Comparing Flowering Responses of Long-day Plants under Incandescent and Two Commercial Light-emitting Diode Lamps

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Additional Index Words. LEDs, lighting, night interruption, photoperiod, phytochrome, red to far-red ratio

Summary. When the natural daylength is short, commercial growers of ornamental long-day plants (LDP) often provide low-intensity lighting to more rapidly and uniformly induce flowering. Incandescent (INC) lamps have been traditionally used for photoperiodic lighting because their spectrum, rich in red (600 to 700 nm) and far-red (700 to 800 nm) light, is effective and they are inexpensive to purchase and install. Light-emitting diodes (LEDs) are much more energy efficient, can emit wavelengths of light that specifically regulate flowering, and last at least 20 times longer. We investigated the efficacy of two new commercial LED products developed for flowering applications on the LDP ageratum (Ageratum houstonianum), calibrachoa (Calibrachoa ×hybrida), two cultivars of dianthus (Dianthus chinensis), and two cultivars of petunia (Petunia ×hybrida). Plants were grown under a 9-hour short day without or with a 4-hour night interruption (NI) delivered by one of three lamp types: INC lamps (R:FR = 0.59), LED lamps with R and white (W) diodes [R + W (R:FR = 53.35)], and LED lamps with R, W, and FR diodes [R + W + FR (R:FR = 0.67)]. The experiment was performed twice, both at a constant 20 °C, but the photosynthetic daily light integral (DLI) during the second replicate (Rep. II) was twice that in the first (Rep. I). In all crops and in both experimental replicates, time to flower, flower or inflorescence and node number, and plant height were similar under the R + W + FR LEDs and the INC lamps. However, in Rep. I, both petunia cultivars developed more nodes and flowering was delayed under the R + W LEDs compared with the INC or R + W + FR LEDs. In Rep. II, petunia flowering time and node number were similar under the three NI treatments. Plant height of both dianthus cultivars was generally shorter under the NI treatment without FR light (R + W LEDs). These results indicate that when the DLI is low (e.g., ≤6 mol·m⁻²·d⁻¹), FR light is required in NI lighting for the most rapid flowering of some but not all LDP; under a higher DLI, the flowering response to FR light in NI lighting is apparently diminished.

A common goal in the commercial production of floriculture crops is to produce plants that flower in a complete, rapid, and uniform manner while maintaining at least a moderate crop quality (Runkle and Heins, 2006). Protected environments, especially greenhouses with heating and lighting systems, are used in temperate climates to produce crops for predetermined market dates. For example, production of annual bedding plants begins in the winter so that crops are marketable (i.e., of a desired size and in flower) for customers in the spring. To finish plants on time, greenhouse growers manipulate temperature, light intensity, and photoperiod to regulate growth and flowering. Growers also commonly regulate extension growth of crops by applying plant growth regulators, by delivering a cooler day than night temperature, or other strategies that inhibit internode elongation (Davis and Andersen, 1989).

Most floriculture crops can be classified into one of three categories based on their flowering response to photoperiod: day-neutral plants, short-day (SD) plants (SDP), and long-day (LD) plants. Flowering of day-neutral plants is not influenced by photoperiod. Rapid flowering of SDP occurs when the day is short and the night is long and continuous, whereas rapid flowering of LDP occurs when the night length is less than some critical value. Some plants have an absolute requirement for induction of flowering (an obligate response), while for many others, flowering is simply hastened by a particular photoperiod (a facultative response). Electrical lighting is commonly operated at the end of the day (day-extension lighting) or in the middle of the night (NI lighting) to create an artificial LD. A 4-h NI promotes rapid flowering of a range of LDP including campanula (Campanula carpatica), coreopsis (Coreopsis grandiflora), and lavender (Lavandula angustifolia) (Damann and Lyons, 1996; Runkle et al., 1998). A photosynthetic photon flux (PPF) of ≈1 μmol·m⁻²·s⁻¹ is needed to elicit a photoperiodic response from conventional light sources such as INC or high-pressure sodium (HPS) lamps (Whitman et al., 1998).

The phytochrome family of photoreceptors mediates perception of the ratio of R light (600 to 700 nm) and FR light (700 to 800 nm). Depending on the spectral quality of light, phytochrome exists in a photoequilibrium of two interconvertible forms, the R- and FR-absorbing forms, Pₚ and PₚFₐ, respectively. The phytochrome photoequilibrium (PₚFₐ/PₚFR) refers to the proportion of phytochrome in the active PₚFₐ form and regulates flowering in photoperiodic plants and extension growth in shade-avoiding plants (Smith, 1994). Under a plant canopy or when plants are grown at a high density, the R:FR is decreased because photosynthetic light (400 to 700 nm) is mostly absorbed but most of the FR light is reflected or transmitted. In response to the decrease in the R:FR, flowering is hastened and...
extension growth is promoted in LDP. Accordingly, an FR-deficient environment inhibited flower initiation in some LDP, including snapdragon (Antirrhinum majus), campanula, coreopsis, and petunia, and inhibited flower development in pansy (Viola xwittrockiana) and henbance (Hyoscyamus niger) (Downs and Thomas, 1982; Kim et al., 2002; Runkle and Heins, 2001, 2003; van Haeringen et al., 1998). There is at least some minimal requirement of R light for rapid flowering, as FR light alone is typically not perceived as an LD (Craig, 2012). Thus, artificial lighting that contains both R and FR light is commonly provided to promote flowering of LDP.

INC lamps have been traditionally used to deliver NI lighting because they emit both R and FR light and are inexpensive to purchase and install. A mixture of R and FR light generates an intermediate \( P_{FR}/P_{R+FR} \) that is most promotive for flowering in LDP (Craig and Runkle, 2012; Thomas and Vince-Prue, 1997). LEDs are replacing INC lamps because LEDs are much more energy efficient, have a much longer operating life, and the spectra can be tailored to elicit desired plant reactions such as flowering (Yeh and Chung, 2009). The objective of this study was to compare flowering responses of popular LD floriculture crops under two new commercial LED lamp types developed specifically for flowering applications with those under traditional INC lamps.

**Materials and methods**

**Plant material and culture.** Nine-day-old seedlings of ‘Hawaii Blue’ ageratum, ‘Super Parfait Strawberry’ and ‘Floral Lace Purple’ dianthus, and ‘Easy Wave Burgundy Star’ and ‘Wave Purple Improved’ petunia in 288-cell (6-mL volume) plug trays and rooted cuttings (≈25 d from sticking) of ‘Callie White’ calibrachoa in 51-strip (27-mL volume) trays were provided by a commercial grower (C. Raker & Sons, Litchfield, MI). In the first experimental replicate (Rep. I), all seedlings were received on 8 Nov. 2012 and the calibrachoa were received on 15 Jan. 2013. The young plants were subsequently grown in a greenhouse at a constant temperature set point of 20°C under a 9-h SD until the initiation of the experiment. All seedlings and calibrachoa were transferred to NI treatments on 30 Nov. 2012 and 16 Jan. 2013, respectively. At transfer, the seedlings were thinned to one seedling per cell and all plants were transplanted into 4-inch round plastic containers filled with a commercial soilless peat-based medium (Suremix; Michigan Grower Products, Galesburg, MI). Except for calibrachoa, the experiment was performed twice with the same propagation procedure and greenhouse environment as previously described. For the second replicate (Rep. II), all seedlings were received on 6 Feb. 2013 and ‘Floral Lace Purple’ dianthus and ‘Wave Purple Improved’ petunia were transplanted on 27 Feb., ‘Super Parfait Strawberry’ dianthus and ‘Easy Wave Burgundy Star’ petunia were transplanted on 28 Feb., and ageratum was transplanted on 1 Mar. 2013. Throughout the experiment, plants were irrigated as necessary with reverse osmosis water supplemented with a water-soluble fertilizer providing (in mg L\(^{-1}\)) 125 nitrogen, 12 phosphorus, 100 potassium, 65 calcium, 12 magnesium, 1.0 iron, 1.0 copper, 0.5 manganese, 0.5 zinc, 0.5 boron, and 0.1 molybdenum (MSU RO Water Special; GreenCare Fertilizers, Kankakee, IL). Within 21 d of the onset of treatments, all petunias received a 60-mL/pot substrate drench at 5 mg L\(^{-1}\) of paclobutrazol (Piccolo; Fine Americas, Walnut Creek, CA) to inhibit stem elongation.

**Lighting treatments.** Ten plants of each species were randomly assigned to four treatments in a glass-glazed greenhouse at a constant temperature set point of 20°C. Each day, blackout curtains were pulled over benches at 1700 HR and opened at 0800 HR to create a 9-h SD. During the SD, HPS lamps delivered a PPF of 60 to 90 μmol·m\(^{-2}\)·s\(^{-1}\) at plant height when the ambient PPF was <185 μmol·m\(^{-2}\)·s\(^{-1}\) and turned off when the PPF was >370 μmol·m\(^{-2}\)·s\(^{-1}\).

Treatments consisted of the 9-h SD or a 9-h day with NI lighting from 2230 to 0230 HR provided by one of three lamp types: INC lamps (60 W; Philips, Somerset, NJ) or LED lamps that contained red, white, and far-red diodes (R + W + FR; GreenPower LED flowering R + W + FR, 120 V, Philips, Eindhoven, the Netherlands) or red and white diodes (GreenPower LED flowering, 120 V, Philips). Bulbs were installed above the benches, and light intensity at plant level was adjusted by altering bench height and/or installing aluminum mesh around the fixtures, to ensure that each treatment provided a similar photon flux between 600 and 800 nm. The spectral characteristics of each lamp were measured by a portable spectroradiometer (PS-200; StellarNet, Tampa, FL) and are shown in Fig. 1. Spectral measurements were taken throughout the bench area of each NI treatment and the phytochrome photoequilibrium (\( P_{FR}/P_{R+FR} \)) was estimated according to Sager et al. (1988) (Table 1). Plants were positioned on the bench only where the NI lighting intensity of R + FR light was ≥0.7 μmol·m\(^{-2}\)·s\(^{-1}\). The mean R + FR light intensity of all NI treatments was between 1.5 and 1.8 μmol·m\(^{-2}\)·s\(^{-1}\).

**Greenhouse environment.** Light intensity at plant height was continuously measured using line quantum sensors that each contained 10 photodiodes (SQ-311; Apogee Instruments, Logan, UT). Air temperature was measured at plant height on each bench using an aspirated, shielded thermocouple [36-gauge (0.127-mm diameter) type E]. The temperature...
and light sensors were connected to a data logger (CR10; Campbell Scientific, Logan, UT), and data were collected every 10 s and hourly means were automatically recorded on a computer. When the air temperature on each bench was <18.9 °C between 1700 and 0800 hr, a 1500-W electric heater under each bench, controlled by a data logger, provided supplemental heat throughout the night. During the experimental replications, the mean photosynthetic DLI was 5.4 to 6.0 mol·m⁻²·d⁻¹ for the seed-propagated plants and 8.8 mol·m⁻²·d⁻¹ for calibrachoa in Rep. I, and 11.1 to 11.6 mol·m⁻²·d⁻¹ in Rep. II. The actual daily mean temperatures during the experiments were 19.8 to 20.2 °C (Rep. I) and 20.6 °C (Rep. II). Within each replicate, the mean daily temperature differed between treatments by ≤0.6 °C.

**Data collection and analysis.**

On the day of transplant, nodes were counted on each seedling and means were 6, 6, 8, 4 to 6, and 6 or 7 nodes for ageratum, ‘Floral Lace Purple’ dianthus, ‘Super Parfait Strawberry’ dianthus, ‘Easy Wave Burgundy Star’ petunia, and ‘Wave Purple Improved’ petunia, respectively, in both replicates. Initial node number was not counted on calibrachoa. Plants were checked daily for first visible flower bud or inflorescence (VB) and first open flower and those dates were recorded. Ageratum and dianthus were considered flowering when two flowers opened on the inflorescence and when 50% of the petals of the first flower were reflexed, respectively. Petunia and calibrachoa were considered flowering when the first flower opened. When each plant flowered, the following data were collected: plant height, VB number, and node number below the first inflorescence or open flower. Plant height was measured from the soil surface to apex (ageratum and dianthus) or length of longest shoot below the first open flower (calibrachoa and petunia). Days from transplant to VB, days from transplant to first flower and node number increase were calculated for each plant. Plants that did not have VB within 90 d after transplant were considered nonflowering. Data were analyzed with SAS (version 9.1; SAS Institute, Cary, NC) and mean separation between treatments was performed with Tukey’s honestly significant difference test at \( P \leq 0.05 \).

**Results**

**Ageratum.** All plants flowered in all treatments. Flowering under all NI treatments was hastened by \( \approx 13 \) or 9 d in Rep. I or II, respectively, compared with plants under SD (Fig. 2). Ageratum formed 12 to 14 nodes before flowering when grown under SD, but only 8 or 9 nodes when grown under NI. Treatments generally had little effect on plant height at flower, but in Rep. II, plants grown under R + W LEDs were \( \approx 2 \) cm shorter than those grown under the R + W + FR LEDs. In Rep. I, plants formed a mean of 108 inflorescences each and treatments had no significant effect on inflorescence number, but during Rep. II, inflorescence number under the three NI treatments was greater than that under SD (Table 2).

**Calibrachoa.** One plant under SD had not reached the visible flower bud stage 90 d after transplant and was considered nonflowering; all other plants in all other treatments flowered (data not shown). Time to flower was delayed by \( \approx 6 \) weeks under SDs compared with plants under an NI, regardless of lamp type (Fig. 2). Plants grown under NI treatments formed 13 nodes before initiating a flower, while those under SD formed \( \geq 40 \) nodes. Under SD, plants formed extensive vegetative growth before flowering, and shoots were \( > 22 \) cm long when plants bloomed. Shoot length under NI treatments was 9 to 12 cm, and shoots on plants grown under the R + W LEDs were \( \approx 3 \) cm shorter than those grown under R + W + FR LEDs. Calibrachoa formed significantly more flowers under NI treatments than under SD (Table 2).

**Floral lace purple’ dianthus.** All plants flowered in all treatments. Time to flower was reduced \( \approx 5 \) by NI provided with INC or R + W + FR lamps compared with plants under SD, while flowering time under the R + W lamps was similar with that under SD (Fig. 2). Plants in all treatments formed 17 to 19 nodes before forming a flower. Plants under NI provided by the INC or R + W + FR LED lamps were significantly taller than those under SD or R + W.
LEDs in both Rep. I and II. Flower bud numbers were 8 to 10 in Rep. I and 10 to 14 in Rep. II, and were unaffected by treatments (data not shown).

‘Super Parfait Strawberry’ Dianthus. All plants flowered in all treatments. In Rep. I, NI from INC or R + W + FR LEDs reduced time to flower by 7 d compared with plants under SD or the R + W LEDs. In contrast, flowering time was similar under the NI treatments in Rep. II. Plants under the R + W + FR LEDs developed fewer nodes before flowering than plants under SD in Rep. II, but otherwise node number at flowering was similar. Mean flower bud number was 11 per plant in Rep. I and 17 in Rep. II, and was similar among treatments (data not shown). Plants under INC or R + W + FR lamps were 24% or 33% taller in Rep. I or II, respectively, compared with those under SD or R + W LEDs.

‘Easy Wave Burgundy Star’ Petunia. During Rep. I, a single plant under SD did not flower; all plants in all other treatments flowered (data not shown). Time to flower under all NI treatments was reduced by 21 to 30 d in Rep. I and 22 to 24 d in Rep. II compared with plants under SD (Fig. 2). In Rep. I, plants flowered earlier under the INC or R + W + FR LEDs than under the R + W LEDs, while flowering time in Rep. II was similar among the NI treatments. In both replications, plants under NI lighting treatments formed 15 to 18 nodes before flowering, while those under SD formed 30. In Rep. I, plants grown under R + W lamps formed four more nodes before flowering than those grown under INC or R + W + FR LEDs. In Rep. I, plants under SD or R + W LEDs had significantly longer stems at flowering than those under the INC or R + W + FR lamps. In Rep. II, plants under all NI lighting treatments were significantly shorter than those under SD. Flower bud number in Rep. I was greater on plants under INC or R + W + FR lamps than on those under SD or R + W LEDs, but there was no treatment effect in Rep. II (Table 2).

‘Wave Purple Improved’ Petunia. Seventy or 90% of plants flowered under SD in Rep. I or II, respectively, while all plants flowered in the other treatments (data not shown). Flowering under all NI treatments was promoted by 35 to 44 d in Rep. I and 20 to 23 d in Rep. II compared with plants under SD (Fig. 2). In Rep. I, NI treatment with R + W LEDs did not promote flowering as much as the other NI treatments, whereas all lamps were similarly effective in Rep. II. In both replications, plants under NI lighting treatments formed 14 to 17 nodes before flowering, while those under SD formed more than twice as many. In Rep. I, plants grown under R + W LEDs formed about four more nodes before flowering than those under INC or R + W + FR LEDs. In Rep. I, stems on plants under the three NI treatments were 9 cm shorter than on plants under SD. In Rep. II, shoot lengths were similar in all treatments. Flower bud number was similar in Rep. I, but plants under NI lighting treatments had significantly more flowers than those under SD in Rep. II (Table 2).

Discussion

The FR-promotion of flowering, particularly at the end of the day or during NI lighting, has been previously established in some LD ornamental annuals including pansy, petunia, and snapdragon (Craig and
Table 2. Visible flower bud or inflorescence number at flowering of ornamental annuals grown under a 9-h short day (SD) or a 9-h day with a 4-h night interruption from incandescent (INC) lamps or light-emitting diodes (LEDs) that contained red (R) and white (W) diodes without or with far-red (FR) diodes. Data with different letters within each species and replication (Rep.) are significantly different at $P \leq 0.05$.

| Treatment                        | Rep. I | Rep. II |
|----------------------------------|--------|---------|
|                                  |        |         |
| **Ageratum**                     |        |         |
| SD                               | 117    | 140 b   |
| INC                              | 124 a  |         |
| R + W LED                        | 95     | 224 a   |
| R + W + FR LED                   | 97     | 209 a   |
| **Calibrachoa**                  |        |         |
| SD                               | 4 b    | —       |
| INC                              | 11 a   | —       |
| R + W LED                        | 12 a   | —       |
| R + W + FR LED                   | 13 a   | —       |
| **‘Easy Wave Burgundy Star’ petunia** |    |         |
| SD                               | 16 c   | 18      |
| INC                              | 28 ab  | 19      |
| R + W LED                        | 23 bc  | 21      |
| R + W + FR LED                   | 35 a   | 19      |
| **‘Wave Purple Improved’ petunia** |    |         |
| SD                               | 17     | 16 b    |
| INC                              | 22     | 26 a    |
| R + W LED                        | 19     | 30 b    |
| R + W + FR LED                   | 21     | 26 a    |

*Not included.

In this study, the first experimental replication of the five seed-propagated crops was performed when plants received a low mean DLI ($\leq 6$ mol m$^{-2}$ d$^{-1}$) while during Rep. II, the DLI was twice as high. In contrast, the mean temperatures between the two replications were similar. The low DLI in Rep. I is common in greenhouses during the winter in temperate climates; assuming 50% transmission of light to crops inside a greenhouse without supplemental lighting, a typical DLI would be $\leq 7.5$ mol m$^{-2}$ d$^{-1}$ in the northern half of the United States (i.e., $\leq 40^\circ$N latitude) in December and January (Korczynski et al., 2002). A mean DLI $< 10$ mol m$^{-2}$ d$^{-1}$ delays flowering of numerous herbaceous annual crops and thus is considered light-limiting (Blanchard, 2009; Blanchard et al., 2011; Moccaldi and Runkle, 2007). In Rep. I, both petunia cultivars developed three to five more nodes and flowered 6 to 10 d later when the NI did not include FR light (R + W LEDs) compared with those that did (INC lamps and R + W + FR LEDs). In contrast, node number and flowering time of petunia, as well as the other crops, was similar under the three NI treatments in Rep. II. This suggests that the spectral distribution of NI lighting is more of a factor when the DLI is low compared with higher light conditions. However, ‘Easy Wave White’ petunia and snapdragon still flowered earlier when NI lighting emitted a moderate R:FR (0.66 to 2.38) when the DLI was moderately high (15 mol m$^{-2}$ d$^{-1}$) (Craig and Runkle, 2012). Therefore, the interaction between the DLI and quality of the NI lighting could also vary among crops and cultivars.

All six crops studied here exhibited an LD flowering response, but the magnitude of the promotion of flowering by LDs varied. Both dianthus flowered 4 to 8 d earlier at 20 °C under the INC or R + W + FR LEDs than under SDs in both experimental replicates. The LD promotion of flowering was greatest in petunia and calibrachoa, in which the INC or R + W + FR LEDs accelerated flowering by 28 to 47 d in Rep. I and 23 or 24 d in Rep. II. Consistent with these results, Erwin and Warner (2002) reported that ‘Blue Danube’ ageratum and ‘Ideal Cherry Picotee’ dianthus had a facultative LD flowering response. Several cultivars of petunia have also been reported to be facultative LD plants (Craig and Runkle, 2012; Runkle and Heins, 2003; Runkle et al., 2012) as well as in model crops such as Arabidopsis (Arabidopsis thaliana) and henbane (Goto et al., 1991; Lane et al., 1965).
a limiting factor, but when the DLI is relatively low, the inclusion of FR light simultaneously promotes flowering as well as extension growth, a phenomenon previously reported in other ornamental annuals such as pansy (Runkle and Heins, 2003).

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