

DETERMINING EFFECTIVE RATIOS OF RED AND FAR-RED LIGHT FROM LIGHT-
EMITTING DIODES THAT CONTROL FLOWERING OF PHOTOPERIODIC
ORNAMENTAL CROPS

By

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ABSTRACT

DETERMINING EFFECTIVE RATIOS OF RED AND FAR-RED LIGHT FROM LIGHT-EMITTING DIODES THAT CONTROL FLOWERING OF PHOTOPERIODIC ORNAMENTAL CROPS

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Many herbaceous ornamental plants exhibit a photoperiodic flowering response. Under ambient short days (SDs), lighting from incandescent (INC) lamps during the night inhibits flowering of SD plants (SDPs) and promotes flowering of long-day plants (LDPs). INC lamps are inexpensive, easy to install, and emit an effective spectrum for controlling flowering, but they also are energy inefficient and are being phased out of production. Three annual SDPs and six annual LDPs were grown under a 9-h day with a 4-h night interruption (NI) with different red-to-far-red ratios (R:FR) from light-emitting diodes (LEDs). A moderate to high R:FR (≥ 0.66) was most effective at interrupting long nights and inhibiting flowering of SD plants. For LDPs, a mixture of R and FR light (R:FR= 0.28 to 1.07) most effectively promoted flowering. For both SDPs and LDPs, flowering percentage and flowering time were similar under SDs and the NI with only FR, indicating that NI with only FR was perceived as an SD. Therefore, some threshold amount of R light is required to inhibit flowering in SDPs and promote flowering in LDPs. A second experiment determined whether the sensitivity to the R:FR changed during a 15-hour night. Lamps with R:FR ratios of 0.65 to 2.38 were all effective at promoting flowering, regardless of whether the photoperiodic treatment was delivered at the end of the natural photoperiod or during the middle of the night. In these experiments, plant responses were similar under INC or R+FR LEDs and thus, LEDs can provide an alternative to INC lamps for photoperiodic lighting.

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SECTION I
LITERATURE REVIEW

Introduction

The ability to precisely schedule and synchronize crops has become increasingly important for greenhouse growers as the expectations of both marketers and consumers have changed over the years (Erwin and Warner, 2002). Growers need to be able to induce a crop to flower at a specific time, and are always striving to reduce production costs, which includes finishing the crops as quickly as possible (Cavins and Dole, 2001). However, there can be tradeoffs between plant quality and economics when growers start to alter their production strategies. Growers are also interested in non-chemical methods of height control to reduce chemical inputs and be more environmentally sustainable. Similarly, energy efficiency has become increasingly important as energy prices increase and become more volatile.

Light and temperature are two of the environmental factors that most influence plant growth and development. Growers can utilize these variables by manipulating greenhouse conditions such as light quality, light quantity (daily light integral), photoperiod, average daily temperature, and day and night temperature fluctuation. Therefore, it is important to understand how these potentially interacting factors influence flower induction, crop timing, and growth attributes. This literature review focuses on the effects of light on plants, the current state of greenhouse lighting technology, and related photobiological research.

To understand effects of light on plants, one must consider three separate, but interacting, parameters: light quantity, light quality, and light duration (Hopkins and Hüner, 2004). Light quantity is the number of photons incident upon a described area per unit of time (usually per second or day). Light quantity from sunlight available to plants inside a greenhouse varies by latitude, season, elevation, cloud cover, greenhouse structure and layout, glazing material, shading, time of day, and other factors. Electric light sources vary in luminous efficacy due to

differences in construction and chemical composition. Plants respond to changes in light quantity in both the short and long term via changes in photosynthetic rate, growth, and development. Light quality refers to the distribution of photons at specific wavelengths. Plants perceive light quality and, in response, change their morphology (e.g., stem extension and leaf shape) and perhaps their flowering time. Light duration, or photoperiod, is the relative length of the light periods under which a plant is grown. Many plants flower in response to a particular photoperiod. Flowering of some floriculture crops is influenced by light duration, light quality, and light intensity, whereas others are relatively insensitive to one or more light parameters.

Light Quantity

Light quantity can be measured using photometric, radiometric, and quantum units. The photometric system is based on the sensitivity of the human eye, and therefore is biased towards people and not plants. The photometric system is measured in footcandles ($\text{lm}\cdot\text{ft}^{-2}$). The radiometric system measures all radiation incident on Earth's surface, including both visible light and thermal radiation. The radiometric system is measured as watts per square meter ($\text{W}\cdot\text{m}^{-2}$) and generally measures radiant power per unit area within the waveband range from 300 to 3,000 nm. The quantum system can be used to measure the number of photons within the 400 to 700-nm waveband, which is referred to as photosynthetic photon flux (Hopkins and Hüner, 2004). Quantum measurement describes photosynthetically active radiation (PAR) per unit time (s or d) incident on a unit of area (m^2) and thus, the units are $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ or $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$.

Irradiance varies by location and latitude. In accordance to the Cosine Law, as the angle of the sun increases, the area covered by a parallel beam of light increases while the energy incident on that area remains the same (Basaiux, et al., 1973). In other words, as the angle of

incidence increases, the irradiance decreases per unit area. This explains why irradiance decreases as latitude increases north or south of the equinoxes. This also explains why there are seasonal differences in light intensity. The Earth's rotation is tilted on an axis and when the incident solar angle increases in winter or decreases in summer, the light intensity decreases or increases, respectively.

The position and structural design of a greenhouse impacts light quantity available to plants. Greenhouse superstructure, glazing materials, and other obstructions such as hanging baskets or condensation and dust accumulating on glazing material can reduce the irradiance inside the greenhouse by 40 to 60% or more (Fisher and Runkle, 2004; Runkle and Heins, 2006). Clean, new glass, double-layer acrylic, and double-layer polycarbonate transmit a maximum of 90, 85, and 82% light, respectively (Fisher and Runkle, 2004). The slope of greenhouse roofs affects the angle of incidence of entering light and thus light transmission to crops below (Fisher and Runkle, 2004). For example, as roof slope decreases and the angle of incident sunlight increases, light transmission decreases. Greenhouse orientation (north-south versus east-west layout) will also affect irradiance and how light and shadows move across the crop (Fisher and Runkle, 2004). North-south oriented greenhouses allow for shadows, created by greenhouse structure, to move across the crop throughout the day, improving uniformity of the light environment. In contrast, shadows in east-west greenhouses move very little during the day, which causes high variability in the photosynthetic daily light integral (DLI). The orientation of hanging-basket lines within a greenhouse affects the light environment similarly. In addition, hanging baskets at a density of 1.5 baskets per m² have been shown to intercept 25% of the incoming radiation (Faust and Korczynski, 2001).

Some photobiological studies have reported the effect of instantaneous irradiance on crop growth and development. Chinese hibiscus (*Hibiscus rosa-sinensis* L.) ‘Red Sheen’ flowered 9 d earlier when the irradiance was doubled from 420 to 840 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Neumaier et al., 1987). For yarrow (*Achillea \times millefolium* L.) ‘Summer Pastels’, plants grown under 300 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ had twice the dry weight (21.6 g) of plants grown under 100 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (10.8 g) when grown under a 16-h day photoperiod (Zhang et al., 1996). Plants also flowered 20 d earlier under the higher irradiance, which could at least partially be attributed to a greater plant temperature. In a separate study, days to flower for the day-neutral plant carpanthea (*Carpanthea pomeridiana* L.) ‘Golden Carpet’ decreased by 23 or 42 d when grown under short days (SDs) or long days (LDs), respectively, as supplemental irradiance was increased from 0 to 150 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at 22-24 \pm 2 $^{\circ}\text{C}$ (Mattson and Erwin, 2005).

In contrast to instantaneous irradiance, the photosynthetic DLI represents the amount of accumulated light available to a plant in one day and is measured in $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$. Increasing DLI can increase dry weight, flower bud number, lateral branching (Fausey et al., 2005), flower diameter (Niu et al., 2001), and root growth (Lopez, 2006); reduce time to flower (Runkle and Heins, 2006); and improve overall plant quality. DLI can be increased by increasing the irradiance, increasing the photoperiod, and/or by reducing the number of objects or materials that cast shade to crops below.

The DLI varies by latitude and increases from December 21 through June 21 in the northern hemisphere. The average outdoor DLI in January is less than 15 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ in Michigan (lat. 43 $^{\circ}\text{N}$) and greater than 25 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ in Florida (lat. 28 $^{\circ}\text{N}$). In June, the DLI outdoors can exceed 50 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ in both Michigan and Florida (Korczynski et al., 2002). The greenhouse structure, glazing material, and obstructions such as hanging baskets or overhead

irrigation can reduce the DLI inside a greenhouse by 40% or more (Hanan, 1998). During the darkest months in Michigan (November through February), DLI inside a typical commercial greenhouse ranges from 2.5 to 10 mol·m⁻²·d⁻¹ (Fausey et al., 2005).

Dry mass of many plants increases linearly with increasing DLI up to about 20 to 30 mol·m⁻²·d⁻¹ (Warrington and Norton, 1991). For example, as DLI increased from 4.2 to 10.8 mol·m⁻²·d⁻¹, tussock bellflower (*Campanula carpatica* Jacq.) 'Blue Clips' dry mass increased by 155% (Niu et al., 2001). Similarly, dry mass of yarrow, gaura (*Gaura lindheimeri* Engelm. & Gray), and English lavender (*Lavandula angustifolia* Mill.) shoots increased by 3-, 3.4-, and 2.6-fold, respectively, as DLI increased from 5 to 20 mol·m⁻²·d⁻¹ (Fausey et al., 2005). Dry weight per internode of impatiens (*Impatiens walleriana* Hook.f.), cockscomb (*Celosia argentea* L. var. *plumosa*), French marigold (*Tagetes patula* L.), and pansy (*Viola* ×*wittrockiana* Gams.) seedlings increased by 47 to 68% as DLI increased from 4.1 to 14.2 mol·m⁻²·d⁻¹ (Pramuk and Runkle, 2005). However, at flowering, seedlings grown under the high DLI had decreased plant shoot dry weight because they flowered earlier than crops grown from low-DLI seedlings.

Flowering Time. An increase in DLI can reduce time to flower by reducing the number of nodes that develop before the first flower bud (Runkle and Heins, 2006). Rose (*Rosa* ×*hybrida*), geranium (*Pelargonium* ×*hortorum* L.), rose periwinkle (*Catharanthus roseus* L.), Chinese hibiscus, and stock (*Matthiola incana* L.) all flower earlier when grown under an increased DLI (Mortensen and Moe, 1995; Armitage et al., 1981; Pietsch, 1995; Dansereau et al., 1998; Warner and Erwin, 2003). As DLI during the seedling stage increased from 4.1 to 14.2 mol·m⁻²·d⁻¹ at 21 °C, pansy, cockscomb, scarlet sage (*Salvia splendens* F.), impatiens, and French marigold flowered 4, 10, 11, 12, and 12 d earlier, respectively (Pramuk and Runkle, 2005). Prairie gentian (*Eustoma grandiflorum* Raf.) grown under LDs reached visible bud 12 d

earlier under a DLI of $8.8 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ compared to $4.4 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ at $21 \pm 1 \text{ }^\circ\text{C}$ (Islam, 2005). However, Niu et al. (2001) reported that increasing DLI from 4.2 to $10.8 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ at $20 \text{ }^\circ\text{C}$ had no effect on flower timing of tussock bellflower 'Blue Clips'. Flowering time of yarrow and gaura, decreased by 5 and 7 d, respectively, when DLI was increased from 5 to $20 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ at $22 \pm 2 \text{ }^\circ\text{C}$ (Fausey et al., 2005). When swamp rose mallow (*Hibiscus moscheutos* L.) and flower of-an-hour (*H. trionum* L.) were grown under SDs, increasing DLI from 14.2 to 20.2 and 9.5 to $16.4 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ decreased time to flowering from 109 to 95 d and from 96 to 57 d, respectively (Warner, 2003). Rose mallow (*Hibiscus cisplatinus* St.-Hil.) flowered earliest when grown under the highest DLI studied, regardless of photoperiod.

Flower Number and Size. An increase in DLI increases flower bud number in many crops including rose 'Rubino', tussock bellflower 'Karl Foerster', lily (*Lilium*) 'Rouge', 'Orange', and 'Pink', prairie gentian (*Eustoma grandiflorum* Raf.), and tussock bellflower 'Blue Clips' (Islam et al., 2005; Mortensen and Moe, 1995; Niu et al., 2001; Serek, 1991; Zhang et al., 1990). For example, increasing DLI from 5.5 to $8.4 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ increased flower bud number of rose 'Rubino' from 10 to 18 flowers per plant (Mortensen and Moe, 1995). A supplemental increase in the DLI often has a large effect on crop growth when ambient DLI is low ($<10 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$). For example, flower bud number of tussock bellflower 'Blue Clips' doubled as DLI increased from 4.2 to $10.8 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ (Niu et al., 2001). However, a further increase in DLI to $15.8 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ increased flower number only by an additional 30%. Warner (2003) reported a 43% increase in flower number of rose mallow (*Hibiscus radiatus* Cav.) when DLI was increased from 6.7 to $8.9 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$. The number of lateral inflorescences was doubled for yarrow and tripled for gaura as DLI increased from 5 to $20 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$. However, there was no such relationship for English lavender (Fausey et al., 2005).

Stem Length and Branching. As DLI increased from 5 to $>10 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$, stem thickness, lateral branching, and overall plant quality increased for yarrow, gaura and English lavender (Fausey et al., 2005). At visible bud, an increase in DLI from 5 to $20 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ decreased stem length by 24, 35, and 35% for yarrow, gaura, and English lavender, respectively. However, there was no correlation between stem length and DLI at first flower.

Rooting of Cuttings. During propagation, shading typically is used to decrease DLI to prevent dehydration and stress of cuttings (Lopez, 2006). However, cuttings grown under less than $3 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ were of lower quality than cuttings grown under increased irradiance (Lopez, 2006). Increasing DLI from 1.2 to $3.9 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ during propagation of petunia (*Petunia* \times *hybrida* Vilm.-Andr.) 'Tiny Tunia Violet Ice' increased root number from 17 to 36, root length from 9.4 to 12.9 cm, root dry mass by 452%, and shoot dry weight by 47%, while shoot length decreased from 6.3 to 4.1 cm. In a similar study, root and shoot dry weight of New Guinea impatiens cuttings (*Impatiens hawkeri* Bull.) grown at 24 °C increased by 38 and 82%, and time to flower decreased from 85 to 70 d as DLI during propagation increased from 1.2 to $10.7 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ (Lopez, 2008).

Light Quality

Light quality refers to the spectral composition of light (Hopkins and Hüner, 2004). Plants are able to utilize certain wavelengths more efficiently for photosynthesis than others due to variation in absorbance by photosynthetic pigments. In addition, specific wavebands are associated with a variety of morphological and developmental processes. In plants, light quality is perceived by several families of photoreceptors: phototropins, cryptochromes, ultra-violet

receptors, and phytochromes, which influence flowering and morphogenesis (Moe and Heins, 1990; Runkle and Heins, 2006).

There are three major pigments in plants: chlorophylls, carotenoids, and anthocyanins. Chlorophylls are green pigments involved in photosynthesis that absorb light most effectively in the blue (B, 400-500 nm) and red (R, 600-700 nm) ranges of the visible spectrum (Hopkins and Hüner, 2004). Carotenoids, which are orange and yellow, are also involved in photosynthesis and primarily absorb light in the B region. Anthocyanins are R, purple, and B pigments, which absorb B, blue-green, and green (G) light (500 to 600 nm). Together, chlorophyll and carotenoids absorb light throughout most of the photosynthetic spectrum (Franklin, 2005). Fewer green photons are absorbed than other wavebands visible to the human eye, which gives plants their green color (Hopkins and Hüner, 2004).

Cryptochromes. The B light receptors, cryptochromes and phototropins, detect low light intensities and are not involved in photosynthesis. The cryptochromes are sensitive to B and ultraviolet-A light (320-380 nm) and can inhibit stem elongation in some plants (Hopkins and Hüner, 2004; Moe, 1990; Runkle and Heins, 2006). For example, B light has a strong inhibiting effect on hypocotyl elongation in cucumber (*Cucumis sativus* L.) (Shinkle and Jones, 1988). In arabidopsis (*Arabidopsis thaliana* L.), the cryptochromes promote flower induction and inhibit stem elongation (Mozley and Thomas, 1995; Bagnall et al., 1996). Stem length of geranium shoot cultures were reduced by 38% under B fluorescent (FL) lamps compared to both white FL and incandescent (INC) lamps (Appelgren, 1991). However, the effects of B light vary among species. For example, Hirai and Watanabe (2006) reported that monochromatic B light inhibited stem elongation of lettuce (*Lactuca sativa* L.) 'Okayama-saradana', but promoted elongation in eggplant (*Solanum melongena* L.) 'Kokuyo'. Phototropins mediate several plant responses

including phototropism, chloroplast movement, stomatal opening, leaf expansion, and growth inhibition (Folta and Spalding, 2001; Kagawa et al., 2001; Kinoshita et al., 2001; Sakai et al., 2001).

Both the presence of B light and the ratio of B to R light can affect extension growth. Compared to control plants grown under a B:R of 0.6, height and internode length of rose 'Meijikatar' grown under a B:R of 1.6 were decreased by 17-28% (Rajapakse and Kelly, 1994). A B-absorbing filter (resulting in a B:R of 0.06) increased elongation growth by 10 to 100% in tussock bellflower, tickseed (*Coreopsis ×grandiflora* Hogg ex Sweet.), garden pea (*Pisum sativum* L.), pansy, and lobelia (*Lobelia ×speciosa* Sweet.) (Runkle and Heins, 2001a). Stem length of coleus (*Coleus blumei* Benth.) grown under a B:R of 1.05 or 0.14 was reduced by 25% or increased by 27%, respectively, compared to control plants (B:R= 0.28) (Oyaert et al., 1997). The B:R of 1.05 also reduced total leaf area and dry weight compared to the neutral (N) filter. In a later study, Oyaert et al. (1999) compared the growth of chrysanthemum (*Chrysanthemum morifolium* Ramat.) under a blue polyethylene film, which increases the proportion of B (B:R= 85.5) with that of plants grown under an N filter (B:R of ~1). Elongation growth was inhibited by 22% under the B filter, while the number of axillary shoots, axillary leaf area, and leaf dry weight was reduced by 30%, 50%, and 30%, respectively.

Ultraviolet Receptors. Ultraviolet (UV, 100 to 380 nm) light can damage DNA and the photosynthetic apparatus, and can change plant morphology and color. Lercari et al. (1992) provided $50 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ of supplementary UV light to petunia, marigold (*Tagetes ×hybrida*), and tomato (*Solanum lycopersicon* L.) for 24 to 96 h. The UV treatment inhibited stem growth in these three species compared to sunlight. UV light had no effect on flower color in petunia or marigold and did not affect tomato yield. UV-transmitting films reduced leaf area and biomass

of lettuce 'Challenge', while a UV-blocking film increased these parameters in some cases (Paul et al., 2005).

Phytochromes. The third family of photoreceptors, the phytochromes, exist in R-absorbing (peak absorption at 660nm) and far red-absorbing [FR (700 to 800 nm), peak absorption at 730 nm] forms (P_R and P_{FR} , respectively) (Hayward, 1984; Sager et al., 1988; Smith, 1994). The intensity and spectral quality of a light source determines the proportion of phytochrome that is converted to the active P_{FR} form (Franklin, 2005). This ratio of R to FR wavelengths creates a phytochrome photoequilibrium (P_{FR}/P_{R+FR}) that mediates flowering in photoperiodic crops and stem extension in some plants. The R:FR of light incident on a plant can be influenced by plant spacing and canopy shading, lamp type, and light-filtering films. For example, natural light varies in R:FR throughout the day; the R:FR at midday is about 1.15 and decreases to around 0.70 during twilight hours (Lund, 2007).

Plants compete with neighboring plants for available sunlight. As light passes through a plant canopy, the plant tissues absorb most of the photosynthetic light, while FR light is primarily transmitted or reflected to the lower canopy (Smith 1994). While natural daylight has a R:FR of about 1.15, the R-depleted light under a plant canopy has a R:FR that can range from 0.05 to 0.7, depending on the canopy characteristics (Smith, 1982). Plants below a canopy detect this low R:FR ratio and respond by increasing stem extension to harvest unfiltered sunlight. This reaction to increased FR light relative to R light is termed the shade-avoidance response (Smith, 1982).

A light source high in R light relative to FR light creates a high P_{FR}/P_{R+FR} , which inhibits stem extension and promotes branching (Appelgren, 1991; Runkle and Heins, 2002, 2006; Runkle et al., 2001). A light source low in R light relative to FR creates a low P_{FR}/P_{R+FR} , which

promotes stem extension and inhibits branching. For example, stem elongation of tussock bellflower was promoted under supplemental lighting provided by INC lamps (R:FR 0.8) compared to light from FL lamps (R:FR 9.1) (Kristiansen, 1988). Blackout material was used to eliminate the low R:FR of twilight on Easter lily (*Lilium longiflorum* Thunb.) 'Ace' and 'Nellie White' and suppressed plant height by 12-24% (Blom, 1995). Lund et al. (2007) tested the effect of various 30 minute end-of-day (EOD) R:FR treatments on chrysanthemum. The plants receiving the lowest R:FR treatments (R:FR of 0.4 and 0.7) were taller than control plants (R:FR of 2.4). However, other parameters including dry weight, stem diameter, internode number, and branching were not affected by any EOD treatment. EOD lighting with R-rich FL bulbs, changing the P_{FR}/P_{R+FR} from 0.72 to 0.78, reduced height of pepper (*Capsicum annuum* L.) from 47.5 to 30.9 cm (Graham and Decoteau, 1995).

In an FR-deficient environment (R:FR of 1.74), branching of poinsettia (*Euphorbia pulcherrima* Willd. ex Klotzsch) increased by 25% compared to plants grown under an N filter (R:FR of 1.07) that transmitted the same DLI (Clifford et al., 2004). When grown under an R light NI, chrysanthemum produced 19.5% more cuttings (increased branching) than plants grown under an INC night interruption (NI) (Heins and Wilkins, 1979).

Effect of FR light on the flowering of LD crops. A low R:FR promotes stem extension and flowering in at least some LD plants (LDPs) (Runkle and Heins, 2006). Thus, many LDPs flower most rapidly when electric lighting contains FR light, particularly at the end of the photoperiod (Downs et al., 1958; Downs and Thomas, 1982; Lane et al., 1965). When LDPs are grown under light deficient in FR, flower initiation, development, or both can be delayed as observed for snapdragon (*Antirrhinum majus* L.), tussock bellflower, tickseed, petunia, pansy, and black henbane (*Hyoscyamus niger* L.) (Downs and Thomas, 1982; Kim et al., 2002; Runkle

et al., 2001; Runkle and Heins, 2003; van Haeringen et al., 1998). The first microscopic sign of flowering as well as differentiation of the flower parts of tussock bellflower were promoted under FR-rich supplemental INC light (R:FR of 0.8) compared to FL light (R:FR of 9.1) at 12 and 17 °C (Kristiansen, 1988). Anthesis of petunia and snapdragon at 27/20 °C day/night was delayed by up to 13 d under an R:FR of 1.51 compared to 1.05 (Cerny et al., 2003).

Effect of Diffuse Light on Crop Growth. Plants with a large leaf area index intercept more light with upper leaves than with middle and lower leaves. Physiologically older leaves deeper in the foliar canopy are generally less photosynthetically active since they receive less light (Hemming, 2007). Specialized greenhouse covering materials can diffuse light to balance the horizontal light distribution within a greenhouse and increase light penetration to lower leaves. PAR transmission under one light-diffusing plastic greenhouse film was reduced by 4% (Hemming, 2008). However, the horizontal light distribution was improved and photosynthesis in middle leaf layers was increased for cucumber ‘Shakira’, chrysanthemum ‘Danielson’, kalanchoe (*Kalanchoe blossfeldiana* Poelln.) ‘Kerinci’, weeping fig (*Ficus benjamina* L.) ‘Exotica’, and schefflera (*Schefflera arboricola* Hayata.) ‘Compacta’. While the middle leaf layers intercepted more light on clear days under the light-diffusing material, on cloudy days there was no difference between standard and diffusion coverings. Plant height, branch number, and leaf and stem dry weight increased by 8%, 22%, 23%, and 28%, respectively, for chrysanthemum under the light-diffusing film. However, photosynthetic DLIs were not reported and may have been different among treatments, which could have influenced dry weights.

Spectral Filters. The light quality in a greenhouse can be altered using photoselective films, or spectral filters. Some commercial growers of ornamentals use spectral filters as a non-chemical method for plant height control. Plant growth regulating chemicals (PGRs) present

human health and environmental concerns (Kambalapally, 1998; Lercari et al., 1992; Moe and Heins, 1990; Nissim-Levi et al., 2008; Oyaert et al., 1997; Rajapakse et al., 2001). Additionally, the use of PGRs may cause undesirable carry-over effects on bedding or pot plants after they are transplanted by the consumer. Therefore, light quality can be used as a PGR alternative. Photosensitive filters that reduce transmission of FR light can inhibit elongation growth and thus, plant height (Adams, 1997; Patil, 2001).

Both plastic films and fluid-filled (e.g., CuSO_4) layers can be used to reduce transmission of undesired wavelengths. FR-absorbing films can be used to increase the R:FR and thus inhibit stem elongation; R-absorbing films can promote extension growth (Table 1). For example, chrysanthemum and pepper grown under an FR-absorbing photosensitive filter with R:FR of 2.2 were 20% and 30% shorter, respectively, than plants grown under a neutral-density filter (Li et al., 2000). Although photosensitive filters can improve some plant-quality attributes, they generally reduce the total PAR, which can reduce crop yield, flower count, and branching, especially when ambient light conditions are limiting.

Effect of FR-absorbing filters on stem elongation. One of the most investigated aspects of spectral filters is their use for controlling stem elongation and thus plant height (Table 1.1). Several experiments with floriculture and vegetable crops quantified extension growth responses in FR-deficient environments. Internode elongation in *Petunia ×hybrida* ‘Ultra Blue’ was decreased by 30% under an FR-absorbing plastic filter with a R:FR of 1.57 compared to an N filter with a R:FR of 1.06 (Patil, 2001). Runkle and Heins (2002) found that an FR-absorbing filter (R:FR 1.74) decreased extension growth of impatiens, pansy, petunia, snapdragon, and tomato by 10, 18, 34, 5, and 24%, respectively, compared to the control (R:FR 1.07). The same

FR-absorbing filter also inhibited elongation growth of tickseed, garden pea, and pansy by 21, 17, and 14%, respectively (Runkle and Heins, 2001a).

Moe (2002) observed that stem length of cucumber was 45 to 50% shorter under an FR-absorbing filter (R:FR of 1.6) compared to that under the control film (R:FR of 1.1). An FR-absorbing filter (R:FR of 1.50) also decreased stem length of common sunflower (*Helianthus annuus* L.) and wild cabbage (*Brassica oleracea* L.) by 39 and 29%, respectively, compared to the control (R:FR not given) (Murakami et al., 1996). Petunia 'Priscilla', 'Purple Sunspot', 'Blue', and 'Blue Vein' were grown under an FR filter (R:FR 5.47) and an N filter (R:FR 1.28) of equal PAR (Kim et al., 2002). Under the FR filter, plants were 40 to 73% shorter, depending on cultivar, compared to plants grown under the neutral filter. Fletcher et al. (2005) found that three spectral filters, with R:FR of 1.1, 1.8, and 3.8, reduced stem elongation of petunia 'Express Blue' by 13, 30, and 37% compared to the control filter (R:FR of 1.0). Therefore, even slight differences in R:FR (e.g., 1.1 versus 1.0) can have a measurable effect on stem elongation.

The use of copper sulfate (CuSO_4) dissolved in water decreases transmission of FR light, which can decrease stem elongation by producing a high R:FR while transmitting most of the B light (Rajapakse and Kelly, 1992). However, PAR is reduced under such filters, especially those where the CuSO_4 concentration is high. For example, CuSO_4 concentrations of 4, 8, and 16% reduced PAR by 26, 36, and 47%, respectively, compared to ambient light intensity (Rajapakse and Kelly, 1992). Plant height of chrysanthemum 'Bright Golden Anne' was reduced by ~35% under all three CuSO_4 concentrations. Therefore, the lowest CuSO_4 concentration, which also gave the highest light transmittance, was sufficient for effective height control. Extension growth of other floriculture crops is also suppressed under CuSO_4 filters. Height of Easter lily 'Nellie White' was reduced by 9 to 32% under a CuSO_4 filter depending on the growing season,

while flowering time, flower number, and flower size were similar to those of control plants (Kambalapally and Rajapakse, 1998). In another study, rose plants were 25% shorter when grown under a CuSO_4 filter with a R:FR of 3.33 than when grown under a control filter with an R:FR of 1.16 (McMahon and Kelly, 1990). CuSO_4 filters are not practical for commercial greenhouse operations because they are expensive and difficult to handle.

Effect of R-absorbing filters on stem elongation. Filters that selectively reduce transmission of R light have been reported to increase stem elongation. An R-absorbing filter (R:FR of 0.53) increased stem length of common sunflower and wild cabbage by 21 and 25%, respectively, compared to the control (R:FR not given) (Murakami et al., 1996). Similarly, an R-absorbing filter (R:FR of 0.75) increased stem elongation (by 21 to 41%) in cucumber compared to the control (R:FR of 1.1) (Moe, 2002). Stem length of tussock bellflower, tickseed, garden pea, and pansy was increased under an R-absorbing filter (R:FR of 0.4) by 65, 26, 23, and 31%, respectively, compared to a neutral-density filter (R:FR of 1.07) with the same PAR (Runkle and Heins, 2001).

Spectral filters and flowering of photoperiodic crops. Several studies have reported the effect of photosensitive filters on the growth and development of photoperiodic crops. FR-absorbing filters delay flowering in some crops, especially LDPs. Flowering of day-neutral rose ‘Cherry Cupido’ and SDPs chrysanthemum ‘Bright Golden Anne’, zinnia (*Zinnia elegans* Jacq.) ‘Pumila Mix’, and cosmos (*Cosmos bipinnatus* Cav.) ‘Sonata White’ was not delayed under an FR-absorbing filter (R:FR not given) (Rajapakse et al., 2001). However, flowering of LDP petunia ‘Supercascade Burgundy’, snapdragon ‘Ribbon White’, and ‘Tahiti Red’ was delayed by 7 to 13 d under this filter. The presence or absence of FR light also had a significant impact on flowering time of the LDP snapdragon ‘Coronette Yellow’ (van Haeringen et al., 1998).

Flowering of snapdragon was delayed by 9 d under an FR-absorbing filter at 18 °C and was 7 d earlier under an R-absorbing filter (R:FR not given).

Table 1.1. Summary of the effects of the ratio of red (R) and far-red (FR) light on various species.

| Species | Control R:FR | Treatment R:FR | Treatment effect | Reference |
|---------------------------------|-----------------|-------------------|--|----------------------------|
| <i>Antirrhinum majus</i> | 1.05 | 5.51 | 13 d delay in anthesis | Cerny et al., 2007 |
| | 1.05 | 1.51 | 10% decrease in stem elongation | Cerny et al., 2003 |
| <i>Campanula carpatica</i> | 1.07 | 1.74 | 2 to 3 d delay in flowering | Runkle and Heins, 2002 |
| | 9.10 | 0.8 | Promoted first microscopic sign of flowering | Kristiansen, 1988 |
| | 0.6 | 8.4 | No effect on flowering time | Padhye and Runkle, 2009 |
| <i>Capsicum annuum</i> | 1.07 | 0.4 | 65% increase in stem elongation | Runkle and Heins, 2001 |
| | 1.00 | 2.2 | 30% decrease in stem elongation | Li et al., 2001 |
| <i>Chrysanthemum morifolium</i> | 1.00 | 1.45 | 22% decrease in stem elongation | Oyaert et al., 1999 |
| | 1.05 | 2.51 | No effect on anthesis | Cerny et al., 2004 |
| | 1.00 | 2.2 | 20% decrease in stem elongation | Li et al., 2000 |
| <i>Coreopsis ×grandiflora</i> | 1.05 | 1.51 | 5% decrease in stem elongation | Cerny et al., 2003 |
| | 0.6 | 8.4 | No effect on flowering time | Padhye and Runkle, 2009 |
| | 1.07 | 1.74 | 21% decrease in stem elongation | Runkle and Heins, 2001a |
| <i>Cosmos bipinnatus</i> | 10.7 | 0.4 | 26% increase in stem elongation | Runkle and Heins, 2001 |
| | 10.5 | 3.51 | No effect on anthesis | Cerny et al., 2005 |
| <i>Cucumis sativus</i> | 10.5 | 1.51 | 4% decrease in stem elongation | Cerny et al., 2003 |
| | 1.1 | 1.6 | 45-50% decrease in stem elongation | Moe, 2002 |
| <i>Euphorbia pulcherrima</i> | 1.1 | 0.75 | 21-41% increase in stem elongation | Moe, 2002 |
| | 1.07 | 1.74 | 25% increase in branching | Clifford et al., 2004 |
| <i>Eustoma grandiflorum</i> | 1.07 | 1.74 | 20% decrease in internode elongation | Clifford et al., 2004 |
| | 1.02 | 1.48 | 10-19% decrease in stem elongation | Wilson and Rajapakse, 2001 |
| <i>Fuchsia ×hybrida</i> | 1.02 | 0.85 | 15% increase in stem elongation | Wilson and Rajapakse, 2001 |
| | 1.1 | 1.6 | <10% decrease in stem elongation | Moe, 2002 |
| <i>Impatiens walleriana</i> | 1.1 | 8.0 | 20% decrease in stem elongation | Moe, 2002 |
| | 1.07 | 1.74 | 10% decrease in stem elongation | Runkle and Heins, 2002 |
| | 1.0 | 1.8 | 12% decrease in stem elongation | Fletcher et al., 2005 |
| | 1.0 | 3.8 | 19% decrease in stem elongation | Fletcher et al., 2005 |

Table 1 (cont'd)

| | | | | |
|-----------------------------|------|------|---|----------------------------------|
| <i>Lilium longiflorum</i> | 1.1 | 4.5 | 9-23% decrease in stem elongation | Kambalapally and Rajapakse, 1998 |
| | 1.1 | 4.5 | No effect on flowering time | Kambalapally and Rajapakse, 1998 |
| <i>Petunia ×hybrida</i> | 1.05 | 4.51 | 13 d delay in anthesis | Cerny et al., 2006 |
| | 1.06 | 1.57 | 30% decrease in internode elongation | Patil, 2001 |
| | 1.07 | 1.74 | 34% decrease in stem elongation | Runkle and Heins, 2002 |
| | 1.28 | 5.47 | 40-73% decrease in stem elongation | Kim et al., 2002 |
| | 1.0 | 1.1 | 13% decrease in stem elongation | Fletcher et al., 2005 |
| | 1.0 | 1.8 | 30% decrease in stem elongation | Fletcher et al., 2005 |
| | 1.0 | 3.8 | 37% decrease in stem elongation | Fletcher et al., 2005 |
| | 1.28 | 5.47 | 7-13 d delay in flowering | Kim et al., 2002 |
| | 1.07 | 1.74 | 2-3 d delay in flowering | Runkle and Heins, 2002 |
| <i>Petunia multiflora</i> | 0.6 | 8.4 | 21 d delay in flowering | Padhye and Runkle, 2009 |
| | 0.6 | 8.4 | 28 d delay in flowering | Padhye and Runkle, 2009 |
| <i>Pisum sativum</i> | 1.07 | 1.74 | 17% decrease in stem elongation | Runkle and Heins, 2001a |
| | 1.07 | 0.4 | 23% increase in stem elongation | Runkle and Heins, 2001 |
| <i>Rosa ×hybrida</i> | 1.1 | 5.8 | 17-27% decrease in stem elongation | Rajapaske and Kelly, 1994 |
| | 1.1 | 5.8 | 18-28% decrease in internode elongation | Rajapaske and Kelly, 1994 |
| | 1.1 | 5.8 | 9-23% increase in lateral shoot number | Rajapaske and Kelly, 1994 |
| | 1.16 | 0.3 | 25% decrease in stem elongation | McMahon and Kelly, 1990 |
| <i>Rudbeckia hirta</i> | 0.6 | 8.4 | No effect on flowering time | Padhye and Runkle, 2009 |
| <i>Solanum lycopersicon</i> | 1.07 | 1.74 | 24% decrease in stem elongation | Runkle and Heins, 2002 |
| <i>Viola ×wittrockiana</i> | 1.07 | 1.74 | 18% decrease in stem elongation | Runkle and Heins, 2002 |
| | 1.07 | 1.74 | 14% decrease in stem elongation | Runkle and Heins, 2001a |
| | 1.07 | 0.4 | 31% increase in stem elongation | Runkle and Heins, 2001 |
| | 1.07 | 1.47 | 10 d delay in flowering | Runkle and Heins, 2003 |
| <i>Zinnia elegans</i> | 1.05 | 1.51 | No effect on anthesis | Cerny et al., 2003 |
| | 1.05 | 1.51 | 7% decrease in stem elongation | Cerny et al., 2003 |

Photoperiod

Another environmental variable created by light is photoperiod, which is the duration of light and darkness during a 24-hour period. Plant development in photoperiodic crops is affected by both the absolute photoperiod (the number of hours of light versus dark in a 24-hour period) and the pattern and duration of light and dark cycles. Photoperiod affects flower induction and the rate at which a plant flowers in many garden species (Erwin and Warner, 2002; Mattson and Erwin, 2005; Runkle and Heins, 2003). Ambient photoperiod is commonly manipulated to elicit a desired vegetative or reproductive response in photoperiodic crops.

Photoperiod is perceived by plant leaves (Hopkins and Hüner, 2004; Vince-Prue, 1975; Zeevaart, 1958). In some plants, leaves grown under an inductive photoperiod that were grafted to a photoperiodic plant grown under a noninductive photoperiod induced a flowering response (Zeevaart, 1958). Zeevaart also reported that induced leaves of the SD plants (SDPs) perilla (*Perilla crispa* L.) and cocklebur (*Xanthium pennsylvanicum*) caused flowering when grafted to plants maintained under LDs. Furthermore, a detached leaf exposed in isolation to inductive photoperiods was grafted to noninduced plants and induced a flowering response. This research led to the concept of “florigen”, a theoretical photoperiodic stimulus transducer that is produced in leaves and transported to the apex to initiate flowering.

Most floriculture crops can be grouped into three photoperiodic classes: LDPs, SDPs, and day-neutral plants (DNPs) (Erwin, 2002; Mattson and Erwin, 2005; Runkle et al., 2001; Runkle and Heins, 2006). DNPs flower regardless of the photoperiod, assuming other environmental and cultural factors are favorable. Flower induction among LDPs occurs when night length is shorter than some critical length, while SDPs are induced to flower when night length is longer than some critical duration (Vince, 1969). A small number of species flower most rapidly under

an intermediate photoperiod (e.g., 13 or 14 h of light) and thus can be called intermediate-day plants. Within the photoperiodic classes, plants can be further divided based on whether they exhibit a quantitative or qualitative response to photoperiod. Plants with a quantitative (facultative) response to photoperiod will eventually flower under any photoperiod, but flower most rapidly under a specific photoperiod (Erwin and Warner, 2002; Mattson and Erwin, 2005; Runkle and Heins, 2006). Those with a qualitative (obligate) response to photoperiod only flower at, above, or below a specific photoperiod. Flowering responses to photoperiod can vary by cultivar within a species (Mattson and Erwin, 2005).

Manipulating Photoperiod. Manipulating the photoperiod can reduce production costs by reducing production time and improving the overall quality of the crop (Runkle and Heins, 2006). When the ambient photoperiod is undesirable for a crop, growers have several options to manipulate the lighting conditions. Under ambient LDs, SDs can be created by covering the crop with a blackout material (Erwin and Warner, 2002). Under ambient SDs, LDs can be created by lighting during the night. Low-intensity, photoperiodic lighting promotes flowering of LDPs and inhibits flowering of SDPs (Mattson and Erwin, 2005; Runkle and Heins, 2006). Day-extension lighting serves to lengthen the photoperiod by providing electric light beginning at the end of the natural day. Night interruption (NI) lighting involves breaking up the dark period with one or more light periods (Runkle et al., 2001). NI generally induces flowering in LDPs more effectively than day extension, even if the intensity and duration of the supplemental lighting is equal (Thomas and Vince-Prue, 1997). Four hours of NI is recommended for the most complete and rapid flowering in LDPs (Runkle and Heins, 2003; Runkle et al., 1998a). For example, flowering time of tussock bellflower decreased from 79 to 49 d as the duration of NI

increased from 1 to 4 h (Runkle et al., 1998a). Less than $1 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (5-10 footcandles) is needed to elicit a photoperiodic response (Whitman et al., 1998).

Manipulated LDs can be used to reduce the time to visible bud and the time to flower for a variety of LDPs. Time to visible bud was shortened by 21 and 15 d, respectively, when prairie gentian ‘Echo Blue’ and ‘Fuji Deep Blue’ were grown under 20-h LDs compared to 10-h SDs, both at 21 °C (Islam, 2005). However, since flower buds were initiated under both LDs and SDs, the two cultivars studied can be classified as quantitative LDPs (at least for flower initiation). Under LDs, prairie gentian flowered at a developmentally younger stage as shown by the production of fewer nodes below the first flower than plants grown under constant SDs. Time to visible bud and first open flower of snapdragon decreased by 25 d and 34 d at 21 °C, respectively, under 18-h LDs compared to 9-h SDs (Maginnes and Langhans, 1961). In addition, plants grown under LDs developed 19.5 fewer leaves before flowering than did plants grown under SDs. Loosestrife (*Lysimachia congestiflora*) flowered 21 and 34 d earlier when grown under 16-h LD at 20 ± 2 °C than when grown under 12- and 8-h photoperiods, respectively (Zhang et al., 1995). In addition, leaf number below the first flower was decreased by 40 to 72% when grown under LDs. Trailing petunias grown under 17-h LDs flowered 57 d earlier than plants grown under 8-h SDs (Adams et al., 1997). This and other research show that the critical photoperiod for flower initiation can be different from that for flower development.

Photoperiod and Flowering Percentage. Complete and uniform flowering is important in commercial floriculture production. Achieving 100% flowering for a particular crop can be challenging if photoperiodic requirements are not met. Several floriculture crop examples can be used to illustrate the variability in how plants respond to photoperiod. Qualitative LDPs flower under SDs or LDs, but flowering is more uniform, and occurs faster, under long photoperiods.

For example, flowering percentage of Persian violet (*Cyclamen persicum* Mill.) was greatest (100%) when grown under a 16-h photoperiod compared to 36 or 75% flowering under 8- or 12-h photoperiods, respectively (Oh et al., 2008). Flowering percentage of vernalized perennial phlox (*Phlox paniculata* Lyon ex Pursh.) was 100% when the photoperiod was longer than 13 h or a 9-h day with a 4-h NI (Runkle et al., 1998). Under 10- or 12-h SDs, flowering percentage only reached 19 or 50%, respectively. Flowering of cape bugloss (*Anchusa capensis* Thunb.) and gypsophila (*Gypsophila repens* L.) was 100% under LDs (9-h days with a 4-h NI) and was reduced (84 and 15%, respectively) under 9-h SDs (Armitage and Garner, 1999). Qualitative LDP do not flower under short photoperiods. For example, flowering percentage of gooseneck loosestrife (*Lysimachia clethroides* Duby.) was 85 to 90 under constant LDs (9-h day with a 4-h NI), whereas it was 0 under constant 9-h SDs (Lewis et al., 2000). Flowering percentage of coneflower (*Rudbeckia fulgida* Ait.) was nearly 100% when the photoperiod was greater than 14 h or with a 9-h day with a 4-h NI. In contrast, plants remained vegetative under photoperiods less than 13 h (Runkle et al., 1999).

Cyclic Lighting. Cyclic lighting refers to intermittent (not continuous) lighting and is another method of providing manipulated LDs to photoperiodic crops. Cyclic lighting can reduce energy consumption by reducing the amount of time lamps operate or the number of lamps needed to light a crop. INC lamps, for example, can be cycled on and off (e.g. 6 minutes on and 24 minutes off) for several hours during the night to create effective LDs in many crops. For example, flowering time of tussock bellflower 'Pearl Deep Blue', and tickseed 'Early Sunrise' was similar under cyclic and continuous INC night interruption (Runkle et al., 1998a). However, flowering of the LDP *Petunia* × *hybrida* 'Easy Wave Coral Reef' and black-eyed susan (*Rudbeckia hirta*) 'Becky Cinnamon Bicolor' was delayed by 9 to 16 d at 20 °C under cyclic NI

(on for 20% of each hour for 4 h) compared to a continuous 4-h NI (Blanchard and Runkle, 2010). Therefore, cyclic INC night interruption may not induce the most rapid flowering of some LD crops.

Another cyclic lighting strategy is the use of stationary high-pressure sodium (HPS) lamps with rotating reflectors. The reflector moves a beam of light across a relatively large area at regular intervals (e.g., every minute). One such device, the Beamflicker (Parsource Lighting Solutions, Petaluma, CA), can be mounted above the crop and used to create cyclic lighting for up to 2700 square feet of space. A cyclic HPS lamp has been used to induce flowering in the LD species tussock bellflower, tickseed, petunia, and black-eyed susan, while using less energy than a traditional 4-h INC night interruption (Blanchard and Runkle, 2010). However, since light intensity from the cyclic HPS lamp declines with increasing lateral distance, flowering was delayed as the intensity from the lamp decreased below $2.4 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. At the furthest distance from the device (at 13 m, when the light intensity was $0.3 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), flowering was delayed by 14 to 31 d at 20 °C. A cyclic HPS lamp can also be used to prevent flowering in SD crops. Initiation and flowering of the SDP chrysanthemum ‘Bianca’ and ‘Auburn’ and *Salvia leucantha* L. was delayed by 23 to 31, 13 to 17, and 12 to 30 d, respectively, when a 4-h NI from a cyclic HPS delivered $\geq 2.4 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Blanchard and Runkle, 2009).

Effect of Non-Inductive Photoperiods. In some situations, it is advantageous to deliver a non-inductive photoperiod when extended vegetative production is preferred (Mattson and Erwin, 2005). For example, stock plants used for the production of stem cuttings are maintained in a perpetually vegetative state by delivering a non-inductive photoperiod. In petunia production, flowering is fastest under LDs. However, in some situations, a higher quality specimen can be grown if plants are exposed to a period of SDs. In addition, early flowering can

reduce the quality of the finished crop in the greenhouse and lead to subsequent inferior garden performance if there is insufficient foliage to support the flowers (Erwin and Warner, 2002).

Traditional Lamps Used In Horticulture

A variety of lamp types are used in floriculture crop production to create long days or to increase photosynthesis. Traditionally, greenhouse lighting has been delivered with INC, FL, metal halide (MH), or HPS lamps (Bula et al., 1991). However, these lamp types were originally developed for human needs, not for plants (Bula et al., 1991; Kim et al., 2007). PAR and light quality vary widely among these lamps, leading to differences in photosynthetic efficiency, photomorphogenesis, energy efficiency, and thermal load on crops. For example, the R:FR of INC, MH, HPS, and CWF lamps are 0.7, 3.3, 5.9, and 8.8, respectively.

Incandescent. INC are the least electrically efficient lamp type, are low intensity (~2.060 lumen per watt), they release a considerable amount of heat, and they have a short (1,000 h) lifespan. The radiant yield of INC is low; only 6 to 7% of the energy consumed is emitted in the form of photosynthetic light (Thimjan and Heins, 1983). Because of their inefficiency, these bulbs are being phased out of production in many countries for general use. However, INC lamps are regularly used in greenhouse production for low-intensity photoperiodic lighting. Rich in FR photons, INC lamps emit an effective light quality for inducing flowering in LDPs and inhibiting flowering in SDPs, although they promote stem extension, which is often undesirable.

Fluorescent. With the advent of compact fluorescent and T5 and T8 bulbs, FL lamps have increased in light output and energy efficiency. FL lamps emit more light in the B and G wavebands (21 and 52% of PAR, respectively) and much less FR than INC lamps. Overall, FL lamps emit almost four times as much PAR than INC at a similar input wattage. Therefore, plants

are able to use much more of the light from FL lamps for photosynthesis than that from INC; and the radiant yield is 22 to 27%. Cool-white fluorescent (CWF) lamps are filled with mercury gas. The mercury gas emits ultra-violet light that is absorbed by phosphors within the lamp. The phosphors re-emit the energy as longwave visible light. The output of CWF bulbs is 35% R light, while warm-white fluorescent (WWF) bulbs emit 44% R (Thimijan and Heins 1983). While WWF bulbs have a greater R component, they are lower in B and G wavelengths.

High Intensity Discharge. Two commonly used lamps that are capable of high light intensities are MH and HPS lamps. HID lamps are the most electrically efficient lamps available for plant lighting with radiant yields of up to 31%. Although HIDs emit a high PAR intensity, they also emit a lot of heat. Therefore, they may increase plant temperature or cause tissue damage if positioned too close to the crop. Metal halide lamps have a slightly wider spectrum than HPS lamps. An electrical arc across high-pressure mercury, thorium, thallium, and sodium gases cause the metal halides to vaporize and emit light in metal halide lamps. HPS lamps are the most electrically efficient HID lamp and the most commonly used lamp for photosynthetic lighting. They are similar to metal halide lamps, but contain primarily sodium, with mercury and xenon added for starting the bulb.

Emerging Lighting Technology: The Light-Emitting Diode

In the search for a more energy and photosynthetically efficient lighting source for plant production, scientists have turned to the developing technology of light-emitting diodes (LEDs) as a promising option. Since its introduction in the 1960s, LED technology has facilitated many photobiological studies as well as demonstrated the potential of becoming an efficient lighting source for commercial plant production (Nhut et al., 2003).

In the last decade, LEDs have become powerful and efficient enough to be a possible substitute for conventional lighting in horticulture (Kim et al., 2007; Lee and Palsson 1994). The original low-power indicator LED is still used in electronic equipment, stoplights, automobile taillights, and other applications where light intensity is not crucial. Around 1999, advances in semiconductor technology significantly augmented the light intensity of LEDs, resulting in “high-power” or “superbright” LEDs capable of providing photon outputs high enough for photosynthetic lighting (Bourget, 2008; Morrow, 2008; Tennessen et al., 1994). The output of superbright LEDs has been doubling approximately every two years, and additional increases in light intensity are expected (Kim et al., 2007; Steigerwald et al., 2002).

The light intensity of LEDs varies according to the chemical composition of the semiconductor chip within each lamp and can be manually altered by adjusting the electrical output of the power supply (Fujiwara et al., 2005; Heo et al., 2002; Okamoto et al., 1996; Yanagi et al., 1996). Red gallium-aluminum-arsenide (GaAlAs) LED arrays can emit up to $900 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, which is intense enough to support many C4 plants (Lee and Palsson 1994). However, until recently, B LEDs were capable of only emitting a low photon flux and were generally used to supplement other LED arrays (Tanaka et al., 1998).

The spectral quality of LED output varies with chemical composition (Bula et al., 1991; Okamoto et al., 1996). LED chips are generally composed of group III-V elements in a particular combination depending on the color of light desired. For example, gallium-aluminum-arsenide-phosphide and gallium-nitride chips emit B light peaking at 440 nm (Tamulaitis et al., 2005), silicon-carbide chips emit violet-blue light, and gallium-phosphide and gallium-arsenide-phosphide chips emit light in the yellow-orange-red range (Barta et al., 1992). Both R and FR LED chips are composed of GaAlAs. Depending on the ratio of Al to Ga, peak wavelengths

ranging from 630 to 940 nm can be achieved (Barta et al., 1992; Bula et al., 1991; Tennessen et al., 1994). Generally, the light produced by R LEDs peaks at 650 nm and at 720 nm for FR LEDs (Heo et al., 2002; Tamulaitis et al., 2005). Currently, LEDs are available that emit wavelengths from UVC (250 nm) through IR (1000 nm) (Bourget, 2008).

Advantages of LEDs. Compared with conventional lighting sources, LEDs are safe and reliable, have a small mass and volume, solid-state construction, long operating lifespan (~50,000 h), allow delivery of specific wavelengths, and are continually improving in electrical efficiency (Bourget, 2008; Morrow 2008). Furthermore, LEDs switch on and off instantly, with no warmup or downtime required (Morrow, 2008). They can also be dimmed from zero to maximum light intensity. LED lifespan is not shortened with increasing on/off cycles as are FL, HPS, and metal halide lamps (Bourget, 2008). While LEDs do emit heat, which is dissipated through an external heat sink, little heat is emitted in the beam of light. Therefore, LEDs can be placed near crops without increasing plant temperature or scorching leaves (Bourget, 2008; Massa et al., 2008; Morrow, 2008). As this technology advances, LEDs continue to improve in electrical efficiency, light intensity, and affordability (Kim et al., 2007). Steigerwald et al. (2002) stated that each decade, LED cost decreases by a factor of ten, while intensity increases by a factor of ten.

The LED's narrow bandwidth makes precise control of light quality possible. Since LEDs emit specific wavebands, it is possible to provide plant lighting that contains only those wavelengths recognized by the photoreceptors (Kim et al., 2007; Tamulaitis et al., 2005). Furthermore, exclusion of certain wavelengths from the light source makes it possible to isolate the effects associated with a particular waveband (Folta et al., 2005). For example, LEDs have been used to isolate responses that are stimulated by phototropins and cryptochromes using

“pure” B light, and those stimulated by phytochromes using “pure” R and FR light (Barta et al., 1992; Folta et al., 2005).

High photosynthetic efficiency is another attainable trait of LED lighting. Red and B LEDs emit light corresponding to the two chlorophyll absorption peaks (Barta et al., 1992). Considerably less non-photosynthetic radiation is produced by R, B, and white LEDs than by conventional lamps (Barta et al., 1002; Brown et al., 1995; Lee and Palsson, 1994). Therefore, greater photosynthetic utilization efficiency can be achieved by LEDs than by traditional lamps (Bula et al., 1991). At equal photosynthetic photon flux, lighting with LEDs can produce higher net assimilation rates than other lighting schemes (Barta et al., 1992). Having a relatively high peak wavelength, R LEDs are particularly efficient. With increasing wavelength, there is an increase in the conversion of electricity to photons and then from photons to photosynthetically fixed carbon (Tennessee et al., 1995).

High electrical efficiency and the resulting energy savings are further benefits of LED lighting (Schubert et al., 2006). The electrical efficiencies of various lamp types are often compared according to their luminous efficiency, which is the flux in lumens per unit of electrical input, or lm/W (Schubert and Kim, 2005). However, this measure of efficiency is based on the human eye’s sensitivity to light, and thus is not appropriate for plants. Unlike conventional lamps, LEDs directly convert electrical energy into light (Krames et al., 2007). Reportedly, the electrical efficiencies of LEDs are similar to those of HPS lamps and greater than those of FL lamps (Barta et al., 1992; Bula et al., 1991; Goins et al., 1997; Yorio et al., 2001). The most efficient white LEDs produce 231 $\text{lm}\cdot\text{W}^{-1}$ (CREE, 2011). The theoretical maximum efficiency of white LEDs, based on a photometric measurement system, is nearly double that of the most efficient LEDs constructed to date.

R and FR LEDs could provide an attractive option for controlling phytochrome-related responses in photoperiodic crops, as discussed previously. The use of LEDs for photoperiodic lighting can potentially consume 75% to 80% less energy than INC lamps that deliver the same light intensity. LEDs could provide additional advantages, such as less frequent maintenance, accelerating flowering, or minimizing stem elongation of some crops.

Limitations of LEDs. Despite their many advantages, there are a few concerns regarding the use of LEDs for horticultural lighting. The high cost of LEDs is a major barrier to their widespread use in both horticulture and other industries (Schubert and Kim, 2005; Tamulaitis et al., 2005). Therefore, the use of LEDs in horticulture has been limited to small-scale research applications, such as for tissue culture or growth chamber lighting, and space-based life support systems (Morrow, 2008). In addition, many LED systems are not intense enough for sole-source photosynthetic lighting (Massa et al., 2008). Less intense LED systems may be useful for supplemental lighting or for low-intensity lighting of photoperiodic crops (Massa et al., 2008; Morrow, 2008). LEDs are continually improving in output and are becoming adequate for photosynthetic lighting.

Several colors of LEDs may be needed to provide the range of wavelengths required for normal plant growth (Kim et al., 2007). Problems can occur if all the photosynthetic light is delivered in only one narrow waveband. For example, in B-deficient light, stomatal conductance may be reduced, which could decrease transpiration rate and increase leaf temperature (Tennessen et al., 1994).

LED Plant Research. The ability to control light quality and quantity using LEDs has made this technology useful for photobiological research. Studies in photosynthesis, photomorphogenesis, chlorophyll synthesis (Brown et al., 1995; Kim et al., 2007; Nhut et al.,

2003; 2007; Tennessen et al., 1994), disease resistance (Kim et al., 2007; Schuerger et al., 1997), and nitrate accumulation (Kim et al., 2007) have been conducted using LEDs. LEDs as either the primary or supplementary lighting source have been used to successfully culture a number of species including strawberry (*Fragaria ×ananassa*) ‘Akihime’ (Nhut et al., 2003); lettuce (Tamulaitis et al., 2005; Tanaka et al., 1998; Yorio et al., 2001); pepper, cucumber, tomato, and wheat (*Triticum aestivum* L.) (Brown et al., 1995; Goins et al., 1997; Nhut et al., 2003); spinach (*Spinacea oleracea* L.) and radish (*Raphanus sativus* L.) (Tamulaitis et al., 2005; Yorio et al., 2001), as well as bedding crops such as flossflower (*Ageratum houstonianum* Mill.), marigold, and scarlet sage (*Salvia splendens*) (Heo et al., 2002, 2006).

Unlike traditional lamps, LEDs offer the opportunity to deliver narrow wavebands of monochromatic light to crops. This characteristic of LEDs has been useful to researchers to determine the effects of monochromatic light on germination, plant growth, and development. Lettuce and egg-plant were grown under B, B-G, G, or R LEDs (Hirai et al., 2006). Stem length of eggplant was longest under B LEDs. On the other hand, stem length of lettuce was longest under R LEDs, while B light suppressed it. Therefore, the effect of monochromatic B light on stem elongation varies among species. In another study, lettuce plants grown under R LEDs developed approximately four more leaves than plants grown under B LEDs at the same light intensity (Yanagi et al., 1996). In African marigold (*Tagetes erecta* L.) ‘Orange Boy’, plants grown under R LEDs had higher dry weight than plants grown under B LEDs at the same irradiance (Heo et al., 2002). In addition, B LEDs produced stems that were three times longer compared to plants grown under FL.

In other experiments, crops were grown under a mixture of multiple colors of LED light. Flossflower, African marigold, and scarlet sage were grown under B+R, B+FR, R+FR LEDs, or

FL lamps at the same light intensity ($90 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and duration (16-h photoperiod) (Heo et al., 2006). Both FL and B+R produced the shortest stems in ageratum, African marigold, and scarlet sage (8.7, 6.4, and 6.2 cm, respectively) compared to R+FR (29.3, 11.8, and 15.9 cm) and B+FR (14.2, 15.1, and 13.5 cm). FL and B+R increased dry weight compared to R+FR and B+FR. Plants have evolved under a broad spectrum of light, so determining the specific effects of narrow-bandwidth LED lighting on growth and development has been of interest (Brown et al., 1995).

With the advent of superbright B LEDs, many LED studies have been carried out to determine how the B:R influences growth and whether B light is necessary for normal growth. Several studies suggest that approximately 10% B light (with other wavebands) is needed to maintain a similar leaf number, leaf length, and dry mass compared to plants grown under broad-spectrum lamps (Goins et al., 1997; Yorio et al., 2001). Lettuce 'Waldmann's Green', radish 'Cherriette' and spinach 'Nordic IV' grown under $300 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ of light supplied by R LEDs increased in dry weight by 50%, 50%, and 200%, respectively, when $30 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ of B FL light was included in the $300 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ total PPF (Yorio et al., 2001). Similarly, in 'USU-Super Dwarf' wheat plants grown under $350 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ supplied by R LEDs needed 10% B FL supplementation for culm-leaf and flag-leaf lengths, tiller number, shoot dry weight, net photosynthesis rate, seed yield, and seed number to equal wheat grown under white FL light at the same intensity (Goins et al., 1997). Pepper also required additional B light to maintain normal growth and development (Brown et al., 1995; Pinho et al., 2005). Compared to the control (light from metal halide lamps at $300 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), leaf dry weight of pepper grown under monochromatic R LEDs at the same intensity was decreased by 44% (Brown et al., 1995).

The addition of 1% B FL to the R LEDs increased leaf dry weight by 50%. These studies quantify the importance of B photons for plant growth.

Green light is able to penetrate plant canopies better than R or B light (Kim et al., 2004a). Therefore, transmitted G light can increase photosynthesis in leaves lower in the canopy. The addition of G light to R+B LED arrays can increase plant growth. Lettuce grown under R+G+B (24% G) LED arrays had increased growth compared to plants under R+B arrays of equal intensity (Kim et al., 2004b). However, excessive G light had negative effects on growth; when G light in the arrays was increased above 50%, plant growth decreased (Kim et al., 2006).

For leaves within a plant canopy, photosynthetic light is often received in the form of sunflecks, which last from milliseconds to minutes in length. LEDs can provide such intermittent lighting because they are capable of reaching their peak emittance in about 80 nanoseconds during each on/off cycle (Barta et al., 1992; Tennessen et al., 1994). Pulsed light of differing frequencies can be used to study three separate processes of the photosynthetic apparatus: 1) the initial photochemistry, 2) the electron transport chain, and 3) carbon metabolism (Jao and Fang, 2003; Tennessen et al., 1994). By varying the time between pulses of light, researchers have found that up to 75% of the light in a given time period can be eliminated without a decrease in photosynthetic rate (Jao and Fang, 2003). Furthermore, depending on the frequency of pulses, photosynthetic efficiency was shown to be equal, if not greater, in intermittent light than in continuous light (Jao and Fang, 2003; Tennessen et al., 1995).

The favorable attributes of LEDs include their small size and volume, solid-state construction, long lifespan, energy and photosynthetic efficiency, and their ability to allow precise control of light quality. However, the future of LEDs for plant production depends on several factors. Currently, LEDs are substantially more expensive (3- to 30-fold) compared to

conventional lamps (Tamulaitis et al., 2005). For this reason, the use of LED lighting has been restricted to specific applications. However, the photosynthetic utilization efficiency and electrical efficiency of LEDs may compensate for their expense (Kim et al., 2007). As additional improvements in efficiency are expected for this technology, LEDs may become an affordable option. Further research is needed to characterize the effects of narrow bandwidth irradiation on a broader variety of crops.

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SECTION II

USING LIGHT-EMITTING DIODES FOR NIGHT-INTERRUPTION LIGHTING OF SHORT-DAY PLANTS

Using Light-emitting Diodes for Night-interruption Lighting of Short-day Plants

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Abstract

Flowering of short-day (SD) plants is inhibited by photoperiodic lighting from incandescent (INC) lamps during the night. INC lamps are inexpensive, easy to install, and emit an effective spectrum for controlling flowering, but they also are energy inefficient and are being phased out of production. Our objective was to compare the effects of different red-to-far-red ratios (R:FR) of photoperiodic lighting from LEDs on the flowering of SD plants.

Chrysanthemum (*Chrysanthemum* × *morifolium*), dahlia (*Dahlia hortensis*), and African marigold (*Tagetes erecta*) were grown at 20 °C under a 9-h day with and without a 4-h night interruption (NI) treatment by INC lamps or light-emitting diodes (LEDs) with seven different R:FR ranging from all R to all FR. The least sensitive species, African marigold, flowered under all treatments, but flowering was delayed under the FR-only NI and under SDs. Flowering in dahlia was incomplete under the FR-only NI and under SDs, but flowering was delayed similarly under the remaining NI treatments. Flowering in the most sensitive species, chrysanthemum, was not inhibited by an R:FR of 0.28 or lower, while an R:FR of 0.66 or above reduced flowering percentage. For all species, stem length under the FR-only NI and SD treatments was shortest compared to all other R:FR treatments. We conclude that a moderate to high R:FR (≥ 0.66) was most effective at interrupting the long night for SD plants.

Introduction

Many herbaceous ornamental plants exhibit a photoperiodic flowering response (Erwin and Warner, 2002; Runkle and Heins, 2003; Mattson and Erwin, 2005). This photoperiodic response is determined primarily by the duration of the dark period, also known as the critical night length (Thomas and Vince-Prue, 1997). Plants have been classified into photoperiodic

response classes depending how the critical night length influences flowering, including short-day (SD) plants (SDPs), in which flowering is most rapid when uninterrupted dark periods are longer than some genotype-specific critical night length (Vince, 1969). Within the SDP response category, plants can be further classified based on whether SDs are required for flowering (a qualitative response), or only hasten it (a quantitative response). Photoperiodic (low-intensity) lighting is used by commercial crop producers to alter the natural photoperiod (e.g., to extend the natural day length, or to interrupt the dark period) to manipulate flowering.

The spectral quality of photoperiodic lighting can influence flowering responses. Light quality is perceived by three identified families of plant photoreceptors: cryptochromes, ultra-violet receptors, and phytochromes (Kami et al., 2010). The phytochrome photoreceptors mediate extension growth and flowering in photoperiodic plants (Smith, 1994). At least for phytochrome A, it exists in a red- [R (600 to 700 nm), peak absorption at 660 nm] and a far red- [FR (700 to 800 nm), peak absorption at 730 nm] absorbing form, P_R and P_{FR} , respectively (Hayward, 1984; Sager et al., 1988). The ratio of R to FR light (R:FR) incident on the plant influences the phytochrome photoequilibria (P_{FR}/P_{R+FR}) within the plant. Upon absorbing R light, P_R converts mainly to the P_{FR} form. The P_{FR} form largely converts back to the P_R form upon absorbing FR light, or during a natural, gradual conversion during the dark period (Thomas and Vince-Prue, 1997). Although the total pool of phytochrome in the plant is relatively constant, since natural light environments are ever-changing, the relative amounts of P_{FR} and P_R , and thus the overall P_{FR}/P_{R+FR} , also fluctuate throughout the day.

In photoperiodic crops, the P_{FR}/P_{R+FR} , through different types of phytochromes, influences flowering. The P_{FR}/P_{R+FR} also influences extension growth, especially in shade-avoiding plants. Five types of phytochrome have been identified, types A-E (Kami et al., 2010).

Studies with phytochrome mutants of *Arabidopsis* have shown that phyA and phyB play dominant roles mediating flowering and stem extension, respectively, in response to light quality (Franklin and Quail, 2010). Under a long, uninterrupted night, the P_{FR} form of phytochrome slowly converts to the P_R form during the long night, leaving insufficient P_{FR} to inhibit flowering. However, if R light is provided during the long night, P_R is converted to P_{FR} (creating a greater P_{FR}/P_{R+FR}), which inhibits flowering in SDPs. The P_{FR} form is the active form of phytochrome, which translocates to the nucleus upon receiving light signals and activates downstream pathways.

Light-emitting diodes (LEDs) are an attractive technology for night-interruption lighting of photoperiodic crops. Compared to conventional lamps, LEDs have many desirable characteristics including a very long operating life, narrow bandwidth capability, full instantaneous irradiance when powered, and continually improving electrical efficiencies (Bourget, 2008; Morrow, 2008). Furthermore, LEDs allow researchers to analyze the effects of specific wavebands without extraneous wavebands such as blue light. Many of the original studies on photoperiodic light quality were limited by the lighting technology of the time. The use of photosensitive filters and tinted lamps may have introduced confounding variables into these early experiments, such as differences in photon flux between treatments and/or inclusion of potentially confounding, extraneous wavelengths (Borthwick et al., 1952; Borthwick, 1957; Cathey and Borthwick, 1957; Downs, 1956).

The objectives of the present study were to use LEDs to quantify the impact of the R:FR of NI lighting on flowering of several SD ornamental crops and to compare plant responses with those under traditional incandescent (INC) lamps. To our knowledge, this is the first study that

has identified how R:FR ratios control the flowering response of SDPs without the confounding effects of other light wavebands.

Materials and Methods

Plant material and culture. On February 8, 2011, 7- to 10-day-old seedlings of the SDP African marigold (*Tagetes erecta*) 'American Antigua Yellow' grown in 288-cell (6 mL) plug trays were received from a commercial greenhouse (C. Raker & Sons, Inc., Litchfield, MI). In addition, rooted cuttings of the SDP chrysanthemum (*Chrysanthemum ×morifolium*) 'Garden Adiva Purple', and dahlia (*Dahlia hortensis*) 'Dahlinova Figaro Mix' grown in 36-cell (32 mL) liner trays were received from the same source. The young plants were subsequently grown under non-inductive long days [natural day length extended from 0600 to 2200 HR by high-pressure sodium (HPS) lamps] in a research greenhouse at 20 °C until transfer to the NI treatments.

African marigold and dahlia were transferred to NI treatments on February 14, 2011 and chrysanthemum on February 25. Upon transfer, ten young plants per treatment of each species were transplanted into 10-cm (430 mL) round plastic pots containing a commercial peat-perlite medium (Suremix; Michigan Grower Products, Inc., Galesburg, MI). All species were thinned to one plant per pot on the day of transplant. The experiment was repeated with the same propagation procedure and greenhouse environment as previously described, except dahlia 'Dahlinova Figaro Mix' was replaced by dahlia 'Carolina Burgundy'. Due to the commercial unavailability during the second replication, chrysanthemums from the first replicate of the experiment were grown as stock plants under long days (LDs), and cuttings were subsequently harvested and rooted for the second replicate. Shoot-tip cuttings (2-3 nodes) were rooted in 51-

cell liner trays filled with 50% Sure-mix and 50% screened coarse perlite (Therm-O-Rock East, Inc., New Eagle, PA). Cuttings were rooted in a propagation greenhouse as described by Lopez and Runkle (2008). For the second replicate, African marigold was transferred to NI treatments on May 26, 2011, and chrysanthemum and dahlia were transferred on July 7.

LED lamps and NI treatments. Opaque black cloth enclosed all greenhouse benches from 1700 to 0800_{HR}, creating a 9-h SD. With the exception of the SD control bench, above the remaining benches, NI lighting was delivered from 2230 to 0230_{HR} by either 40-W INC lamps or customized LED fixtures containing three R and/or FR LED diodes per lamp developed by CCS Inc. (Kyoto, Japan). Lamps were paired to produce a total of six diodes and thus, seven R:FR ratios were created (Figure 1). The R and FR LEDs had peak wavelengths of 660 nm and 735 nm, respectively, which correspond with peaks of phytochrome absorption (Sager et al., 1988). Since the photon flux from the R LEDs was approximately twice that from the FR LEDs, all R diodes were filtered with two layers of aluminum mesh.

Light spectra under each treatment were measured by two different portable spectroradiometers (LI-1800, LI-COR, Inc., Lincoln, NE and PS-200, StellarNet, Inc., Tampa, FL). Spectral measurements were taken at regular intervals across the bench area of each treatment. Mean photon flux from 600 to 800 nm was 1.3 to 1.6 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for all NI treatments, and plants were positioned on benches only where it was $\geq 0.7 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. The R:FR was measured and described using 100 or 10-nm-wide wavebands (Figure 1). In addition, the phytochrome photoequilibria ($P_{\text{FR}}/P_{\text{R+FR}}$) was calculated for each treatment following Sager et al. (1988) (Figure 2.1).

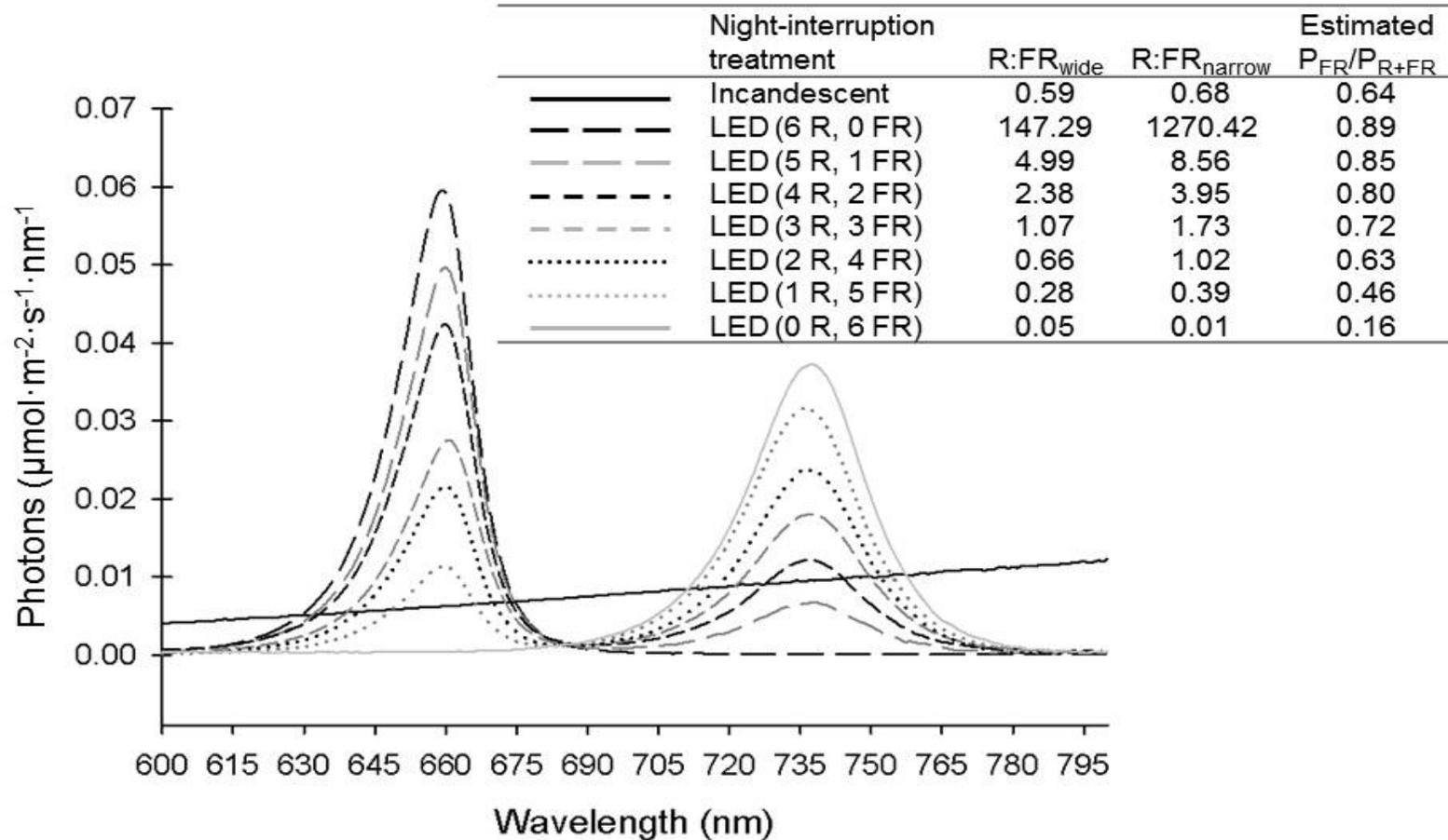


Figure 2.1. Light quality of incandescent and LED lamps between 600 and 800 nm. Red (R) to far-red (FR) ratios and estimated phytochrome photoequilibria (P_{FR}/P_{R+FR}) values (Sager et al., 1988) for incandescent and LED night-interruption treatments are given in the inset table. R:FR_{wide} was measured as the ratio of R photon flux between 600 and 700 nm to FR photon flux between 700 and 800 nm. The R:FR_{narrow} was measured as the ratio of R photons between 655 and 665 nm, to FR photons between 725 and 735 nm. The number of R and FR diodes per lamp pair is indicated in parentheses for each treatment.

Greenhouse environment. The experiment was conducted in a glass-glazed, environmentally controlled greenhouse at a constant temperature set point of 20 °C. In late April, whitewash was applied externally to the greenhouse glazing to reduce light transmission by 30-40% and thus, decrease temperature rise. All treatments received supplemental lighting from 0800 to 1600 HR provided by high-pressure sodium lamps (HPS) delivering a PPF of 60 to 90 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at plant height. The HPS lamps were operated by an environmental control computer and were switched on when the ambient PPF outside the greenhouse was $<185 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, and switched off when $>370 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Line quantum sensors (Apogee Instruments, Inc.) were positioned at plant height throughout the greenhouse. The sensors measured PPF every 10 s, and hourly averages were recorded by a data logger (CR10; Cambell Scientific, Logan, UT). The mean photosynthetic daily light integrals (DLIs) were 15.2 and 14.5 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ for the first and second experiment replications, respectively.

Air temperature was measured on each greenhouse bench by an aspirated thermocouple [36-gauge (0.127-mm diameter) type E] every 10 s, and hourly averages were recorded by a data logger. The actual mean daily temperature was 19.9 °C and 21.9 °C for the first and second experiments, respectively. When the nighttime air temperature at bench level was $<18.9 \text{ }^\circ\text{C}$, a 1500-W electric heater, controlled by a data logger, provided supplemental heat during the night. Plants were irrigated as necessary with reverse-osmosis water supplemented with a water-soluble fertilizer providing (in $\text{mg}\cdot\text{L}^{-1}$) 125 N, 12 P, 100 K, 65 Ca, 12 Mg, 1.0 Fe and Cu, 0.5 Mn and Zn, 0.3 B, and 0.1 Mo (MSU RO Water Special; GreenCare Fertilizers, Inc., Chicago, IL).

Data collection and analysis. Ten plants were randomly assigned to each treatment in both experiment replications. Plant height (from media surface to shoot tip) was measured on the day of transplant, and nodes were counted on each plant. The date of first visible flower bud

or inflorescence (VB) and date of first flowering were recorded. Plants were considered flowering when at least 50% of the ray flowers of an inflorescence were reflexed. At flowering, the total number of VBs, plant height, and number of nodes below the first flower (replicate #2 only) were recorded. Plants that did not have an open flower within 150% of average flowering time were considered non-flowering. Time from transplant to VB and to first flower, as well as node number increase, were calculated for each plant. Data were analyzed with SAS (Version 9.1; SAS Institute, Cary, NC) and data were pooled between replications if statistical interactions between main effects and replication were not significant ($P \geq 0.05$). Regression analysis was performed with SAS to relate the data parameters to the estimated P_{FR}/P_{R+FR} of the night interruption.

Results

All chrysanthemum plants flowered under the FR-only NI treatment and under SDs in both replicates (Figure 2.2). However, among the other treatments, flowering percentage generally decreased with increasing R:FR. For plants that did flower under an LED NI with a $R:FR_{wide} \geq 0.66$ ($P_{FR}/P_{R+FR} \geq 0.63$), flowering was delayed by 42 d compared to plants under SDs or FR-only NIs. Similarly, under the INC NI, flowering was delayed by 30 d compared to under SDs or FR-only NIs. Extension growth of plants was greater in the second experimental replicate but trends were similar (Table 2.1). Plants grown under the FR-only NIs were 4.3 cm shorter in replicate #1 and 7.8 cm less in replicate #2 compared to plants under INC NIs. Under SDs, extension growth was 8.2 cm less in replicate #1 and 14.9 cm shorter in replicate #2, compared to the INC NIs. Inflorescence number was greatest (≥ 163) under a moderate $R:FR_{wide}$ and approximately 43 under the FR-only NIs or SDs.

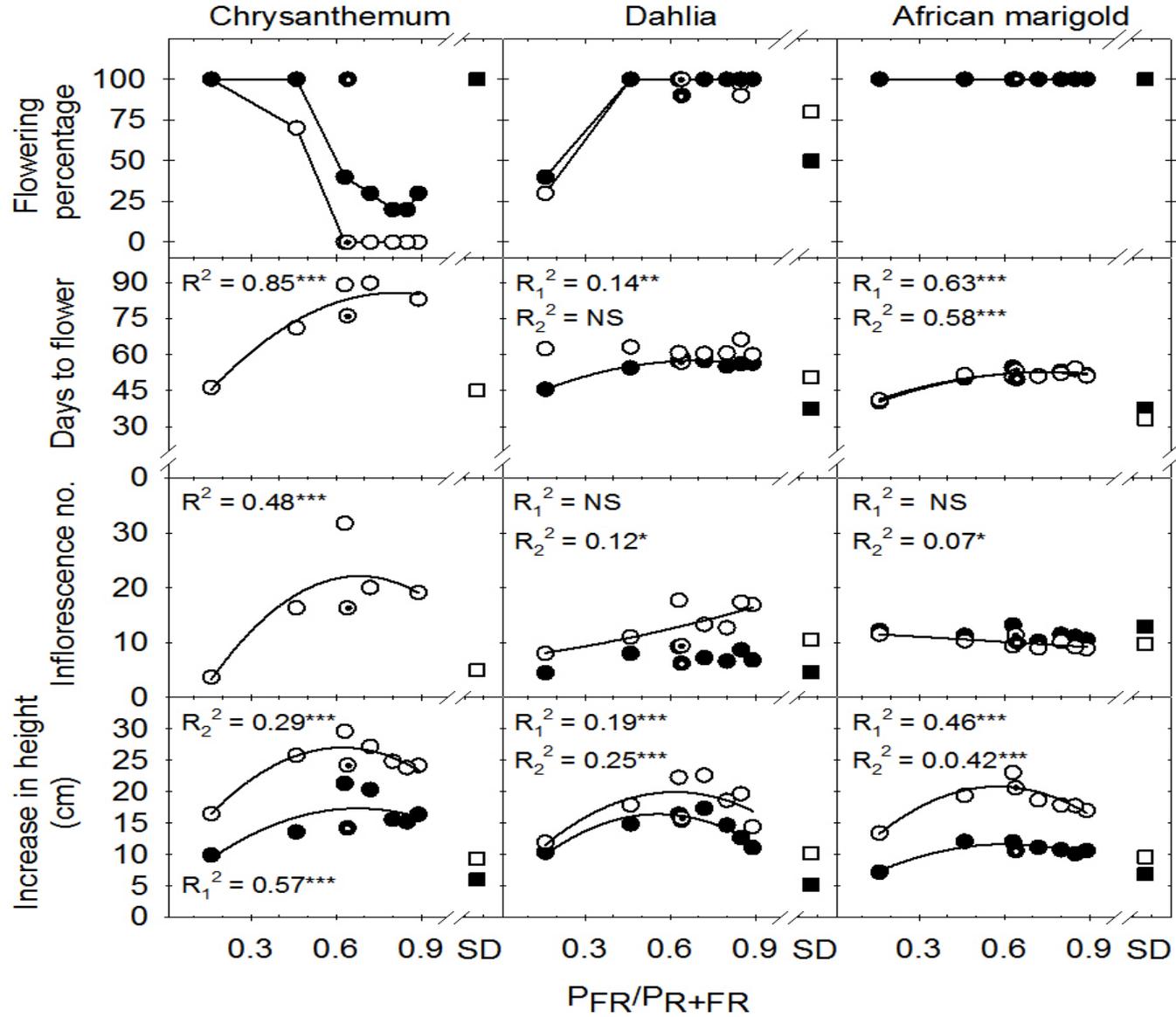


Figure 2.2. The estimated P_{FR}/P_{R+FR} of night-interruption lighting affects flowering and extension growth of the short-day (SD)

Figure 2.2 (cont'd)

plants. The estimated P_{FR}/P_{R+FR} of night-interruption lighting affects flowering and extension growth of the short-day (SD) plants chrysanthemum 'Adiva Purple', dahlia 'Figaro Mix' (solid symbols), dahlia 'Carolina Burgundy' (open symbols), and African marigold 'American Antigua Yellow'. Single open data symbols indicate pooled data with an associated correlation coefficient (R^2). Multiple plots indicate replicate #1 data (solid symbols) and replicate #2 data (open symbols) with associated R_1^2 and R_2^2 values, respectively. Dotted circle symbols indicate the incandescent control treatment. Square data symbols indicate the SD control treatment. Data for chrysanthemum inflorescence number has been divided by 10. NS, *, **, *** indicate non-significant or significant at $P \leq 0.05$, 0.01, and 0.001, respectively. See Table 2.1 for regression equations.

Table 2.1. Parameters of regression analysis relating days to flower, inflorescence number, and increase in height to the calculated P_{FR}/P_{R+FR} of the night-interruption lighting treatments.

| Species | Parameter | Replicate | Regression equation | R ² |
|---|--------------------|-----------|---------------------------------|----------------|
| Chrysanthemum ' Adiva Purple' | Days to flower | pooled | $y = 25.3 + 144.8x - 94.5x^2$ | 0.85*** |
| | Inflorescence no. | pooled | $y = -78.8 + 817.8x - 608.4x^2$ | 0.48*** |
| | Increase in height | 1 | $y = 7.9 + 61.5x - 49.5x^2$ | 0.57*** |
| | Increase in height | 2 | $y = 3.6 + 40.5x - 29.9x^2$ | 0.29*** |
| Dahlia 'Figaro' | Days to flower | pooled | $y = 36.8 + 59.8 - 43.5x^2$ | 0.14*** |
| | Increase in height | pooled | $y = 2.9 + 48.0x - 42.5x^2$ | 0.19*** |
| Dahlia 'Carolina Burgundy' | Inflorescence no. | pooled | $y = 7.5 + 5.0x + 5.6x^2$ | 0.12* |
| | Increase in height | pooled | $y = 4.6 + 50.1x - 40.7x^2$ | 0.25*** |
| | Days to flower | 1 | $y = 32.8 + 53.0x - 35.2x^2$ | 0.63*** |
| African marigold 'American Antigua Yellow' | Days to flower | 2 | $y = 35.0 + 47.3x - 31.9x^2$ | 0.58*** |
| | Inflorescence no. | 2 | $y = 12.0 - 3.1x$ | 0.07* |
| | Increase in height | 1 | $y = 3.7 + 26.5x - 21.8x^2$ | 0.46*** |
| | Increase in height | 2 | $Y = 6.4 + 50.2x - 43.6x^2$ | 0.42*** |

NS, *, **, *** indicate non-significant or significant at $P \leq 0.05$, 0.01, and 0.001, respectively.

Flowering of dahlia 'Figaro Mix' was incomplete under the FR-only NI and SD treatments (40% and 50%, respectively), which was surprising since dahlia is considered an SD plant. However, the 'Figaro Mix' plants that flowered did so slightly earlier than those under the LD treatments: flowering was delayed similarly and by 19 and 11 d under the R:FR_{wide} treatments ≥ 0.28 ($P_{FR}/P_{R+FR} \geq 0.46$), compared with plants grown under SDs and the FR-only NIs, respectively. Extension growth exhibited a quadratic trend and was greatest under moderate R:FR_{wide} treatments. Plants grown under FR NIs and SDs were 5.2 and 10.4 cm shorter, respectively, than plants grown under the INC NIs. There was a small, positive correlation between inflorescence number and the R:FR_{wide} of the NI.

Flowering of dahlia 'Carolina Burgundy' was incomplete under FR-only NI and SD treatments, whereas nearly all plants flowered under the other treatments. Time to flower was 11 d earlier under SDs compared to all other treatments (which were similar in flowering time). Extension growth of 'Carolina Burgundy' exhibited a quadratic trend and was greatest under intermediate LED R:FR_{wide} values. Inflorescence number was variable and statistically similar under all treatments.

All African marigold plants flowered under all treatments, but plants flowered 10 to 19 d earlier under SDs or the FR-only NI treatment compared to the other treatments. Time to flower under the remaining LED treatments (R:FR_{wide} ≥ 0.28) and under INC lamps was similar. Extension growth of plants grown under the FR-only NI treatment or under SDs was 3.9 to 5.8 cm less than that of plants under the other NI treatments. There was a small negative correlation between inflorescence number and the R:FR_{wide} of the NI in the second experimental replicate.

Discussion

In several classic photoperiod studies, flowering of cocklebur (*Xanthium strumarium*) (Borthwick et al., 1952a; Downs, 1956), chrysanthemum (Cathey and Borthwick, 1957), and soybean (*Glycine max*) (Downs, 1956) could be inhibited by an R night break, which promotes formation of P_{FR} and thus increases the P_{FR}/P_{R+FR} . A subsequent FR exposure, however, could reverse the flowering inhibition imposed by R light, showing that the inhibition of flowering in SDPs depends on R light and the resulting formation of the P_{FR} form of phytochrome (Thomas and Vince-Prue, 1997). Although it is well established that R light is most effective at inhibiting flowering in SDPs, some plants are more sensitive than others (Cathey and Borthwick, 1957; Downs, 1956). In addition, these classic R:FR studies used broad spectrum lamps with or without photoselective filters, which could have introduced confounding wavelengths into these experiments.

As in previous studies (Borthwick et al., 1952a; Cathey and Borthwick, 1957; Downs, 1956), R light was effective for flower inhibition among the SDP species studied. LED treatments with an $R:FR_{wide}$ of ≥ 0.66 and the INC lamps ($R:FR_{wide} = 0.59$) inhibited flowering the most. Therefore, LEDs with a moderate-to-high R:FR are a viable replacement for INC lamps to inhibit flowering of SDPs. A variety of crop characteristics (e.g., internode length, branching, and bud number), can be influenced using LEDs with different R:FR. However, in terms of flower inhibition and height control, the NI treatments that primarily emitted R light were most effective for the SDP species studied.

Short-day plants differ in their sensitivity to the R:FR and duration of NI lighting. Only one minute of $\sim 11 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ light from an INC lamp during a long night was needed to inhibit flowering of cocklebur and soybean (Downs 1956), while several hours of light at the same irradiance, for multiple cycles, was needed to inhibit flowering of chrysanthemum (Cathey

and Borthwick 1957). Chrysanthemum appears to be particularly sensitive to the light quality of the NI. Flowering can be inhibited by several hours of NI from an FL or INC lamp, or by one minute of low-intensity FL light (Cathey and Borthwick, 1957). However, one minute of high-intensity INC light was not sufficient to inhibit flowering. The R:FR of INC light is much lower than that of FL light. Therefore, a brief INC NI converts less phytochrome to the P_{FR} form than would a brief FL NI. Theoretically, R light is most effective at inhibiting flowering of SDPs because the high R:FR of FL light was sufficient to convert enough phytochrome into the P_{FR} form to inhibit flowering, even at low intensity and short duration.

In our study, we also observed variations in sensitivity to the light quality of the NI. In agreement with Cathey and Borthwick (1957), chrysanthemum was highly sensitive to the R:FR of the NI, at least compared to the other species tested. Flowering of chrysanthemum was inhibited more by NI treatments with higher R:FR compared to those with lower R:FR. Since chrysanthemum is an obligate SDP, one might expect a more dramatic response to the R:FR than did dahlia or African Marigold (two facultative SDPs). Oddly, flowering percentage of chrysanthemum grown under the INC NI treatment was 100 in experimental replicate #1 and 0 in replicate #2. We have no idea why all plants flowered in the first replicate, and any attempt to explain this response would be purely speculative. Within our populations of dahlia plants, sensitivity to NI light quality was variable. Flowering percentage was lowest under the FR-only NI and SD treatments. Among the remaining treatments, the effect on flowering time was similar regardless of the R:FR of the NI. These results are the opposite of what one would expect and we cannot propose a reason for this response in dahlia. African marigold exhibited a weakly facultative SD flowering response and was the least photoperiodic species in our study

since all plants flowered in all treatments, and flowering was delayed similarly under all NI treatments with an $R:FR_{\text{wide}} \geq 0.28$.

Interestingly, flowering percentage and time to flower for each species was similar under SDs and the FR NI, indicating that the FR-only NI was perceived as an SD. Since R light is most effective at inhibiting flowering of SDPs, we postulated that as the proportion of R light relative to FR light increased (as the R:FR increased), inhibition of flowering in SDPs would progressively increase. Indeed, the higher R:FR NI treatments were more effective and those without R light were relatively ineffective. Therefore, it appears that some threshold amount of R light (or some threshold R:FR value) is required for SDPs to perceive an NI. The threshold $R:FR_{\text{wide}}$ for delaying flowering was ≥ 0.66 ($P_{\text{FR}}/P_{\text{R+FR}} \geq 0.63$) for chrysanthemum and African marigold, but one was not identified for dahlia.

Regardless of photoperiodic classification, most plants exhibit some degree of shade-avoidance response. Natural daylight has an R:FR of about 1.15, and when plants detect a reduced R:FR (resulting from mutual shading, canopy cover, photosensitive filters, etc.), extension growth increases in an effort to better harvest photosynthetic light (Smith, 1982). Alternatively, stem extension can be inhibited by growing plants under an increased R:FR, especially in shade-avoiding plants. For example, chrysanthemum grown under an FR-absorbing photosensitive filter ($R:FR = 2.2$) were 20% shorter than plants grown under a neutral filter (Li et al., 2000). Yamada et al. (2008) used FR FL lamps ($R:FR = 0.01$), INC lamps ($R:FR = 0.65$), and FL lamps ($R:FR = 5.00$) as NI treatments on lisianthus (*Eustoma grandiflorum*) ‘Niel Peach Neo’, an LD plant. Lamps with an R:FR of 0.01 and 0.65 increased internode length by 26 and 23%, respectively, compared to plants grown without a NI. In contrast, plants grown with FL NI had 14% shorter internodes than plants grown without a NI.

In our study, plant height of chrysanthemum and dahlia ‘Figaro’ under an NI with a high proportion of R light ($R:FR_{wide} \geq 2.38$) was shorter than when grown under a moderate $R:FR_{wide}$ (0.66 and 1.07). Surprisingly, plants grown under the FR-only NI were generally shorter than plants in the other NI treatments. We anticipated that plants grown under the FR-only NI ($R:FR_{wide} = 0.05$) would exhibit a shade-avoidance response and thus have greater stem elongation. However, since plants did not perceive an FR NI as an LD, flowering occurred earlier in development, so there was less time for stems to elongate before flowering. For example, in the second experimental replicate, internode length of marigold plants under an FR NI was 0.7 cm longer than that of plants grown with a higher $R:FR_{wide}$ NI (data not shown). However, since the plants grown with an FR NI flowered with 6 fewer nodes than plants in the other treatments, their overall height at first flowering was actually less.

In commercial production, artificial LDs are delivered to maintain SDPs in a vegetative state for production of vegetative stem cuttings (Mattson and Erwin, 2005). The presence of flower buds on stem cuttings is undesirable because the cutting may direct more carbohydrates to reproductive organs than to vegetative growth or rooting. Non-inductive photoperiods can also be used to prevent premature flowering and to increase plant size and biomass before flower induction, such as with chrysanthemum.

Commercial growers have traditionally used INC lamps to provide photoperiod lighting since they are effective and inexpensive to install. However, INC lamps convert <10% of the energy consumed into visible light (Thimijan and Heins, 1983; Kanter, 2009). With the phaseout of INC lamps, greenhouse growers will need other sources of light to control flowering of photoperiodic crops. As we have shown, LED technology provides an alternative to INC lamps for photoperiodic lighting. In addition to the improvements in lamp lifespan and energy

efficiency, the narrow waveband nature of LEDs can be used to create lamps that are tailored to ornamental crop production needs. In SDPs, LEDs with a moderate to high R:FR are effective at preventing premature flowering and thus, are a viable replacement for INC lamps.

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SECTION III

USING LIGHT-EMITTING DIODES TO CHARACTERIZE HOW THE RED TO FAR- RED RATIO OF NIGHT-INTERRUPTION LIGHTING INFLUENCES FLOWERING OF LONG-DAY PLANTS

Using Light-emitting Diodes to Characterize How the Red to Far-red Ratio of Night-interruption Lighting Influences Flowering of Long-day Plants

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Abstract

Flowering of long-day (LD) plants is promoted by photoperiodic lighting from incandescent (INC) lamps during an otherwise long night. INC lamps are inexpensive, easy to install, and emit an effective spectrum for controlling flowering, but they are also energy inefficient and are being phased out of production. Our objective was to compare the effects of different red-to-far-red ratios ($R:FR_{\text{wide}} = 600 \text{ to } 700 \text{ nm} : 700 \text{ to } 800 \text{ nm}$) of photoperiodic lighting from LEDs on the flowering of LD plants. Petunia (*Petunia milliflora*) 'Shock Wave Ivory', petunia (*P. multiflora*) 'Easy Wave White' and 'Wave Purple Improved', rudbeckia (*Rudbeckia hirta*) 'Denver Daisy', snapdragon (*Antirrhinum majus*) 'Liberty Classic Cherry', and fuchsia (*Fuchsia \times hybrida*) 'Trailing Swingtime' were grown at 20 °C under a 9-h day with or without a 4-h night interruption (NI) treatment delivered during the middle of the night by INC lamps or light-emitting diodes (LEDs) with seven different R:FR ranging from all R to all FR. For all three petunia cultivars and snapdragon, flowering was earliest under a moderate R:FR NI and most delayed under short days (SDs), the FR NI, or the R NI treatments. A moderate R:FR NI increased plant height at flowering while plants were most compact under SDs, the FR NI, or R NI treatments. For rudbeckia and fuchsia, all NI treatments except the FR NI promoted flowering but plant height was similar. We conclude that a mixture of R and FR light ($R:FR_{\text{wide}} = 0.28 \text{ to } 1.07$) was most effective at interrupting the long night and promoting flowering in a variety of LDPs.

Introduction

The flowering of many herbaceous ornamental plants is influenced by photoperiod (Erwin and Warner, 2002; Runkle and Heins, 2003; Mattson and Erwin, 2005). Photoperiodic

flowering responses are determined primarily by the length of the dark period, also known as the critical night length (Thomas and Vince-Prue, 1997). Plants have been categorized into photoperiodic classes depending how they respond to the critical night length, including long-day (LD) plants (LDPs), in which flowering is most rapid when uninterrupted dark periods are shorter than some genotype-specific critical night length (Vince, 1969). Within the LDP response category, plants can be further classified based on whether LDs are required for flowering (a qualitative response), or only hasten it (a quantitative response). Commercial growers of LDPs use photoperiodic (low-intensity) lighting to create artificial LDs by extending the natural day length, or interrupting the dark period to accelerate flowering.

Light quality, or the distribution of wavelengths, can cause a broad range of morphological and developmental changes in plants. Light quality is detected by three identified families of photoreceptors in plants including the phytochromes (Kami, et al., 2010). The phytochromes exist in red- [R (600 to 700 nm), peak absorption at 660 nm] and far red- [FR (700 to 800 nm), peak absorption at 730 nm] absorbing forms, P_R and P_{FR} , respectively (Hayward, 1984; Sager et al., 1988). Phytochromes have the potential to control a wide variety of plant responses including seed germination, plant architecture, flowering, tuberization, bud dormancy, and shade-avoidance responses such as extension growth (Smith, 2000). The ratio of R to FR light (R:FR) incident on the plant influences the phytochrome photoequilibria (P_{FR}/P_{R+FR}) within the plant. Upon absorbing R light, P_R converts mainly to the P_{FR} form. The P_{FR} form largely converts back to the P_R form under FR light, or during a natural, gradual conversion during the dark period (Thomas and Vince-Prue, 1997). The total pool of phytochrome in the plant is constant, but the relative amount of phytochrome in the P_{FR} and P_R forms fluctuates with changes to the light environment.

In nature, the light environment changes during the day, with the R:FR ranging from 1.15 under full sun to 0.70 at twilight (Lund, 2007). The R:FR can also vary dramatically within layers of a plant canopy. These differences can occur between leaf layers on the same plant or between layers of a complex plant community. Leaves at the top of a canopy receive unfiltered sunlight with a relatively high R:FR. As light passes through a plant canopy, the plant tissues absorb most of the photosynthetic light, while FR light is primarily transmitted through or reflected to the lower canopy (Smith, 1994). The R-depleted light under a plant canopy has a reduced R:FR, ranging from 0.05 to 0.70 (Smith, 1982). These changes in R:FR are a more dependable indicator of the proximity of potentially competing neighbors than associated reductions in light intensity (Smith, 2000). In greenhouses or growth chambers, the R:FR of light can also be altered by human-imposed factors such as plant density, canopy shading from plants in hanging baskets, use of artificial lighting, and use of light-filtering films. Plants detect a low R:FR ratio and respond by increasing extension growth to compete for unfiltered sunlight. This ecological strategy is termed the shade-avoidance response and enables plants to react to potential competition for light before it actually occurs. If elongation growth fails to bring a plant into an un-shaded environment, other aspects of the shade-avoidance response can cause early flowering and seed production, thus increasing the chance of perpetuating the plant in the future (Smith, 2000).

Phytochrome is also the photoreceptor that detects photoperiodic signals and regulates flowering of photoperiodic plants. Phytochrome detects changes in light quality in order to sense dark/light and light/dark transitions as part of the photoperiodic time-keeping mechanism (Smith, 1982; Smith 2000). During the night, P_{FR} promotes flowering in LDPs when present in sufficient concentrations, and is associated with a high P_{FR}/P_{R+FR} . During long nights (short

days; SDs), the P_{FR} form of phytochrome slowly converts to the P_R form, leaving insufficient P_{FR} to promote flowering. However, if this dark period is interrupted with light, the conversion of P_{FR} to P_R is also interrupted, leaving enough P_{FR} to effectively promote flowering. Although the flower-promoting P_{FR} form of phytochrome is dependent on the R light conversion of P_R to P_{FR} , several studies have shown that the addition of FR light to R light is more effective at promoting flowering in some LDP than without it (Kim et al., 2002; Runkle and Heins, 2003; van Haeringen et al., 1998).

The production of floriculture crops in greenhouses creates a controlled setting in which environmental factors such as temperature, light intensity, light quality, and photoperiod can all be manipulated beyond the constraints of natural conditions. As discussed previously, light quality and photoperiod in natural environments can have significant impacts on plant morphology and flowering. The ability to elicit these plant responses to the R:FR and photoperiod in the greenhouse allows commercial growers to quickly and efficiently produce plants that are in flower on scheduled market dates. In temperate regions, peak production of annual bedding plants and ornamental herbaceous perennials begins when the natural day lengths are short. Therefore, under natural SDs, flowering of LDPs can be promoted by providing artificial lighting during the middle of the night (night interruption, NI) to create an LD.

Commercial growers have traditionally used incandescent (INC) lamps to provide photoperiodic lighting since they are inexpensive and have an R:FR of 0.70 ($P_{FR}/P_{R+FR} = 0.64$) and thus are effective at controlling flowering of photoperiodic crops. However, INC lamps convert only about 10% of the energy consumed into visible light (Thimijan and Heins, 1983; Kanter, 2009). With the phase-out of INC lamps, greenhouse growers will need other sources of light to control flowering of photoperiodic crops. Although the R:FR of cool-white fluorescent

lamps is much higher, they can be effective for promoting flowering in some LDPs, while being more energy efficient than INC lamps (Whitman et al., 1998). Similarly, compact-fluorescent lamps (CFLs) have also been tested as a more energy efficient alternative to INC lamps for flower induction (Runkle et al., 2012). However, FL lamps are less effective for promoting flowering in some LD crops than INC lamps and they present safety and disposal issues due to their mercury content (Environmental Protection Agency, 2009). Therefore, there is an impending need for replacing both INC and FL bulbs in commercial floriculture.

Light-emitting diodes (LEDs) are an attractive technology for NI of photoperiodic crops. Compared to conventional lamps, LEDs have many desirable characteristics including a very long operating life, narrow bandwidth capability, full instantaneous irradiance when powered, and especially, improving electrical efficiencies (Bourget, 2008; Morrow, 2008). Furthermore, LEDs allow researchers to analyze the effects of specific wavebands without extraneous wavebands such as blue light. The objectives of the present study were to use LEDs to quantify the impact of the R:FR of NI lighting on flowering of several LD ornamental crops, and to compare plant responses with those under INC lamps. This information can be used to 1) guide lighting manufacturers in the development of lamps for photoperiodic lighting of plants, 2) compare the relative efficacy of LEDs to INC lamps and determine whether other wavelengths (such as blue light) would be advantageous, and 3) enable one to predict the photoperiodic efficacy of lamps already developed. To our knowledge, this is the first study that has identified how R:FR ratios control the flowering responses of a range of LDPs without the possibly confounding effects of other light wavebands.

Materials and Methods

Plant material and culture. On February 8, 2011, 7- to 10-day old seedlings of the LDPs petunia (*Petunia ×hybrida*) 'Shock Wave Ivory', 'Easy Wave White', and 'Wave Purple Improved', rudbeckia (*Rudbeckia hirta*) 'Denver Daisy', and snapdragon (*Antirrhinum majus*) 'Liberty Classic Cherry' grown in 288-cell (6 mL) plug trays were received from a commercial greenhouse (C. Raker and Sons, Inc., Litchfield, MI). In addition, rooted cuttings of fuchsia (*Fuchsia ×hybrida*) 'Trailing Swingtime' grown in 36-cell (32 mL) liner trays were received from the same source. The young plants were subsequently grown under non-inductive SDs (natural day length truncated to a 9-h photoperiod using blackout cloth) in a research greenhouse at 20 °C until transfer to the NI treatments.

Rudbeckia were transferred to NI treatments on February 14, 2011; petunia 'Easy Wave White' and snapdragon on February 18; petunia 'Wave Purple Improved' on February 21; petunia 'Shock Wave Ivory' on February 22; and fuchsia on February 25. The young plants were transplanted into 10-cm (430 mL) round plastic pots containing a commercial peat-perlite medium (Suremix; Michigan Grower Products, Inc., Galesburg, MI). All species were thinned to one plant per pot on the day of transplant. The experiment was repeated with the same propagation procedure and greenhouse environment as previously described. For the second replicate, fuchsia was transferred to NI treatments on April 25, 2011; petunia 'Wave Purple Improved' and rudbeckia on May 18; petunia 'Shock Wave Ivory' and 'Easy Wave White' on May 19; and snapdragon on May 20.

LED lamps and NI treatments. Opaque black cloth enclosed all greenhouse benches from 1700 to 0800 HR, creating 9-h SDs (control). Above the remaining benches, NI lighting was delivered from 2230 to 0230 HR by either 40-W INC lamps or customized LED fixtures containing three R and/or FR LED diodes per lamp, which were developed by CCS Inc. (Kyoto,

Japan). Lamps were paired to produce a total of six diodes and thus, seven R:FR ratios were created (Figure 1). The R and FR LEDs had peak wavelengths of 660 nm and 735 nm, respectively, which correspond with peaks of phytochrome absorption (Sager et al., 1988). Since photon flux from the R LEDs was approximately twice that from the FR LEDs, all R diodes were filtered with two layers of aluminum mesh.

Light spectra under each treatment were measured by two portable spectroradiometers (LI-1800, LI-COR, Inc., Lincoln, NE and PS-200, StellarNet, Inc., Tampa, FL). Spectral measurements were taken at regular intervals across the bench area of each treatment. Mean photon flux from 600 to 800 nm was 1.3 to 1.6 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for all NI treatments, and plants were positioned on benches only where it was $\geq 0.7 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. The R:FR was measured and described using 10 or 100-nm-wide wavebands (Figure 3.1). In addition, the $P_{\text{FR}}/P_{\text{R+FR}}$ was estimated for each treatment following Sager et al. (1988).

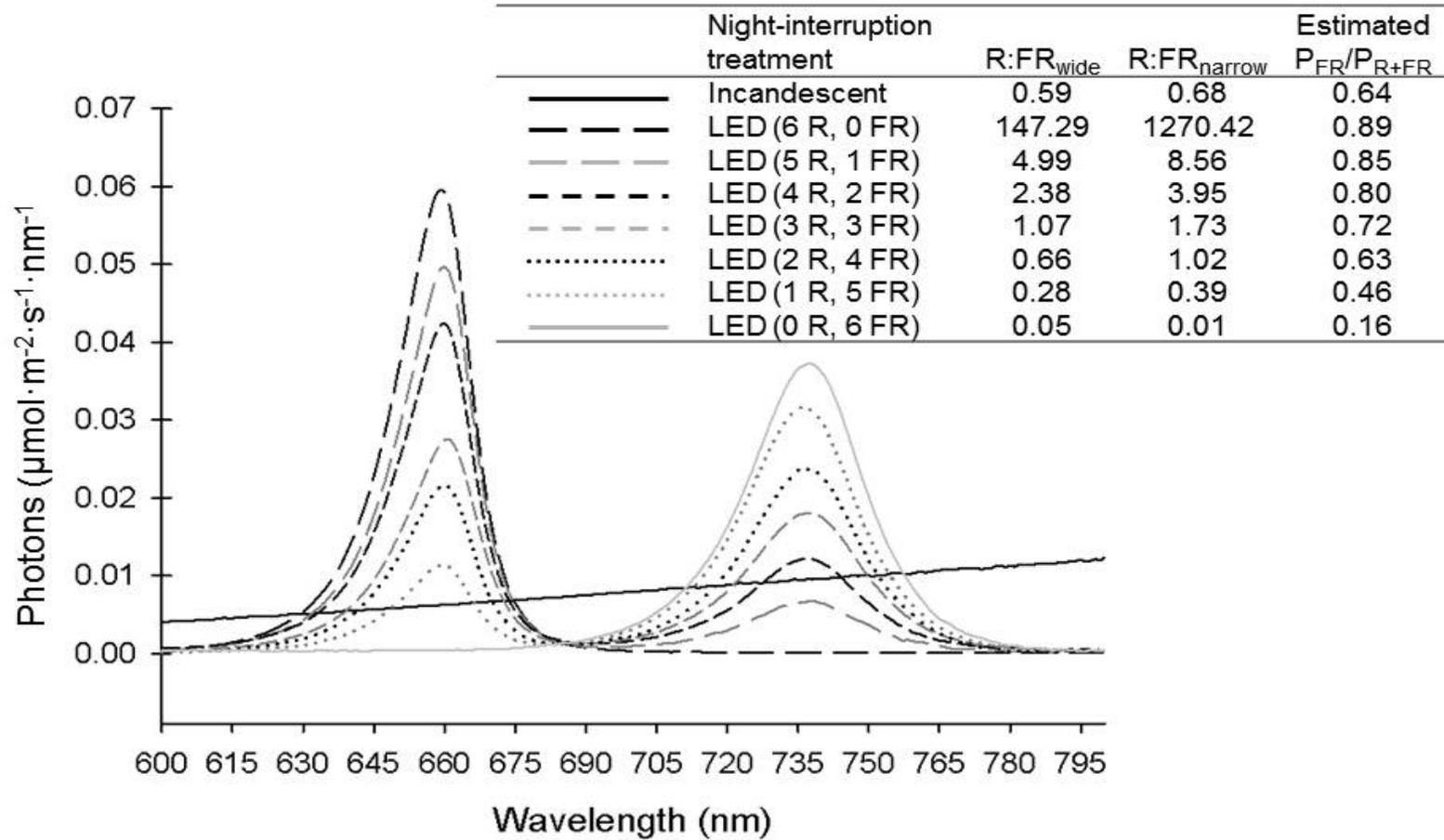


Figure 3.1. Spectral distribution of light from incandescent and light-emitting diode (LED) lamps between 600 and 800 nm. Red (R) to far-red (FR) ratios and estimated phytochrome photoequilibria (P_{FR}/P_{R+FR}) values (Sager et al., 1988) for incandescent and LED night-interruption treatments are given in the inset table. $R:FR_{wide} = 600-700 \text{ nm} : 700-800 \text{ nm}$; $R:FR_{narrow} = 655-665 \text{ nm} : 725-735 \text{ nm}$. The number of R and FR diodes per lamp pair is indicated in the table in parentheses for each treatment.

Greenhouse environment. The experiment was conducted in a glass-glazed, environmentally-controlled greenhouse at a constant temperature set point of 20 °C. In late April, whitewash was applied externally to the greenhouse glazing to reduce light transmission by 30-40% and thus, decrease temperature rise. All treatments received supplemental lighting from 0800 to 1600 HR provided by high-pressure sodium lamps (HPS) delivering a PPF of 60 to 90 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at plant height. The HPS lamps were operated by an environmental control computer and were switched on when the irradiance outside the greenhouse was $<185 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and switched off when $>370 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Line quantum sensors (Apogee Instruments, Inc.) were positioned on benches at plant height throughout the greenhouse. The sensors measured the PPF every 10 s, and hourly averages were recorded by a data logger (CR10; Cambell Scientific, Logan, UT). The mean photosynthetic daily light integrals (DLIs) were 15.2 and 14.5 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ during the first and second experimental replications, respectively.

Air temperature was measured on each greenhouse bench by an aspirated thermocouple [36-gauge (0.127-mm diameter) type E] every 10 s and hourly averages were recorded by the data logger. The actual mean daily temperature was 19.9 °C and 21.9 °C for the first and second experiments, respectively. When the nighttime air temperature at bench level was $<18.9 \text{ }^\circ\text{C}$, a 1500-W electric heater, controlled by the data logger, provided supplemental heat during the night. Plants were irrigated as necessary with reverse-osmosis water supplemented with a water-soluble fertilizer providing (in $\text{mg}\cdot\text{L}^{-1}$) 125 N, 12 P, 100 K, 65 Ca, 12 Mg, 1.0 Fe and Cu, 0.5 Mn and Zn, 0.3 B, and 0.1 Mo (MSU RO Water Special; GreenCare Fertilizers, Inc., Chicago, IL).

Data collection and analysis. Ten plants were randomly assigned to each treatment in both experimental replications. Plant height (from media surface to shoot tip) was measured on the day of transplant and nodes were counted on each plant. The date of first flowering was

recorded. Rudbeckia was considered flowering when at least 50% of the ray flowers of an inflorescence were reflexed. At flowering, the total number of visible buds (VBs), plant height, and number of nodes below the first flower (replicate #2 only) were recorded. Plants that did not have an open flower within 150% of the average flowering time were considered nonflowering. For experimental replicate 1, this cut-off date occurred 65, 59, 67, 78, 116, and 90 d after transplant for petunia ‘Easy Wave White’, ‘Shock Wave Ivory’, and ‘Wave Purple Improved’, and snapdragon, rudbeckia, and fuchsia, respectively. In replicate 2, the cut-off dates were 54, 50, 52, 64, 87, and 72 d after transplant. The number of nodes formed below the first flower was calculated for each plant. Data were analyzed with SAS (Version 9.1; SAS Institute, Cary, NC) and data were pooled between replications if the statistical interactions between treatment and replication were not significant ($P \geq 0.05$). Regression analysis was performed with SAS to relate the data parameters to the estimated P_{FR}/P_{R+FR} of the night interruption.

Results

All petunia ‘Easy Wave White’ plants flowered in all treatments. Flowering occurred earlier in the first experimental replicate, when the average daily temperature was 2.0 °C higher, but response trends to the NI treatments were similar (Figure 3.2). Flowering time exhibited a quadratic trend, and was most rapid under the NI treatments with a moderate R:FR_{wide} (0.28 to 1.07), which had a $P_{FR}/P_{R+FR} = 0.46$ to 0.72. There was an opposite quadratic response for stem elongation; the NI treatments with moderate R:FR_{wide} elicited the longest stems at first flowering, whereas plants under the FR or R NI treatments or SD control were the most compact. The average node, VB, and lateral branch numbers were 17.4, 47.0, and 7.0, respectively, and

were similar among treatments (data not shown). Flowering and extension growth under INC lamps and LEDs with a similar estimated P_{FR}/P_{R+FR} (0.64 or 0.63) were similar.

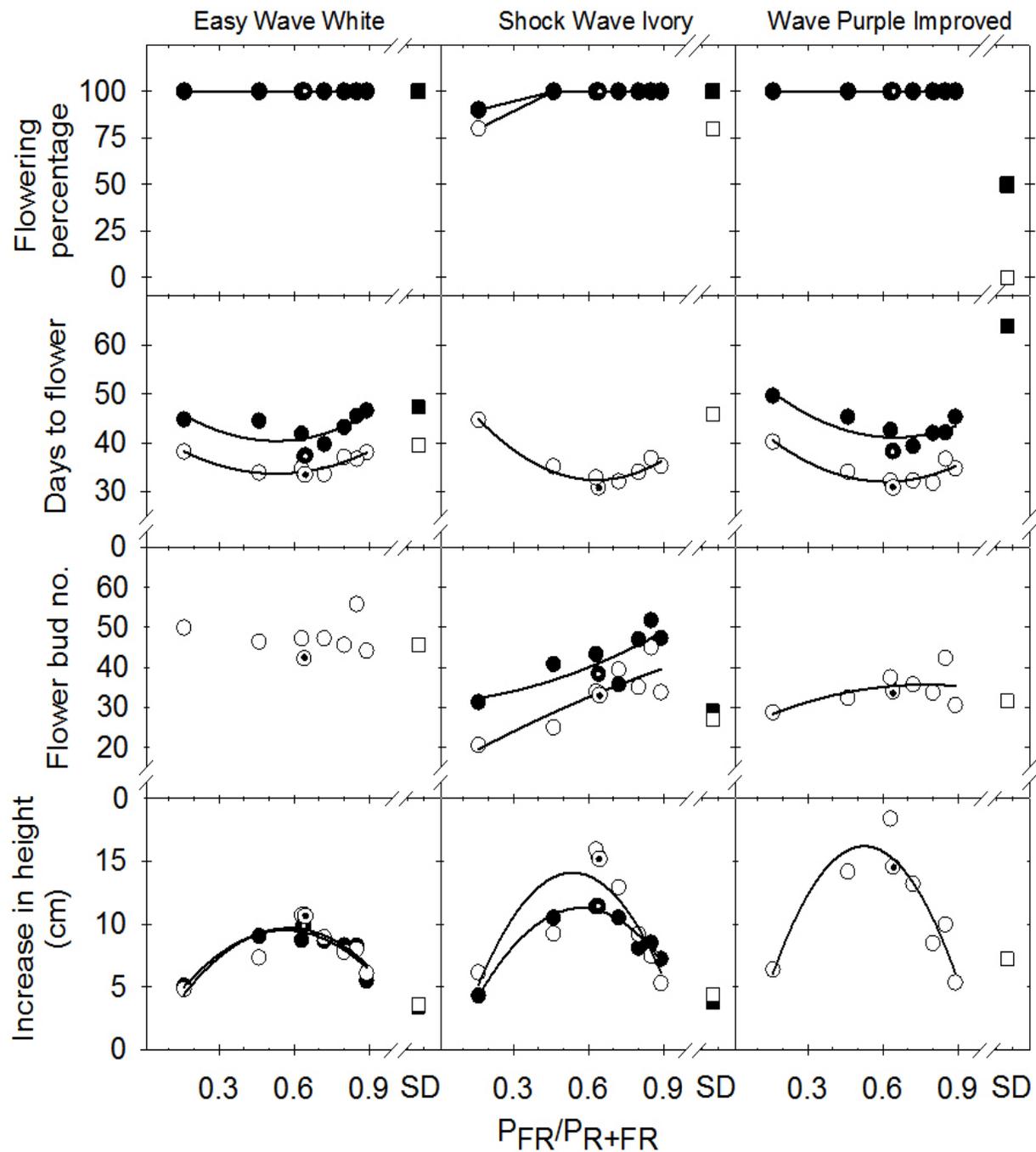


Figure 3.2. The effects of the estimated phytochrome photoequilibria (P_{FR}/P_{R+FR}) of night-interruption lighting on flowering and extension growth of three petunia cultivars. Single open data symbols indicate pooled data; multiple plots indicate replicate #1 (solid symbols) and replicate #2 data (open symbols). Dotted circle symbols indicate the incandescent control treatment. SD = short-day control treatment. See Table 3.1 for regression equations.

Table 3.1. Parameters of regression analysis relating days to flower, inflorescence number, or increase in height to the estimated P_{FR}/P_{R+FR} of the night interruption.

| Species | Parameter | Replicate | Regression equation | r^2 |
|----------------------------|--------------------|-----------|---------------------------------|---------|
| Petunia | | | | |
| 'Easy Wave White' | Days to flower | 1 | $y = 51.6 - 42.2x + 39.9x^2$ | 0.23*** |
| | Days to flower | 2 | $y = 43.1 - 35.4x + 33.4x^2$ | 0.34*** |
| | Inflorescence no. | pooled | NS | NS |
| | Increase in height | 1 | $y = 1.8 + 28.2x - 28.9x^2$ | 0.17** |
| | Increase in height | 2 | $y = -0.3 + 34.4x - 29.7x^2$ | 0.23*** |
| Petunia 'Shock Wave Ivory' | | | | |
| Days to flower | Days to flower | pooled | $y = 54.8 - 71.0x + 56.3x^2$ | 0.37*** |
| | Inflorescence no. | 1 | $y = 31.2 + 4.6x + 16.8x^2$ | 0.22*** |
| | Inflorescence no. | 2 | $y = 14.0 + 35.4x - 7.6x^2$ | 0.32*** |
| | Increase in height | 1 | $y = -2.2 + 47.2x - 41.3x^2$ | 0.34*** |
| | Increase in height | 2 | $y = -4.0 + 67.7x - 63.1x^2$ | 0.44*** |
| Petunia | | | | |
| 'Wave Purple Improved' | Days to flower | 1 | $y = 57.4 - 50.4x + 39.0x^2$ | 0.44*** |
| | Days to flower | 2 | $y = 47.6 - 50.8x + 41.6x^2$ | 0.39*** |
| | Inflorescence no. | pooled | $y = 24.1 + 29.6x - 18.8x^2$ | 0.04* |
| | Increase in height | pooled | $y = -4.7 + 79.7x - 75.8x^2$ | 0.27*** |
| Snapdragon | | | | |
| 'Liberty Classic Cherry' | Days to flower | 1 | $y = 67.4 - 90.3x + 90.4x^2$ | 0.51*** |
| | Days to flower | 2 | $y = 49.2 - 44.4x + 46.9x^2$ | 0.59*** |
| | Inflorescence no. | pooled | $y = 29.8 - 52.5x + 52.9x^2$ | 0.15*** |
| | Increase in height | pooled | $y = 55.1 - 42.5x + 38.4x^2$ | 0.13*** |
| Rudbeckia | | | | |
| 'Denver Daisy' | Days to flower | pooled | $y = 96.0 - 82.4x + 50.0x^2$ | 0.06* |
| | Inflorescence no. | pooled | $y = 16.7 - 27.5x + 28.8x^2$ | 0.15*** |
| | Increase in height | 1 | $y = -18.6 + 157.5x - 103.4x^2$ | 0.74*** |
| | Increase in height | 2 | $y = -22.8 + 190.7 - 142.7x^2$ | 0.73*** |
| Fuchsia | | | | |
| 'Trailing Swingtime' | Days to flower | pooled | $y = 60.3 - 13.2x$ | 0.06* |
| | Inflorescence no. | 1 | $y = 67.4 - 182.6x + 187.44x^2$ | 0.24*** |
| | Inflorescence no. | 2 | $y = -6.1 + 69.8x - 39.7x^2$ | 0.31*** |
| | Increase in height | pooled | $y = 31.8 - 8.7x$ | 0.03* |

NS, *, **, *** indicate non-significant or significant at $P \leq 0.05$, 0.01, and 0.001, respectively.

Flowering percentage of petunia ‘Shock Wave Ivory’ was not quite complete under the FR NI and SD treatments in replicate 2 (Figure 3.2). Flowering time and stem elongation exhibited quadratic trends similar to those for ‘Easy Wave White’. Plants grown under the FR NIs or SDs flowered 14 d later than plants grown under the INC NIs. Extension growth was greatest in plants grown under INC or LEDs with an R:FR_{wide} of 0.66 (~16 cm at flowering), and decreased as the R:FR of the NI lighting increased or decreased. Under SDs or FR NIs, plants produced 24 nodes below the first flower, which was seven more than in all other treatments (data not shown). In replicate #2, plants grown under SDs, R NIs, or FR NIs produced two more lateral branches at first flowering than plants grown under INC NIs (data not shown). VB number at first flowering increased as the NI R:FR and P_{FR}/P_{R+FR} increased.

All petunia ‘Wave Purple Improved’ plants that received NI flowered, regardless of NI light quality, while flowering percentage under the SD treatment was reduced to 0 or 50 (Figure 3.2). Flowering time and stem elongation both exhibited quadratic trends similar to those for ‘Easy Wave White’. In replicate #1, flowering of plants grown under SDs occurred 26 d later than for plants grown under INC NIs. Flowering was also delayed by 9 to 11 d in plants grown under the FR NI compared to those grown under INC. Stem extension was greatest under INC and LED NIs with an R:FR_{wide} of 0.28 to 1.07 (P_{FR}/P_{R+FR} = 0.46 to 0.72). Compared to plants grown under INC NI, plants were 7 cm shorter when grown under SDs, FR, or under the highest three R:FR_{wide} (2.38, 4.99, or 147.29) (P_{FR}/P_{R+FR} = 0.80, 0.85, or 0.89). Under SDs, plants produced two more lateral branches than under INC at first flowering (data not shown). The average node and VB numbers were 19 and 34, respectively, and were similar among all NI treatments.

All snapdragon plants flowered in all treatments. The time to first flowering exhibited a quadratic trend similar to the three petunia cultivars (Figure 3.3). Plants grown under SDs or the R NI flowered 9 to 16 d later than plants grown under the INC NIs. Plants under R or FR NIs were 6.5 cm taller than plants grown under the INC NIs. Plants grown under the R NI or SDs developed approximately eight more nodes and eight more VB than plants grown under the INC NI (data not shown; Figure 3). Under SDs, plants had two more lateral branches than those under other treatments (data not shown). The average VB number exhibited a quadratic trend and was least under NI treatments with a moderate R:FR_{wide} (0.28 to 2.38) ($P_{FR}/P_{R+FR} = 0.46$ to 0.80), which were the treatments that elicited flowering the earliest.

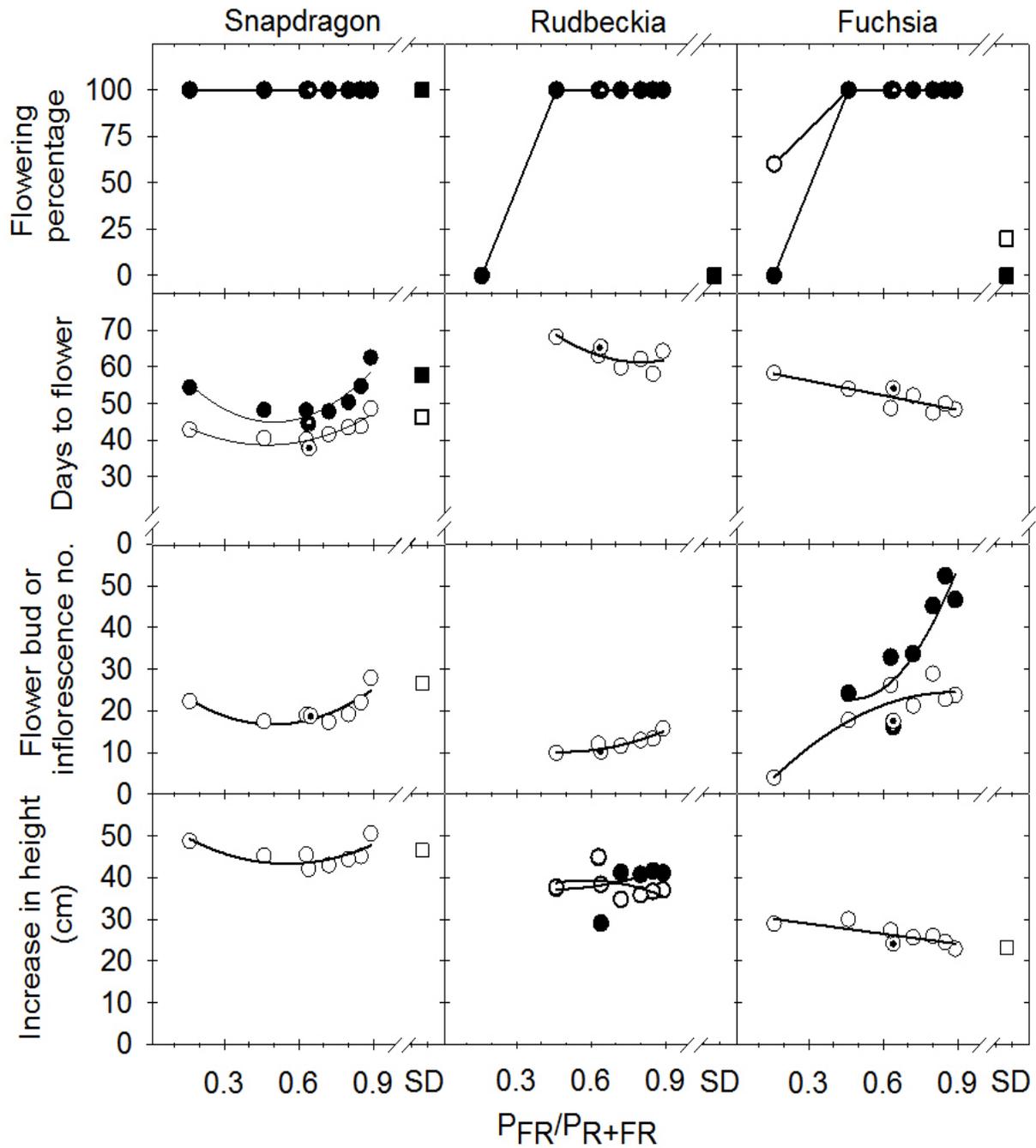


Figure 3.3. The effects of the estimated phytochrome photoequilibria (P_{FR}/P_{R+FR}) of night-interruption lighting on flowering and extension growth of snapdragon ‘Liberty Classic Cherry’, Rudbeckia ‘Denver Daisy’, and fuchsia ‘Trailing Swingtime’. Single open data symbols indicate pooled data; multiple plots indicate replicate #1 (solid symbols) and replicate #2 data (open symbols). Dotted circle symbols indicate the incandescent control treatment. SD = short-day control treatment. See Table 3.1 for regression equations.

No rudbeckia plants flowered under the FR NI treatment or under SDs, whereas all plants flowered in the remaining treatments (Figure 3.3). When grown under an FR NI or SDs, the plants remained as rosettes and never showed signs of flowering. Under the remaining NI treatments, there was little effect on the time to flowering, VB number, or plant height at flowering. Among the plants that flowered, the number of nodes formed below the first flower was similar (~16 nodes) in all treatments (data not shown). Although data were not collected, leaf size was small under SD, larger under the FR NI, and even larger under the remaining NI treatments.

Under the FR NI, flowering percentage of fuchsia was 0 and 60, in replicate #1 and #2, respectively (Figure 3.3). Flowering percentage was also reduced under SDs (0 and 20 for replicate #1 and #2, respectively). Flowering time and extension growth both decreased slightly with increasing P_{FR}/P_{R+FR} of the NI treatment. Node number below the first flower was similar in all treatments (data not shown). VB number increased with increasing R:FR_{wide} of the NI, especially in the first experimental replicate.

Discussion

Several studies have shown that the presence of FR light promotes flowering of LDPs both during the photoperiod, and during NI (Downs et al., 1958; Lane et al., 1965; Runkle and Heins, 2003;). For example, flower initiation in the LDP snapdragon (van Haeringen et al., 1998), tussock bellflower (*Campanula carpatica*), tickseed (*Coreopsis grandiflora*) (Runkle et al., 2001), and petunia (Kim et al., 2002) was delayed when grown under photosensitive filters creating an FR-deficient environment. Light quality during NI treatments can also affect flowering in LDPs: flowering of pansy (*Viola ×wittrockiana*) was promoted most when NI

lighting contained a mixture of R and FR light (imposing a relatively low PPE in the plant) compared with FR-deficient light (Runkle and Heins, 2003). In a separate study, flowering of lisianthus (*Eustoma grandiflorum*) ‘Nail Peach Neo’, another LDP, occurred 24 d earlier when grown with an INC NI (R:FR = 0.6) compared to NI supplied by R-fluorescent (FL) lamps (R:FR = 8.0) (Yamada et al., 2011). Similarly, when FR-FL and R-FL lamps were used to create NI treatments ranging in R:FR from 0.5 to 10.0, flowering was increasingly delayed as the R:FR increased (Yamada et al., 2011). Between the two extreme R:FR (0.5 and 10.0), the difference in flowering dates was 28 d. These studies, among others, establish a paradigm that light containing both R and FR light is more effective at promoting flowering in LDPs than R light alone (Runkle and Heins, 2003; van Haeringen et al., 1998).

Far-red light is known to promote flowering in LDPs, so we postulated that as the proportion of FR light relative to R light increased (as the R:FR decreased), flowering in LDPs would be increasingly promoted. However, rudbeckia and fuchsia did not perceive the FR NI as an LD. In addition, flowering of several of the other LD plants studied was delayed when the NI treatment did not contain R light. These responses indicate that some threshold amount of R light (or some threshold R:FR), in addition to FR light, is required to saturate an NI flowering response in LDPs. With the exception of fuchsia, the most effective R:FR_{wide} for promoting flowering were intermediate values (0.66 to 2.38 for petunia ‘Early Wave White’ and ‘Shock Wave Ivory’, 0.66 to 4.99 for petunia ‘Wave Purple Improved’ and rudbeckia, and 0.28 to 1.07 for snapdragon) and thus, our findings support the paradigm that a mixture of R and FR light is most effective at promoting flowering in LDPs. Similar results were published in a recent study on baby’s breath (*Gypsophila paniculata*), showing that a mixture of R and FR light (specifically,

R:FR between 0.23 and 0.71) was more effective at promoting flowering than FR alone (Nishidata, et al., 2012).

Thomas and Vince-Prue (1997) proposed that flowering in LDPs could be controlled by P_{FR} in two ways, one where a certain threshold amount promotes flowering, and another where some greater amount inhibits flowering. A mixture of R and FR light (e.g. sunlight, INC light) generates an intermediate P_{FR}/P_{R+FR} within the plant that induces the flower-promoting response. At the same time, this intermediate P_{FR}/P_{R+FR} has insufficient P_{FR} to induce the flower-inhibiting response. If the P_{FR}/P_{R+FR} drops below this intermediate level, (i.e. if the light source is too rich in FR), there is insufficient P_{FR} to drive the promoting response. If the P_{FR}/P_{R+FR} increases above this intermediate level (i.e. if the light source becomes more R-dominant), the excess P_{FR} drives the inhibitory response. Our findings are consistent with this theory; there was little or no LD flower promotion under the FR NI (R deficient) as well as delayed flowering under the R NI (FR deficient) in most species.

Some of our understanding of the shade-avoidance response has come from experiments performed in growth chambers or greenhouses that utilized spectral filters or artificial light sources. For example, Yamada et al. (2008) grew lisianthus under NI treatments from FR-FL lamps (R:FR = 0.01), FL lamps (R:FR = 0.43), and daylight FL lamps (R:FR = 5.00). The lamps with an R:FR of 0.01 and 0.43 increased internode length by 26 and 23%, respectively, compared to plants grown without an NI. Plants grown with an R:FR of 5.0 had 14% shorter internodes than plants grown without an NI. In another study of lisianthus, different combinations of FR- and R-FL lamps were used to deliver a range of R:FR. Mean internode length of lisianthus was shorter in plants receiving an NI with an R:FR > 5.0, while an R:FR < 2.0 increased internode length, compared to plants grown without an NI (Yamada et al., 2011). Similarly, there was less

elongation growth in the three petunia varieties and fuchsia under NI treatments with a high R:FR. However, elongation growth was also inhibited under very low R:FR (FR only) in petunia and rudbeckia.

Commercial growers have traditionally used INC lamps, and sometimes CFL lamps, to provide photoperiodic lighting. However, these two lamp types have several negative characteristics including low energy efficiency (for INCs) and reduced effectiveness and safety issues (for CFLs). There is an impending need for replacing both INC and CFL bulbs in commercial floriculture. As we have shown, LED technology provides an alternative to these lamps for photoperiodic lighting of daylength-sensitive crops. LEDs lamps that emit somewhat similar amounts of R and FR light were most effective at controlling flowering of LDP, at least in the species studied

Long-day and short-day plants (SDPs) vary in their response to the spectral quality of NI lighting. In a previous study (Chapter 2), an NI with a moderate-to-high R:FR ($R:FR_{\text{wide}} \geq 0.66$; $P_{\text{FR}}/P_{\text{R+FR}} \geq 0.63$) delayed flowering in the SDPs chrysanthemum, African marigold, and dahlia (Figure 3.4). For the LDPs petunia, rudbeckia, snapdragon, and fuchsia, generally an NI with a moderate R:FR ($R:FR_{\text{wide}} = 0.66$ to 1.07) promoted flowering, while a higher R:FR was less effective. Interestingly, for both SDPs and LDPs, the FR NI ($R:FR_{\text{wide}} = 0.05$) was perceived as an SD, indicating that some threshold amount of R light is necessary for both SD and LD to perceive an NI treatment.

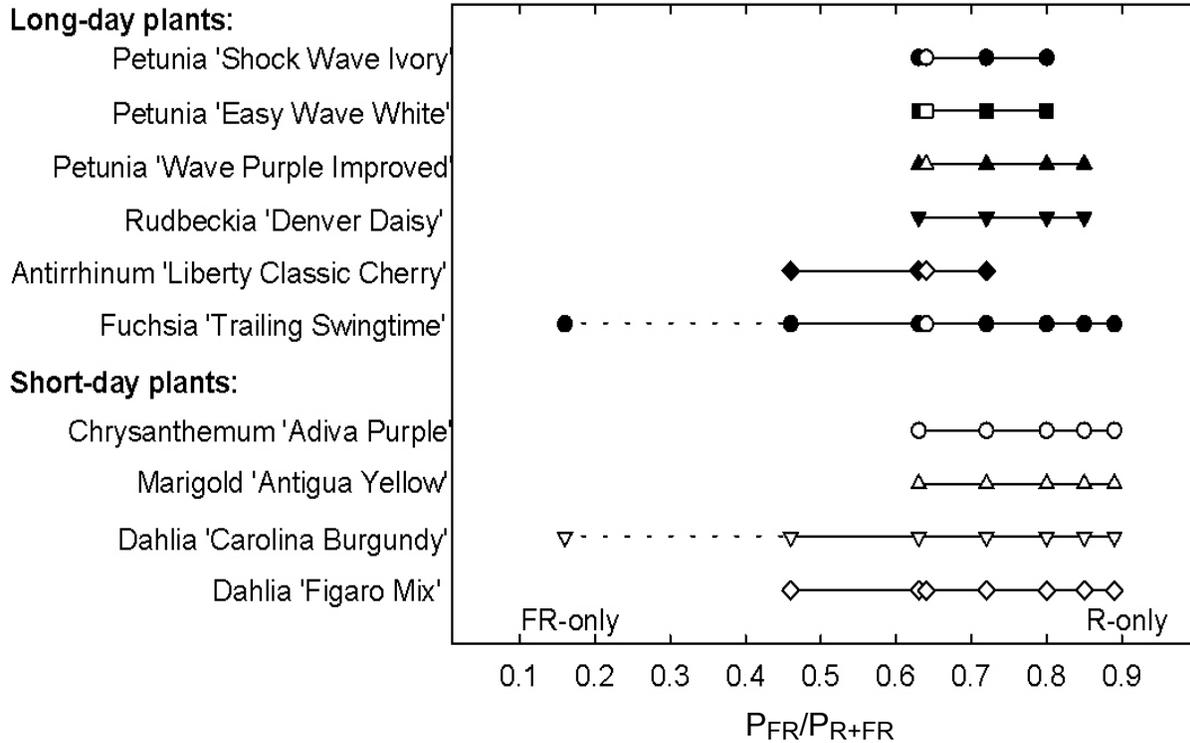


Figure 3.4. Summary of the efficacy of 4-h night-interruption lighting treatments that promoted flowering in long-day plants and inhibited flowering in short-day plants based on results here and in Chapter 2. Lamps emitted different ratios of red (600 to 700 nm) and far-red (700 to 800 nm) light. The phytochrome photoequilibria (P_{FR}/P_{R+FR}) values were estimated using the light distribution of the lighting treatments and the model by Sager et al. (1988). A lamp was considered effective for each species if flowering percentage was $\geq 90\%$ for long-day plants and if time to flower was statistically similar to plants that flowered most rapidly (for long-day plants) or was most delayed (for short-day plants).

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LITERATURE CITED

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SECTION IV

COMPARING THE EFFICACY OF DAY-EXTENSION AND NIGHT-INTERRUPTION LIGHTING USING LIGHT-EMITTING DIODES TO PROMOTE FLOWERING OF LONG-DAY PLANTS

Comparing the Efficacy of Day-extension and Night-interruption Lighting Using Light-Emitting Diodes to Promote Flowering of Long-day Plants

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Abstract

Flowering of long-day (LD) plants is promoted by lighting during an otherwise long night, especially when provided by lamps that emit a mixture of red (R, 600 to 700 nm) and far-red (FR, 700 to 800 nm) light. Traditionally, this has been accomplished using incandescent (INC) bulbs either at the end of the natural photoperiod (EOD) or during the middle of the night (night interruption, NI). Our objective was to compare the effects of three R and FR ratios, delivered as EOD or NI lighting, on the flowering of several obligate LD plants. *Rudbeckia* (*Rudbeckia hirta*) 'Denver Daisy', campanula (*Campanula carpatica*) 'Clips Deep Blue', petunia (*Petunia ×hybrida*) 'Wave Purple Classic', tickseed (*Coreopsis verticillata*) 'Moonbeam', and spinach (*Spinacia oleracea*) 'Bloomsdale Longstanding' were grown in glass greenhouses at 20 °C under a truncated 9-h natural day with or without a 7-h EOD or 4-h NI lighting treatment provided by either INC lamps, R and FR light-emitting diode (LED) emitters, or blue (B) LED emitters. The R and FR LEDs had peak wavelengths of 660 and 735 nm, respectively, had an R:FR of 0.65 to 2.38, an estimated phytochrome photoequilibria (P_{FR}/P_{R+FR}) of 0.63 to 0.80, and emitted $\sim 1 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ within the 600 to 800 nm waveband. The B LEDs had an emission peak at 455 nm and emitted $\sim 3 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ within the 300 to 700 nm waveband. With the exception of petunia and campanula, flowering responses under EOD or NI lighting treatments were similar. For petunia, flowering was promoted more under EOD treatments than by NI lighting. For campanula, VB development was promoted by NI in one replicate. In general, plants had a weak or no flowering response when grown without an LD or under the B NI treatment. In most instances, the INC and R+FR LED treatments elicited similar flowering and morphological responses. We conclude that light with an $R:FR_{\text{wide}}$ ranging from 0.59 to 2.38

was effective at promoting flowering in LDPs, regardless of whether delivered as NI or EOD lighting.

Introduction

Most organisms exhibit changes in their metabolism, physiology, and/or behavior depending on diurnal rhythms (e.g., day versus night). In addition, most organisms innately measure time and therefore, can anticipate transitions between day and night and adjust their biological responses accordingly (McClung, 2006). Many diurnal rhythms continue to oscillate in the absence of external time cues (e.g., rising and setting of the sun) due to the presence of an internal 24-h circadian clock. However, since the cycle length is not exact, the circadian clock requires daily resetting from environmental cues. In plants, there are two main environmental stimuli that entrain the circadian clock: photoperiod and temperature (McClung, 2006; Thomas, 2006; Thomas and Vince-Prue, 1997). In this study, we focused on light and its effect on photoperiodic signaling and flowering.

Phytochrome, which is primarily a red- (R) and far-red- (FR) absorbing photoreceptor, relays incoming light signals to the circadian clock and aids in the R light-dependent resetting of the clock each day at dawn (McClung, 2006). The R light triggers phytochrome to reset the clock by inactivating a repressor of the clock mechanism. Light signals during other times can also affect the circadian clock. For example, providing a pulse of light prior to dawn can advance the phase of the circadian clock, while a pulse of light given after dusk can delay the phase (McClung, 2006).

The circadian clock produces daily oscillations of the CONSTANS (CO) protein, which regulates the photoperiodic induction of flowering (McClung 2006; Thomas 2006). In LDPs, the presence of light during the peak of CO transcription is perceived by cryptochrome 2, a blue (B)

light receptor, and phytochrome A, and prevents CO from being degraded. The involvement of cryptochrome in the clock mechanism suggests that B light can also play a role in photoperiodic flowering responses, at least in some plants.

Plants have been classified into photoperiodic response classes depending on how the critical night length influences flowering. One photoperiodic group includes the long-day (LD) plants (LDPs), in which flowering is most rapid when uninterrupted dark periods are shorter than some genotype-specific critical night length (Vince, 1969). Within the LDP response category, plants can be further divided based on whether LDs are required for flowering (an obligate, or qualitative response), or only hasten it (a facultative, or quantitative response). When the ambient photoperiod is short, commercial crop producers of LDPs commonly alter the natural photoperiod to promote flowering by using end-of-day (EOD) lighting to extend the day length, or by lighting during the middle of the night (night interruption, NI).

Several studies on photoperiodism tested the effects of lighting during different times of the dark period on the flowering response (Salisbury, 1963; Halaban, 1968; Vince, 1965). The maximal night break response in both LDPs and short-day (SD) plants (SDPs) occurs cyclically, with a peak during the middle of the night, approximately 8 to 10 hours after darkness begins. Therefore, NI lighting can be more effective for inducing flowering in LDP than EOD lighting when a relatively short (e.g., <4 h) period of lighting is delivered (Thomas and Vince-Prue, 1997).

In addition to the timing of the night break, plants are also sensitive to the quality of LD lighting, specifically the ratio of R to FR light (R:FR). The R:FR is detected by phytochrome photoreceptors, which exist in red- (peak absorption at 660 nm) and far red- (peak absorption at 730 nm) absorbing forms, P_R and P_{FR} , respectively (Hayward, 1984; Sager et al., 1988). The

R:FR incident on the plant influences the phytochrome photoequilibria (P_{FR}/P_{R+FR}) within the plant. Upon absorbing R light, P_R converts to the P_{FR} form. The P_{FR} form converts back to the P_R form upon absorbing FR light, or during a natural gradual conversion during the dark period (Thomas and Vince-Prue, 1997). The total pool of phytochrome in the plant is constant, but the relative amount of phytochrome in the P_{FR} and P_R forms fluctuate with changes to the light and dark environment. Throughout the night, a high P_{FR} promotes flowering in LDPs. Under natural SDs, the P_{FR} form slowly converts to the P_R form during the long night, leaving insufficient P_{FR} to promote flowering. However, night break lighting interrupts the conversion of P_{FR} to P_R , leaving enough P_{FR} to effectively promote flowering.

Light-emitting diodes (LEDs) are an attractive technology for photoperiodic lighting. In a previous study, we compared the effects of NI lighting with different R:FR, provided by narrow-bandwidth LED lamps, for promoting flowering in LDPs. We concluded that a mixture of R and FR light ($R:FR_{wide} = 0.28$ to 1.07) was most effective at interrupting the long night and promoting flowering in a variety of LDPs. However, commercial growers commonly use EOD or NI lighting. Our objective in this experiment was to determine whether LDP responded differently to the R:FR when delivered as EOD or NI lighting from LEDs. Responses were compared with lighting from INC lamps, as well as from B LEDs. A B treatment was included because a recent study reported that B EOD lighting was not perceived as an LD in chrysanthemum (Van Ieperen, 2009).

Materials and Methods

Plant material and culture. On December 22, 2011, 7-d old seedlings of the obligate LD annual rudbeckia (*Rudbeckia hirta*) 'Denver Daisy' and LD perennial campanula (*Campanula*

carpatica) 'Clips Deep Blue' grown in 288-cell (6 mL) plug trays were received from a commercial greenhouse (C. Raker & Sons, Inc., Litchfield, MI). On January 2, 2012, seedlings of petunia (*Petunia ×hybrida*) 'Wave Purple Classic' grown in 288-cell plug trays and rooted cuttings of tickseed (*Coreopsis verticillata*) 'Moonbeam' grown in 36-cell (32 mL) plug trays were received from the same company. In addition, seeds of spinach (*Spinacia oleracea*) 'Bloomsdale Longstanding' were hand sown in a 288-cell plug tray on January 9, 2012 using a 50/50 mix of commercial peat and perlite medium (Suremix; Michigan Grower Products, Inc., Galesburg, MI) and fine vermiculite (Sun Gro Horticulture, Bellevue, WA). Prior to their transfer to the treatments, seedlings were grown under a 9-h SD in a controlled environment chamber at 20 °C with a photosynthetic daily light integral (DLI) of $8.3 \text{ mol} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ from fluorescent lamps (215 W T12 bulbs; Philips Lighting, Somerset, NJ). Rudbeckia were transferred to treatments on January 6, 2012, tickseed on January 17, petunia on January 20, spinach on January 25, and campanula on February 3. Upon transfer, ten seedlings of each species were transplanted into 10-cm (430 mL) round plastic pots containing Suremix. All species were thinned to one seedling per pot on the day of transplant. Average leaf number of petunia, rudbeckia, spinach, tickseed, and campanula at transplant were 5, 3, 2, 3, and 6, respectively.

The experiment was repeated with the same propagation procedure and greenhouse environment as previously described. For the second replicate, spinach was sowed on February 28, 2012 and campanula, tickseed, and rudbeckia were received on March 8. Tickseed seedlings were transferred to NI treatments on March 14, rudbeckia and spinach on March 21, petunia on April 5, and campanula on April 9. Average leaf number of petunia, rudbeckia, spinach, tickseed, and tussock bellflower at transplant were 4, 3, 2, 3, and 4, respectively.

LED lamps and photoperiodic treatments. Opaque black cloth enclosed all greenhouse benches from 1700 to 0800_{HR}, creating 9-h SDs (control). Above the remaining benches, EOD lighting was delivered from 1700 to 2400_{HR} and NI lighting was delivered from 2230 to 0230_{HR} by either 40-W INC lamps or LEDs. The customized screw-in LED fixtures containing R and/or FR LED diodes were obtained from CCS Inc. (Kyoto, Japan). Three R:FR ratios were delivered (Figure 1): 1) one R LED for every 2 FR LEDs (1R2FR), 2) an equal number of R and FR LEDs (RFR), and 3) two R LEDs for every one FR LED (2R1FR). The R and FR LEDs had peak wavelengths of 660 nm and 735 nm, respectively, which correspond to the peaks of phytochrome absorption (Sager et al., 1988). Since photon flux from the R LEDs was approximately twice that from the FR LEDs, all R diodes were filtered with two layers of aluminum mesh. Another treatment utilized screw-in LED fixtures designed for horticulture applications (red/white/deep red GreenPower LED flowering lamp, Philips Lighting, Somerset, NJ). These lamps contained white (W), R, and FR LEDs (WRFR). The photon flux from the WRFR lamps was approximately twice that from the R+FR LEDs and so they were filtered using four layers of aluminum mesh. One additional NI treatment was supplied by two custom B LED tubes (peak wavelength of 455 nm) manufactured by CCS Inc that fit into standard 1.2-m fluorescent tube fixtures.

Light spectra under each treatment were measured by a portable spectroradiometer (PS-200, StellarNet, Inc., Tampa, FL). Spectral measurements were taken in a grid pattern at ~0.5-m increments across the bench area of each treatment. Mean photon flux from 600 to 800 nm was 0.9 to 1.5 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for all photoperiodic treatments, with the exception of the B LED treatment, which had no output from 600 to 800 nm, and 3.26 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ between 300 and 700 nm. Plants were positioned on benches only where photon flux from the lamps was ≥ 0.7

$\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. The R:FR was measured and described using 100 (R:FR_{wide}) or 10 (R:FR_{narrow}) nm-wide wavebands (Table 4.1, Figure 4.1). In addition, the $P_{\text{FR}}/P_{\text{R+FR}}$ was calculated for each treatment following Sager et al. (1988).

Table 4.1. Red (R)-to-far-red (FR) ratios and estimated phytochrome photoequilibria ($P_{\text{FR}}/P_{\text{R+FR}}$) values under long-day lighting treatments (Sager et al., 1988).

| Lamp type | R:FR _{wide} | R:FR _{narrow} | Estimated $P_{\text{FR}}/P_{\text{R+FR}}$ |
|-------------------|---------------------------------------|---------------------------------------|--|
| | R: 600 to 700 nm FR: 700 to 800 nm | R: 655 to 665 nm FR: 725 to 735 nm | |
| Incandescent | 0.59 | 0.67 | 0.64 |
| WRFR ^z | 0.65 | 0.94 | 0.63 |
| 1R2FR | 0.66 | 1.02 | 0.63 |
| RFR | 1.07 | 1.73 | 0.72 |
| 2R1FR | 2.38 | 3.95 | 0.80 |
| Blue | - | - | 0.51 |

^zWRFR = White/red/far-red LED, 1R2FR = Lamps with one red LED for every two far-red LEDs, RFR = lamps with an equal number of red and far-red LEDs, 2R1FR = lamps with two red LEDs for every one far-red LED.

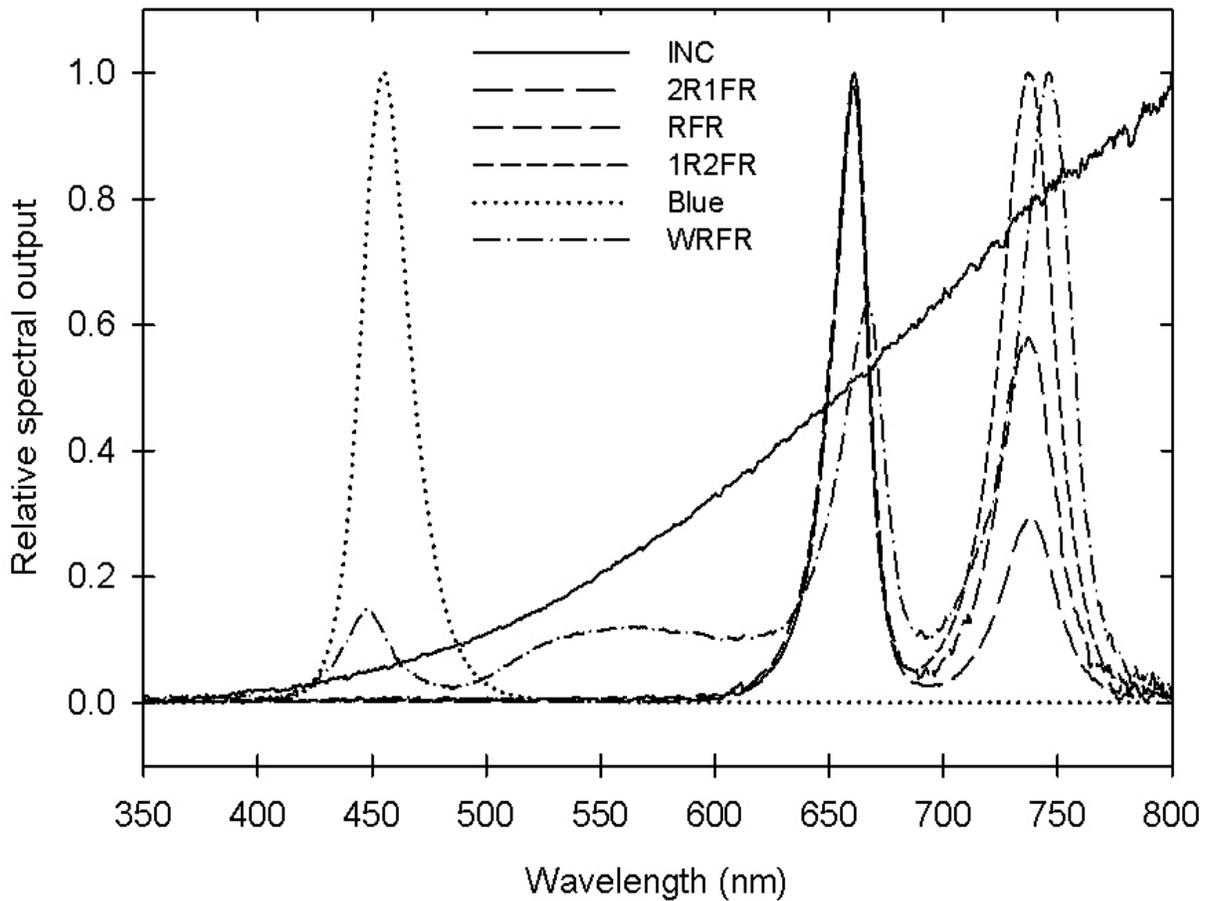


Figure 4.1. Relative spectral distribution of light from incandescent (INC) and light-emitting diode (LED) lamps between 350 and 800 nm. Red (R) to far-red (FR) ratios and estimated phytochrome photoequilibria (P_{FR}/P_{R+FR}) values (Sager et al., 1988) are given in the inset table. Night-break treatments were provided using B LEDs (B), INC, white/red/far-red LEDs (WRFR), lamps with two far-red LEDs for every one red LED (1R2FR), lamps with an equal number of red and far-red LEDs (RFR), and lamps with two red LEDs for every one far-red LED (2R1FR). $R:FR_{wide} = 600-700 \text{ nm} : 700-800 \text{ nm}$; $R:FR_{narrow} = 655-665 \text{ nm} : 725-735 \text{ nm}$.

Greenhouse environment. The experiment was conducted in a glass-glazed, environmentally controlled greenhouse at a constant temperature set point of 20 °C. In late April, whitewash was applied externally to the greenhouse glazing to reduce light transmission by 30-40% and thus, decrease temperature rise. All treatments received supplemental lighting from 0800 to 1600 HR provided by high-pressure sodium lamps (HPS) delivering a *PPF* of 60 to

90 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at plant height. The HPS lamps were operated by an environmental computer and were switched on when the light intensity outside the greenhouse was $<185 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and switched off when ambient light intensity was $>370 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Line quantum sensors (Apogee Instruments, Inc.) were positioned at plant height throughout the greenhouse. The sensors measured *PPF* every 10 s, and hourly averages were recorded by a data logger (CR10; Cambell Scientific, Logan, UT). The mean DLIs were 9.0 and 11.4 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ for the first and second experiment replications, respectively.

Air temperature was measured on each greenhouse bench by an aspirated thermocouple [36-gauge (0.127-mm diameter) type E] every 10 s. Hourly averages were recorded by a data logger. The actual mean daily temperature was 20.5 °C and 20.6 °C for the first and second experiments, respectively. When the nighttime air temperature at bench level was $<18.9 \text{ }^{\circ}\text{C}$, a 1500-W electric heater, controlled by a data logger, provided supplemental heat during the night. Plants were irrigated as necessary with reverse-osmosis water supplemented with a water-soluble fertilizer providing (in $\text{mg}\cdot\text{L}^{-1}$) 125 N, 12 P, 100 K, 65 Ca, 12 Mg, 1.0 Fe and Cu, 0.5 Mn and Zn, 0.3 B, and 0.1 Mo (MSU RO Water Special; GreenCare Fertilizers, Inc., Chicago, IL).

Data collection and analysis. Ten plants were randomly assigned to each treatment in both experimental replications. Plant height (from media surface to shoot tip) was measured on the day of transplant and nodes were counted on each plant. The date of first flowering was recorded. Tickseed and rudbeckia were considered flowering when at least 50% of the ray flowers of an inflorescence were reflexed, petunia and campanula were considered flowering when the first flower opened, and spinach was considered flowering when stigma were visible on female plants and pollen had dehisced on male plants. At flowering, the total number of visible flower buds (VBs), plant height, and number of nodes below the first flower were recorded.

Plants that did not form VBs within 150% of the average flowering time were considered nonflowering. For experimental replicate 1, this cut-off date occurred 108, 81, 79, and 120 d after transplant for campanula, tickseed, petunia, and rudbeckia, respectively. In replicate 2, the cut-off dates were 97, 77, 66, and 110 d after transplant. The number of nodes formed below the first flower was counted for each plant. For spinach, the only data parameter recorded was flowering percentage. Data were analyzed with SAS (Version 9.1; SAS Institute, Cary, NC) using a two-factor factorial design and the significance of the main effects and interactions were determined using ANOVA. Pairwise comparisons between treatments were performed with Tukey's honestly significant difference test at $P \leq 0.05$. Data were pooled between replications if the statistical interactions between treatment and replication were not significant ($P \geq 0.05$).

Results

All petunia 'Wave Purple Classic' flowered under all R+FR lighting treatments. No plants flowered under SDs or the B NI (Table 4.2). The timing of the night break had a significant impact on many of the parameters measured. For the first and second experimental replicates, VBs developed 5 and 2 d earlier, respectively, under EOD lighting compared to NI lighting. Flowering occurred 3 d earlier under EOD lighting compared to NI lighting. Extension growth increased by 198% and plants formed one more lateral branch and two fewer nodes below the first flower when grown under NI compared to EOD lighting. The lamp type also had significant effects on some petunia growth and flowering characteristics, but trends generally were inconsistent between experimental replications (Figure 4.2 and 4.3).

Table 4.2. The effects of the time of the lighting period and lamp type on flowering and extension growth of petunia ‘Wave Purple Classic’ (n = 240 for pooled parameters). Data were pooled between replications if the statistical interactions between treatment and replication were not significant at $P \geq 0.05$. Significant interaction effects are shown in separate figures below.

| Parameter | Flowering percentage | Days to visible bud | | Days to flower | Increase in height (cm) | Flower bud no. | Lateral branch no. | | Increase in node no. | |
|----------------------|----------------------|---------------------|--------|----------------|-------------------------|----------------|--------------------|--------|----------------------|------|
| | | Rep #1 | Rep #2 | | | | Rep #1 | Rep #2 | | |
| Lighting period (LP) | | | | | | | | | | |
| None (short day, SD) | - | - ^z | - | - | 1.8 c | - | 9.4 a | - | - | |
| End of day | - | 29.7 b ^y | 27.7 b | 47.4 b | 6.4 a | 38.4 | 5.1 c | 5.8 b | 20.3 a | |
| Night interruption | - | 34.7 a | 29.6 a | 50.6 a | 19.1 b | 40.4 | 6.5 b | 6.7 a | 18.9 b | |
| Lamp type (LT) | | | | | | | | | | |
| | | | | <i>Rep #1</i> | <i>Rep #2</i> | | | | | |
| SD | 0 | - | - | - | - | 1.8 c | - | 9.4 a | - | - |
| Blue | 0 | - | - | - | - | 2.4 c | - | 8.4 a | - | - |
| Incandescent | 100 | 32.4 b | 27.4 b | 51.8 b | 43.3 ab | 10.3 b | 38.3 | 6.0 b | 6.5 ab | 38.3 |
| WRFR ^x | 100 | 33.5 ab | 27.5 b | 54.8 a | 41.3 b | 15.9 a | 39.0 | 5.5 b | 6.1 ab | 39.0 |
| 1R2FR | 100 | 32.3 b | 29.2 b | 53.5 ab | 47.7 ab | 19.2 a | 36.1 | 5.3 b | 5.7 b | 36.1 |
| RFR | 100 | 28.4 c | 26.8 b | 48.2 c | 44.0 ab | 10.9 b | 41.0 | 5.3 b | 5.9 ab | 41.0 |
| 2R1FR | 100 | 34.2 a | 32.4 a | 55.7 a | 50.3 a | 8.6 b | 42.6 | 5.9 b | 7.0 a | 42.6 |
| LP × LT | - | *** ^w | *** | NS | NS | *** | NS | ** | ** | *** |

^zNo data.

^yMeans followed by the same letter within a column are not significantly different at $P \leq 0.05$ using Tukey’s honestly significant difference test. Data without mean separation letters indicate non-significant differences.

^xWRFR = White/red/far-red LED, 1R2FR = Lamps with one red LED for every two far-red LEDs, RFR = lamps with an equal number of red and far-red LEDs, 2R1FR = lamps with two red LEDs for every one far-red LED.

^wNS, **, *** indicate non-significant or significant at $P \leq 0.01$ and 0.001, respectively.

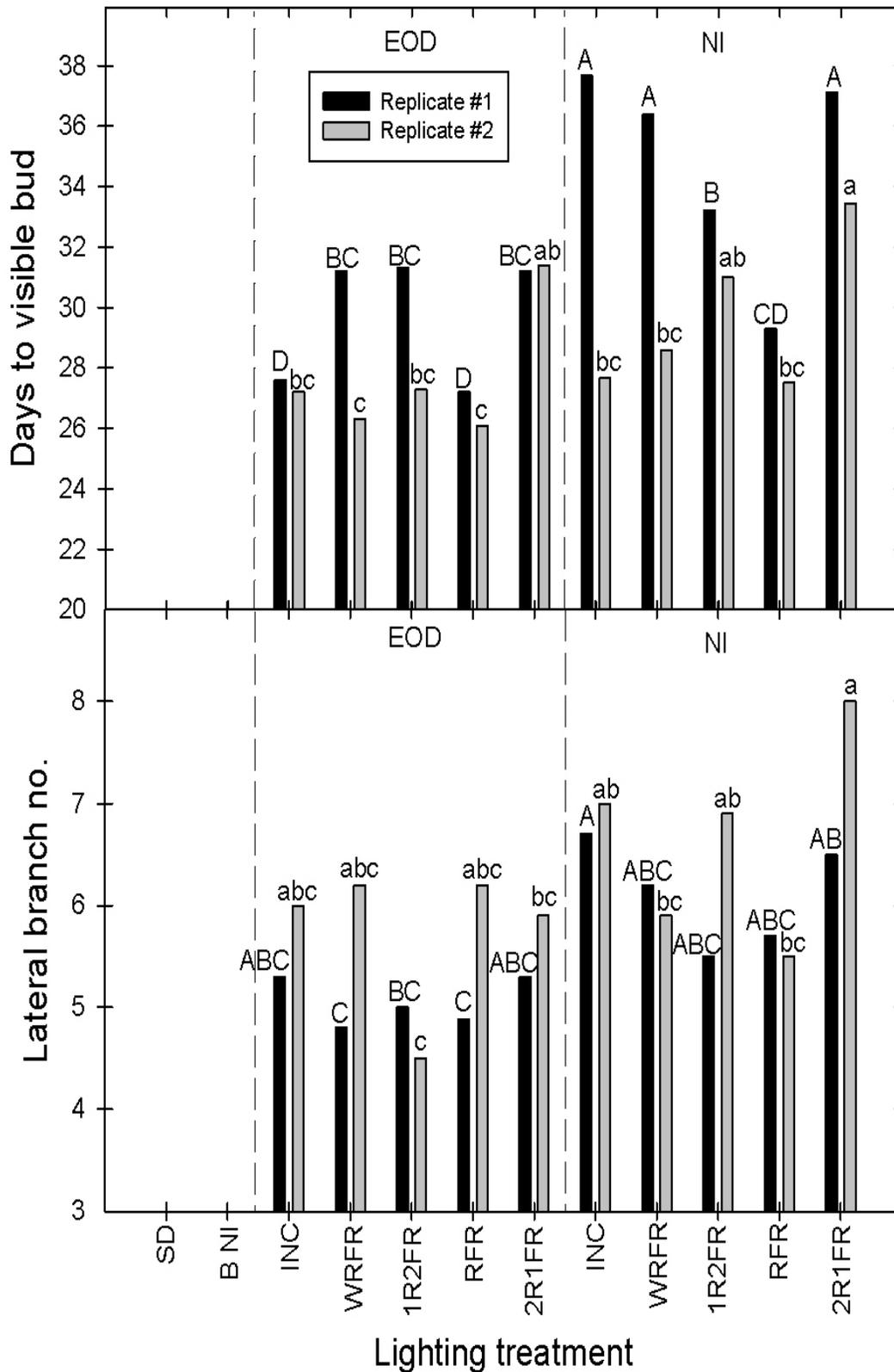


Figure 4.2. Interaction effect of the time of the night-break and lighting treatment on flowering and lateral branch formation of petunia 'Wave Purple Classic' (n = 240 for pooled parameters).

Figure 4.2 (cont'd)

In addition to the short-day control (SD), night-break treatments were provided as either an end-of-day (EOD) or night interruption (NI) treatment. Lighting treatments were delivered by B LEDs (B), incandescent lamps (INC), white/red/far-red LEDs (WRFR), lamps with two far-red LEDs for every one red LED (1R2FR), lamps with an equal number of red and far-red LEDs (RFR), and lamps with two red LEDs for every one far-red LED (2R1FR). Mean separation within variable by Tukey's honestly significant difference test at $P \leq 0.05$.

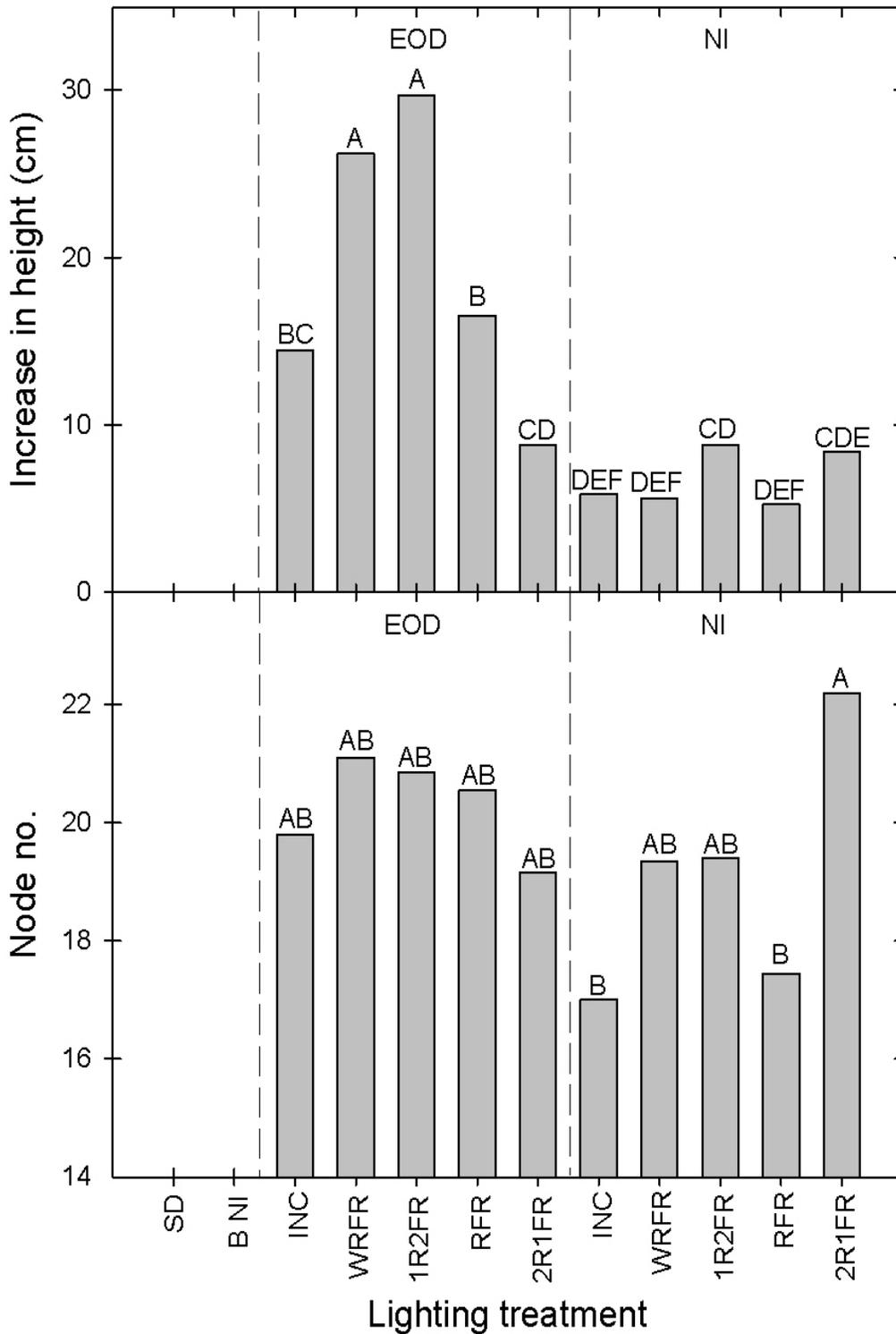


Figure 4.3. Interaction effect of the time of the night-break and lighting treatment on extension growth and node number below the first flower of petunia ‘Wave Purple Classic’ (n = 240 for pooled parameters). In addition to the short-day control (SD), night-break treatments were provided as either an end-of-day (EOD) or night interruption (NI) treatment. Lighting treatments were delivered by B LEDs (B), incandescent lamps (INC), white/red/far-red LEDs (WRFR),

Figure 4.3 (cont'd)

lamps with two far-red LEDs for every one red LED (1R2FR), lamps with an equal number of red and far-red LEDs (RFR), and lamps with two red LEDs for every one far-red LED (2R1FR). Mean separation within variable by Tukey's honestly significant difference test at $P \leq 0.05$.

The interaction effect of lamp type and timing of the night break was significant for some parameters. For example, in Rep 1, VB appearance was delayed under NI lighting compared to EOD lighting for the INC, WRFR, and 2R1FR treatments. When given as an NI, the plants grown under the 2R1FR treatment developed more nodes before the first flower than those under the RFR treatment. However, when given as an EOD night break, the 2R1FR treatment responses were similar to that under the RFR lamps, indicating an interaction effect between lighting treatment and night break timing. Among the plants that flowered, flower-bud number at first flowering was similar for all treatments.

All rudbeckia 'Denver Daisy' flowered under all R+FR lighting treatments, whereas no plants flowered under SDs or the B NI (Table 4.3). The timing of the night break did not have a significant impact on any of the parameters measured. In general, all R+FR lamps promoted flowering, and there were no consistent trends for R:FR and flowering time. Plants flowered 6 to 7 d earlier in Rep 2 than in Rep 1. Flowering time under the R+FR treatments was similar in Rep 1, whereas flowering was delayed (by ≥ 5 d) under the 1R2FR and 2R1FR lamps. Plants in all R+FR treatments developed a VB in 45 to 49 d, 26 to 31 VBs, and 10 to 11 nodes below the first flower. Although there were significant differences in extension growth among the R+FR lamps, there were no apparent trends. The increase in height was between 43 and 52 cm in all treatments.

Table 4.3. The effects of the time of the lighting period and lamp type on flowering and extension growth of rudbeckia ‘Denver Daisy’ (n = 239 for pooled parameters). Data were pooled between replications if the statistical interactions between treatment and replication were not significant at $P \geq 0.05$.

| Parameter | Flowering percentage | Days to visible bud | Days to flower | | Increase in height (cm) | | Flower bud no. | Increase in node no. |
|----------------------|----------------------|---------------------|----------------|--------|-------------------------|--------|----------------|----------------------|
| | | | Rep #1 | Rep #2 | Rep #1 | Rep #2 | | |
| Lighting period | | | | | | | | |
| None (short day, SD) | - | - ^z | - | - | - | - | - | - |
| End of day | - | 46.1 | 79.9 | 74.1 | 47.7 | 47.3 | 28.1 | 10.1 |
| Night interruption | - | 46.3 | 81.3 | 74.3 | 50.5 | 44.9 | 29.8 | 10.6 |
| Lamp type | | | | | | | | |
| SD | 0 | - | - | - | - | - | - | - |
| Blue | 0 | - | - | - | - | - | - | - |
| Incandescent | 100 | 46.4 | 78.1 | 69.8 | 49.5 | 46.1 | 30.2 | 10.4 |
| WRFR ^x | 100 | 45.9 | 80.2 | 73.4 | 47.9 | 42.9 | 27.4 | 10.3 |
| 1R2FR | 100 | 46.9 | 81.0 | 78.5 | 51.9 | 50.6 | 29.9 | 10.4 |
| RFR | 100 | 44.5 | 78.6 | 70.2 | 49.8 | 42.9 | 30.9 | 10.8 |
| 2R1FR | 100 | 48.9 | 82.9 | 79.7 | 46.4 | 48.5 | 26.1 | 9.9 |

^zNo data.

^yMeans followed by the same letter within a column are not significantly different at $P \leq 0.05$ using Tukey’s honestly significant difference test. Data without mean separation letters indicate non-significant differences.

^xWRFR = White/red/far-red LED, 1R2FR = Lamps with one red LED for every two far-red LEDs, RFR = lamps with an equal number of red and far-red LEDs, 2R1FR = lamps with two red LEDs for every one far-red LED.

All tickseed 'Moonbeam' flowered under all R+FR lighting treatments (Table 4.4). Flowering percentage was reduced to five and 25 under SDs and B NI, respectively. The timing of the night break did not have a significant impact on any parameters. Plants developed VBs and flowered earlier, were significantly taller, and formed more flower buds and fewer nodes when grown with R+FR night breaks compared with SDs or B NIs. There were no significant differences among the various R+FR treatments for these parameters. Plants in all R+FR treatments developed a VB in 21 to 24 d and flowered in 49 to 56 d. Plants in these treatments also increased in height by 44 to 55 cm and developed 48 to 58 VBs and 7 to 8 nodes below the first flower.

Table 4.4. The effects of the time of the lighting period and lamp type on flowering and extension growth of tickseed ‘Moonbeam’ (n = 238 for pooled parameters). Data were pooled between replications if the statistical interactions between treatment and replication were not significant at $P \geq 0.05$.

| Parameter | Flowering percentage | Days to visible bud | Days to flower | | Increase in height (cm) | | Flower bud no. | Increase in node no. | |
|----------------------|----------------------|---------------------|----------------|---------------|-------------------------|--------|----------------|----------------------|--------|
| | | | | | Rep #1 | Rep #2 | | Rep #1 | Rep #2 |
| Lighting period | | | | | | | | | |
| None (short day, SD) | - | 60.8 a ^y | - ^z | - | 8.0 b | 8.0 b | - | - | - |
| End of day | - | 21.2 b | 52.5 | 52.5 | 46.4 a | 46.4 a | 53.0 | 7.4 | 7.4 |
| Night interruption | - | 25.5 b | 54.7 | 54.7 | 43.9 a | 43.9 a | 51.5 | 7.8 | 7.8 |
| Lamp type (LT) | | | | | | | | | |
| | | | <i>Rep #1</i> | <i>Rep #2</i> | | | | | |
| SD | 5 | 60.8 a | - | - | 7.4 c | - | - | - | - |
| Blue | 25 | 50.1 a | - | 73.2 a | 6.8 c | 30.6 b | 18.3 b | - | 9.7 a |
| Incandescent | 100 | 21.0 b | 52.7 | 49.0 b | 49.5 ab | 43.8 a | 58.3 a | 7.9 | 7.3 b |
| WRFR ^x | 100 | 21.0 b | 54.8 | 51.6 b | 47.9 ab | 45.7 a | 51.0 a | 8.1 | 6.9 b |
| 1R2FR | 100 | 21.9 b | 54.1 | 55.2 b | 51.9 a | 47.6 a | 53.5 a | 8.2 | 7.4 b |
| RFR | 100 | 24.4 b | 53.2 | 49.6 b | 49.8 ab | 45.3 a | 55.6 a | 8.0 | 6.7 b |
| 2R1FR | 100 | 22.1 b | 53.8 | 55.5 b | 46.4 b | 46.6 a | 48.3 ab | 7.5 | 7.8 ab |

^zNo data.

^yMeans followed by the same letter within a column are not significantly different at $P \leq 0.05$ using Tukey’s honestly significant difference test. Data without mean separation letters indicate non-significant differences.

^xWRFR = White/red/far-red LED, 1R2FR = Lamps with one red LED for every two far-red LEDs, RFR = lamps with an equal number of red and far-red LEDs, 2R1FR = lamps with two red LEDs for every one far-red LED.

Flowering percentage of spinach ‘Bloomsdale Longstanding’ was variable and incomplete, with less than half of the plants flowering in many treatments (Table 4.5). No plants flowered under SDs or B NIs. Although trends were not clear, flowering percentage appears to have increased slightly with increasing P_{FR}/P_{R+FR} of the night break.

Table 4.5. The effects of the time of the lighting period and lamp type on flowering of spinach ‘Bloomsdale Longstanding’ (n = 234 for pooled parameters).

| Parameter | Flowering percentage |
|----------------------|----------------------|
| Lighting period | |
| None (short day, SD) | 0 |
| End of day | 31 |
| Night interruption | 43 |
| Lamp type (LT) | |
| SD | 0 |
| Blue | 38 |
| Incandescent | 35 |
| WRFR ^z | 45 |
| 1R2FR | 50 |
| RFR | 60 |
| 2R1FR | 0 |

^zWRFR = White/red/far-red LED, 1R2FR = Lamps with one red LED for every two far-red LEDs, RFR = lamps with an equal number of red and far-red LEDs, 2R1FR = lamps with two red LEDs for every one far-red LED.

Flowering percentage of campanula ‘Clips Deep Blue’ was 98 under all R+FR lighting treatments (Table 4.6). Flowering percentage was zero or 25 under SDs or the B NI, respectively. The timing of the night break did not affect many of the parameters measured. In Rep 2, VB formation occurred 5 d earlier for plants grown under NI than EOD treatments. In addition, ~8 more VBs were formed for plants grown under NI than EOD treatments. Plants developed VBs earlier, flowered earlier, and developed fewer nodes when grown with R+FR night breaks compared with SDs or B NI. There were no consistent differences among the

various R+FR treatments for these parameters. Plants developed a VB ~8 d earlier for Rep 2 than for Rep 1. Plants in all R+FR treatments flowered in 90 to 96 d, and was ≥ 9 d later for plants that flowered under the B NI. Plants in these treatments also increased in height by 10 to 14 cm and developed 30 to 48 VBs and ~14 nodes below the first flower.

Table 4.6. The effects of the time of the lighting period and lamp type on flowering and extension growth of campanula ‘Clips Deep Blue’ (n = 229 for pooled parameters). Data were pooled between replications if the statistical interactions between treatment and replication were not significant at $P \geq 0.05$.

| Parameter | Flowering percentage | Days to visible bud | | Days to flower | Increase in height | | Flower bud no. | Increase in node no. | | | | | | | |
|----------------------|----------------------|---------------------|--------|----------------|--------------------|--------|----------------|----------------------|-----|------|----|------|-----|------|---|
| | | Rep #1 | Rep #2 | | Rep #1 | Rep #2 | | | | | | | | | |
| Lighting period | | | | | | | | | | | | | | | |
| None (short day, SD) | - | - ^z | - | - | - | - | - | - | - | | | | | | |
| End of day | - | 75.4 | 70.8 | a ^y | 94.5 | 12.5 | 12.0 | 33.9 | b | 14.0 | | | | | |
| Night interruption | - | 75.7 | 65.9 | b | 92.7 | 12.1 | 13.0 | 41.5 | a | 13.8 | | | | | |
| Lamp type | | | | | | | | | | | | | | | |
| SD | 0 | - | - | - | - | - | - | - | - | - | | | | | |
| Blue | 25 | 94.7 | a | - | 114.4 | a | 10.8 | c | - | 21.0 | c | 19.0 | a | | |
| Incandescent | 98 | 75.3 | b | 62.9 | b | 90.1 | b | 9.8 | c | 12.1 | ab | 29.7 | bc | 13.5 | b |
| WRFR ^x | 98 | 72.9 | b | 71.1 | a | 92.5 | b | 13.6 | a | 13.5 | a | 38.4 | ab | 13.4 | b |
| 1R2FR | 98 | 74.8 | b | 69.5 | ab | 94.5 | b | 13.5 | a | 13.3 | a | 36.1 | abc | 14.2 | b |
| RFR | 98 | 75.3 | b | 67.1 | ab | 92.0 | b | 12.2 | abc | 10.2 | b | 38.3 | ab | 13.7 | b |
| 2R1FR | 98 | 76.1 | b | 69.5 | ab | 95.5 | b | 12.8 | ab | 13.3 | a | 48.2 | a | 13.9 | b |

^zNo data.

^yMeans followed by the same letter within a column are not significantly different at $P \leq 0.05$ using Tukey’s honestly significant difference test. Data without mean separation letters indicate non-significant differences.

^xWRFR = White/red/far-red LED, 1R2FR = Lamps with one red LED for every two far-red LEDs, RFR = lamps with an equal number of red and far-red LEDs, 2R1FR = lamps with two red LEDs for every one far-red LED.

Discussion

A circadian rhythm in plants makes them most sensitive to light perception during the middle of the night. An early study on the LDP *Fuchsia* and the short-day plant *Kalanchoe* suggested that a night break given near the middle of a 12 to 16-h night was most effective because it broke up the long night into two shorter dark periods, which were each shorter than the critical night length (Vince-Prue, 1975). However, this explanation was deemed inadequate in a later study of *Xanthium* and *Pharbitis* (Salisbury and Ross, 1991). Under non-24-h cycles, the NBmax response still occurred 8 to 9 h after the beginning of an extended night (40 to 48 h night), even though the remaining 30- to 40-h dark period greatly exceeded the critical night length. These studies established that the night break response is a period of sensitivity to light that occurs in accordance with the beginning of the dark period.

Several studies suggest that short periods of lighting are more promotive to flowering when delivered near the middle of the dark period (NI) than at the beginning of the dark period (EOD) (Thomas and Vince-Prue, 1997). For example, in the SDP *Xanthium strumarium*, a 5 min night break was most effective 6 to 8 h after the beginning of darkness (Salisbury 1963). In the LDPs *Coleus frederici* (Halaban, 1968) and *Lolium temulentum* (Vince, 1965), 1-h night breaks were most effective 10 to 12 and 8 to 9 h after the beginning of darkness, respectively. There was no difference between EOD and NI lighting for promoting flowering in tickseed, rudbeckia, and campanula. Furthermore, flowering in petunia was actually delayed by NI lighting compared to EOD lighting. Our observations could differ since our night breaks were significantly longer in duration than the previous studies. Similarly, in a recent study on tickseed and campanula, 6-h EOD treatments or 2- or 4-h NI treatments provided by either INC, fluorescent (FL), or 50% INC and 50% FL lamps had no consistent effect on time to flower

(Padhye and Runkle, 2011). As with our study, the rate of plant development, illustrated by node number at flowering, was similar regardless of night break timing. Collectively, these results show that in many plants, NI and EOD are equally promotive.

It is possible that our findings diverge from convention because we used narrow-waveband LED lamps for most treatments. LEDs allow researchers to analyze the effects of specific wavebands without including extraneous wavebands. Many of the original photoperiodic lighting studies were limited by the lighting technology of the time. The use of photosensitive filters and tinted lamps may have introduced confounding variables into these early experiments, such as differences in photon flux between treatments and/or inclusion of potentially confounding, extraneous wavelengths (Borthwick et al., 1952; Cathey and Borthwick, 1957; Downs, 1956).

In general, plants did not flower when grown under SDs or with B NIs. The remaining lamp types all emitted a mixture of R and FR light, with one lamp type also emitting white light. Regardless of R:FR, which ranged from 0.59 to 2.38 (P_{FR}/P_{R+FR} of 0.63 to 0.80), flowering was promoted in all species compared to plants grown with SDs or B NIs. In some cases, there were significant differences among lamp types, but the trends were generally inconsistent.

Previous studies suggest that B light is involved in photoperiodic responses in at least some plant families (Runkle and Heins, 2001; Thomas and Vince-Prue, 1997). The cryptochromes and phytochromes are both involved in daylength perception. In addition, phytochrome absorbs in the B region of the spectrum, suggesting a possible interaction of B light with the phytochrome-mediated flowering response. In our study, B light was not effective as a night break light source. While tickseed exhibited a weak flowering response under B NI, flowering was delayed dramatically (by approximately 21 d). In another study, an 11-h SD with

or without a 4-h B EOD treatment induced flowering in the short-day plant chrysanthemum (Van Ieperen, 2009). Even though the B EOD treatment created LD conditions, the B night break was not perceived as a LD signal. Since the photoreversible forms of phytochrome respond only to R and FR light, it is reasonable to assume that B light is not involved in the phytochrome-mediated flowering response.

Commercial growers have traditionally used INC lamps to provide both EOD and NI photoperiod lighting. However, INC lamps convert only about 10% of the energy consumed into visible light (Thimijan and Heins, 1983; Kanter, 2009). With the phase-out of INC lamps, greenhouse growers will need other sources of light to control flowering of photoperiodic crops. Although all of the R- and FR-emitting lamps were effective for promoting flowering, we found few differences among the lamps, even though their $R:FR_{\text{wide}}$ ranged from 0.65 to 2.38 ($P_{\text{FR}}/P_{\text{R+FR}}$ of 0.63 to 0.80). Among the differences we did observe, trends were not consistent. Plant responses were essentially the same under either INC or LED light. Therefore, LED technology can provide an alternative to INC lamps for photoperiodic lighting. In addition to the improvements in lamp lifespan and energy efficiency, the narrow waveband nature of LEDs can be used to create lamps that are tailored to ornamental crop-production needs. In the LDPs studied, LEDs with a moderate to high R:FR were effective at promoting flowering when given either as an EOD or NI treatment.

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