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Day-extension Blue Light Inhibits Flowering of Chrysanthemum When the Short Main Photoperiod Includes Far-red Light

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Abstract. Chrysanthemum (*Chrysanthemum* ×*morifolium*) is a common ornamental crop with a qualitative short-day flowering response. Extending a short day with moderate blue [B (400–500 nm)] light inhibits flowering in greenhouse conditions with sunlight but does not indoors (without sunlight) under B + red [R (600–700 nm)] light or white light. We postulated that the contrasting responses to B light as a day extension depended on far-red [FR (700–800 nm)] light during the day, which is plentiful under sunlight but lacking indoors under B+R or white light-emitting diodes. To study this response in three chrysanthemum cultivars, we delivered indoor lighting treatments at two locations with an 11-hour main photoperiod of B, green [G (500–600 nm)], R, and FR light, where subscript values indicate the photon flux density (in $\mu mol \cdot m^{-2} \cdot s^{-1}$) of each waveband: $B_{60}R_{120}$, $B_{60}G_{60}R_{60}$, and $B_{60}R_{60}FR_{60}$. After each short main photoperiod, plants received 0 or 4 hours of day-extension lighting of 60 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of B light (B_{60}). Under all treatments except $B_{60}R_{60}FR_{60}$ with day-extension B_{60}, it took 'Chelsey Pink', 'Gigi Gold', and 'Gigi Yellow' 13 to 17 days to reach the first visible inflorescence and 42 to 51 days to the first open flower. In contrast, plants grown under $B_{60}R_{60}FR_{60}$ with day-extension B_{60} took 41 to 67 days to reach the first visible inflorescence with few plants developing open flowers. Plants were tallest at the first open flower and after 9 weeks of treatments when grown under $B_{60}R_{60}FR_{60}$ with day-extension B_{60}. These results indicate that the inclusion of FR light, but not G light, in the main photoperiod is necessary for day-extension B light to inhibit flowering in chrysanthemum. On the basis of these results and those of other studies, we postulate that the spectral dependence of flowering in chrysanthemum depends on whether and how the phytochrome photoequilibrium changes during the day. In particular, a sufficiently high daytime phytochrome photoequilibrium (e.g., under B+R and B+G+R light) could establish a predominant mode of floral signaling that prevents perception of subsequent B light as a long day.

Most ornamental crops can be classified as long-day, short-day, or day-neutral plants based on their flowering responses to the photoperiod (or the skotoperiod). Chrysanthemum (*Chrysanthemum* ×*morifolium*) is a common ornamental crop with an obligate short-day flowering response and only flowers when the skotoperiod is consistently longer than a critical duration (Thomas and Vince-Prue 1997). Manipulation of the skotoperiod allows greenhouse growers to control flowering time precisely. In summer–fall garden chrysanthemum production, growers can use opaque black cloth to truncate the natural photoperiod and lengthen the skotoperiod, thereby inducing flowering under otherwise long days. However, this approach decreases light available for photosynthesis and incurs high capital cost for automated blackout systems or high labor cost for daily manual operation of black cloth. Conversely, for chrysanthemum plants grown under natural short days, lighting at a low (e.g., 1 to 2 $\mu mol \cdot m^{-2} \cdot s^{-1}$) total photon flux density [TPFD (400–800 nm)] at the end of the day (day extension) or in the middle of the night (night interruption) creates a sufficiently short skotoperiod that inhibits flowering. Light-emitting diode (LED) lamps that primarily emit red [R (600–700 nm)] and

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far-red [FR (700–800 nm)] light have largely replaced conventional lamps in photoperiodic control of flowering, including incandescent and compact-fluorescent lamps.

The photon spectrum of nighttime photoperiodic lighting influences flowering time of chrysanthemum grown under natural short days. Although phytochrome photoreceptors primarily absorb both R and FR light to mediate flowering, R light is generally a more effective signal than FR light for short-day plants (Thomas and Vince-Prue 1997). For example, during a 15-h skotoperiod, a 4-h night interruption at a TPFD of 1.3 to 1.7 $\mu mol \cdot m^{-2} \cdot s^{-1}$ inhibited flowering of chrysanthemum 'Adiva Purple' more effectively when the R:FR was high, whereas FR LEDs alone did not inhibit flowering (Craig and Runkle 2013). Floral inhibition by FR LEDs alone required a higher FR photon flux density [PFD ($13\ \mu mol \cdot m^{-2} \cdot s^{-1}$)] for another short-day plant, poinsettia (*Euphorbia pulcherrima*) 'Marble Star' (Zhang and Runkle 2019).

Phosphor-converted white LED lamps emit considerable R light (but little FR light) and are effective when delivered at night to delay flowering of short-day plants (Meng and Runkle 2015, 2017a). During a 15-h skotoperiod, a 4-h night interruption from low-intensity cool- or warm-white LED lamps delayed flowering of chrysanthemum 'Cheryl Golden Yellow' more than R light alone or blue [B (400–500 nm)] + R light (Meng and Runkle 2015, 2017a). White LED lamps also emit a substantial fraction (e.g., 40%) of green [G (500–600 nm)] light, which by itself elicited moderate floral inhibition in multiple chrysanthemum cultivars at a TPFD of 2 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Meng and Runkle 2019). Therefore, the effectiveness of white light at regulating flowering of short-day plants can be at least partly attributed to possible synergistic effects of R+G light.

When days are short, the effects of nighttime B light on regulating flowering depend on its PFD. When delivered alone or with R+FR light as a 4-h night interruption at 1.5 $\mu mol \cdot m^{-2} \cdot s^{-1}$, B light did not influence flowering of various long-day and short-day plants, including chrysanthemum 'Golden Cheryl' (Meng and Runkle 2015). However, at a higher PFD of 30 $\mu mol \cdot m^{-2} \cdot s^{-1}$, B light alone inhibited flowering of chrysanthemum 'Cheryl Golden Yellow', but not to the extent of R+white+FR light (Meng and Runkle 2017a). The mechanism(s) of photoperiodic flowering control by B light remains unclear but could involve B light-absorbing photoreceptors such as cryptochromes and FLAVIN-BINDING, KELCH REPEAT, F-BOX 1 (Cashmore et al. 1999; Huché-Thélier et al. 2016).

In contrast to plants grown with sunlight (i.e., greenhouse production), the photon spectrum of the main photoperiod indoors (without sunlight) can affect whether B light is perceived as a long-day signal. For example, at a PFD of 70 $\mu mol \cdot m^{-2} \cdot s^{-1}$, a 4-h day extension from R, G, or white LEDs, but not B LEDs, inhibited flowering of indoor chrysanthemum 'Gaya Yellow' grown under a 12-h main photoperiod from white fluorescent lamps (Jeong et al. 2012). At a PFD of 39 to 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$, a 4-h night interruption from B light inhibited flowering of chrysanthemum 'Reagan' when the 12-h main photoperiod consisted of B light, but not white light (Higuchi et al. 2012). Similarly, a 4-h day extension from B light at 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ did not influence flowering of chrysanthemum 'Zembla' when the 11-h main photoperiod consisted of B+R light (Jeong et al. 2014). Moreover, B light at 40 $\mu mol \cdot m^{-2} \cdot s^{-1}$ inhibited flowering of chrysanthemum 'Radost' when the 11-h main photoperiod was from sunlight, but not when it was B+R light indoors (SharathKumar et al. 2021). Collectively, these studies indicate that the effects of B light on flowering of chrysanthemum depend on whether the main photoperiod is from sunlight or indoor lighting from white or B+R light fixtures. We postulated that the presence of FR light, not G light, during the main photoperiod would determine whether B light delivered at the end of the day elicits a short-day response in chrysanthemum.

Materials and Methods

We conducted two overlapping replications of this experiment in the Delaware Indoor Ag Laboratory (DIAL) at the University of Delaware [UD (Newark, DE, USA)] and in the Controlled-Environment Lighting Laboratory (CELL) at Michigan State University [MSU (East Lansing, MI, USA)].

Plant material and environment at UD. We acquired 3-week-old rooted cuttings of chrysanthemum 'Chelsey Pink' and 'Gigi Gold' (Syngenta Flowers LLC, Gilroy, CA, USA) in 51-cell trays from a commercial greenhouse (Lucas Greenhouses, Monroeville, NJ, USA) on 22 Jun 2022. Upon receiving cuttings, we transplanted 54 plants per cultivar into 15-cm round plastic pots filled with a peat-based media (Pro-Mix; Premier Tech Ltd., Quakertown, PA, USA). We randomly assigned nine plants per cultivar to each of the sole-source lighting treatments described below. To compare plant development after treatment initiation, we marked the youngest leaf of every plant with a correction fluid. We manually irrigated with a nutrient solution [pH = 5.8; electrical conductivity (EC) = 1.3 $mS \cdot cm^{-1}$] composed of reverse-osmosis water and two water-soluble fertilizers [12N–1.8P–13.3K (RO Hydro FeED; JR Peters, Allentown, PA, USA)] and magnesium sulfate (JR Peters) to provide the following nutrients (in $mg \cdot L^{-1}$): 125 N, 18 P, 138 K, 73 Ca, 21 Mg, 39 S, 0.1 B, 0.5 Cu, 1.8 Fe, 0.5 Mn, 0.1 Mo, and 0.6 Zn.

In DIAL, we grew plants at a temperature setpoint of 24 °C with ambient relative humidity and CO_2 concentration. Environmental sensors (HOBO MX1101; Onset Computer Corp., Bourne, MA, USA) placed at the plant canopy level monitored and recorded the air temperature and relative humidity at 10-min intervals. A sensor malfunction resulted in the loss of environmental data from 22 Jun to 16 Jul 2022. An additional sensor (MCH3 Smart CO_2 Detector; GZAIR, Guangzhou, China) logged the CO_2 concentration inside DIAL. From 17 Jul to 21 Sep 2022, the air temperature, relative humidity, and CO_2 concentration [mean ± *SD*] was 24.4 ± 1.2 °C, 64.7% ± 8.1%, and 548.8 ± 123.3 $\mu mol \cdot mol^{-1}$, respectively.

Plant material and environment at MSU. On 20 Jul 2022, we received 4-week-old rooted cuttings of chrysanthemum 'Chelsey Pink' and 'Gigi Yellow' (Syngenta Flowers LLC) grown in 51-cell trays from a commercial grower (Raker-Roberta's Young Plants, Litchfield, MI, USA) and placed them in CELL. For 1 week, the young plants were grown under warm-white light (peak = 639 nm, color temperature = 2700 K) from tunable LED fixtures (PHYTOFY RL; OSRAM, Beverley, MA, USA) at a TPFD of 120 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at plant height for 18 $h \cdot d^{-1}$ (0000 to 1800 HR) at an air temperature setpoint of 19 °C, as controlled by a ventilation and air-conditioning unit (HBH030A3C20CRS; Heat Controller, LLC, Jackson, MI, USA) via a wireless thermostat. The air temperature and relative humidity were recorded using thermocouples (0.13-mm type E; Omega Engineering, Inc., Stamford, CT, USA) and the CO_2 concentration was recorded with a CO_2 sensor (GMD20; Vaisala, Inc., Louisville, CO, USA). All

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sensors were connected to a datalogger (CR-1000; Campbell Scientific, Inc., Logan, UT, USA) with a multiplexer (AM16/32; Campbell Scientific, Inc.) and data were collected every 10 s with averages recorded every hour. The air temperature, relative humidity, and CO_2 concentration (mean ± *SD*) in CELL from 20 to 27 Jul 2022 were 18.9 ± 0.2 °C, 68.8% ± 8.1%, and 404.4 ± 8.1 μmol·mol^{-1}, respectively. The rooted cuttings were manually irrigated as needed with a solution containing deionized water mixed with water-soluble fertilizer [pH = 5.8; EC = 1.3 mS·cm^{-1} (13N–1.3P–12.5K MSU Orchid RO Water Special; Greencare Fertilizers, Kankakee, IL, USA)], which supplied (in mg·L^{-1}) 125 N, 13 P, 120 K, 77 Ca, 19 Mg, 0.2 B, 0.4 Cu, 1.7 Fe, 0.8 Mn, 0.2 Mo, and 0.4 Zn.

On 27 Jul 2022, we transplanted 54 rooted chrysanthemum cuttings of each cultivar into 15-cm round plastic pots that were filled with soilless media consisting of 70% peatmoss, 21% perlite, and 9% vermiculite (Suremix; Michigan Grower Products, Inc., Galesburg, MI, USA). We marked the newest unfolded leaf of each plant with a white correction fluid. Plants were manually irrigated as necessary with the same fertilizer (pH = 5.8; EC = 1.6 mS·cm^{-1}) that delivered (in mg·L^{-1}) 200 N, 20 P, 191 K, 123 Ca, 31 Mg, 0.3 B, 0.7 Cu, 2.7 Fe, 1.4 Mn, 0.3 Mo, and 0.7 Zn. We randomly placed nine plants per cultivar under each of the six lighting treatments described below and grew the plants at an average air temperature of 23 °C with ambient relative humidity and CO_2 concentration. All environmental parameters were recorded as previously described. The air temperature, relative humidity, and CO_2 concentration (mean ± *SD*) in CELL from 27 Jul to 26 Oct 2022 were 22.6 ± 0.4 °C, 50.8% ± 11.4%, and 409.8 ± 24.8 μmol·mol^{-1}, respectively.

Lighting treatments. We designed six treatments to investigate whether light waveband(s) during the short main photoperiod influenced flowering of chrysanthemum grown with or without day-extension B light. From 0800 to 1900 HR, all plants received a TPFD of 180 μmol·m^{-2}·s^{-1} from B+R ($B_{60}R_{120}$), B+G+R ($B_{60}G_{60}R_{60}$) or B+R+FR ($B_{60}R_{60}FR_{60}$) LEDs. For each of these main photoperiod lighting treatments, half of the plants received no day-extension lighting while the other half received B light (B_{60}) at the end of the day from 1900 to 2300 HR. Day-extension B_{60} is subsequently referred to as $\rightarrow B_{60}$.

We used color-tunable LED fixtures (PHYTOFY RL) to establish each of these treatments. The measured peak wavelengths of the B, G, R, and FR LEDs were 446, 523, 660, and 735 nm, respectively. We used lighting software (PHYTOFY Control Software, OSRAM) to program three LED light fixture arrays per canopy to ensure reasonably good light uniformity and deliver each scheduled treatment. For each treatment, we made nine spectroradiometer measurements [SS-110 (Apogee Instruments, Logan, UT, USA) and LI-180 (LI-COR Biosciences, Lincoln, NE, USA)] at canopy height and adjusted the software until we reached the specified PFD setpoints. The PFD for each waveband in each treatment and the estimated internal phytochrome photoequilibria (iPPE) at UD and MSU are in Table 1. Spectral distribution curves are in Fig. 1.

Data collection and analysis. We recorded the dates of the first visible inflorescence and open flower for each plant. We counted inflorescences as open once the outermost row of ray flowers opened to 135° to 180°. On the first open flower date, we measured plant height (distance from media surface to plant apex), and the increase in nodes since transplant (starting after the marked leaf). After 8 and 9 weeks of treatments at UD and MSU, respectively, we photographed representative plants of both cultivars from each treatment. At 9 weeks, we measured plant height, total branch number, inflorescence number, and open flower number. After 13 weeks of treatment, we ended the experiment. For all plants without open flowers, we measured the inflorescence diameter and general stage (1 to 7) of inflorescence development for each plant based on those established by Zhang et al. (2020).

We performed this experiment at the two locations using a randomized complete block design. We counted each replication as a block to compensate for differences in location and starting plant material. We analyzed cultivars independently and pooled data from both replications when there were no interactions between treatment and replication. To assess mean separation between treatments, we used statistical software [JMP Pro ver. 16.0.0 and SAS ver. 9.4 (both SAS Institute Inc., Cary, NC, USA)] to run Tukey's honest significant difference test ($P \leq 0.05$).

Table 1. Combined spectral characteristics of indoor lighting treatments of chrysanthemum during an 11-h main photoperiod and 4-h day-extension lighting at the University of Delaware (Newark, DE, USA) and Michigan State University (East Lansing, MI, USA). Lighting treatments consisted of blue [B (400–500 nm)], green [G (500–600 nm)], red [R (600–700 nm)], and far-red [FR (700–800 nm)] light with their photon flux densities (in μmol·m^{-2}·s^{-1}) subscripted.

	Main photoperiod			Day extension
	$B_{60}R_{120}$	$B_{60}G_{60}R_{60}$	$B_{60}R_{60}FR_{60}$	B_{60}
	Single-band photon flux density (μmol·m^{-2}·s^{-1})			
B	58.4	61.2	59.5	59.7
G	0.5	57.8	0.6	0.0
R	121.8	61.6	60.8	0.0
FR	0.7	0.8	57.9	0.0
	Integrated photon flux density (μmol·m^{-2}·s^{-1})[i]			
PPFD	180.8	180.6	120.9	59.7
TPFD	181.5	181.4	178.8	59.7
YPFD	157.8	148.6	110.7	44.2
	Light ratio			
B:R	0.5	1.0	1.0	–
B:G	107.0	1.0	97.7	–
G:R	0.0	0.9	0.0	–
R:FR	183.0	75.0	1.0	–
iPPE[ii]	0.856	0.812	0.315	0.452

[i] The photosynthetic photon flux density [PPFD (400–700 nm)] and the total photon flux density [TPFD (400–800 nm)] were integrals in their respective ranges over 1-nm increments. The yield photon flux density [YPFD (300–800 nm)] was the product of the spectral distribution multiplied by the relative quantum efficiency based on Sager et al. (1988).

[ii] The internal phytochrome photoequillibrium (iPPE) was estimated based on Kusuma and Bugbee (2021).

Results

Flowering time. For all three chrysanthemum cultivars, flowering was markedly inhibited under $B_{60}R_{60}FR_{60}\rightarrow B_{60}$ but not under any other treatment (Figs. 2–5). The first visible inflorescence of 'Chelsey Pink' appeared 35 to 38 d later under $B_{60}R_{60}FR_{60}\rightarrow B_{60}$ than the other treatments at UD, but simultaneously among all treatments at MSU (Fig. 3A). 'Gigi Gold'

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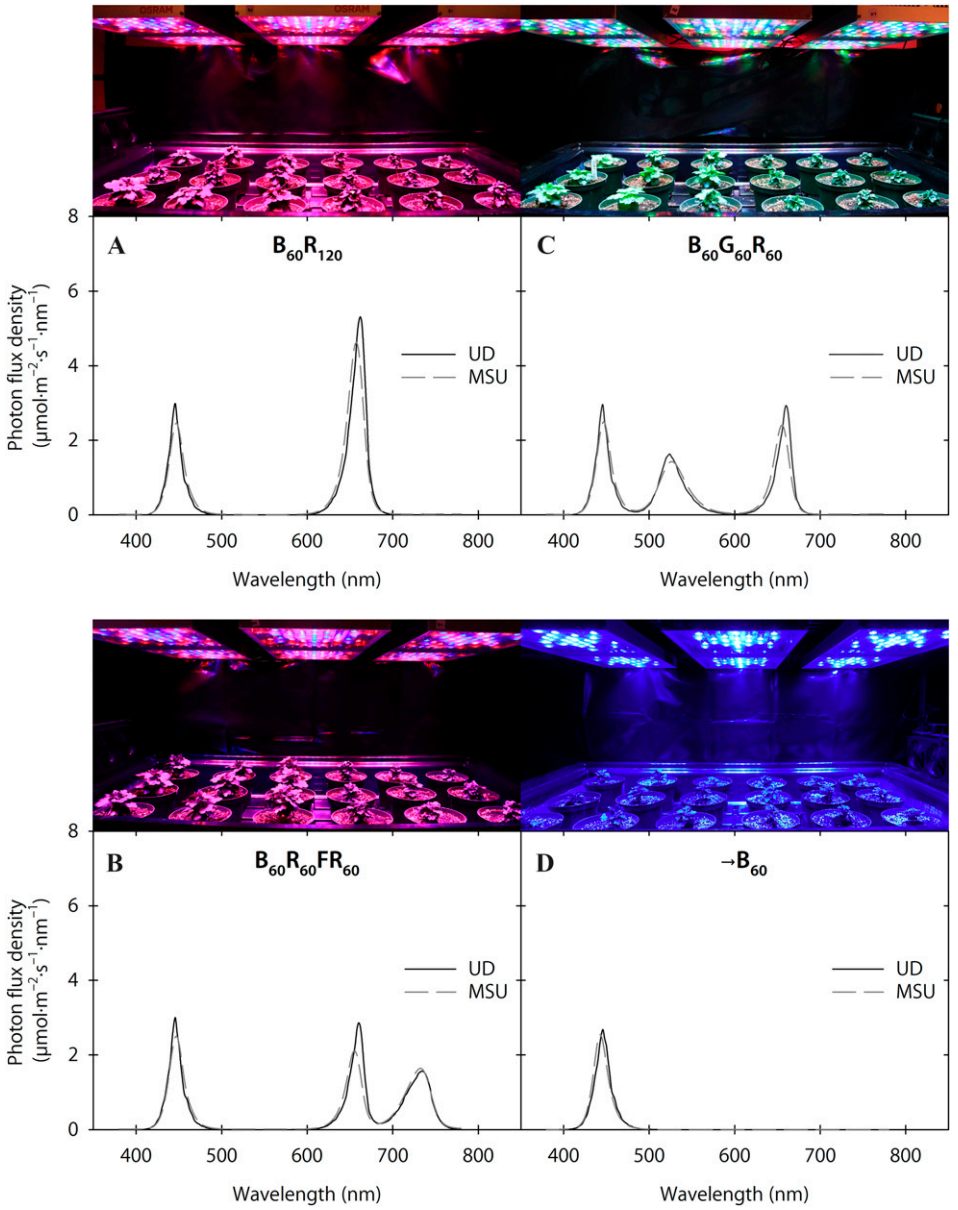

Fig. 1. Distributions of four spectra from blue [B (400–500 nm)], green [G (500–600 nm)], red [R (600–700 nm)], and/or far-red [FR (700–800 nm)] light-emitting diodes at the University of Delaware (UD, Newark, DE, USA) and Michigan State University (MSU, East Lansing, MI, USA): (**A**) B60R120, (**B**) B60R60FR60, (**C**) B60G60R60, and (**D**) 4-h day-extension B60 (→B60). The subscripts denote integrated photon flux densities in $m^{-2}·s^{-1}$.

and 'Gigi Yellow' developed the first visible inflorescence after 67 and 41 d, respectively, under $B_{60}R_{60}FR_{60}$→B_{60} and after 13 to 15 d under the other treatments (Figs. 4A and 5A). For all three cultivars, trends for time to the first open flower were similar between UD and MSU. Only 17% of all 'Chelsey Pink' plants between UD and MSU flowered under $B_{60}R_{60}FR_{60}$→B_{60}, with a 31- to 33-d delay, compared with complete flowering under the other treatments (Fig. 3B). 'Gigi Gold' did not flower under $B_{60}R_{60}FR_{60}$→B_{60}, despite forming visible inflorescences but had similarly complete and early flowering under the other treatments (Fig. 4B). Only one 'Gigi Yellow' plant flowered under $B_{60}R_{60}FR_{60}$→B_{60} after 84 d, whereas all plants flowered after 42 to 45 d under the other treatments (Fig. 5B). In addition, flowering of 'Gigi Yellow' was 1 to 2 d earlier under $B_{60}R_{120}$ and $B_{60}G_{60}R_{60}$ compared with the other treatments except $B_{60}R_{60}FR_{60}$→B_{60}.

Morphological traits. Floral inhibition under $B_{60}R_{60}FR_{60}$→B_{60} was accompanied by promotion of extension growth. 'Chelsey Pink' and 'Gigi Yellow' were 71% to 201% and 60% to 126% taller, respectively, at flowering under $B_{60}R_{60}FR_{60}$→B_{60} than the FR-deficient treatments, whereas no height data were collected for the non-flowering 'Gigi Gold' under $B_{60}R_{60}FR_{60}$→B_{60} (Figs. 3C, 4C, and 5C). In addition, all three cultivars were 24% to 57% taller at flowering under $B_{60}R_{60}FR_{60}$ than the FR-deficient treatments, irrespective of similar flowering time. $B_{60}R_{60}FR_{60}$→B_{60} increased plant height of 'Chelsey Pink' and 'Gigi Yellow' by 71% to 91% and 57%, respectively, compared with $B_{60}R_{60}FR_{60}$. 'Chelsey Pink' produced 14% to 28% more nodes at flowering under $B_{60}G_{60}R_{60}$→B_{60} and $B_{60}R_{60}FR_{60}$ compared with $B_{60}R_{120}$ with and without →B_{60} (Fig. 3D). 'Gigi Gold' developed similar numbers of nodes at flowering among treatments under which

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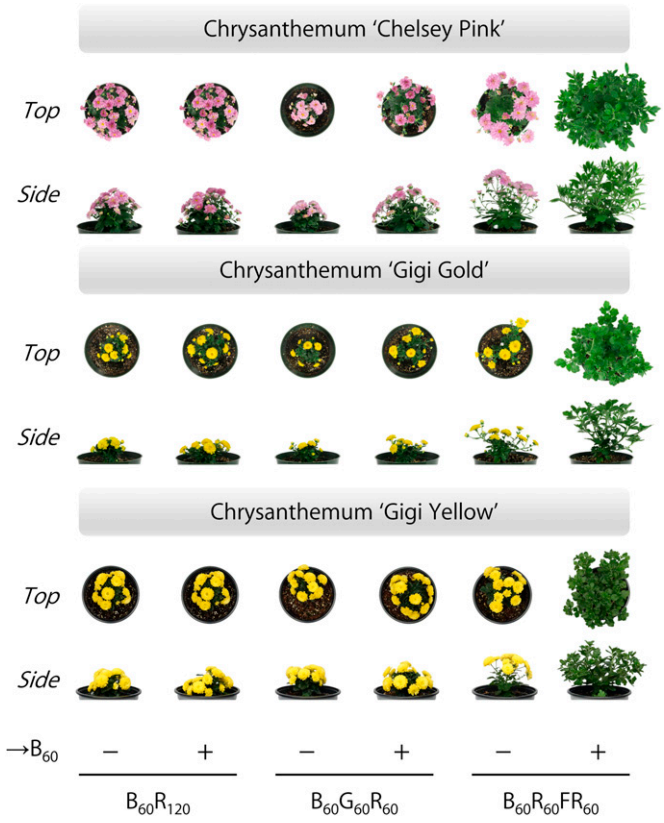

Fig. 2. Top and side view of representative chrysanthemum 'Chelsey Pink' (at University of Delaware, Newark, DE, USA), 'Gigi Gold' (at University of Delaware), and 'Gigi Yellow' (at Michigan State University, East Lansing, MI, USA) after 8, 8, and 9 weeks of treatment, respectively. Plants were grown indoors under an 11-h photoperiod of three photon spectra consisting of blue (B), green (G), red (R), and far-red (FR) light ($B_{60}R_{120}$, $B_{60}G_{60}R_{60}$, and $B_{60}R_{60}FR_{60}$, where each subscript signifies the photon flux density in $\mu mol \cdot m^{-2} \cdot s^{-1}$) with (+) and without (–) 4-h day-extension B_{60} ($\rightarrow B_{60}$).

flowering occurred (Fig. 4D). 'Gigi Yellow' developed 57% to 83% more nodes at flowering under $B_{60}R_{60}FR_{60} \rightarrow B_{60}$ than the other treatments (Fig. 5D).

In addition to the preceding data at flowering, we also recorded plant height, branch number, visible inflorescence number, and open flower number on a fixed date (9 weeks after treatments began). All three cultivars were tallest under $B_{60}R_{60}FR_{60} \rightarrow B_{60}$, followed by $B_{60}R_{60}FR_{60}$ and then the FR-deficient treatments. Plants grown under $B_{60}R_{60}FR_{60} \rightarrow B_{60}$ were 30% to 106%, 64% to 95%, 42% to 112%, and 27% to 78% taller than the other treatments for 'Chelsey Pink' at UD, 'Chelsey Pink' at MSU, 'Gigi Gold', and 'Gigi Yellow', respectively (Figs. 6A, 7A, and 8A). 'Chelsey Pink' at MSU grown under $B_{60}G_{60}R_{60} \rightarrow B_{60}$ had four to six more branches than $B_{60}G_{60}R_{60}$ and $B_{60}R_{60}FR_{60} \rightarrow B_{60}$ (Fig. 6B). In contrast, 'Chelsey Pink' at UD and 'Gigi Gold' grown under $B_{60}R_{60}FR_{60} \rightarrow B_{60}$ had three to four and two to three more branches, respectively, compared with $B_{60}G_{60}R_{60}$ and $B_{60}R_{60}FR_{60}$ (Figs. 6B and 7B). When the main short photoperiod was $B_{60}G_{60}R_{60}$, $\rightarrow B_{60}$ increased the branch number of 'Chelsey Pink' at MSU by four but did not influence it at UD. This could be at least partly attributed to the different liner ages at transplant at the two locations. The branch number of 'Gigi Yellow' was similar among all treatments (Fig. 8B).

'Chelsey Pink' and 'Gigi Yellow' at MSU grown under $B_{60}R_{60}FR_{60} \rightarrow B_{60}$ had 54 to 56 and 32 to 38 more visible inflorescences, respectively, compared with the other treatments (Figs. 6C and 8C). In contrast, 'Gigi Gold' had 9 to 14 fewer visible inflorescences under $B_{60}R_{60}FR_{60} \rightarrow B_{60}$ than the other treatments (Fig. 7C). Similarly, 'Chelsey Pink' at UD had seven to 18 fewer visible inflorescences under $B_{60}R_{60}FR_{60} \rightarrow B_{60}$ compared with the other treatments except $B_{60}R_{60}FR_{60}$ (Fig. 6C). At the 9-week mark, the three cultivars had open inflorescence under all treatments except $B_{60}R_{60}FR_{60} \rightarrow B_{60}$ (Figs. 6D, 7D, and 8D). 'Chelsey Pink' at UD had five to 12 more open flowers under $B_{60}R_{120} \rightarrow B_{60}$ than the other treatments (Fig. 6D). Similarly, 'Chelsey Pink' at MSU had six and eight more open flowers under $B_{60}R_{120} \rightarrow B_{60}$ compared with $B_{60}R_{120}$ and $B_{60}G_{60}R_{60}$, respectively. 'Gigi Gold' had four to six more open flowers under $B_{60}R_{120}$ and $B_{60}R_{120} \rightarrow B_{60}$ than $B_{60}G_{60}R_{60}$ (Fig. 7D). 'Gigi Yellow' had four or five more inflorescences under $B_{60}R_{120}$ and $B_{60}G_{60}R_{60}$ with $\rightarrow B_{60}$ than without (Fig. 8D). After 13 weeks of lighting treatments, the flowering stages of a representative inflorescence for 'Chelsey Pink', 'Gigi Gold', and 'Gigi Yellow' grown under $B_{60}R_{60}FR_{60} \rightarrow B_{60}$ were one out of seven and had diameters of 2.9, 2.7, and 3.3 mm, respectively (data not shown). The flowering stages of the largest inflorescence for 'Chelsey Pink', 'Gigi Gold', and 'Gigi Yellow' grown under $B_{60}R_{60}FR_{60} \rightarrow B_{60}$ were 3.0, 1.3, and 3.6 with diameters of 9.2, 3.5, and 9.9 mm, respectively (data not shown).

Discussion

In this study, 4-h day-extension B light inhibited flowering of all three chrysanthemum cultivars only when FR light, but not G light, was present in the main 11-h photoperiod of B+R light. Adding G light to B+R light created white light and did not alter the lack of plant sensitivity to subsequent B light. Similarly, it can be inferred from previous studies, although indirectly, that when FR light was absent from a short main photoperiod of B+R light or white light indoors, several chrysanthemum cultivars did not perceive 4-h day-extension or night-interruption B light as a long day signal, regardless of the B PFD (Jeong et al. 2012, 2014; Higuchi et al. 2012). Increasing the day-extension duration of B light can enhance its perception by plants to a limited extent. For example, delivering nightlong B light at 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ with a short main photoperiod of B+R light only partially inhibited flowering of chrysanthemum 'Zembla' (Jeong et al. 2014).

For day-extension B light to be perceived as a long day, the requirement of FR light during the short main photoperiod can explain previous response discrepancies between experiments with FR-abundant sunlight or FR-deficient indoor lighting conditions. Under a 9-h truncated short day in a greenhouse, a 4-h night-interruption with B light at 30 $\mu mol \cdot m^{-2} \cdot s^{-1}$ inhibited flowering of chrysanthemum 'Cheryl Golden Yellow' (Meng and Runkle 2017b). Similarly, under an 11-h day in a greenhouse, 4-h day-extension B light at 40 $\mu mol \cdot m^{-2} \cdot s^{-1}$ inhibited flowering of chrysanthemum 'Radost' (SharathKumar et al. 2021). However, day-extension B light did not influence flowering of chrysanthemum 'Radost' when grown under a short day of B+R light in a climate chamber (SharathKumar et al. 2021). Because sunlight has similar flux densities of B, G, R, and FR photons (Kronenberg and Kendrick 1986), both G and FR light were potentially involved in mediating flowering. Our results indicate that the different flowering responses to photoperiodic

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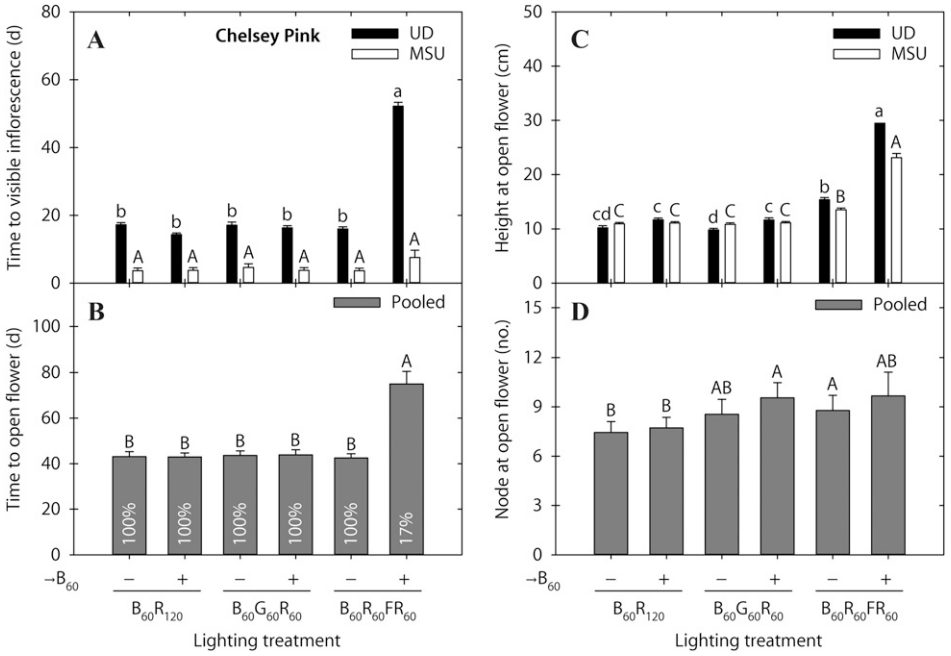

Fig. 3. The (**A**) time to visible inflorescence, (**B**) time to open flower and flowering percentage, (**C**) height, and (**D**) number of nodes at first open flower for chrysanthemum 'Chelsey Pink' grown at the University of Delaware [UD, Newark, DE, USA (solid black bars)], Michigan State University [MSU, East Lansing, MI, USA (solid white bars)], or pooled from both locations (solid gray bars). Plants were grown indoors under an 11-h photoperiod of three photon spectra consisting of blue (B), green (G), red (R), and far-red (FR) light ($B_{60}R_{120}$, $B_{60}G_{60}R_{60}$, and $B_{60}R_{60}FR_{60}$, where each subscript signifies the photon flux density in $\mu mol \cdot m^{-2} \cdot s^{-1}$) with (+) and without (–) 4-h day-extension B_{60} ($\rightarrow B_{60}$). Bars and error bars represent the mean and *SE*, respectively. Means followed by the same letter are not significantly different between lighting treatments using Tukey's honest significant difference test at $P \leq 0.05$. Uppercase and lowercase letters are used to distinguish MSU and UD, respectively (**A** and **C**). $B_{60}R_{60}FR_{60} \rightarrow B_{60}$ had a total sample size of 3 (1 = UD, 2 = MSU) for **B**, **C**, and **D**.

B light could be attributed to FR light, not G light, during the main photoperiod.

Night-interruption B light inhibited flowering of chrysanthemum 'Reagan' grown under a short main photoperiod of B light, but not white light consisting of B+G+R light (Higuchi et al. 2012). In addition, day-extension B light did not inhibit flowering of chrysanthemum 'Radost' grown under a short main photoperiod of B+R light (SharathKumar et al. 2021). These results indicated that 1) G light in the main photoperiod did not influence flowering and 2) adding R light to B light in the main photoperiod promoted flowering. However, this response was reversible by adding FR light to B+R light in the main photoperiod. This R/FR reversibility suggests involvement of phytochromes in mediating flowering of chrysanthemum. Phytochromes are activated by R light and inactivated by FR light. The distributions of interconvertible active (Pfr) and inactive (Pr) forms of phytochromes determine the iPPE [Pfr/(Pr+Pfr)], which increases with the R:FR. Phytochrome A (phyA) inhibited flowering of the short-day plant soybean (*Glycine max*) grown under long days (Kong et al. 2010). Adding R light to B light in the main photoperiod created a high iPPE and suppressed the expression of *PHYA* in chrysanthemum 'Reagan' (Higuchi et al. 2012). Despite a lower iPPE, FR light is more efficient than R light at stabilizing phyA in the nucleus and signaling downstream responses (Rausenberger et al. 2011). Therefore, in this study, we postulate that adding R light in the main photoperiod of B light promoted flowering of chrysanthemum by suppressing phyA-mediated floral inhibition. In contrast, adding FR light in the main photoperiod of B+R light created a lower iPPE and elicited phyA-mediated floral inhibition. Nonetheless, phyA-mediated promotion of flowering by R light cannot readily explain why a long day of R or B+R light inhibited flowering (Higuchi et al. 2012; SharathKumar et al. 2021).

The spectral dependence of flowering in chrysanthemum appears to be associated with whether and how the iPPE changes during the day, rather than the daytime iPPE alone. If the iPPE during the main photoperiod and the iPPE of day-extension or night-interruption lighting are both above 0.8 or below 0.8 (e.g., B→B, R→R, B+R→B+R, B+R+FR→B+R+FR, B+R+FR→R+FR, and B+R+FR→B), flowering is inhibited (Higuchi et al. 2012; Meng and Runkle 2017b; SharathKumar et al. 2021). If the iPPE during the main photoperiod is below 0.8 and the iPPE of day-extension or night-interruption lighting is above 0.8 (e.g., B+R+FR→R and B→R), flowering is also inhibited (Craig and Runkle 2013; Higuchi et al. 2012). However, if the iPPE during the main photoperiod is above 0.8 and the iPPE of day-extension or night-interruption lighting is below 0.8 (e.g., B+R→B and B+G+R→B), chrysanthemum does not perceive the day as long, and flowering occurs (Jeong et al. 2012, 2014; Higuchi et al. 2012; SharathKumar et al. 2021). Higuchi et al. (2012) proposed that adding R light to B light in a main short photoperiod could desensitize the perception of night-interruption B or FR light. Hence, in this study, a sufficiently high iPPE during the main photoperiod (under B+R and B+G+R light) could establish a predominant mode of floral signaling that renders subsequent B light (at a lower iPPE) as an ineffective long-day signal.

Besides phyA, phytochrome B (phyB) also regulates floral inhibition of short-day plants by B or R light. Although cryptochromes are major B-light-absorbing photoreceptors, phytochromes also absorb B light, albeit to a lesser extent than R and FR light (Vierstra and Quail 1983). Night-interruption B and R light inhibited flowering of short-day plants *Oryza sativa*

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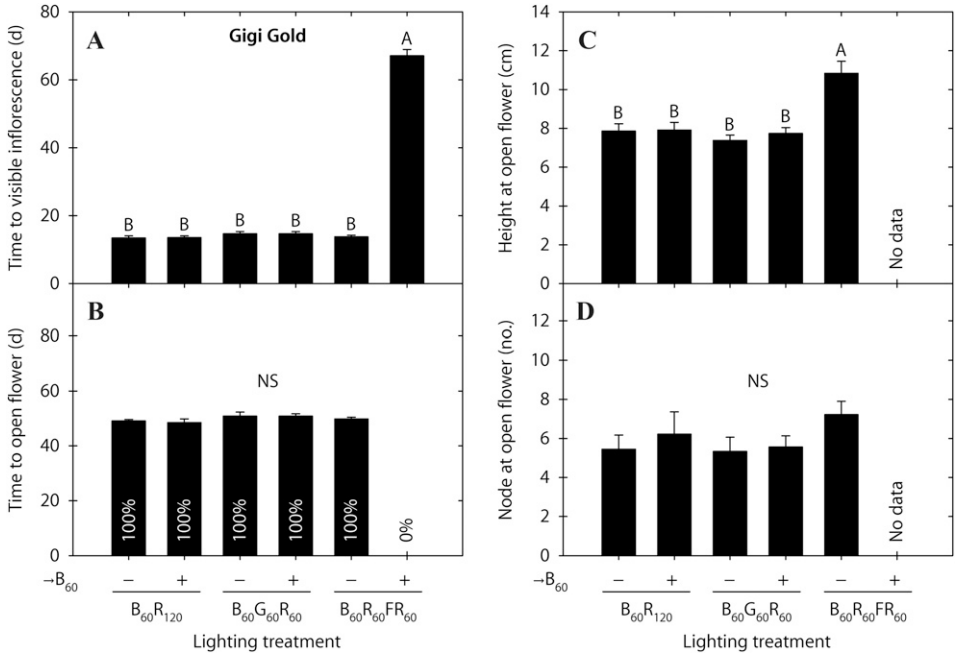

Fig. 4. The **(A)** time to visible inflorescence, (**B**) time to open flower and flowering percentage, (**C**) height, and (**D**) number of nodes at first open flower for chrysanthemum 'Gigi Gold' grown at the University of Delaware (Newark, DE, USA). Plants were grown indoors under an 11-h photoperiod of three photon spectra consisting of blue (B), green (G), red (R), and far-red (FR) light ($B_{60}R_{120}$, $B_{60}G_{60}R_{60}$, and $B_{60}R_{60}FR_{60}$, where each subscript signifies the photon flux density in $\mu mol \cdot m^{-2} \cdot s^{-1}$) with (+) and without (–) 4-h day-extension B_{60} ($\rightarrow B_{60}$). Bars and error bars represent the mean and *SE*, respectively. Means followed by the same letter are not significantly different between lighting treatments using Tukey's honest significant difference test at $P \leq 0.05$; NS is nonsignificant at $P \leq 0.05$.

and *Chrysanthemum seticuspe* f. *boreale*, respectively, grown under short days through phyB (Higuchi et al. 2013; Ishikawa et al. 2009). In chrysanthemum, photoperiodic control of flowering is determined by relative florigen (FTL3) accumulation vs. phyB-mediated antiflorigen (AFT) accumulation (Higuchi et al. 2013). Photoinduction of *AFT* mRNA follows a rhythm set by the dusk signal and peaks 8 to 11 h after dusk, irrespective of the photoperiod (Higuchi et al. 2013). Under natural

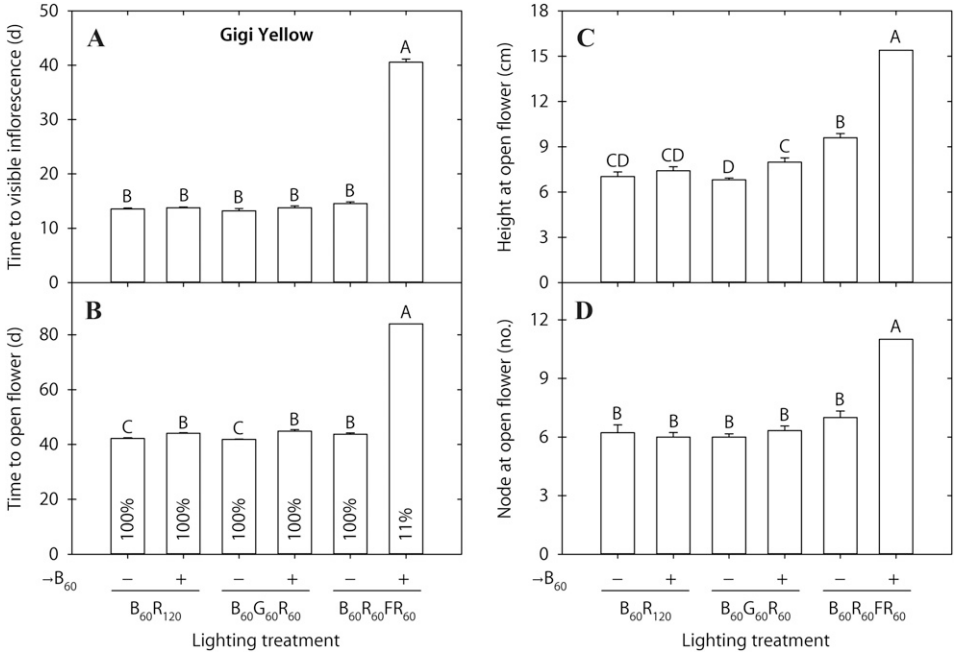

Fig. 5. The **(A)** time to visible inflorescence, (**B**) time to open flower and flowering percentage, (**C**) height, and (**D**) number of nodes at first open flower for chrysanthemum 'Gigi Yellow' grown at Michigan State University (East Lansing, MI, USA). Plants were grown indoors under an 11-h photoperiod of three photon spectra consisting of blue (B), green (G), red (R), and far-red (FR) light ($B_{60}R_{120}$, $B_{60}G_{60}R_{60}$, and $B_{60}R_{60}FR_{60}$, where each subscript signifies the photon flux density in $\mu mol \cdot m^{-2} \cdot s^{-1}$) with (+) and without (–) 4-h day-extension B_{60} ($\rightarrow B_{60}$). Bars and error bars represent the mean and *SE*, respectively. Means followed by the same letter are not significantly different between lighting treatments using Tukey's honest significant difference test at $P \leq 0.05$. $B_{60}R_{60}FR_{60} \rightarrow B_{60}$ had a total sample size of 1 for **B**, **C**, and **D**.

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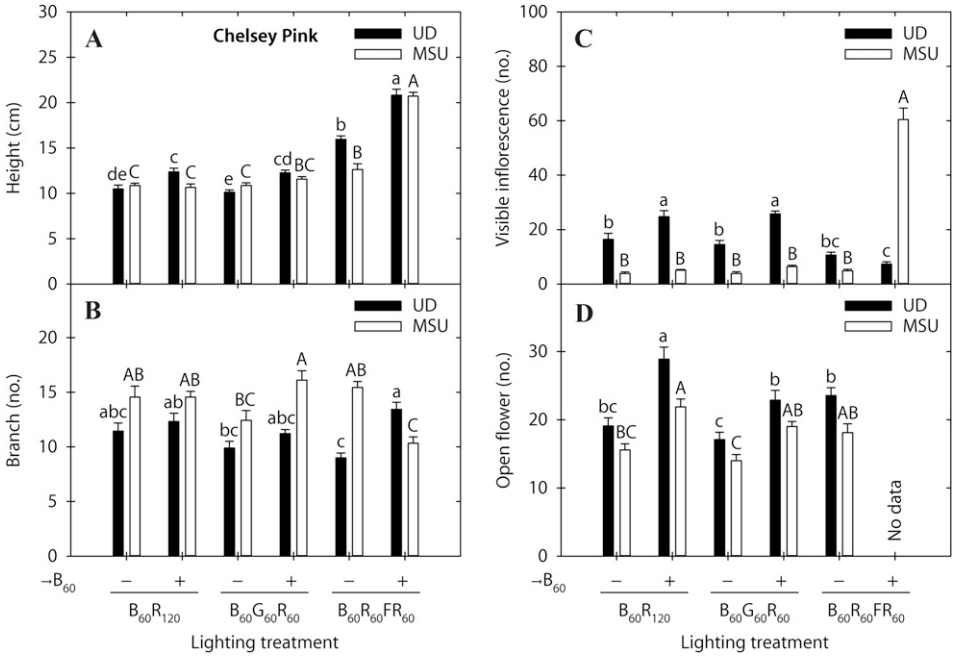

Fig. 6. The **(A)** height, (**B**) number of branches, (**C**) number of visible inflorescences, and (**D**) number of open flowers after 9 weeks for chrysanthemum 'Chelsey Pink' grown at the University of Delaware [UD, Newark, DE, USA (solid black bars)] and Michigan State University [MSU, East Lansing, MI, USA (solid white bars)]. Plants were grown indoors under an 11-h photoperiod of three photon spectra consisting of blue (B), green (G), red (R), and far-red (FR) light ($B_{60}R_{120}$, $B_{60}G_{60}R_{60}$, and $B_{60}R_{60}FR_{60}$, where each subscript signifies the photon flux density in $\mu mol \cdot m^{-2} \cdot s^{-1}$) with (+) and without (–) 4-h day-extension B_{60} ($\rightarrow B_{60}$). Bars and error bars represent the mean and standard error, respectively. Means followed by the same letter are not significantly different between lighting treatments using Tukey's honest significant difference test at $P \leq 0.05$. Uppercase and lowercase letters are used to distinguish MSU and UD, respectively.

short days (e.g., under sunlight), day-extension or night-interruption lighting allows this most sensitive phase to coincide with light and thus maximizes the expression of *AFT* mRNA in the leaf, which is inhibitory to flowering once translocated to the apical meristem (Higuchi et al. 2013). A change in the iPPE during the day could influence the onset trigger and peak timing of the photoinducible phase of *AFT* mRNA. For example, the end of a short main photoperiod of B+R light could trigger the

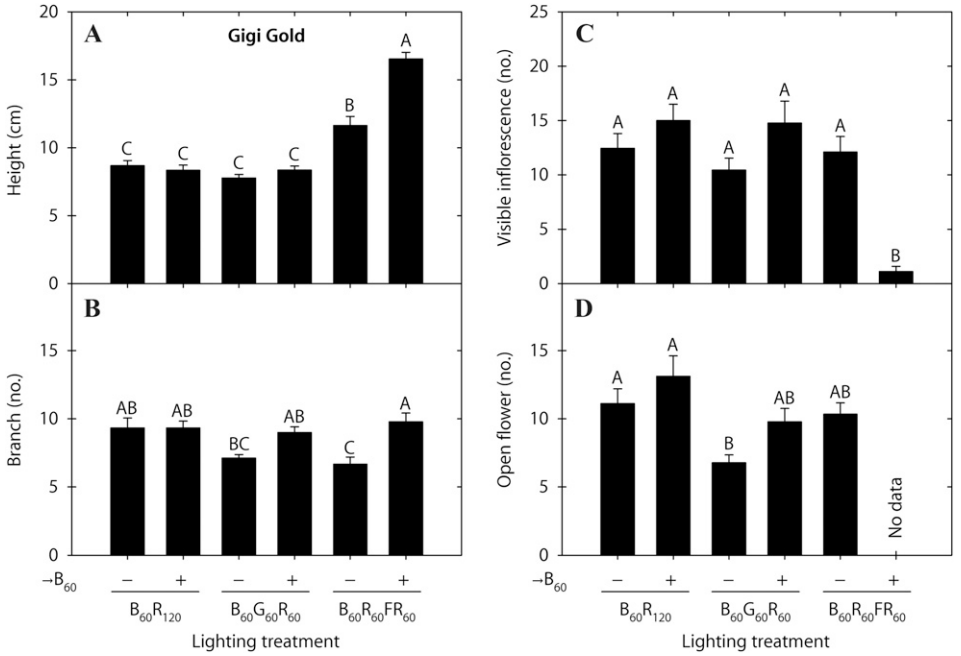

Fig. 7. The **(A)** height, (**B**) number of branches, (**C**) number of visible inflorescences, and (**D**) number of open flowers after 9 weeks for chrysanthemum 'Gigi Gold' grown at the University of Delaware (Newark, DE, USA). Plants were grown indoors under an 11-h photoperiod of three photon spectra consisting of blue (B), green (G), red (R), and far-red (FR) light ($B_{60}R_{120}$, $B_{60}G_{60}R_{60}$, and $B_{60}R_{60}FR_{60}$, where each subscript signifies the photon flux density in $\mu mol \cdot m^{-2} \cdot s^{-1}$) with (+) and without (–) 4-h day-extension B_{60} ($\rightarrow B_{60}$). Bars and error bars represent the mean and *SE*, respectively. Means followed by the same letter are not significantly different between lighting treatments using Tukey's honest significant difference test at $P \leq 0.05$.

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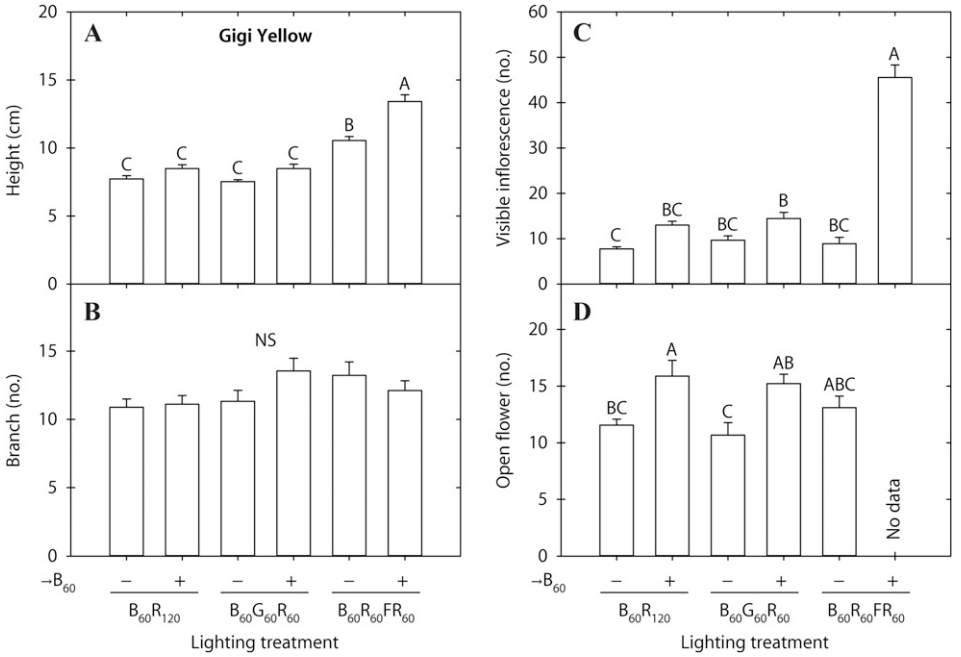

Fig. 8. The (**A**) height, (**B**) number of branches, (**C**) number of visible inflorescences, and (**D**) number of open flowers after 9 weeks for chrysanthemum 'Gigi Yellow' grown at Michigan State University (East Lansing, MI, USA). Plants were grown indoors under an 11-h photoperiod of three photon spectra consisting of blue (B), green (G), red (R), and far-red (FR) light ($B_{60}R_{120}$, $B_{60}G_{60}R_{60}$, and $B_{60}R_{60}FR_{60}$, where each subscript signifies the photon flux density in $\mu mol \cdot m^{-2} \cdot s^{-1}$) with (+) and without (–) 4-h day-extension B_{60} ($\rightarrow B_{60}$). Bars and error bars represent the mean and *SE*, respectively. Means followed by the same letter are not significantly different between lighting treatments using Tukey's honest significant difference test at $P \leq 0.05$. NS is nonsignificant at $P \leq 0.05$.

onset of the photoinducible phase, the peak of which would occur 8 to 11 h later and thus be out of sync with 4-h day-extension B light. On the other hand, the onset trigger of the B+R+FR→B treatment could be at the end of day-extension B light to synchronize the peak of the photoinducible phase and B+R+FR light at dawn, thereby producing sufficient antiflorigen to inhibit flowering.

In this study, all chrysanthemum cultivars showed flowering and morphological adaptations to lighting treatments. Leaf node number at flowering was proportional to flowering time for 'Gigi Gold' and 'Gigi Yellow', indicating that photon spectra did not influence the leaf development rate. However, this trend was less clear for 'Chelsey Pink', possibly because our node-counting method did not match well with its unique branching pattern. Although few plants flowered under B+R+FR→B, 'Chelsey Pink' at MSU and 'Gigi Yellow' at MSU developed substantially more visible inflorescences under B+R+FR→B than under the other treatments 9 weeks after treatment onset. 'Gigi Gold' developed few inflorescences under B+R+FR→B, but because it flowered later than the other two cultivars, it could have subsequently developed more inflorescences. Interestingly, day-extension B light did not influence flowering time under a short day of B+R or B+G+R light but increased the number of open flowers in 'Chelsey Pink' and 'Gigi Yellow'. This could be attributed to the day-extension lighting that slightly increased the photosynthetic daily light integral.

Plant height at flowering or at a fixed time (9 weeks after treatment onset) increased with both flowering time and the inclusion of FR light in the main photoperiod. Extension growth continued until plants flowered and thus was greater in plants with delayed flowering under B+R+FR→B. Plants grown under B+R+FR light had similarly early flowering but were taller compared with those grown under B+R and B+G+R light with or without $\rightarrow B_{60}$. The inclusion of FR light decreased the iPPE and promoted shoot elongation, which is a typical shade-avoidance response (Ruberti et al. 2012). Less branching is another shade-avoidance response, but we did not observe consistent trends of branch number across chrysanthemum cultivars. Besides FR light, G light can also act as a shade signal (Wang and Folta 2013), but this did not occur in our study with chrysanthemum. Sufficient B light can inhibit extension growth through cryptochrome-mediated suppression of phytochrome-interacting factors 4 and 5 (Pedmale et al. 2016). In contrast, 4-h day-extension B light at 60 $\mu mol \cdot m^{-2} \cdot s^{-1}$ generally did not influence plant height when flowering time was unaffected under a main short photoperiod of B+R or B+G+R light. Similarly, day-extension or night-interruption B light at 30 $\mu mol \cdot m^{-2} \cdot s^{-1}$ did not influence extension growth of a variety of photoperiodic ornamentals compared with R+FR light at 2 to 3 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Lopez et al. 2020; Meng and Runkle 2017b). The B photon flux density (e.g., 60 $\mu mol \cdot m^{-2} \cdot s^{-1}$) during the main photoperiod could have been sufficiently high and long to saturate this response.

In conclusion, floral inhibition of chrysanthemum by day-extension B light requires the inclusion of FR light in a short main photoperiod of B+R light. Without FR light in the daytime photon spectrum, chrysanthemum cannot perceive subsequent B light as an effective long-day signal. In contrast, G light during the day did not influence photoperiodic control of flowering by B light. These results can reconcile discrepancies in previous chrysanthemum studies, in which the effects of day-extension or night-interruption B light on flowering depended on the preceding light conditions. Although we cannot exclude possible roles of cryptochromes, phytochromes are likely involved in long-day signaling perception of B light based on daytime R/FR

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reversibility of flowering responses, which requires further research to elucidate.

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