–0.89), 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 ( $<5 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) 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  $3 \mu\text{mol m}^{-2} \text{s}^{-1}$  (PPE  $\approx 0.52$ ) 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  $100 \mu\text{mol m}^{-2} \text{s}^{-1}$  (PPE not reported, but probably  $\approx 0.5$ ) (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  $250 \text{ mW m}^{-2}$  (probably  $<2 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) from B fluorescent tubes (peak wavelength = 460 nm; PPE not reported, but probably  $\approx 0.5$ ), 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  $\approx 0.5$ ) 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-Théliér 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  $2 \mu\text{mol m}^{-2} \text{s}^{-1}$  (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 and Lane, 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. Both phototropin and cryptochrome activated by B radiation are involved in photomorphogenesis (Folta and Spalding, 2001). 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 et al., 2004; Shimizu et al., 2006). 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.,  $30 \mu\text{mol m}^{-2} \text{s}^{-1}$ ), 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 sowing, 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

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