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Research Report

Light Quality during Night Interruption Affects Morphogenesis and Flowering in *Petunia hybrida*, a Qualitative Long-Day Plant

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Abstract. We investigated the effects of light quality during night interruption (NI) on morphogenesis, flowering, and the transcription of photoreceptor genes in *Petunia hybrida* Hort. 'Easy Wave Pink' (a qualitative long-day plant, LDP). Plants were grown in a closed-type plant factory under a constant light intensity of 180 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PPF provided by white (W) light emitting diodes (LEDs) under long day (LD, 16 h light/8 h dark), short day (SD, 10 h light/14 h dark), or SD conditions with a 4 h NI using green (NI-G), blue (NI-B), red (NI-R), far-red (NI-Fr), or white (NI-W) LEDs at an intensity of 10 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PPF. Shoot length was greatest under NI-Fr. Flowering was observed under LD, NI-G, NI-Fr, and NI-W. The expression of photoreceptor genes was induced by NI. Specifically, *phyA*, *phyB*, and *cry1* were more highly expressed under NI-G, NI-B, and NI-R compared to LD and SD. These results suggest that morphogenesis, flowering, and transcriptional factors are strongly affected by light quality during NI.

***Additional key words*:** flowering control, night break, photoperiodism, photoreceptor, spectral quality

Introduction

The photoperiod regulates growth and flowering in photoperiodic plants (Kim et al., 2011). Most floriculture crops can be grouped into one of three photoperiodic classes: long day plants (LDPs), short day plants (SDPs), and day neutral plants (DNPs) (Runkle and Heins, 2001). Within the photoperiodic classes, plants can be further divided based on whether the photoperiod is required for flowering to occur (a qualitative or obligate response) or if the photoperiod simply accelerates flowering (quantitative or obligate response) (Craig and Runkle, 2012).

Artificial lighting during the middle of the night (night interruption, NI) regulates the flowering of photoperiod-sensitive species (Yamada et al., 2008; Blanchard and Runkle, 2010; Park et al., 2016). NI breaks up the long dark period to deliver photoperiodic lighting, resulting in modified long day (LD) conditions for plants (Vince-Prue and Canham, 1983).

The effects of light quality on the regulation of flowering vary depending on the plant species (Higuchi et al., 2012). Many LDPs flower most rapidly when artificial light includes far-red (Fr) light, particularly at the end of the photoperiod (Lane et al., 1965; Downs and Thomas, 1982). Goto et al. (1991) reported that a night break using either Fr, red (R), blue (B), or white (W) light promotes flowering in *Arabidopsis thaliana*, with Fr light being the most effective. In SDPs, night interruption with R light inhibits flowering, which is promoted by subsequent exposure to Fr light (Cathey and Borthwick, 1957), suggesting the involvement of R/Fr reversible phytochromes in this response. Hisamatsu et al. (2008) found that irradiation with end-of-day Fr light reduces the time to the flowering transition and suggested that the photo-conversion of phytochromes is involved in this process in cut chrysanthemum. Shin et al. (2010) recommended the use of NI with R + B light emitting diodes (LEDs) to promote the growth and flowering of cyclamen to reduce heating and electricity costs during winter cultivation.

Manipulating the photoperiod can also reduce production costs by reducing production time and improving the overall quality of a crop (Runkle and Heins, 2006). A fundamental

objective of most commercial establishments that grow ornamental plants is to produce a flowering crop that meets the quality standards of the market in the shortest time possible. Therefore, in the current study, we examined the effects of light quality during NI on morphogenesis, flowering, and the transcription of photoreceptor genes in the LDP *Petunia hybrida* Hort. 'Easy Wave Pink'.

Materials and Methods

Plant Materials and Growth Conditions

Seeds of petunia (Pan Seed Co., West Chicago, IL, USA) were sown in 288-cell plug trays containing commercial medium (Tosilee Medium, Shinan Grow Co., Jinju, Korea). Seedlings were grown on a greenhouse bench and transplanted into 50-cell plug trays in a closed-type plant factory at 28 days after sowing. During the acclimatization periods in the plant factory, the petunia plants were grown under a 10 h photoperiod (SD, short day conditions) to suppress flower initiation. After 14 days, the plants (shoot length of approximately 6.0 cm) were subjected to photoperiodic light treatments. The plants were propagated in a greenhouse and transferred to a close-type plant factory, first for acclimatization at 20 ± 1°C, 60 ± 10% RH, 140 ± 20 μmol·m^{-2}·s^{-1} PPFD, and 350 ± 50 μmol·mol^{-1} provided by fluorescent lamps (F48T12-CW-VHO, Philips Co Ltd., Eindhoven, the Netherlands) and then for photoperiodic treatments using LED lighting systems installed at a 25 cm distance above the plant canopy. The plants were fertigated once per day with a multipurpose nutrient solution for greenhouses [in mg·L^{-1}: $Ca(NO_3)_2·4H_2O$ 737.0, KNO_3 343.4, KH_2PO_4 163.2, K_2SO_4 43.5, $MgSO_4·H_2O$ 246.0, NH_4NO_3 80.0, Fe-EDTA 15.0, H_3BO_3 1.40, $NaMoO_4·2H_2O$ 0.12, $MnSO_4·4H_2O$ 2.10, and $ZnSO_4·7H_2O$ 0.44] throughout the experiment.

Photoperiodic Light Treatments

The plants were grown under a light intensity of 180 μmol·m^{-2}·s^{-1} PPF provided by white (W) LEDs (MEF50120, More Electronics Co. Ltd., Changwon, Korea) during the light period under either long day (16 h light/8 h dark, LD), short day (10 h light/14 h dark, SD), or SD with a 4 h (from 11:00 p.m. to 3:00 a.m.) night interruption (NI) using LEDs at an intensity of 10 μmol·m^{-2}·s^{-1} PPF. The LD and uninterrupted SD conditions were used as controls. The NI was provided by either blue (B, 450 nm), green (G, 530 nm), red (R, 660 nm), far-red (Fr, 730 nm), or white (W, 400-700 nm, with 28% B, 37% R, and 15% Fr) LEDs: NI with B (NI-B), NI with R (NI-R), NI with Fr (NI-Fr), and NI with W (NI-W). The spectral distribution and the average value of maximum absolute irradiance measured at three locations within the plant growing bench under each light treatment are shown in Fig. 1. The light spectral distributions for all treatments were scanned using a spectroradiometer (USB 2000 Fiber Optic Spectrometer, Ocean Optics Inc., Dunedin, FL, USA) at the same (25 cm) distance above the bench top at an interval of 1 nm. The spectral distribution and the average value of maximum absolute irradiance were measured at three locations within the plant-growing bench under each light treatment.

Data Collection and Analysis

At 33 days after the photoperiodic treatments were initiated, the shoot length, relative growth rate, leaf length, leaf width, petiole length, number of leaves per plant, chlorophyll content,

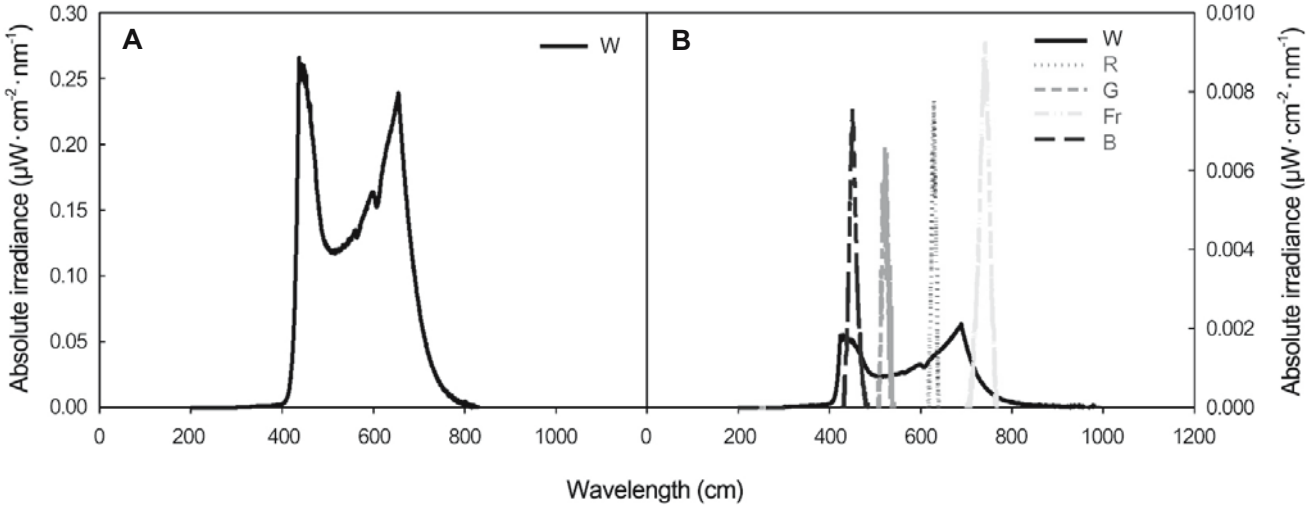

Fig. 1. Spectral distribution of light used in a closed-type plant factory: white light emitting diodes (LEDs) were used as daily light (A), and various LEDs (G, green; B, blue; R, red; Fr, far-red; and W, white) were used as light sources during night interruption (NI) (B). The NI-G, green; NI-B, blue; NI-R, red; NI-Fr, far-red; and NI-W, white. The LD and SD indicate 16 h (long days) and 10 h (short days), respectively.

fresh and dry weights of shoots and roots, flowering percent, days after treatment initiation to visible flower bud (days to visible buds [DVB]), number of flowers and flower buds per plant (hereafter referred to as "number of flowers"), and expression of photoreceptor genes were measured in the petunia plants. The ratio between leaf length and leaf width was considered to represent the leaf expansion index, and the ratio between leaf length and petiole length was considered to represent the overgrowth or stretchiness index.

The relative growth rate is the mean net increase in dry biomass per unit of plant dry biomass over a time interval. Total plant dry weight was determined before (W1) and after (W2) treatment, and relative growth rate across the time interval t2-t1 was calculated as follows:

$$\text{Relative growth rate} = (\ln W2 - \ln W1)/(t2-t1)$$

For chlorophyll estimation, 10 mg fresh leaf samples were collected from young, fully developed leaves and extracted using 80% ice-cold acetone. After centrifuge at 3,000 rpm, the absorbance of the supernatant was measured using a spectrophotometer (Biochrom Libra S22, Biochrom Co. Ltd., MA, USA) at 663 and 645 nm. The calculation was performed according to Dere et al. (1998). Dry weights of the shoot and root were determined after drying in an oven (Model FO-450M, Jeio Technology Co. Ltd., Seoul, Korea) at 75°C for 3 days.

A randomized complete block design with three replications and two plants per replication was employed in the experiment. The treatment locations in the controlled environment were randomly mixed between replications to minimize positional effects. The data were analyzed for statistical significance using the SAS (Statistical Analysis System, V. 9.1, Cary, NC, USA) program. The experimental results were subjected to an analysis of variance (ANOVA) and the Duncan's multiple range test. Graphing was performed with Sigma Plot 10.0 (Systat Software, Inc., San Jose, CA, USA).

Total RNA Isolation and Semi-quantitative Reverse-transcription Polymerase Chain Reaction (RT-PCR) Analysis of Selected Genes

Total RNA was extracted from the shoot tips or leaves of plants grown for 33 days after the initiation of NI treatments using an RNA isolation kit according to the manufacturer's instructions (Promega, Madison, WI, USA). First-strand cDNA was synthesized by reverse transcription of 1 μg of DNase-treated RNA using a reverse transcriptase kit (Promega, Madison, WI, USA) and used as a template for PCR. Independent PCRs with equal amounts of cDNA were performed using primers based on the sequences of *phytochrome A* (*phyA*), *phytochrome B* (*phyB*), *cryptochrome 1* (*cry1*), *Anti-florigenic FT/TFL1* family protein gene (*AFT*), and *FLOWERING LOCUS T* (*FTL*) from *A. thaliana*. The *phyA* gene primers 5'-GAC AGTGTCAGGCTTCAACAAG-3' (forward) and 5'-ACC ACCAGTGTGTGTTATCCTG-3' (reverse), *phyB* gene primers 5'-GTGCTAGGGAGATTACGCTTTC-3' (forward) and 5'-CC AGCTTCTGAGACTGAACAGA-3' (reverse), *cry1* gene primers 5'-CGTAAGGGATCACCGAGTAAAG-3' (forward) and 5'-C TTTTAGGTGGGAGTTGTGGAG-3' (reverse), *AFT* primers 5'-AGAACACCTCCATTGGATCG-3' (forward) and 5'-CTG GAACTAGGTGGCCTCAC-3' (reverse), *FTL* primers 5'-A CAACGGACTCCTCATTTGG-3' (forward) and 5'-CGCG AAACTACGAGTGTTGA-3' (reverse), and *Actin* primers 5'-CGTTTGGATCTTGCTGGTCG-3' (forward) and 5'-CAGG ACATCTGAAACGCTCA-3' (reverse) were used to detect the presence of *phyA*, *phyB*, *cry1*, *AFT*, *FTL*, and *Actin*, respectively. *Actin* was used as the control, since it is commonly used to normalize gene expression levels due to its high conservation as an endogenous housekeeping gene. The PCR conditions were as follows: initial denaturation for 5 min at 95°C, followed by 35 cycles consisting of 20 sec at 95°C, 30 sec at 57°C, and 30 sec at 72°C, a final extension for 10 min at 72°C. The PCR products were run on a 1% agarose gel to assess the differential expression of the transcripts.

Results and Discussion

Morphogenesis

Shoot length decreased by 19% under NI-R compared to LD (Fig. 2A). Hypocotyl inhibition in response to R light in *A. thaliana* is mediated by phytochrome (Mockler et al., 1999). The *phyB* functions in the inhibition of hypocotyl elongation under R light, a response enhanced by synergistic interactions with *phyA* (Koornneef et al., 1980). The light-stable phytochromes (*phyB*, *phyC*, *phyD*, and *phyE*), particularly *phyB*, repress the shade avoidance response in direct sunlight (Franklin, 2008; Franklin and Quail, 2010). The reduced shoot length in petunia observed under NI-R in the present study may be related to the role of *phyB*.

The relative growth rate was highest under LD (Fig. 2B). The accumulated total light intensity was also highest under LD. The relative growth rate significantly increased under NI-W (0.055 $g \cdot g^{-1} \cdot day^{-1}$) compared to the other NI treatments due to higher shoot dry weight.

The ratio of leaf length to leaf width increased under NI-R (Fig. 2D). The ratio of leaf length to petiole length was greatest under NI-W due to the relatively long leaf length compared to the other treatments (Fig. 2D). The number of leaves per plant decreased by 17% under NI-G (Fig. 2E), and the leaf area increased by 36% under NI-R compared to LD (Fig. 2F). Leaf expansion, including leaf length and leaf

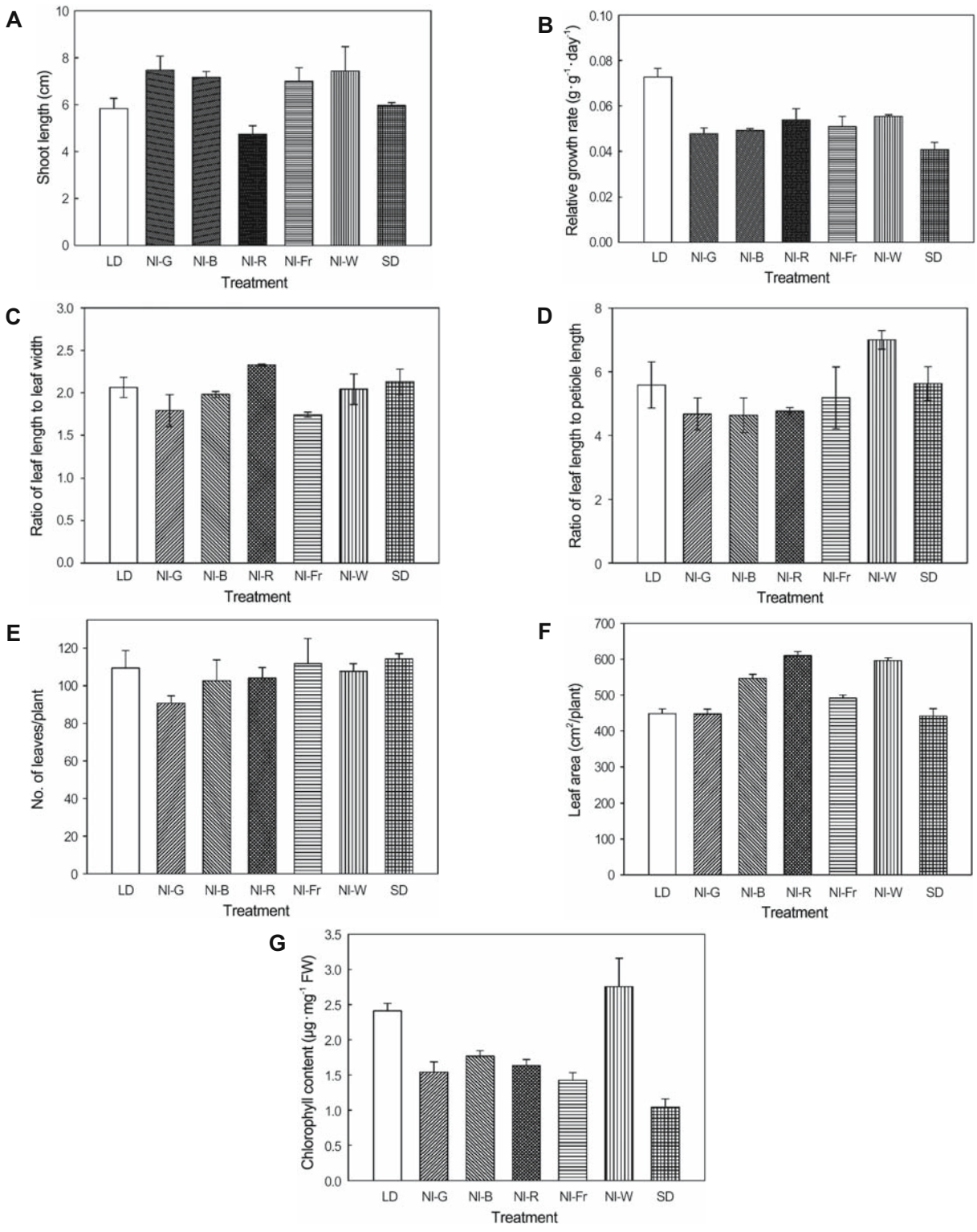

Fig. 2. Effects of light quality during night interruption (NI) provided at 10 μmol·m^{-2}·s^{-1} PPF on shoot length (A), relative growth rate (B), ratio of leaf length to leaf width (C), ratio of leaf length to petiole length (D), number of leaves per plant (E), leaf area (F), and chlorophyll content (G) in petunia (*Petunia hybrida* Hort. 'Easy Wave Pink') measured at 33 days after treatment. Please refer to Fig. 1 for details about light quality during NI. Vertical bars are means ± S.E. (n = 3).

width, increased under NI-R and NI-W. Mor et al. (1980) suggested that R light during the photoperiod is the most effective light for increasing the transport of assimilates to the shoot tips of rose plants, and it promotes shoot sink activity by increasing the unloading process. According to Park et al. (2012), W LEDs may be more efficient for use in

Table 1. Effects of light quality during night interruption (NI) provided at 10 μmol·m^{-2}·s^{-1} PPF on flowering characteristics in petunia (*Petunia hybrida* Hort. 'Easy Wave Pink') measured at 33 days after treatment

Treatment[z]	Flowering (%)	DVBy (Day)	No. of flowers/plant
LD	100	12.4	19.0 a[x]
NI-G	16	22.0	0.8 b
NI-B	-[w]	-	-
NI-R	33	23.6	2.8 b
NI-Fr	33	21.5	0.5 b
NI-W	16	21.5	1.4 b
SD	-	-	-
F-test			***

[z]Please refer to Fig. 1 for details about light quality during NI.
[y]Days after treatment initiation to visible flower buds (days to visible buds).
[x]Mean separation within columns by Duncan's multiple range test at the 5% level.
[w]No flowering.
***: Significant at $p \leq 0.001$.

photosynthesis than monochromatic LEDs, since the spectrum of W LEDs is as broad as that of sunlight. Therefore, the effects of light quality during NI observed in the current study are similar to the effects of daily light.

Chlorophyll contents were lower under all NI treatments except NI-W, in which this value was greater than that under LD treatment (Fig. 2G), suggesting that W is effectively used for photosynthesis during the night due to its broad spectrum (400-700 nm). The current results indicate that the light quality used during NI, despite its low intensity, induced photosynthesis in petunia.

Flowering

Flowering was induced by LD, NI-G, NI-R, NI-Fr, and NI-W (Table 1 and Fig. 3). The percent flowering was greatest in LD (100%), followed by both NI-R (33.3%) and NI-Fr (33.3%) and both NI-G (16.6%) and NI-W (16.6%). Similarly, flowering in petunia was previously shown to be hastened by some LD lighting regimes and lamp types compared to 4-h NI (Oh and Runkle, 2016). In the current study, the percent flowering under NI treatments was lower than that under LD due to delayed flowering, which was probably caused by the lower light intensity used in the NI treatments. Flowering in LDPs is generally enhanced when the photoperiod has a moderate-to-low R (600 to 700 nm) to Fr (700 to 800 nm) ratio (Vince-Prue, 1975; Runkle and Heins, 2001). Park et al. (2016) reported that light sources with low R:FR ratios promote flowering and stem elongation in petunia, but they reduce its ornamental value due to overgrowth and poor branching. Goins et al. (1998) and Mockler et al. (1999) reported that monochromatic B light delays flowering in *A. thaliana*, possibly through its influence on cryptochromes. The R pathway mediates the R light-induced inhibition of floral initiation, whereas the B and Fr pathways mediate the

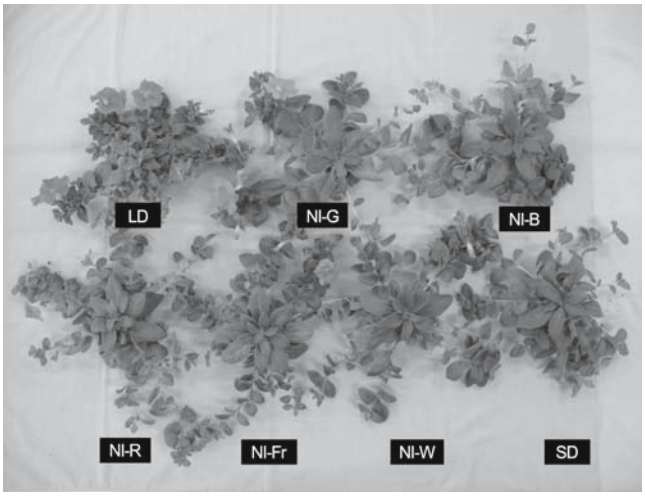

Fig. 3. Effect of light quality during night interruption (NI) provided at 10 μmol·m^{-2}·s^{-1} PPF on flowering in petunia (*Petunia hybrida* Hort. 'Easy Wave Pink') measured at 33 days after treatment. Please refer to Fig. 1 for details about light quality during NI.

B- or Fr-dependent suppression of the R pathway as well as the B- or the Fr-dependent direct promotion of flowering (Mockler et al., 2003). For LDPs such as *A. thaliana*, the coincidence of the B and Fr light pathways and the sensitive phase of the photoperiodic response rhythm are more likely to occur in LD than in SD (Mockler et al., 2003). In *A. thaliana*, Fr, B, and R light were all effective at promoting flowering in NI experiments, although R light was the least effective (Goto et al., 1991; Carre, 1998). In the current study, G, R, Fr, and W light promoted flowering, whereas B light inhibited this process, implying that light quality has differential effects on day extension by NI. The DVB increased under all NI treatments compared to LD. The number of flowers per plant was greatest in LD and was not

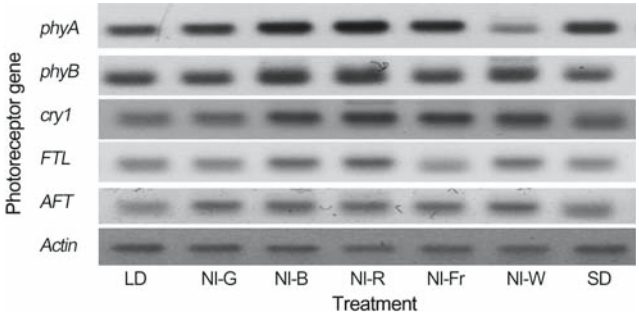

Fig. 4. Effects of light quality during night interruption (NI) provided at 10 μmol·m^{-2}·s^{-1} PPF on the expression of photoreceptor genes in petunia (*Petunia hybrida* Hort. 'Easy Wave Pink') measured at 33 days after treatment. Please refer to Fig. 1 for details about light quality during NI. Photoreceptor genes include *phyA*, *phytochrome A*; *phyB, phytochrome B*; *cry 1*, *cryptochrome 1*; *AFT, Anti-florigenic FT/TFL1* family protein; and *FTL*, *FLOWERING LOCUS T*. The constitutively expressed *Actin* gene was used as the control to compare gene expression levels.

significantly affected by light quality during NI. The reduced number of flowers per plant detected under the NI treatments suggests that flowering was delayed, probably because the NI treatments in this study employed a lower light intensity (10 μmol·m^{-2}·s^{-1} PPF). A similar result was reported for *Cymbidium*, i.e., there was a greater increase in the number of inflorescences and florets under high light intensity (120 μmol·m^{-2}·s^{-1} PPF) than under low light intensity (3-7 μmol·m^{-2}·s^{-1} PPF) (Kim et al., 2011).

In the current study, *phyA*, *phyB*, and *cry1* were highly expressed under NI-G, NI-B, and NI-R compared to LD and SD, which acted as the positive and negative control, respectively (Fig. 4). Similarly, *cry1*, *FTL*, and *AFT* were highly expressed under NI-B, NI-R, and NI-Fr. The results suggest that flowering induction by NI in petunia (LDP) may be related to the differential expression of the photoreceptor genes evaluated in this study. However, no significant differences in the expression of these genes were detected between LD and SD, and plants with relatively high expression of these genes under NI-B produced no flowers (Table 1), imply that flowering induction by NI involves a complicated genetic mechanism. Therefore, further study at the molecular level is required to elucidate the specific responses of these genes to different qualities of light and their roles in the flowering induction pathway.

In summary, the effects of light treatment on morphogenesis were as follows: NI-G increased shoot length, NI-B increased leaf expansion, NI-R increased leaf expansion, NI-Fr increased plant height and decreased chlorophyll content, and. The NI-W increased leaf expansion. Morphogenesis and flowering were significantly affected by light quality during NI. Despite the reduced number of flowers per plant, flowering was promoted by G, R, Fr, and W light, whereas it was inhibited by B light, implying that light quality has differential effects on NI-induced day extension. To obtain high quality plants, however, treatment with NI using a high light intensity should be considered.

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