

Chapter 14

Control of Flowering Using Night- Interruption and Day-Extension LED Lighting

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Abstract Flowering of photoperiodic plants is regulated by the duration of the continuous night (dark) period during each 24-h period. When the natural photoperiod is short, longer days (shorter nights) may be desired by commercial growers of ornamentals and other specialty crops to promote flowering of long-day plants or inhibit flowering of short-day plants. To create short nights, electric lighting can extend the daylength (day extension, DE) or interrupt the night (night interruption, NI). Conventional lamps such as incandescent (INC), halide, and compact fluorescent (CFL) can serve this purpose, but they are energy inefficient, have a short life span, and/or emit photons at wavelengths that have little or no effect on regulating flowering. Recent advancements in solid-state lighting enable horticultural applications including regulation of flowering, especially in (semi-) controlled environments. Light-emitting diodes (LEDs) with customized spectra suitable for control of flowering are at least as effective as conventional lamps, last longer, and are more energy efficient. Narrowband radiation from LEDs facilitates research on the role of specific wavelengths in mediating flowering and plant morphology, which are important in commercial production of many specialty crops produced in controlled environments. In addition, applied lighting research helps elucidate how photoreceptors, such as phytochromes and cryptochromes, mediate these physiological processes in plants. LEDs will increasingly replace conventional lamps to regulate flowering of commercial photoperiodic crops as their energy efficiency increases and manufacturing costs decrease.

Keywords Cryptochrome • Far-red radiation • Long-day plants • Photoperiod • Phytochrome • Regulation of flowering • Short-day plants

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14.1 Introduction

Flowering of a wide range of ornamental crops, including annuals (bedding plants) and herbaceous perennials, is sensitive to the photoperiod (Thomas and Vince-Prue 1997). Long-day plants flower earlier when the dark period is shorter than a critical length, whereas short-day plants flower earlier when the dark period exceeds a critical duration. The critical photoperiod is species and sometimes cultivar specific. Unlike the conversion of light energy to chemical energy for photosynthesis, photoperiodic signaling in plants has a very low threshold light intensity ($<2 \mu\text{mol m}^{-2} \text{s}^{-1}$) (Whitman et al. 1998). When the natural photoperiod is short, the long night can be truncated using electric lights to promote flowering of long-day plants and inhibit flowering of short-day plants. This technique, known as the photoperiodic regulation of flowering, is an important strategy for commercial growers to produce crops efficiently and to schedule them in flower for specific, predetermined market dates. Besides manipulating flowering time, photoperiodic lighting can alter other characteristics such as morphology, vegetative growth, and pigmentation. For example, a delay in flowering of short-day plants is often accompanied by a desired increase in vegetative growth, which is known as “bulking”.

Photoperiodic lighting is often delivered during one of two periods during the night: following sunset [day-extension (DE) or end-of-day (EOD) lighting] or during the middle of the night [night-interruption (NI) lighting]. A DE creating a 16-h photoperiod often ensures a long-day response for a wide range of ornamentals (Whitman et al. 1998). Because flowering of photoperiodic plants is determined by the night length, a brief (e.g., several seconds to minutes) pulse of NI light that divides a long night into two short dark periods can regulate flowering of some model crops that need only one or a few inductive cycles (Thomas and Vince-Prue 1997). However, most plants, particularly most ornamental crops, require a longer (>30 min) NI lighting duration to be effective. Generally, a 4-h NI is sufficiently long to saturate the promotion of flowering for long-day crops and inhibit flowering of short-day crops (Runkle et al. 1998). When comparing the efficacy of DE and NI lighting, a 4-h NI generated a slightly stronger long-day signal than a 5.5-h DE using the same light source (Meng and Runkle 2016a), although several studies with herbaceous perennials (e.g., *Rudbeckia fulgida*) have reported a similar response to NI and DE lighting (Runkle et al. 1999).

14.2 Conventional Lamps

The application of electric lights in photoperiodic control of flowering has evolved rapidly over the past decade. A wide array of light sources, including incandescent (INC), high-pressure sodium (HPS), and fluorescent lamps, have been extensively researched and used commercially. Although these lamps were designed for general

illumination, in many instances they are effective at creating long days for photoperiodic plants. The selection of an appropriate light source for commercial applications depends on factors such as the spectral distribution, intensity, energy efficiency, rated lifetime, annual hours of operation, and costs for installation and operation.

With a spectral distribution similar to a blackbody radiator, INC lamps convert electric energy to photons mostly with long wavelengths. The primary spectral emission of INC lamps in the near-visible range is red (R, 600–700 nm) and far-red (FR, 700–800 nm) radiation, but this accounts for only about 8 % of the total energy emitted (Thimjan and Heins 1983). Despite their energy inefficiency and short life span, INC lamps gained popularity in greenhouses and growth chambers for photoperiodic control because of their low cost. However, they have been phased out of production in compliance with increased energy standards being enforced worldwide and, to some extent, have been replaced by slightly more energy-efficient halide lamps, which emit a very similar spectrum. Compact fluorescent (CFL) lamps are more energy efficient and last longer than INC lamps. However, flowering of some long-day plants, such as petunia (*Petunia × hybrida*), was delayed when INC lamps were replaced with CFL lamps (Runkle et al. 2012). CFL lamps emit little FR radiation, which is required to accelerate flowering in some long-day crops. As the light source most commonly used for greenhouse supplemental lighting, HPS lamps can also provide long days to inhibit flowering of short-day plants (Blanchard and Runkle 2009) and promote flowering of long-day plants (Blanchard and Runkle 2010; Whitman et al. 1998).

14.3 Light-Emitting Diodes

14.3.1 *Critical Wavebands for Regulation of Flowering of Long-Day Plants*

Phytochromes are a class of photoreceptors that primarily absorb R and FR radiation and mediate flowering and photomorphogenesis (Fig. 14.1). In plants, phytochromes exist as an active form absorbing FR radiation (P_{FR}) and an inactive form absorbing R radiation (P_R), the ratio of which depends on the incident spectrum. A phytochrome photoequilibrium (PPE) is established based on the proportion of P_{FR} in the total pool of phytochromes ($P_{FR}+P_R$). An estimated PPE can be calculated using the spectral data of a light source and relative absorption of P_R and P_{FR} (Sager et al. 1988). Using conventional lamps, a mixture of R and FR radiation was more promotive of flowering in long-day plants than either R or FR radiation alone (Thomas and Vince-Prue 1997). Likewise, R and FR LEDs, establishing an intermediate PPE of 0.63 or 0.72, usually elicited the most rapid flowering of the long-day plants tested (Craig and Runkle 2016). The efficacy of INC lamps is not

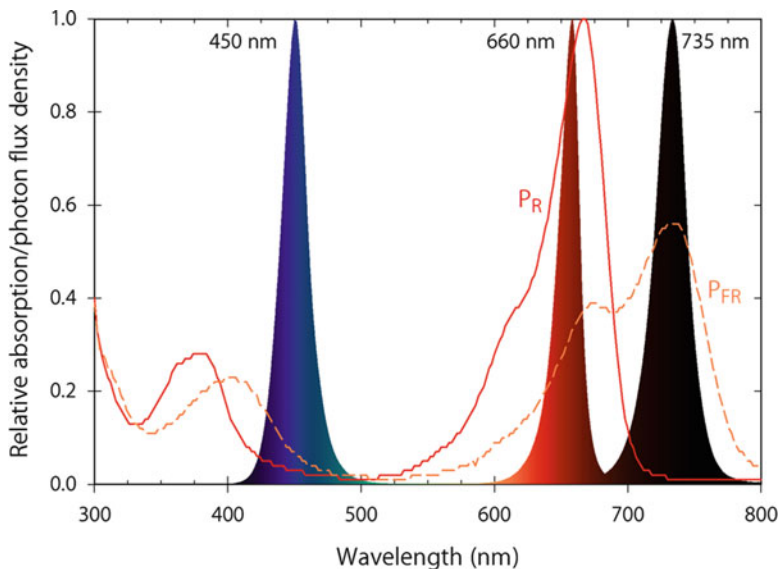


Fig. 14.1 The relative absorption of the two forms of phytochrome and the relative spectral distribution of three LED types used for photoperiodic lighting research at Michigan State University. The names for the two forms of phytochrome are based on their peak absorption of radiation: P_R = the red-absorbing form and P_{FR} = the far-red-absorbing form (Sager et al. 1988). Phytochrome can be manipulated by red (peak = 660 nm) or far-red (peak = 735 nm) LEDs at a low intensity, while a higher intensity of blue radiation (peak = 450 nm) is required, possibly because of its relatively low absorption by phytochrome

surprising because the estimated PPE established by INC lamps is 0.64, which is within this effective range.

The addition of FR to R radiation can accelerate flowering of long-day plants, but typically promotes undesired extension growth of ornamental plants such as calibrachoa (*Calibrachoa × hybrida*) and coreopsis (*Coreopsis grandiflora*). The shade-avoidance response triggered by FR radiation, even at a low intensity, modifies physiological and morphological characteristics of plants (Cerdán and Cory 2003). A low R-to-FR ratio (R/FR) can increase the biosynthesis of gibberellins, which are plant hormones mediating stem elongation (Kurepin et al. 2012). This led to a question of whether LEDs that do not emit FR radiation could provide an effective long-day signal while maintaining the compactness of plants. For some long-day plants such as ageratum (*Ageratum houstonianum*) and dianthus (*Dianthus chinensis*), R+white (W) LEDs controlled flowering as effectively as R+W+FR LEDs but produced shorter plants at flowering, showing that R radiation by itself was sufficient for photoperiodic control of flowering of some crops (Kohyama et al. 2014). However, for other long-day plants, the most rapid flowering occurred when both R and FR radiation were delivered. For example, NIs essentially devoid of FR radiation [i.e., R, blue (B, 400–500 nm)+R, and W LEDs] were not perceived as long days for snapdragon (*Antirrhinum majus*), while flowering was accelerated

under R+W+FR LEDs (Meng and Runkle 2016b). Therefore, long-day plants can be classified into FR-dependent and FR-neutral varieties based on their flowering responses to FR radiation. Within the FR-dependent category, FR radiation is either required for promotion of flowering (an obligate response) or is not required but promotes flowering if added to R radiation (a facultative response). Examples of obligate FR-dependent long-day plants are snapdragon and pansy (*Viola × wittrockiana*). Examples of facultative FR-dependent plants are petunia and coreopsis. In contrast, flowering of FR-neutral plants, such as ageratum, rudbeckia (*Rudbeckia hirta*), and calibrachoa, is primarily regulated by R radiation, and adding FR radiation has no effect on flowering time.

Because LED arrays without FR radiation can control flowering of some long-day plants without promoting extension growth, the application of W LEDs for photoperiodic lighting was explored. LED arrays emitting W radiation are usually B LEDs covered with a phosphor coating, which scatters most photons to longer wavelengths, but can also be created by mixing R, green (G, 500–600 nm), and B LEDs that, when combined, appear W. W LEDs emit little or no FR radiation and thus, cannot necessarily replace INC lamps or R+FR LEDs for some FR-dependent long-day plants. Various types of W LEDs are available including cool-, warm-, and neutral-W LEDs, which depend on the phosphor coating and the resulting spectral distribution and correlated color temperature. Cool- and warm-W LEDs have the same PPE of 0.84 but different B-to-R ratios (0.67 and 0.27, respectively) (Table 14.1). Despite the spectral differences, the effectiveness of cool- and warm-W LEDs at regulating flowering was generally equivalent to that of R and B+R LEDs (Meng and Runkle 2016b).

B radiation is absorbed by the cryptochrome and phototropin families of photoreceptors, but can also be weakly absorbed by phytochromes. Both cryptochromes and phytochromes mediate flowering, whereas phototropins regulate phototropism in plants. The efficacy of B radiation at regulating flowering of photoperiodic crops is dependent on the intensity delivered. A threshold intensity greater than that usually sufficient for R+FR photoperiodic lighting (i.e., $2 \mu\text{mol m}^{-2} \text{s}^{-1}$) is required to establish a B-mediated flowering response (Meng and Runkle 2016a). At $2\text{--}3 \mu\text{mol m}^{-2} \text{s}^{-1}$, a 4-h NI from B LEDs was not perceived as a long-day signal by any long-day plants tested (Craig 2012; Meng and Runkle 2015). Furthermore, the addition of this low-intensity B radiation to R, FR, or R+FR radiation did not influence flowering (Meng and Runkle 2015). However, at a higher intensity of $30 \mu\text{mol m}^{-2} \text{s}^{-1}$, B radiation delivered alone as a 4-h NI was perceived as a long day for all long-day plants tested (Meng and Runkle 2016a). Furthermore, this B radiation further promoted flowering of some plants (e.g., petunia) grown under an NI at $2 \mu\text{mol m}^{-2} \text{s}^{-1}$ from R+W+FR LEDs. Collectively, these experiments challenge the notion that the PPE is an accurate predictor of the efficacy of a light source at regulating flowering. First, the PPE only changed from 0.53 to 0.48 when the intensity of B radiation increased from 2 to $30 \mu\text{mol m}^{-2} \text{s}^{-1}$, but the capacity to control flowering was activated. Second, low-intensity B radiation created an intermediate PPE of 0.53, which should have been at least somewhat

Table 14.1 Spectral characteristics of incandescent (INC), compact fluorescent (CFL), high-pressure sodium (HPS) lamps, and blue (B)+red (R)+far-red (FR), R+white (W), R+W+FR, cool-W (CW), and warm-W (WW) light-emitting diodes (LEDs)

Parameter	INC	CFL	HPS	LEDs				
				B+R+FR ^a	R+W ^b	R+W+FR ^c	CW ^d	WW ^e
<i>Percentage (%) of photon flux (400–800 nm)</i>								
Blue (400–500 nm)	3	14	5	11	6	6	20	12
Green (500–600 nm)	14	37	51	2	14	13	46	39
Red (600–700 nm)	30	42	38	60	78	36	30	43
Far red (700–800 nm)	54	7	6	27	1	44	4	6
<i>Light ratio</i>								
Red:far red	0.56	6.19	5.90	2.24	55.08	0.82	7.47	7.18
Blue:red	0.09	0.32	0.12	0.19	0.08	0.18	0.67	0.27
PPE	0.64	0.83	0.86	0.76	0.88	0.67	0.84	0.84

Phytochrome photoequilibria (PPE) are estimated according to Sager et al. (1988)

^aTotalGrow Day & Night Management Light

^bPhilips GreenPower LED flowering DR/W

^cPhilips GreenPower LED flowering DR/W/FR

^dPhilips, model 9290002296

^ePhilips, model 9290002204

effective at stimulating flowering of at least some species (Craig and Runkle 2013, 2016). Third, there were no consistent correlations between the estimated PPE of a light source and a flowering index for long-day plants such as dianthus, petunia, and rudbeckia (Meng and Runkle 2015). Therefore, factors such as the radiation intensity, duration, and spectral distribution should be considered with the PPE to predict the photoperiodic efficacy of a light source.

14.3.2 Critical Wavebands for Regulation of Flowering of Short-Day Plants

The spectral requirements to inhibit flowering of short-day plants are slightly different from those to promote flowering of long-day plants. During a long night, low-intensity R radiation delivered as a DE or NI generally inhibits flowering in short-day plants (Thomas and Vince-Prue 1997). For example, R LEDs alone delivered as a 4-h NI inhibited flowering of chrysanthemum (*Chrysanthemum morifolium*) and marigold (*Tagetes erecta*) compared with the 9-h short-day control (Craig and Runkle 2013; Meng and Runkle 2016b). Using R+FR LEDs, a high R/FR (or PPE) was often more effective than a low R/FR (or PPE) at delaying flowering of several short-day plants studied (Craig and Runkle 2013). In addition, FR radiation alone was not perceived as a long day. For some plants that only

require one or a few photoinductive cycles, flowering can be at least somewhat influenced by R/FR photoreversibility; an inhibition of flowering by R radiation can be fully or partially reversed by subsequent exposure to FR radiation (Thomas and Vince-Prue 1997). The delivery of R radiation establishes a high PPE that inhibits the signaling pathway for flowering of short-day plants, but subsequent FR radiation attenuates this inhibition by converting some P_{FR} back to P_R .

Similar to long-day plants, the efficacy of B radiation at regulating flowering of short-day plants depends on its intensity. To inhibit flowering of the short-day plant duckweed (*Lemna paucicostata*) by 50 %, B, G, R, and FR radiation needed to be 10, 0.5, 0.1, and 3 $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively (Saji et al. 1982). Similarly, only at a sufficiently high intensity (e.g., 30 $\mu\text{mol m}^{-2} \text{s}^{-1}$) did short-day plants perceive B radiation as a long-day signal (Meng and Runkle 2015, 2016a). Compared with R + W + FR radiation at 2 $\mu\text{mol m}^{-2} \text{s}^{-1}$, B radiation at 30 $\mu\text{mol m}^{-2} \text{s}^{-1}$ was similarly effective for marigold but less effective for chrysanthemum.

Relatively few studies have explored the efficacy of G radiation at regulating photoperiodic flowering. As noted previously, G radiation alone was an effective long-day signal at a low intensity for the model plant duckweed (Saji et al. 1982), although the capacity of G radiation to create long days was questionable in other studies (Thomas and Vince-Prue 1997). More research on the efficacy of G radiation has been performed recently with the advancements of LEDs. Under short days, NIs or DEs with low- or high-intensity G LEDs (peak wavelength = 518, 520, or 530 nm) inhibited flowering of the short-day plants cosmos (*Cosmos bipinnatus*), perilla (*Perilla ocymoides*), okra (*Abelmoschus esculentus*), and chrysanthemum (Hamamoto et al. 2003; Hamamoto and Yamazaki 2009; Jeong et al. 2012). G radiation was as effective as R radiation at inhibiting flowering in some of these studies, but was less effective in others. This indicates that the degree of a long-day response activated by G radiation could depend on its intensity, duration, and spectral characteristics and could vary among species. G radiation emitted from W LEDs could also play a role in photoperiodic regulation of flowering. A 4-h NI from W LEDs emitting comparable amounts of G and R radiation inhibited flowering of chrysanthemum more than that from R LEDs alone (Meng and Runkle 2016b). Because G radiation can exert an inhibitory effect similar to R radiation at a low intensity in some species, a combination of these two wavebands could be more effective at inhibiting flowering of short-day plants than either waveband alone.

14.3.3 Comparisons Between Conventional Lamps and Light-Emitting Diodes

Traditional broad-spectrum light sources can effectively create long days for most photoperiodic crops; however, much of the radiation emitted – and therefore energy consumed – is not necessary for photoperiodic lighting. LED arrays developed for

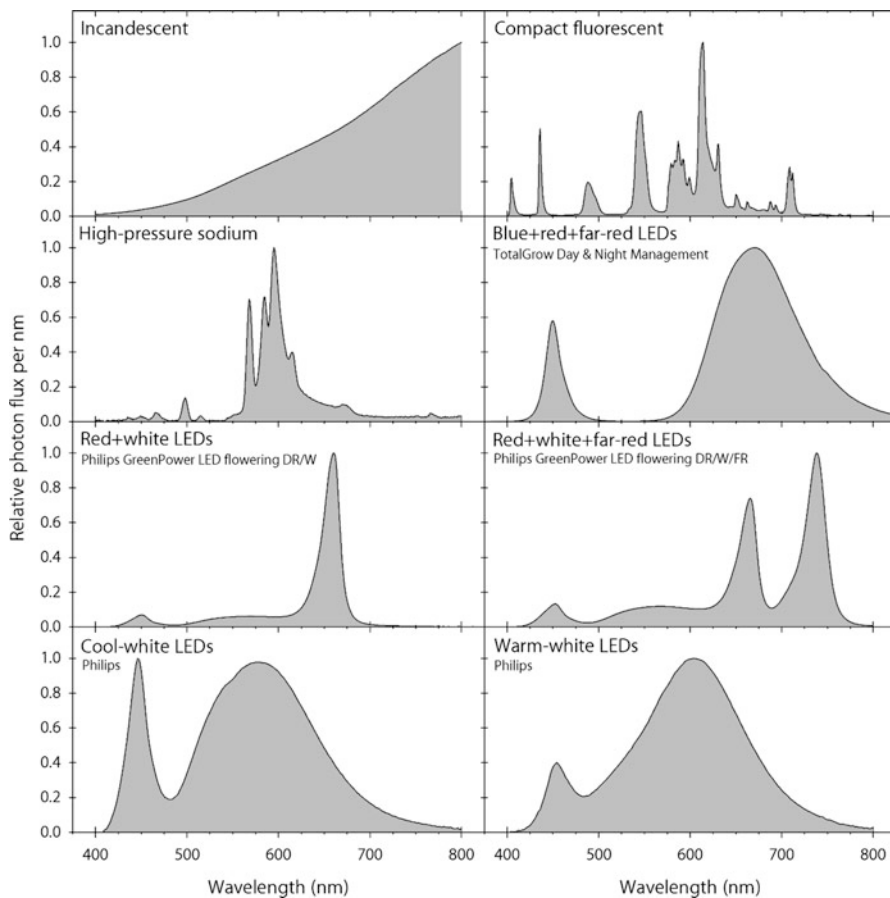


Fig. 14.2 The spectra of several light sources used for regulation of flowering, including lamps traditionally used by commercial growers (incandescent, compact fluorescent, and high-pressure sodium) and newly developed light-emitting diodes (LEDs). A portable spectroradiometer measured photon fluxes every 1 nm from 400 to 800 nm

plant lighting applications can be at least as energy efficient as, and last longer than, conventional lamps (Nelson and Bugbee 2014; Pimpitkar et al. 2009; Schubert and Kim 2005). The use of LEDs also enables specification of spectral composition. For example, LEDs can be customized and tailored to emit a spectrum that controls flowering effectively and efficiently. The spectral distributions and characteristics of several conventional lamps and commercial LEDs used for photoperiodic control of plants are in Fig. 14.2 and Table 14.1.

In a coordinated commercial greenhouse grower trial, LED lamps emitting primarily R and FR radiation, plus a little W, were compared with lamps traditionally used by greenhouse growers to create long days, including INC, HPS, and CFL lamps (Meng and Runkle 2014). Flowering of most herbaceous ornamental crops tested was similar under NIs from the LED, INC, and HPS lamps, showing that

the LEDs were at least as effective as traditional lamps at regulating flowering. Although the spectral distribution of these commercial LEDs differed from that of INC lamps, the intensity of each 100-nm waveband, from 400 to 800 nm, was similar between the two lamp types. The R/FR emitted from the LEDs and INC lamps was similar (0.8 and 0.6, respectively), so their comparable efficacy was not surprising. Experimental LED arrays delivering a similar R/FR were also as effective as INC lamps at creating long days for long-day and short-day plants (Craig and Runkle 2013, 2016).

14.4 Concluding Summary

In long-day plants, R radiation at a low intensity can regulate flowering of some ornamental crops, while the inclusion of FR radiation can promote flowering of other crops. In contrast, R radiation alone is effective at inhibiting flowering of a wide range of short-day plants. The threshold intensity of B radiation, above which it can regulate flowering of photoperiodic plants, is much greater than that of R radiation. LED products designed specifically to regulate flowering can be at least as effective as conventional INC, HPS, and CFL lamps. Table 14.2 summarizes the efficacy of conventional lamps and LEDs commonly used for photoperiodic control of long-day and short-day ornamental crops. A simplified economic analysis revealed that, in the long term, the total operating cost of LEDs could be less than that of INC or HPS lamps to deliver NIs because of the greater energy efficiency and longer life span of LEDs (Meng and Runkle 2014). The cost of LED products is expected to continue decreasing as the technology matures. As a result, flowering applications using LEDs should become more prevalent as we gain a better understanding of photocontrol of flowering.

Table 14.2 Summary of the efficacy of different lamp types at regulating flowering of photoperiodic crops when delivered during the night at a low intensity ($1\text{--}3\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$)

Lamp type	Short-day plants	Long-day plants
Incandescent, halogen	✓	✓
Fluorescent (including CFLs) ^a	✓	Some
Mix incandescent + CFL ^a	✓	✓
High-intensity discharge (HPS, MH, mercury) ^b	✓	✓
LEDs	White	✓
	Red	✓
	Red + far red	✓
	Far red	–
	Blue	–
	Green	Varies

✓ generally effective, – generally not effective

^aCFL Compact fluorescent lamps

^bHPS High-pressure sodium, MH Metal halide

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