



Night interruption light quality changes morphogenesis, flowering, and gene expression in *Dendranthema grandiflorum*

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Abstract

We investigated the effects of the quality of light used for interrupting the night period, termed the night interruption light (NIL), on morphogenesis, flowering, and the expression of photoperiodic genes in chrysanthemum (*Dendranthema grandiflorum*) cultivar ‘Gaya Yellow’, a qualitative short-day (SD) plant. Plants were raised in a closed-type plant factory under white (W) light-emitting diodes (LEDs) providing a light intensity of $180 \mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetic photon flux density, under a condition of long-day (LD, 16 h light/8 h dark), short-day (SD, 10 h light/14 h dark), or SD with a 4-h night interruption (NI) provided by $10 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPF green (NI-G), blue (NI-B), red (NI-R), far-red (NI-Fr), or W (NI-W) LEDs. Plants grown in the LD condition were the tallest. The SD, NI-B, and NI-Fr conditions induced flowering. *Phytochrome A* (*phyA*) and *cryptochrome 1* (*cry1*) were expressed at high levels in plants in NI-B, NI-Fr, and SD conditions. These results suggest that the NIL quality has significant implications on morphogenesis, flowering, and the expression of photoperiodic genes. Flowering was positively affected by the expression of *phyA*, *cry1*, and *FLOWERING LOCUS T* (*FT*), whereas it was negatively affected by the expression of *phyB* and *anti-florigenic FT/FTL1* (*AFT*).

Keywords Blue light · Chrysanthemum · Floral signal · Light spectrum · Photomorphogenesis

1 Introduction

Light manipulation is a critical factor to optimizing photosynthesis, and is an important signal for photoperiodic and photomorphogenic responses in plants (Gautam et al. 2015). It is well established that light characteristics affect the photomorphogenesis of plants (Fukuda et al. 2016). The different photosynthetic pigments and photoreceptors of a plant determine its ability to sense and respond to light (Gautam et al. 2015). Phytochromes, the red (R)/far-red (Fr) light receptors, and cryptochromes, the blue (B)/ultraviolet-A light receptors, are the primary photosensory receptors of vascular plants (Kendrick and Kronenberg 1994).

Phytochrome A (*phyA*) promotes flowering under Fr light (Mockler et al. 2003). On the other hand, *phytochrome B* (*phyB*), *phytochrome D* (*phyD*), and *phytochrome E* (*phyE*) act in a partially redundant manner to inhibit flowering under R light (Devlin et al. 1998).

In some plants, the photoperiod may be manipulated to artificially maintain plants in the vegetative stage or induce flowering (Warner and Erwin 2003). Studies on flowering have mainly examined the influence of light duration, intensity, timing, and quality using night interruption (NI, night break) lighting in greenhouses under natural light (Park et al. 2016a, b). Introducing a NI with light during short-day (SD) seasons promotes the flowering of long-day (LD) plants and allows for an accelerated marketing or seed production. Delaying the flowering of SD plants under natural LD conditions can be achieved in a similar manner (Hama-moto et al. 2005; Kang et al. 2008; Park et al. 2017). An intensity of $1\text{--}2 \mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetic photon flux density (PPFD) provided by conventional broad-spectrum light sources during the NI is usually adequate to control flowering (Whitman et al. 1998).

Different species display varying flowering responses to the light quality (Higuchi et al. 2012). A NI with R or

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white (W) light induced flowering of the LD plant petunia (*Petunia hybrida*) (Park et al. 2016a, b). A NI with Fr light delayed flowering of the day neutral plant geranium (*Pelargonium × hortorum*) (Park et al. 2017). A NI with a combination of B and R lights (B:R = 1:1) was more effective in promoting flowering of the LD plant cyclamen (*Cyclamen persicum*) than a NI with B, R, or Fr light alone (Shin et al. 2010). A NI with B and R lights (B:R = 1:1), and R light alone inhibited the flowering of chrysanthemum (Ho et al. 2012). Our previous study (Park et al. 2015) focused on splitting the traditional 4-h NI period into two periods of 2 h each and shifting the night interruption light (NIL) quality to observe its effect on flowering and morphogenesis in chrysanthemum (*Dendranthema grandiflorum*). The light quality (B, R, Fr, and W) of the first 2 h of the NI exposure affected neither morphogenesis nor flowering, while the light quality (B, R, Fr, and W) of the last 2 h of NI exposure significantly affected both morphogenesis and flowering (Park et al. 2015). Higuchi et al. (2012) also reported the effect of the NIL quality, such as B, R, and Fr, on flowering of chrysanthemum. However, the light intensity of B, R, and Fr they used was quite high: 39.1, 55.3, and 62.5 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPF, respectively (Higuchi et al. 2012). This study aimed to investigate the effect of the NIL quality of low intensity on morphogenesis, flowering, and the expression of photoreceptor genes in chrysanthemum cultivar ‘Gaya Yellow’. We hypothesized that the NIL quality, a very low intensity (10 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPF) of B, G, R, Fr, or W given for a continuous period of 4 h, would also affect morphogenesis and flowering.

2 Materials and methods

2.1 Plant materials and growth conditions

Cuttings of potted chrysanthemum (*Dendranthema grandiflorum* ‘Gaya Yellow’, a qualitative SD plant) were stuck in 50-cell plug trays that contained a commercial medium (Tosilee Medium, Shinan Grow Co., Jinju, Korea) and stationed on a glasshouse bench to root. Twelve days after sticking, the rooted cuttings were relocated to a closed walk-in growth chamber. After 12 days of acclimatization in the growth chamber, the plants, approximately 7.9 cm tall, were subjected to the photoperiodic light treatments described below. The growth chamber was maintained at 20 ± 1 °C, $60 \pm 10\%$ relative humidity, and 140 ± 20 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPF provided by fluorescent lamps (F48T12-CW-VHO, Philips Co Ltd., Eindhoven, the Netherlands). The photoperiodic treatments were provided by an LED system installed 25 cm above the plant canopy. A greenhouse multipurpose nutrient solution (Park et al. 2015, 2016a, b, 2017) was used to fertigate the plants once a day throughout the experiment.

2.2 Photoperiodic light treatments

Chrysanthemum is a qualitative SD plant, which means that it will not produce flowers when the daylength is longer than a critical value that is cultivar-dependent. Flowering is inhibited when the required long-night phase is interrupted by a short period of exposure to light. The critical daylength required for flowering in the SD plant used throughout this study was 12 h, and therefore, an uninterrupted dark period longer than 12 h was sufficient to initiate flowering. The plants were grown under W LEDs with a light intensity of 180 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPF (MEF50120, More Electronics Co. Ltd., Changwon, Korea). The different photoperiods except the lighted period provided by the NI (mentioned as ‘photoperiod’ hereafter) were as follows: LD (16 h light/8 h dark), SD (10 h light/14 h dark), or SD with a 4-h NI (from 11:00 p.m. to 3:00 a.m.) with a light intensity of 10 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPF provided by LEDs. The LD and uninterrupted SD conditions were used as controls. NIL qualities were B (NI-B, 450 nm), G (NI-G, 530 nm), R (NI-R, 660 nm), Fr (NI-Fr, 730 nm), or W (NI-W, 400-700 nm, with 28% B, 37% R, and 15% Fr) (Fig. 1). A spectroradiometer (USB 2000 Fiber Optic Spectrometer, Ocean Optics Inc., Dunedin, FL, USA) scanned the spectral distributions of all photoperiodic treatments at a fixed distance of 25 cm above the bench top at 1-nm intervals. For each photoperiodic treatment, measurements of the spectral distribution and the average maximum absolute irradiance were taken at three locations of the plant growing bench.

2.3 Data collection and statistical analysis

After 46 days of photoperiodic treatments, the plant height, number of leaves per plant, chlorophyll content,

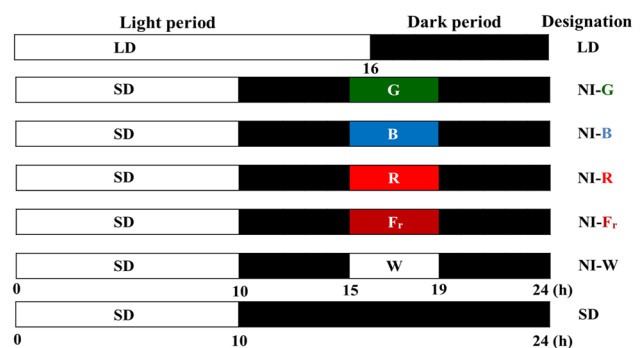


Fig. 1 A representation of the night interruption light (NIL) quality by light emitting diodes (LEDs) during the 4-h night interruptions (NI) of the 10-h short-day (SD) treatments in *Dendranthema grandiflorum* ‘Gaya Yellow’: NI-G, green; NI-B, blue; NI-R, red; NI-Fr, far-red; and NI-W, white. LD indicates the 16-h long-day treatment. (Color figure online)

dry mass, fresh and dry weights of the shoot and root, time from treatment initiation to visible flower bud or to visible buds (DVB), number of flowers and flower buds per plant (hereafter referred to as “number of flowers”), and expression of important photoreceptor genes were measured. Ten mg samples of fresh, fully developed young leaves were taken and extracted using 80% ice cold acetone for chlorophyll estimation. Following a 3000-rpm centrifugation, a spectrophotometer (Biochrom Libra S22, Biochrom Co. Ltd., MA, USA) was used to measure the absorbance of the supernatant at 663 and 645 nm. The method of Dere et al. (1998) was used for calculations. To measure dry weights, the shoot and root were dried in an oven (Model FO-450 M, Jeio Technology Co. Ltd., Seoul, Korea) at 75 °C for 3 days and weighed.

A randomized complete block design was employed in this experiment using 3 replications with 2 plants in each. To minimize the effects of changing treatment locations, the treatment locations were randomly mixed between replications in a controlled environment. The statistical significance of the collected data was analyzed using SAS (Statistical Analysis System, V. 9.1, Cary, NC, USA). Tukey’s studentized range test at $p < 0.05$ was used to assess the differences among the treatment means. Sigma Plot 10.0 (Systat Software, Inc., San Jose, CA, USA) was used for graphing.

2.4 Total RNA isolation, cDNA synthesis, and quantitative polymerase chain reaction (PCR) of selected genes

Independent PCRs with equal amounts of cDNA were performed using primers of *phytochrome A* (*phyA*), *phytochrome B* (*phyB*), *cryptochrome 1* (*cry1*), *Anti-florigenic FT/TFL1* family protein (*AFT*), and *FLOWERING LOCUS T* (*FT*) genes of the sequence from *Arabidopsis thaliana* (Table 1). The methods described in Park et al. (2015) were used for total RNA isolation and semi-quantitative reverse transcription PCR analysis of selected genes.

3 Results

3.1 Morphogenesis

Plants grown under LD and all NI treatments were taller than those grown in the SD condition (Fig. 2a). The greatest plant height was observed in the NI-R treatment (18.2 cm), followed by the NI-Fr treatment (17.7 cm) for the NI treatments. Dry mass was the greatest for plants in the LD treatment (Fig. 2b). Among the NI treatments, the dry mass was the greatest for plants in the NI-W treatment (1.938 g) due to the relatively higher growth rate of both the shoot and root. The dry mass of plants in the NI-G (1.535 g), NI-B (1.679 g), and SD (1.239 g) treatments were similar. The weights of the shoot and root, both dry and fresh, showed a similar trend with the relative growth rate (Park 2014). The number of leaves per plant was 93% higher for plants grown in the LD treatment compared to that for plants grown in the SD treatment (Fig. 2c), and was the lowest for plants grown in the NI-Fr (82.6) and SD (80.3) treatments. The leaf area showed a similar tendency to the number of leaves per plant (Fig. 2d). Plants grown in the NI-W treatment (370.0 cm²) showed the greatest leaf area, followed by plants in the NI-G treatment (355.6 cm²), and then by plants in the NI-R treatment (353.5 cm²). The chlorophyll content was the greatest for plants grown in the SD control (Fig. 2e) and was lower for plants in all NI treatments, especially NI-Fr. The NI-R treatment was an exception; plants displayed similar chlorophyll levels as plants in the SD control. The chlorophyll content was 60% lower for plants grown in the NI-Fr treatment compared to those grown in the SD treatment.

3.2 Flowering

The NI-B, NI-Fr, and SD treatments induced complete flowering (Fig. 3 and Table 2). The DVB was higher for plants grown in the NI-B and NI-Fr treatments than that of plants in the SD control (Table 2). The number of flowers per plant was 31% higher for plants in the NI-Fr treatment than that

Table 1 List of primers used to quantify levels of gene expression

Gene	Accession no.	Forward primer	Reverse primer
<i>phyA</i>	EU915082	5'-GACAGTGTTCAGGCTTCAACAAG-3'	5'-ACCACCAGTGTGTGTTATCCTG-3'
<i>phyB</i>	NM_127435	5'-GTGCTAGGGAGATTACGCTTTC-3'	5'-CCAGCTTCTGAGACTGAACAGA-3'
<i>cry1</i>	NM_116961	5'-CGTAAGGGATCACCCAGTAAAG-3'	5'-CTTTTAGGTGGGAGTTGTGGAG-3'
<i>AFT</i>	AB839766	5'-AGAACACCTCCATTGGATCG-3'	5'-CTGGAAGTGGGCTCAC-3'
<i>FT</i>	AB839767	5'-ACAACGGACTCCTCATTGG-3'	5'-CGCGAAACTACGAGTGTGA-3'
<i>Actin</i>	AB205087	5'-CGTTTGGATCTTGCTGGTCG-3'	5'-CAGGACATCTGAAACGCTCA-3'

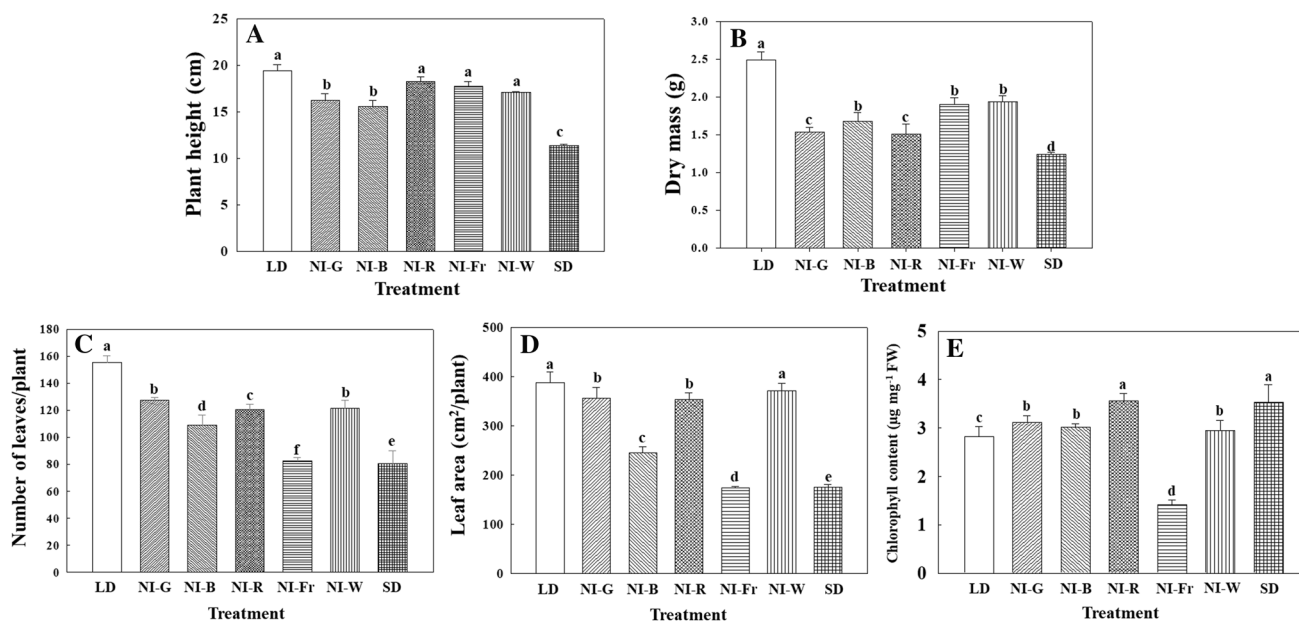


Fig. 2 The effects of the night interruption light (NIL) quality on the **a** plant height, **b** dry mass, **c** number of leaves per plant, **d** leaf area, and **e** chlorophyll content in *Dendranthema grandiflorum* ‘Gaya Yellow’ (see Fig. 1 for details of the light quality of the NI). Vertical bars

indicate \pm S.E. of the means for $n=3$. Means accompanied by different letters are significantly different ($p < 0.05$) according to the Tukey’s studentized range test

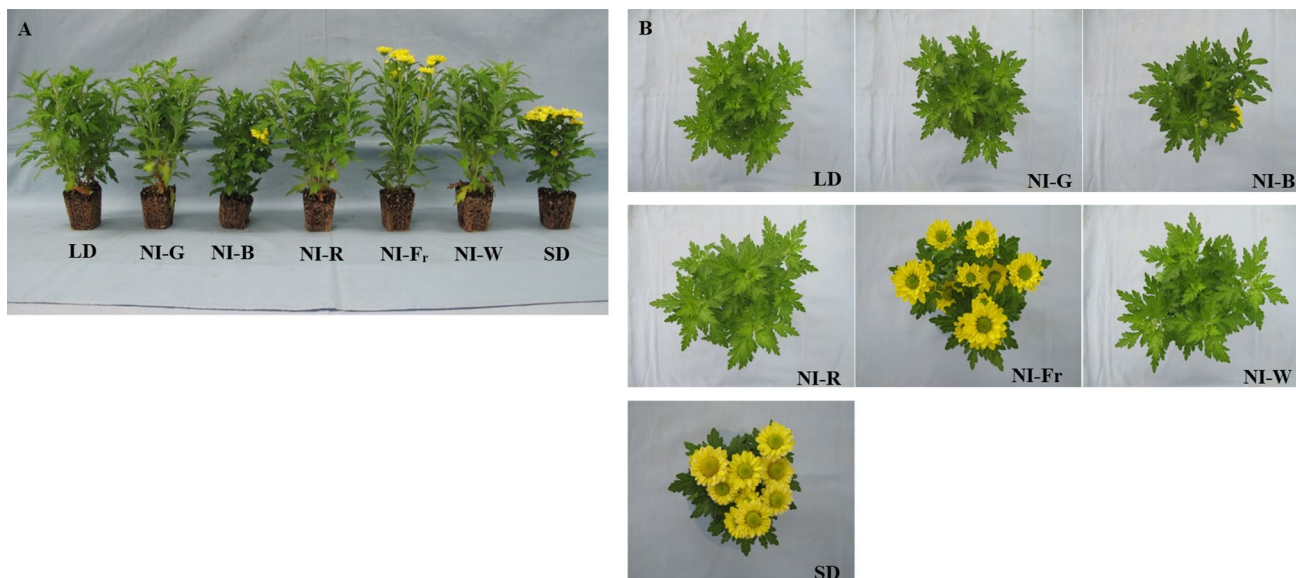


Fig. 3 The effects of the night interruption light (NIL) quality provided at $10 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPF on the flowering of *Dendranthema grandiflorum* ‘Gaya Yellow’ measured 46 days after treatment: **a** side view and **b** top view (see Fig. 1 for the details of the light quality)

of plants in the SD control (Table 2). The difference in the number of flowers per plant was insignificant between plants in the NI-B treatment and in the SD control (Table 2).

3.3 Photoreceptor gene expression analysis

The expression of *phyA* was lower for plants in the LD, NI-G, and NI-W treatments than for plants in the SD control (Fig. 4a). *phyA* expression was more pronounced for plants in the NI-B, NI-R, and NI-Fr treatments compared

Table 2 The effects of the night interruption light (NIL) quality provided at $10 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPF on the flowering characteristics of chrysanthemum (*Dendranthema grandiflorum* ‘Gaya Yellow’) measured 46 days after treatment

Treatment ^z	DVB ^y (day)	No. of flowers/plant
LD	— ^x	—
NI-G	—	—
NI-B	25.3	16.4 b ^w
NI-R	—	—
NI-Fr	22.6	21.3 a
NI-W	—	—
SD	21.0	16.2 b

^zSee Fig. 1 for details of the light quality of the NI

^yTime after treatment initiation to visible flower bud or to visible buds

^xNo flowering

^wMean separation within columns by Tukey’s studentized range test at the 5% level

to that for plants in the SD control (Fig. 4a). The expression of *phyB* was the greatest for plants in the NI-R treatment (Fig. 4b). *CryI* expression was the highest for plants in the NI-B treatment followed by the SD control (Fig. 4c).

The expression of *FT* and *AFT* was the highest for plants in the NI-Fr treatment (Fig. 4d, e).

4 Discussion

4.1 Plant height

For all of the NI treatments, the NI-R treatment produced the tallest plants (Fig. 2a). These results agree with results reported by Kim et al. (2004), where the lengths of the stem and the internode were the greatest when chrysanthemum was exposed to R and R + Fr lights during the photoperiod. However, the effects of R light on stem elongation were inconsistent. Heo et al. (2002) found that R light during the photoperiod stunted stem elongation in marigold (*Tagetes* sp.); this difference may be attributed to different synergistic interactions of the phytochromes acting to inhibit stem elongation. A high level of phytochrome photo-equilibrium ($\Phi = \text{PFR}/\text{P}$ total ratio: ratio of PFR to total phytochrome) during the photoperiod hindered chrysanthemum growth. The results of the current study suggest that plant growth responses differ by the quality of light given during the photoperiod and by the quality of light given during the NI.

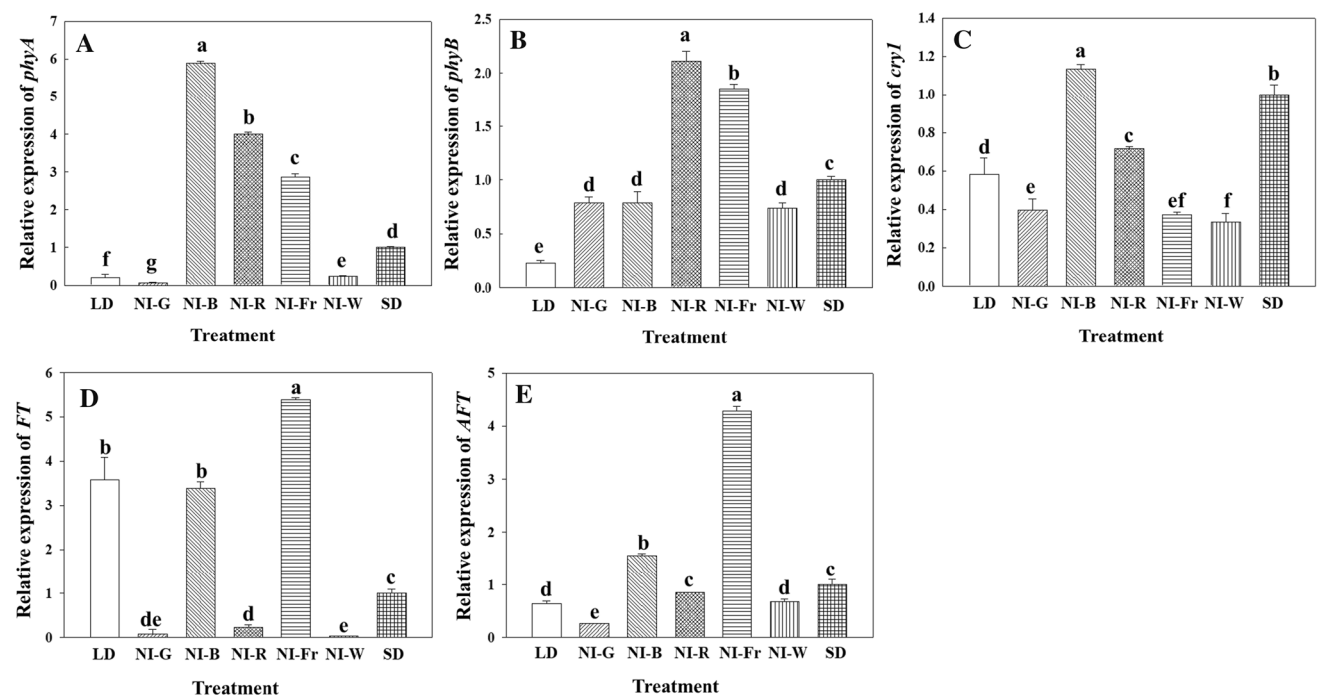


Fig. 4 The effects of the night interruption light (NIL) quality provided at $10 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPF on the relative gene expression of **a** *phyA*, **b** *phyB*, **c** *cryI*, **d** *FT*, and **e** *AFT* of *Dendranthema grandiflorum* ‘Gaya Yellow’ (see Fig. 1 for details of the light quality of

the NI). Vertical bars indicate \pm S.E. of the means for n=3. Means accompanied by different letters are significantly different ($p < 0.05$) according to the Tukey’s studentized range test

4.2 Leaf growth

The NI-W treatment promoted overall vegetative growth, indicated by increases in the dry mass, number of leaves per plant, and leaf area over the other NI treatments (Fig. 2b–d), even at low intensities. The W LEDs may be more efficient for photosynthesis than LEDs with just one or two narrow bandwidth wavelengths (e.g. G, B, R, or a combination of B and R), since W LEDs have the advantage of having a broad spectrum more similar to the sunlight (Park et al. 2012). The chlorophyll content was lower for plants in the NI-Fr treatment than for plants in the SD control (Fig. 2e). Similar results were reported by Li and Kubota (2009) who described that a “dilution” effect by increased biomass led to a decline in phytochemicals, such as chlorophyll and carotenoid, accompanying supplemental Fr during the photoperiod, since an increase in the dry weight was shown for plants grown under a combination of W and Fr lights.

4.3 Flowering and photoreceptor gene expression

In petunia (a LD plant), flowering was observed in the LD, NI-G, NI-Fr, and NI-W treatments (Park et al. 2016a, b). Petunia plants under a 6-h day extension and 4-h NI generally flowered earlier than under 2-h NI (Oh and Runkle 2016). In geranium (a day neutral plant), flowering was not affected by the quality of the NIL, and all plants flowered in the SD, LD, NI-B, NI-G, NI-Fr, and NI-W treatments (Park et al. 2017). In chrysanthemum (a SD plant), previous studies have reported that flowering was induced by NI-B, NI-Fr, and SD treatments (Stack et al. 1998; Higuchi et al. 2012; Jeong et al. 2012), which is similar to our findings in this study. The mutant *hy4-101* alleles of *Arabidopsis* in the Columbia ecotype background caused delayed flowering in both SD and LD conditions with either day extensions or NI, and a NI-B treatment had a stronger effect than NI-W or NI-R treatments (Bagnall et al. 1996). In our study, the NI-B treatment induced flowering with high-level expressions of *phyA*, *cry1*, and *FT* (which are thought to be flowering promoter genes), possibly due to lower levels of the flowering inhibitor genes *phyB* and *AFT* (Fig. 4). *phyA* promotes flowering by Fr light (Johnson et al. 1994; Mockler et al. 2003). *phyB* mediates the NI-induced inhibition of flowering (Higuchi et al. 2013). Cryptochromes induce flowering, and the function of cryptochromes in floral induction has been observed using mutations in *cry1* and *cry2* (Mockler et al. 1999). In addition, *FT* and *TFL*-like genes are crucial to the integration of both exogenous and endogenous signals that control flowering (Ferrier et al. 2011). *AFT* systemically inhibits flowering and is central to the obligate photoperiodic response (Higuchi et al. 2013). The flowering that was observed in the NI-Fr treatment despite high levels of *phyB* and *AFT* expression may be due to the high expression

level of *FT* observed in that treatment (Fig. 4b, d, e). The high level of *phyB* expression observed in the NI-G, NI-W, and NI-R treatments explains the lack of flowering in those environments (Fig. 4b). The DVB observed for plants in the NI-Fr and NI-B treatments in this study was prolonged by 1 day and 4 days, respectively. The number of flowers per plant was higher for plants in the NI-Fr treatment than for plants in the NI-B and SD treatments. Similarly, Park et al. (2015) reported that a shifting of light from B to Fr during the NI resulted in a higher number of flowers per plant, which may be due to a high light energy induction and shade avoidance response, a behavior marked by darkness evasion by shoots via lengthening of the internodes. The early flowering of *phyB* mutants of *Arabidopsis* in SD conditions seems to reflect the constitutive shade avoidance phenotype (Franklin 2008; Franklin and Quail 2010). The overall expression patterns of photomorphogenic genes observed in this study differed from those described in previous studies (Higuchi et al. 2012, 2013). Possible explanations for this disparity are differences in the chrysanthemum genotypes used, the experimental environment, the sample collection time, the plant part from which the samples were collected, and the specific wavelengths of LEDs used in both studies.

In summary, the NI-G, NI-B, NI-R, and NI-W treatments promoted plant growth and leaf expansion. The NI-Fr treatment promoted plant growth, decreased the chlorophyll content, and suppressed leaf expansion. In conclusion, morphogenesis, flowering, and the expression of photoperiodic genes were highly affected by the NIL quality. Flowering was positively affected by the expression of *phyA*, *cry1*, and *FT*, while it was negatively affected by the expression of *phyB* and *AFT*. One possible practical application of this technique in the production of floricultural crops, either in plant factories or greenhouses, would be the inhibition of flowering of SD plants by using the R and W lights as the NIL. Further studies on the effect of the intensity and positioning of B light are needed to understand its effect on flowering control of SD plants.

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