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Several short-day species can flower under blue-extended long days, but this response is not universal

Malleshaiah SharathKumar [a,b,*], Jingwen Luo [a], Yu Xi [a], Wim van Ieperen [a], Leo F.M. Marcelis [a], Ep Heuvelink [a,*]

[a] Horticulture and Product Physiology, Department of Plant Sciences, Wageningen University and Research, Wageningen 6700 AA, the Netherlands
[b] Deliflor Chrysanten B.V., Korte Kruisweg 163, 2676 BS Maasdijk, the Netherlands

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ABSTRACT

Sole-source LED lighting enables spectral flexibility to achieve desirable plant characteristics and product quality. An earlier study from our lab showed that short-day plant chrysanthemum flowers normally under long days with dynamic lighting of 11 h dichromatic red-blue LED light extended with 4 h sole blue LED light. Such dynamic LED lighting is possible in vertical farms and opens the possibility to supply a higher daily light integral (DLI) to short-day plants by providing more hours of light and thus increase growth rate. This study aims to investigate for several short-day species whether normal flowering is obtained when 11 h of red-blue is extended with 4 h of sole blue LED light. Twelve genotypes of nine short-day plants species (kalanchoe - *Kalanchoe blossfeldiana*, perilla - *Perilla frutescens*, stevia - *Stevia rebaudiana*, artemisia - *Artemisia annua*, chrysanthemum - *Chrysanthemum seticuspe* and *Chrysanthemum morifolium*, cosmos - *Cosmos bipinnatus*, poinsettia - *Poinsettia pulcherrima* and wild tomato - *Solanum habrochaites*) were grown at three light conditions in a climate room: 11 h red-blue short day, 11 h red-blue extended with 4 h of sole blue, and 15 h red-blue long day. Mixed red and blue light (ratio 60:40) was provided at a total photosynthetic photon flux density (PPFD) of 100 μmol m^{-2} s^{-1} and sole blue light was provided at 40 μmol m^{-2} s^{-1} PPFD. Flowering response differed among species: kalanchoe, perilla and stevia flowered only in red-blue short day. Artemisia, chrysanthemum, cosmos, poinsettia, and wild tomato flowered in red-blue short day, and blue-extended long day but not in red-blue long day. However, there was a flowering delay in cosmos, poinsettia, and wild tomato under blue-extended long days compared to short days. In blue-extended long days plants received 15 % higher DLI resulting in a 4 to 36 % increase in total dry weight compared to short days. This study shows that increasing growth rate under light-limiting growth conditions through daylength-extension with sole blue light, without compromising flowering and quality, is possible for some, but not all short-day species.

1. Introduction

Flowering is a complex process triggered in response to both environmental (photoperiod, vernalization, and ambient temperature) and endogenous (sugars, microRNAs) cues (Cho et al., 2017; Perrella et al., 2020; Kinoshita and Richter, 2020). Plants precisely plan the time of flowering to the appropriate season in tune with one or more environmental and endogenous cues to ensure reproductive success. A major cue in the seasonal control of flowering is the photoperiod (Song et al., 2015; Brambilla et al., 2017; Osnato et al., 2022). Depending on the photoperiod requirement plants are classified into short-day, long-day and day-neutral plants (Garner and Allard, 1920; Thomas and Vince-Prue, 1997*a*). However, photoperiodic flowering is primarily mediated by the duration of the dark period (skotoperiod). The flowering of short-day plants happens when the skotoperiod is longer than the critical threshold, whereas long-day plants flower when the skotoperiod is shorter and depending on the external coincidence model (Song et al., 2015). Furthermore, species with certain photoperiod requirements can be grouped into obligatory (or qualitative) short-day plants, where flowering does not occur unless certain photoperiodic conditions are met. Other plants may be facultative (or quantitative) short-day plants, in which plants flowering is accelerated under short photoperiod, but flowering is still possible in different conditions (Thomas and Vince-Prue, 1997a).

* Corresponding authors.
E-mail addresses: sharath.malleshaiah@wur.nl (M. SharathKumar), ep.heuvelink@wur.nl (E. Heuvelink).

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In addition to photoperiod, the light spectrum also influences the flowering process through a series of signaling and transduction events (Cerdán and Chory, 2003; Song et al., 2015). Classical physiological studies in many short-day plants showed that short exposure to red light as night-break inhibited flowering, and this inhibitory effect was reversed by subsequent exposure to far-red light, highlighting the involvement of red/far-red absorbing phytochromes (PHY) in the flowering response (Borthwick and Cathey, 1962; Thomas and Vince--Prue, 1997*b*). Phytochromes exist in two interconvertible forms; P_r a biologically inactive red light absorbing form, and P_{fr} a biologically active far-red light absorbing form (Rockwell et al., 2006). Besides red and far-red sensing phytochromes, cryptochromes that sense blue light are also involved in the regulation of flowering (Shibuya and Kanayama, 2014). Phytochromes and cryptochromes regulate flowering and plant development both independently and in interaction with each other (Ni, 2005; Song et al., 2015; Mawphlang and Kharshiing, 2017; Kinoshita and Richter, 2020). To some extent, blue light is also perceived by phytochromes and stimulates the reversible conversion from active P_{fr} into inactive P_r, thereby contributing to lower phytochrome activity. The phytochrome photostationary state (PSS = $P_{fr}/(P_{fr}+P_r)$ indicates the fraction of active phytochrome out of the total phytochrome (Sager et al., 1988). Differences in the ratio of red, far-red, and blue light can alter the PSS and can influence plant architecture and development. This offers the possibility of using different light spectra to regulate plant processes through artificial lighting in greenhouse horticulture and vertical farms (Demotes-Mainard et al., 2016).

In greenhouse production, crop scheduling is crucial for obtaining marketable product quality at the right time of year. Depending on the crop of interest, growers strive to meet multiple quality characteristics simultaneously. For instance, in the production of cut flowers and potted flowering ornamentals, it is crucial to produce crops with improved aesthetics, a uniform crop with synchronized flowering time, and cut flower stems with a certain flower number and size, as well as a minimum stem length and weight with a long vase life. Most of these characteristics of ornamentals are under spectral influence (Ouzounis et al., 2015; Dueck et al., 2016; Paradiso and Proietti, 2022). For year-round production and to obtain guaranteed quality produce, greenhouse horticulture has evolved towards using advanced technologies to control temperature, and duration and intensity of illumination. However, the light spectrum in greenhouses remained largely uncontrolled until the advent of light-emitting diodes (LEDs). With growing interest in vertical farms that rely on LED lighting as their sole source of illumination, the ability to grow reliably high-value crops for all seasons has improved, since all growth factors such as light intensity and spectrum, temperature, carbon dioxide concentration, air humidity and photoperiod are fully controlled to steer plant growth and development that includes flowering (Mitchell and Sheibani, 2020; SharathKumar et al., 2020).

During winter, greenhouse production at northern latitudes is limited primarily by a low daily light integral (DLI), which limits CO_2 assimilation, resulting in long crop cycles and crops with low product quality. Under those conditions, artificial lighting is beneficial to enhance plant growth and development by extending the photoperiod (extra hours of light). However, this method does not work well with short-day plants that require a certain number of dark hours to flower (a shorter photoperiod). Thus, artificial lighting should not exceed 12 to 14 h due to the photoperiodic flowering requirement of short-day plants. When using LED lighting we can apply dynamic lighting, meaning that light spectrum and/or intensity changes as a function of time of the day or the developmental stage of the plant (SharathKumar et al. (2020). In earlier research on dynamic lighting from our lab, it was shown that the short-day plant chrysanthemum flowers normally under long days with dynamic lighting of 11 h dichromatic red-blue light extended with 4 h sole blue LED light (van Ieperen et al., 2011; Jeong et al., 2014; SharathKumar et al., 2021). It would be highly beneficial for vertical farms and greenhouse industry to have such dynamic LED lighting to increase DLI (through blue-extended long days) for short-day plants without compromising flowering. However, whether this dynamic light spectrum would result in normal flowering for other short-day plant species is unknown. Therefore, this study aims to investigate whether normal flowering (until anthesis) is obtained for several short-day species when 11 h of red-blue is extended with 4 h of sole blue LED light. We hypothesize that all short-day species will show normal flowering under such a dynamic spectrum, just like chrysanthemums. Twelve genotypes of nine obligate short-day plant species were investigated.

2. Material and methods

2.1. Plant materials and growth conditions

Twelve genotypes of nine obligate short-day plants species were studied. Seeds of artemisia - *Artemisia annua*, cosmos - *Cosmos bipinnatus* cultivars 'Red Shades' and 'Purple shades' (PanAmerican Seed BV, The Netherlands), perilla - *Perilla frutescens* (Ons zaden, The Netherlands), wild tomato - *Solanum habrochaites* (Plant breeding, Wageningen university and research), and stevia - *Stevia rebaudiana 'Sweetleaf'* were sown in 35 × 21 × 6 cm trays filled with peat-based horticultural substrate (Lentse Potgrond, Horticoop). Seedlings with five to six true leaves were transplanted in 8 × 8 × 10 cm black plastic pots with a peat-based horticultural substrate (810 g m^{-3} N-P-K (15–10–20), pH = 5.7 and EC=0.8 dS m^{-1}, Lentse Potgrond, Horticoop). Peat block-rooted cuttings of *Chrysanthemum seticuspe* (diploid) and *Chrysanthemum morifolium* 'Radost' (cut flower) and 'Double Orange' (potted) (Deliflor Chrysanten B.V, The Netherlands) were transplanted in 8 × 8 × 10 cm black plastic pots filled with peat-based horticultural substrate (Lentse Potgrond, Horticoop). Rooted cuttings of poinsettia - *Poinsettia pulcherrima* 'Mirage Red' (Syngenta, The Netherlands), and kalanchoe - *Kalanchoe blossfeldiana* 'Serenity' and 'Lipstick' (Slijkerman Kalanchoë B.V, The Netherlands) were also transplanted in 8 × 8 × 10 cm black plastic pots filled with peat-based horticultural substrate (Lentse Potgrond, Horticoop). After transplanting, all plant species were grown for a week under 15 h long day photoperiod under white LED light (Greenpower LED top lighting module, Signify, the Netherlands) at 100 ± 10 μmol m^{-2} s^{-1} photosynthetic photon flux density (PPFD) at canopy level, 22/18 ± 0.2 °C day/night temperature, 65 % relative humidity, and ambient CO_2 concentration. Plants were watered manually every other day with a nutrient solution (Hoagland, pH = 5.8 ± 0.2, EC = 1.6 dS m^{-1}).

2.2. Lighting treatments and measurements

Two growth chambers were divided each into three compartments each fitted with one of the three light treatments (Fig. 1A). Each light treatment started with 11 h of mixed red and blue light at a 60:40 ratio: (1) 11 h red-blue short day (RB, SD); (2) 11 h red-blue extended with 4 h of sole blue (RB+B, LD); (3) 15 h red-blue long day (RB, LD). A double-layered white plastic screen was placed between each treatment to avoid light interference from the neighbouring light treatment. Plants were illuminated with a custom-assembled light system with a mixture of red and blue LEDs (Greenpower LEDs research modules, Signify, The Netherlands). Peak wavelength was 450 nm for blue LEDs and 660 nm for red LEDs (Fig. 1B). Mixed red and blue light had a total PPFD of 100 ± 10 μmol m^{-2} s^{-1}; extended sole blue light with a PPFD of 40 ± 5 μmol m^{-2} s^{-1}. The phytochrome photostationary state (PSS) for mixed red-blue light was 0.87 and for blue light 0.49 (calculated according to Sager et al., 1988). The photosynthetic daily light integrals were 3.9 mol m^{-2} d^{-1} for RB, SD, 4.5 mol m^{-2} d^{-1} for RB+B, LD and 5.4 mol m^{-2} d^{-1} for RB, LD. Light spectra were measured at plant height with a spectroradiometer (Jeti Spectro-Radiometer, Germany). Lamp height was adjusted once a week to keep PPFD constant. To minimize potential position effects, plants were randomly rearranged within the tray of the same species, and the trays of each species were rotated clockwise to prevent positional bias on weekly basis. Additionally, the height of the plants within each compartment were adjusted twice a week using black

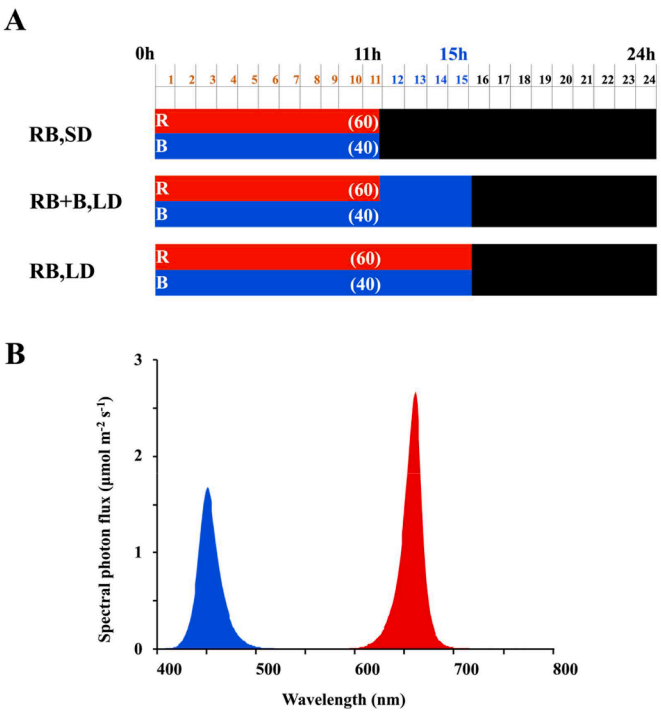

Fig. 1. Schematic representation of light treatments applied (A); Red-blue or blue bars indicate daylight period and black indicates dark period. The numbers in parenthesis indicate the light intensities supplied by red and blue LEDs (μmol m^{-2} s^{-1}). Photosynthetic photon flux density of 100 μmol m^{-2} s^{-1} supplied by a combination of red (660 nm) and blue (450 nm) LEDs at a 60:40 ratio; and spectral photon distribution of narrow-band red and blue LEDs (B).

plastic pots or plastic trays to maintain crop canopy height.

2.3. Flowering observations

Plants were observed daily to record the number of days until visible floral bud appearance (first flower bud larger than 2 mm) and anthesis (first flower fully open). Ten plants per light treatment were used to record number of days until visible floral bud, number of floral buds and floral buds fresh and dry weight and morphological parameters. Five additional plants per light treatment were used to observe whether emerged floral buds could successfully attain anthesis and to record the number of days to anthesis, flower diameter (measured on all flowers per plant), fresh and dry weight of flowers at anthesis. No flowering means there was no visible bud after twice the number of days for the first visible floral bud in the short day treatment. Dry weights were determined after drying in a ventilated oven at 105 °C for 24 h.

2.4. Growth and morphology observations

Morphological parameters were determined on ten plants on the same day as floral bud parameters. Main stem length (cm) (from top of the soil to the shoot apex), total number of leaves and internodes, stem diameter (mm) (measured at the middle of the total stem length), total leaf area (LI192 COR 3100 area meter, LI-COR Inc., USA) were recorded. Buds, leaves, stem, and total shoot fresh weight and dry weight (ventilated oven at 105 °C for 24 h) were determined. Specific leaf area (SLA) was calculated as total leaf area divided by leaf dry weight. Average internode length was calculated as plant height divided by number of internodes.

2.5. Statistical design and analysis

Three light treatments were randomised over the 3 plots in each of the two climate chambers (two blocks). Twelve genotypes of nine short-day plant species were studied in two rounds; round-1 consisted of three types of chrysanthemums (cut flower, potted and diploid), two cultivars of kalanchoe ('Serenity' and 'Lipstick') and poinsettia. Round-2 consisted of artemisia, two cultivars of cosmos ('Red Shades' and 'Purple shades'), perilla, stevia and wild tomato. There were 15 plants per genotype in each plot: 10 plants for floral bud and morphology observations, 5 plants for flower anthesis observation. The statistical analysis was performed with IBM SPSS Statistics 26.0 (IBM, New York, USA). For each genotype, a one-way Analysis of Variance (ANOVA) in blocks was conducted, followed by mean separation according to Fisher's Protected LSD test ($p = 0.05$).

3. Results

3.1. Short-day plants flowering under blue-extended long day

Kalanchoe (both cultivars), perilla and stevia produced flowers only under short day (Figs. 2, 3 and 4). However, artemisia, chrysanthemum (all three genotypes), cosmos (both cultivars), poinsettia and wild tomato flowered under short day as well as blue-extended long day but not in red-blue long day (Figs. 2 and 10). Floral parameters such as bud number, flower diameter, and flower dry weight of artemisia showed no significant difference between short day and blue-extended long day (Fig. 5B, C and D). Days to visible floral bud for cut flower, diploid and potted chrysanthemum were not significantly different between short day and blue-extended long day (Fig. 6A). For cosmos light treatments significantly differed in all plants grown under blue-extended long day successfully developed visible flower bud and attained anthesis. However, there was a delay of around 20 days compared to plants grown in short days (Fig. 7A). Floral bud number, flower diameter and dry weight showed no significant difference between short day and blue-extended long day (Fig. 7B, C and D). In the short day treatment poinsettia attained the required bract color on around day 27, while plants grown under blue-extended long day required an additional 9 days (Fig. 8A). Accordingly, visible flower bud (Cyathea) was observed on day 33 under short day and day 50 under blue-extended long day (Fig. 8A). However, no visible bud was observed under long day until the termination of the experiment (14 days after the first observed change of bract color) (Fig. 8A). Number of buds, bud size, and bud dry weight were lower under blue-extended long day than short day (Fig. 8B, C and D). Wild tomato plants grown under blue-extended long day reached anthesis 3 days later compared to short day (Fig. 9A). Flower parameters showed no significant difference between short day and blue-extended long day treatments (Fig. 9B, C and D).

3.2. Growth and plant morphology of short-day plants under blue-extended long days

All the recorded growth and plant morphology parameters are available as Supplementary material. Short-day plant species flowering under blue-extended long day showed an increased internode length (6 to 48 %) compared to short day (Fig. 11A). Similarly, total dry weight also increased (4 to 36 %) under blue-extended long day compared to short day (Fig. 11B). For kalanchoe 'Lipstick' plant height was largest under blue-extended long day (Fig. S1A). However, number of leaves, leaf area and total dry weight was highest under red-blue long days for both kalanchoe cultivars (Figs. S1B, S1D and S1E). Perilla under blue-extended long day were taller compared to red-blue short day and long day (Fig. S3A). For cut-chrysanthemum plant height and total dry weight were higher under blue-extended and red-blue long days, whereas for diploid chrysanthemum plant height and number of leaves were higher under red-blue long day (Figs. S9A, S9C and S9G).

Most of the morphological parameters in perilla, stevia, artemisia, cosmos, poinsettia, and wild tomato did not show any statistical difference among light treatments. In perilla (Fig. S3D), stevia (Fig. S5D),

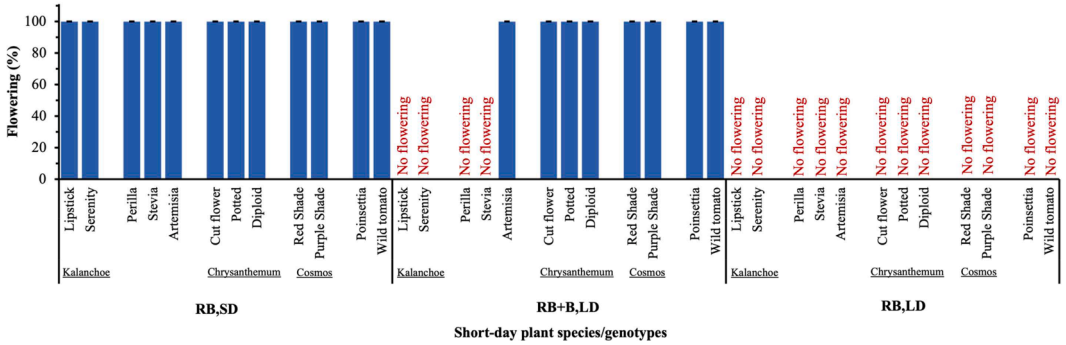

Fig. 2. Flowering responses of short-day plants under different light treatments. Light treatment RB,SD represents 11 h dichromatic red-blue short day; RB+B,LD represents 11 h dichromatic red-blue extended with 4 h of sole blue; and RB, LD represents 15 h dichromatic red-blue long day. Data represented as mean of two blocks consisting of 10 plants each ± SE (n = 2).

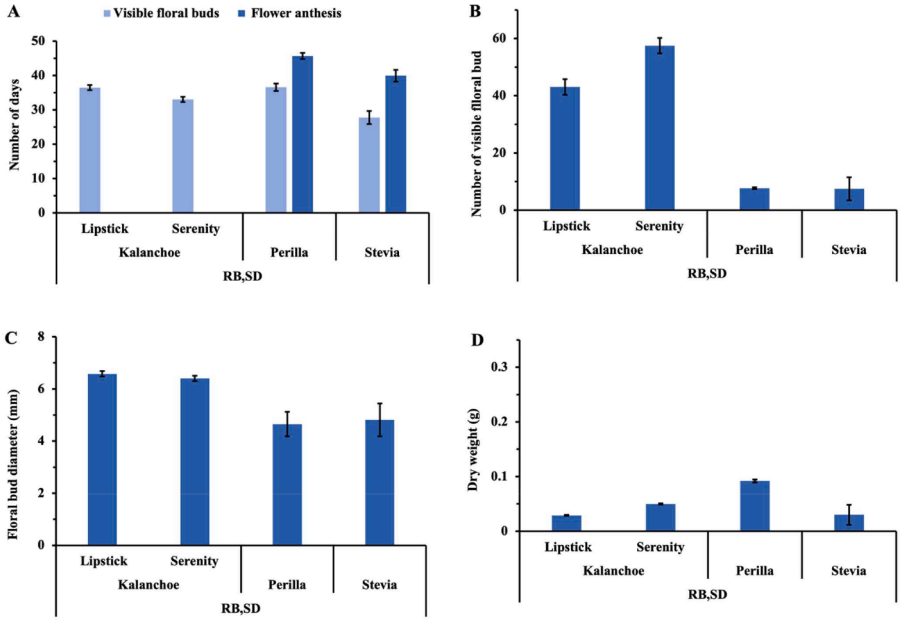

Fig. 3. Flowering responses of *Kalanchoe blossfeldiana* cv. 'Lipstick' and 'Serenity', *Perilla frutescens* and *Stevia rebaudiana* under RB,SD (11 h dichromatic red-blue short day). No flowering occurred under RB+B,LD (11 h dichromatic red-blue extended with 4 h of sole blue) and RB,LD (15 h dichromatic red-blue long day) light treatments. Number of days to visible floral buds and flower anthesis (A); number of visible floral buds (B); floral bud diameter (C); and dry weight of floral bud (kalanchoe on day 42, perilla on day 46 and stevia on day 32) (D) after the start of light treatments. Data represented as mean of two blocks consisting of 10 plants each ± SE (n = 2).

diploid chrysanthemum (Fig. S9D), cosmos cv. Red Shade (Fig. S11B) and poinsettia (Fig. S13D) plants grown under red-blue long day developed a thicker stem compared to short day and blue-extended long day. Artemisia plants grown under long day showed significantly higher total dry weight compared to other light treatments (Fig. S7E). Cosmos plants grown under red-blue long day showed statistically higher leaf area compared to other treatments (Fig. S11C). Poinsettia was taller when grown under red-blue long day to other light treatments (Fig. S13A). Wild tomato grown under short day developed higher number of leaves compared to long day (Fig. S15B).

4. Discussion

This study demonstrates the possibility of inducing flowering in several short-day species when 11 h of red-blue light is extended with 4 h of sole blue LED light. Flowering response of short-day plants grown under 4 h blue-extended long day differed among species: kalanchoe, perilla, and stevia did not flower (Figs. 2, 3 and 4), whereas artemisia, chrysanthemum, cosmos, poinsettia, and wild tomato flowered (Figs. 2, 5, 6, 7, 8, 9 and 10). This study shows that flowering under blue-extended long days is not limited to chrysanthemum, however this response is also not universal among all short-day species. Additionally, short-day plant species that flowered under blue-extended long day showed an increased internode length (6 to 48 %) compared to short day (Fig. 11A). Likewise, there was also an increase in total dry weight (4 to 36 %) under blue-extended long days compared to short days (Fig. 11B).

4.1. Blue-extended long day allows flowering in several short-day species

Several short-day plants (artemisia, chrysanthemum, cosmos, wild tomato, and poinsettia) showed normal flowering under blue-extended long days. However, when the day was extended with red-blue (red-blue long days) light, flowering was inhibited (Figs. 2 and 10). Therefore, the question arises whether it is the presence of blue or the absence of red light that controls the photoperiodic flowering under blue-extended long days. A possible reason could be that the day extension with 4 h of sole blue light is sensed as 'dark period' or blue light may have a much weaker long day signal compared to red light (Lopez et al.,

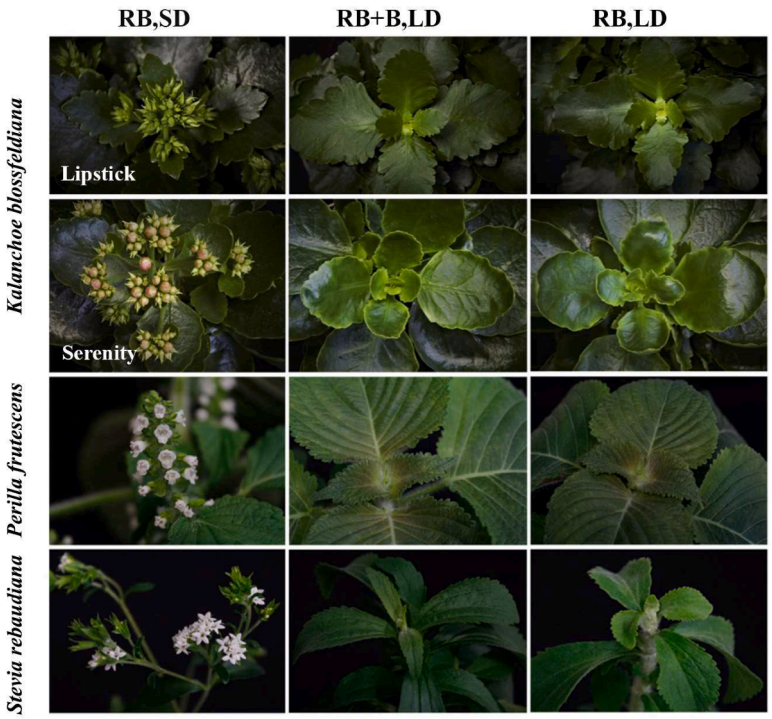

Fig. 4. Flowering responses of *Kalanchoe blossfeldiana* cv. Lipstick (on day 60) and Serenity (on day 77), *Perilla frutescens* (on day 51), and *Stevia rebaudiana* (on day 43), under different light treatment. The label at the top of the image indicates light treatment: RB,SD represents 11 h dichromatic red-blue short day; RB+B,LD represents 11 h dichromatic red-blue extended with 4 h of sole blue; and RB,LD represents 15 h dichromatic red-blue long day.

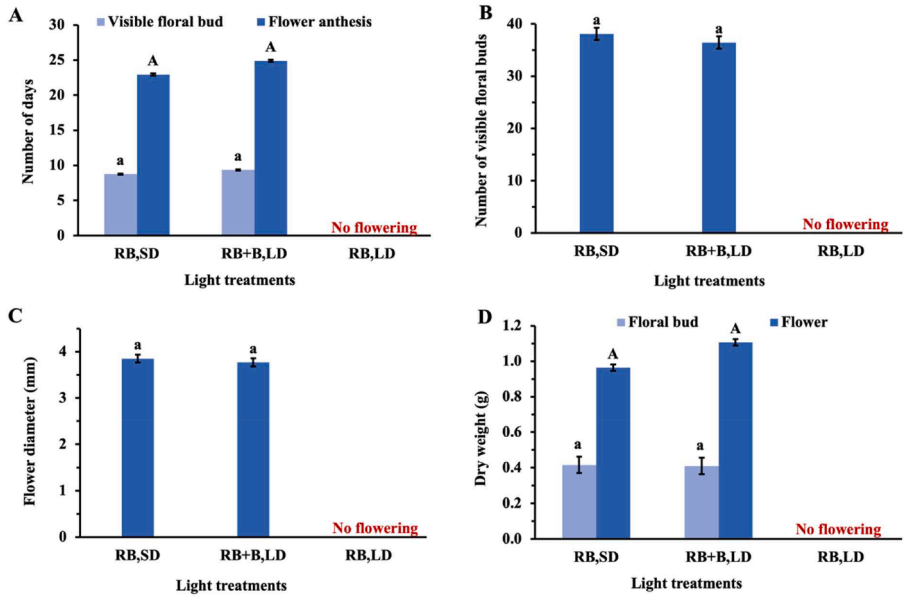

Fig. 5. Flowering responses of *Artemisia annua* under different light treatments. Number of days for visible floral bud and flower anthesis (A); number of visible floral buds (B); flower diameter (C); and dry weight of floral bud on day 20 and flower on day 27 (D) after the start of light treatments. Light treatment RB,SD represents 11 h dichromatic red-blue short day; RB+B,LD represents 11 h dichromatic red-blue extended with 4 h of sole blue; and RB,LD represents 15 h dichromatic red-blue long day. Data represented as mean of two blocks consisting of 10 plants each ± SE ($n = 2$). Different letters indicate significant differences between light treatments (Fisher's Protected LSD test, $p = 0.05$).

2020). Furthermore, the magnitude of phytochrome-mediated flowering responses relies on the relative amount of active phytochrome (P_{fr}), or PSS. To some extent, blue light is also perceived by phytochromes and stimulates the reversible conversion from active (P_{fr}) to inactive (P_r) more than vice versa (Sager et al., 1988). Therefore, the lower phytochrome activity associated with blue light (PSS = 0.49) compared to red-blue light (PSS = 0.87) may lead to successful flowering in some short-day plant species under blue-extended long days (Fig. 10).

The failure of flowering when the day was extended by red-blue light, while it did flower when extended by sole blue light could also be attributed to PHYB that acts as a primary photoreceptor mediating non-inductive (LD or night-break) signals in short-day plants. Previous studies elucidated the inhibitory effect of red light on flowering by giving red as night-break in many short-day plants such as cocklebur

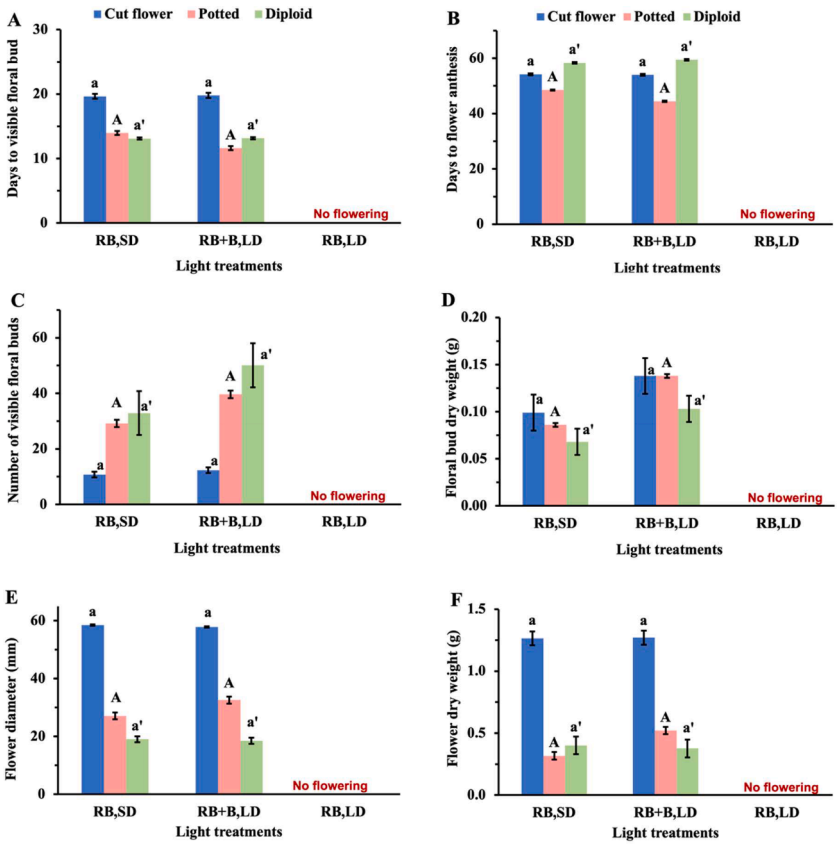

Fig. 6. Flowering responses of three genotypes of chrysanthemum (cut flower - *Chrysanthemum morifolium* cv. Radost, potted- *Chrysanthemum morifolium* cv. Double Orange, and diploid - *Chrysanthemum seticuspe*) under different light treatments. Number of days to visible floral bud (A), Number of days to flower anthesis (B); number of visible floral buds (C) and floral bud dry weight (D) 29 days after start of light treatments; flower diameter (E) and flower dry weight (F) 58 days after start of light treatments. Light treatment RB,SD represents 11 h dichromatic red-blue short day; RB+B,LD represents 11 h dichromatic red-blue extended with 4 h of sole blue; and RB,LD represents 15 h dichromatic red-blue long day. Data represented as mean of two blocks consisting of 10 plants each ± SE ($n = 2$). Different letters indicate significant differences between light treatments (Fisher's Protected LSD test, $p = 0.05$).

(Borthwick et al., 1952), soybean (*Glycine* max) (Downs, 1956), chrysanthemum (Cathey and Borthwick, 1957; Higuchi et al., 2012), dahlia (*Dahlia hortensis*) and marigold (*Tagetes erecta*) (Craig and Runkle, 2013). In chrysanthemum grown under 11 h of red-blue short days extending with 4 h of sole red light (40 μmol m^{-2} s^{-1}; PSS = 0.89), flowering was initiated, but no flowers were developed or anthesis occurred (SharathKumar et al., 2021). It is reasonable to speculate that non-flowering under red-blue long days is attributed to higher ratio of red light compared to blue light (60:40). This may lead to stronger activity and influence of phytochrome-regulated flowering response (particularly Phytochrome B, PHYB). For example, PHYB is involved in the inhibition of flowering in many short-day plants either by suppressing flower promoting genes such as *Heading date 3a (Hd3a,* in rice, Ishikawa et al., 2005) and *FLOWERING LOCUS T-like 3 (CmFTL3,* in chrysanthemum, Sumitomo et al., 2012), or by inducing anti-florigenic *Flowering locus T* (*CmAFT)* in chrysanthemum with stronger PHYB activity (Higuchi et al., 2013). Therefore, we assume that the effects of red light on PHYB-mediated flowering inhibition in short-day plants were strong enough to attenuate any possible promotional effects of blue light on flowering. Thus, it is well possible that some short-day plants sense blue light as a 'dark' signal or blue light may have a much weaker long day signal than red or red-blue light combined.

Both, cryptochromes and phytochromes have been shown to influence flowering time by regulating the stability of CO (CONSTANS) protein, a key factor in promoting flowering in plants (Valverde et al., 2004). Red light promotes CO degradation through PHYB, whereas blue and far-red light promote CO accumulation through cryptochromes and Phytochrome A (PHYA), respectively (Valverde et al., 2004). The difference in flowering responses among short-day species in this study may be attributed to different types of phytochrome-cryptochrome interactions. However, it is unclear whether cryptochrome plays a role in flowering under sole-blue light with low phytochrome activity. It has been shown by altering the levels of active phytochrome (P_{fr}) that it is possible to modify cryptochrome action through an interaction between these two photoreceptor systems (Ahmad and Cashmore, 1997; Yang et al., 2017b). Despite the involvement of phytochromes, the role of blue light sensing cryptochromes and ZTL-FKF1-LKP2 family proteins, in the regulation of photoperiodic flowering cannot be ruled out (Song et al., 2015). Cryptochromes (CRY) are known to regulate photoperiodic flowering in many short-day plants. For instance, *CRY1a* in soybean (Zhang et al., 2008), CRY1a, CRY1b and CRY2 genes in chrysanthemum are involved in the regulation of flowering (Yang et al., 2017a, 2018). However, the detailed mechanism by which light quality regulates flowering in short-day plants remains unclear.

Based on the flowering responses under blue-extended long days, we could categorize the studied qualitative short-day species as responders and non-responders; responders being species that flower under blue-extended long days, and non-responders being species that fail to flower under blue-extended long days (Figs. 2 and 4). Artemisia, chrysanthemum, cosmos, wild tomato, and poinsettia are categorized as responders and may share similar flowering physiology in response to photoperiod and light spectrum, more specifically to blue light. For instance, in cosmos and chrysanthemum, blue light as night break or daylength extension failed to inhibit flowering (Hamamoto et al., 2003; Higuchi et al., 2012; Jeong et al., 2014; SharathKumar et al., 2021). These short-day plants may have lesser sensitivity towards the daylength

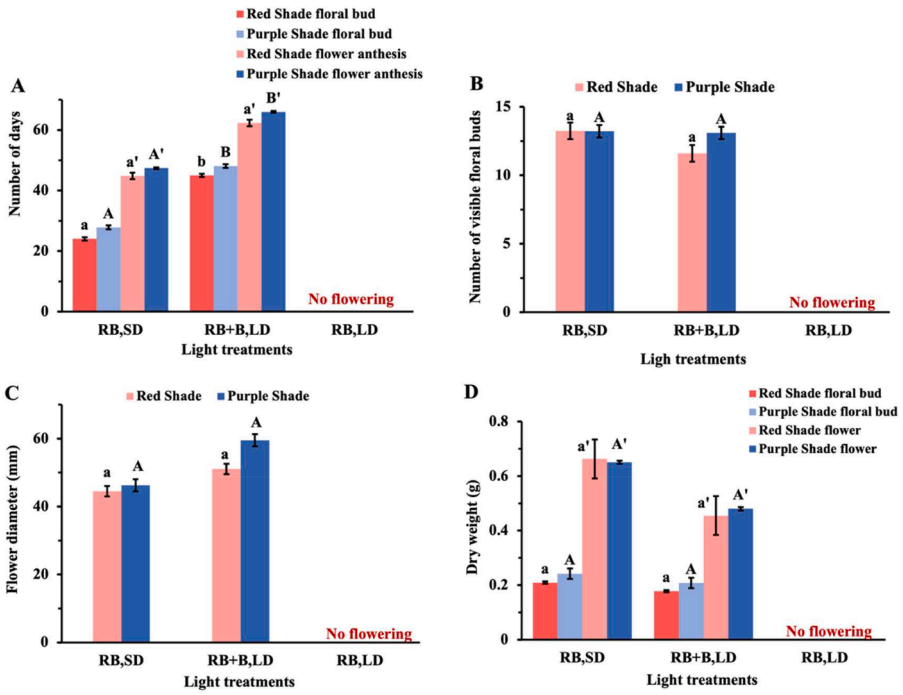

Fig. 7. Flowering responses of *Cosmos bipinnatus* cv. 'Red Shade' and 'Purple Shade' under different light treatments. Number of days to visible floral bud and anthesis (A); number of visible floral buds (B); flower diameter (C); dry weight of floral bud on day 40 (RB,SD), day 53 (RB+B,LD) and dry weight of flower on day 53 (RB,SD), day 70 (RB+B,LD) (D) after start of light treatments. Light treatment RB,SD represents 11 h dichromatic red-blue short day; RB+B,LD represents 11 h dichromatic red-blue extended with 4 h of sole blue; and RB,LD represents 15 h dichromatic red-blue long day. Data represented as mean of two blocks consisting of 10 plants each ± SE ($n = 2$). Different letters indicate significant differences between light treatments (Fisher's Protected LSD test, $p = 0.05$).

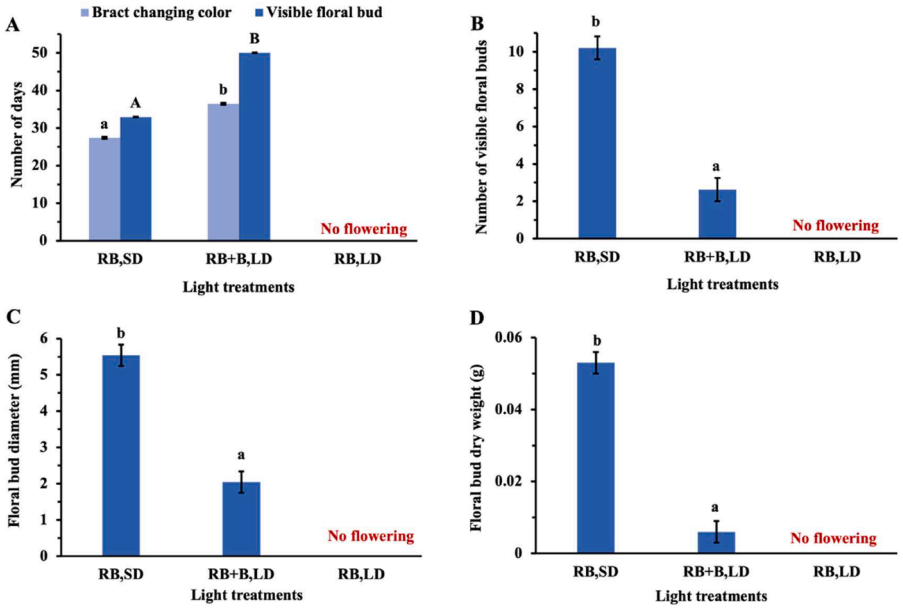

Fig. 8. Flowering responses of *Poinsettia pulcherrima* cv. 'Mirage Red' under different light treatments. Number of days to bract changing color and visible floral bud (A); number of floral buds (B); floral bud diameter (C) and dry weight (D) on day 42 after start of light treatments. Light treatment RB,SD represents 11 h dichromatic red-blue short day; RB+*B*,LD represents 11 h dichromatic red-blue extended with 4 h of sole blue; and RB,LD represents 15 h dichromatic red-blue long day. Data represented as mean ± SE ($n = 2$). Data represented as mean of two blocks consisting of 10 plants each ± SE ($n = 2$). Different letters indicate significant differences between light treatments (Fisher's Protected LSD test, $p = 0.05$).

extension or night-break by blue light than the non-responders (kalanchoe, perilla, and stevia) that flowered only under short day conditions (Figs. 2, 3 and 4). This indicates that non-responders must be under strict critical daylength requirements or being extremely sensitive to blue light, even under lower PPFD of 40 μmol m^{-2} s^{-1} for flowering. It is also possible that variations in plant responses of short-day plants to blue light extension may be linked to differences in their sensitivity to twilight due to variations in their circadian clock systems (Takimoto and Ikeda, 1961).

Further, the differences in flowering responses among responders

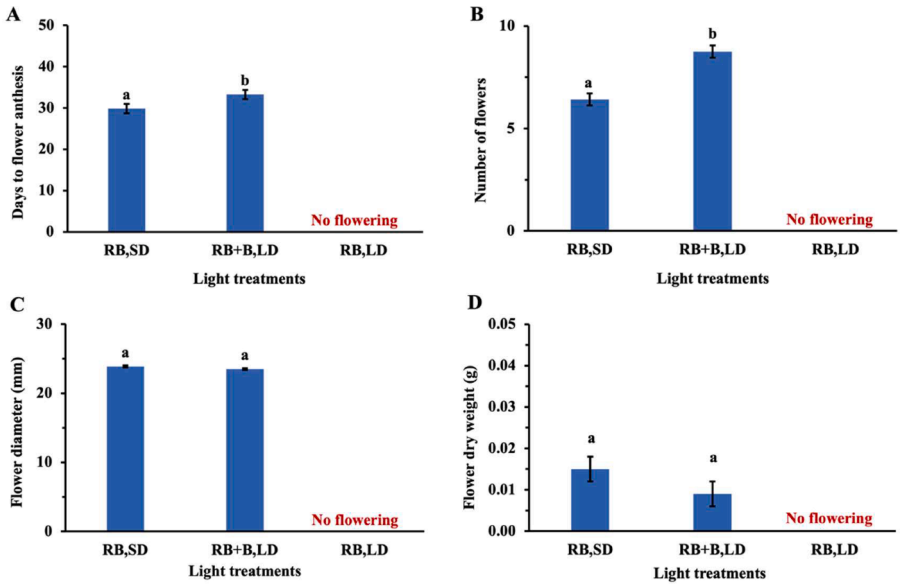

Fig. 9. Flowering responses of *Solanum habrochaites* under different light treatments. Number of days to flower anthesis (A); number of flowers (B); flower diameter (C) and dry weight (D) on day 40 after the start of light treatments. Light treatment RB,SD represents 11 h dichromatic red-blue short day; RB+B,LD represents 11 h dichromatic red-blue extended with 4 h of sole blue; and RB,LD represents 15 h dichromatic red-blue long day. Data represented as mean of two blocks consisting of 10 plants each ± SE ($n = 2$). Different letters indicate significant differences between light treatments (Fisher's Protected LSD test, $p = 0.05$).

and non-responders seems at least partly the result of varied flowering sensitivity to sole blue light. For example, in short-day plants such as chrysanthemum, cosmos (*Cosmos bipinnatus* and *Cosmos sulphureus*), Japanese morning glory (*Pharbitis nil*), marigold (*Tagetes erecta*) and zinnia (*Zinnia elegans*) night-break or day extension with sole blue light did not inhibit flowering even when the photoperiod was much longer than the critical minimum (13.5 h) (Hamamoto et al., 2003; Sumitomo et al., 2012; Higuchi et al., 2012; Jeong et al., 2014; Meng and Runkle, 2015; Park and Jeong, 2019). However, blue light given as a night-break inhibited flowering in some short-day plants, but not in others (Hamamoto et al., 2003; Meng and Runkle, 2015; Kang et al., 2019; Park and Jeong, 2020*a*,*b*). For instance, a low intensity (< 10 μmol m^{-2} s^{-1}) of blue light given as a night-break for a short period of time (10 min upto 4 h) was effective in inhibiting the flowering in some of short-day plants like duckweed (*Lemna paucicostata*), perilla (*Perilla ocymoides*), rice (*Oryza sativa*) and kalanchoe (*Kalanchoe blossfeldiana*) (Hamamoto et al., 2003; Ishikawa et al., 2009; Kang et al., 2019). Similarly, in this study kalanchoe (as well as perilla, and stevia) did not flower under blue-extended long days, exhibiting higher sensitivity towards sole blue light to initiate flowering (Fig. 2, 4). Additionally, day extension with blue light delayed flowering in short-day plant okra (*Abelmoschus esculentus*) but not when blue light was applied as a night-break (Hamamoto and Yamazaki, 2009). So, applying blue light as a daylength extension or night-break may also result in different flowering responses within the same species.

Additionally, given the different behavior of responders and non-responders, perhaps for short-day plants, the flowering response depends on the intensity and duration of blue light during daylength extension. For example, some short-day species might be sensitive to blue light at a lower intensity (40 μmol m^{-2} s^{-1}), which might explain flowering inhibition in kalanchoe, stevia, and perilla. However, for chrysanthemum, it appears that the duration of exposure may play a more prominent role than the intensity of blue light during daylength extension. If blue light extension is applied for only 4 h, high-intensity blue light is not likely to disturb the flowering response of chrysanthemum. For instance, when chrysanthemums were grown under 11 h of RB short days at 100 μmol m^{-2} s^{-1} extended with 100 μmol m^{-2} s^{-1} of blue light, all plants flowered, whereas overnight illumination with blue light led to flowering in 67 % of the plants (Jeong et al., 2014). Therefore, it is unlikely that the intensity of blue light matters more than the duration of blue light exposure in chrysanthemum but not certain that other short-day plants behave in similar way. However, it would be interesting to test flowering responses at higher light intensity.

Another commonality is that three species (artemisia, cosmos, and chrysanthemum) out of five of the responders belong to the Asteraceae family. However, stevia, which is also a member of the Asteraceae family, does not share similar flowering behavior under blue-extended long days. On the other hand, wild tomato of Solanaceae and poinsettia of Euphorbiaceae are also responders, even though they belong to different families. It is therefore reasonable to assume that some short-day species might exhibit similar flowering behavior under blue-extended long days despite belonging to different families. Non-responders like kalanchoe of Crassulaceae and perilla from the Lamiaceae family did not flower under blue-extended long day. Therefore, it can be concluded that short-day plants exhibit photoperiod and spectrum specificity, regardless of whether they belong to the same or different families. Hence, no universal flowering response under blue-extended long days exists among short-day species.

4.2. Morphology of short-day plants under blue-extended long day

The increased plant height in cut and diploid chrysanthemum, cosmos and poinsettia under blue-extended long day compared to short day resulted from 6 to 48 % increased internode length (Figs. 11A, S9A, S13A, and S15A). This increased internode length might be due to sole blue light stimulating the elongation in many species, for example, chrysanthemum, petunia, cucumber, potato, and some microgreens (Jeong et al., 2014; Fukuda et al., 2016; Ying et al., 2020). The enhanced internode elongation under sole blue light might be caused by increasing levels of bioactive gibberellins (GA_1 and GA_4) (Fukuda et al., 2016). Additionally, blue light is also partly sensed by phytochromes resulting in shade avoidance responses such as stem elongation. It is likely that an increase in stem elongation under blue-extended long days (Fig. 11A) is the result of low phytochrome activity (PSS = 0.49) (Plantenga et al., 2016; Kong et al., 2018; Larsen et al., 2020). In our study, plants grown under blue-extended long days received 15 % higher DLI which resulted in an increase of 4 to 36 % in biomass compared to plants grown under short days (Fig. 11B). The biomass increase is species dependent; 4 %

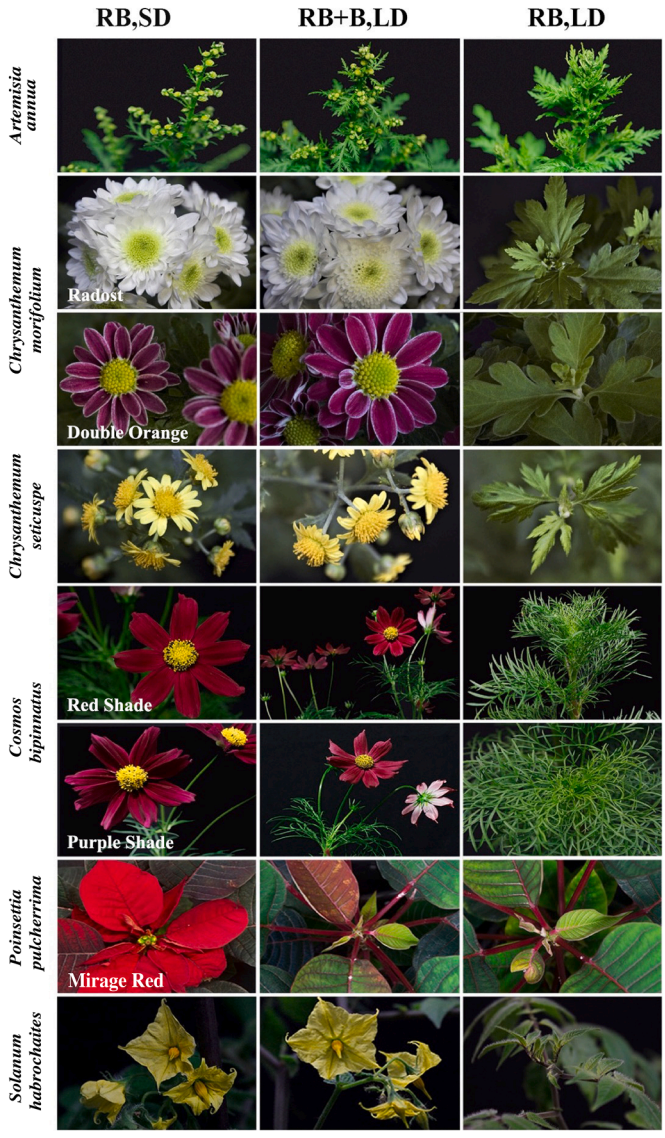

Fig. 10. Flowering responses of *Artemisia annua* (on day 27), three genotypes of chrysanthemum (cut flower - *Chrysanthemum morifolium* cv. Radost, potted - *Chrysanthemum morifolium* cv. Double Orange, and diploid- *Chrysanthemum seticuspe*) (on day 58), *Cosmos bipinnatus* cv. Red Shade, and Purple Shade (on day 70), *Poinsettia pulcherrima* cv. Mirage Red (on day 42), and wild tomato - *Solanum habrochaites* (on day 40) under different light treatments. The label at the top of the image indicates the light treatment: RB,SD represents 11 h dichromatic red-blue short day; RB+B,LD represents 11 h dichromatic red-blue extended with 4 h of sole blue; and RB,LD represents 15 h dichromatic red-blue long day.

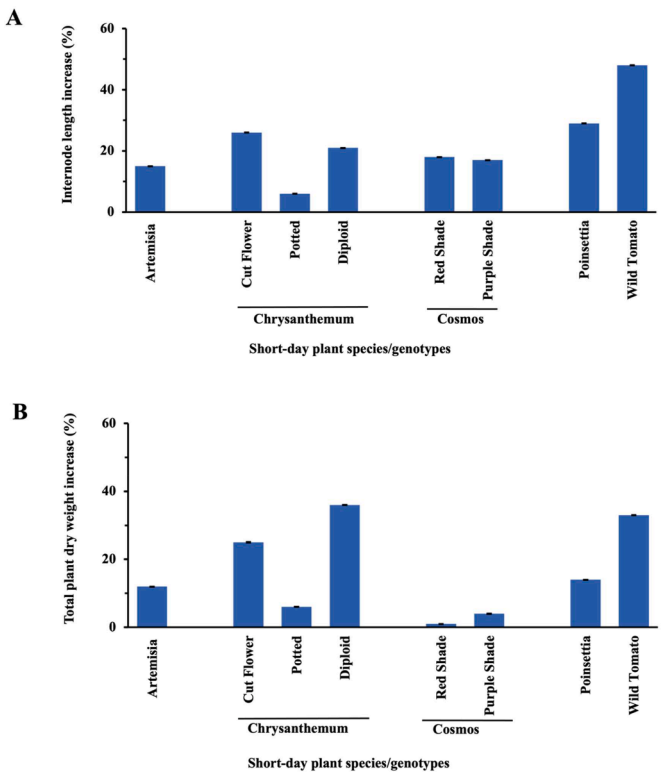

Fig. 11. Increase in internode length (A) and total plant dry weight (B) due to extending a short-day by 4 h of sole-blue light for short-day genotypes that flowered under blue-extended days. The percent increase in internode length and total plant dry weight were calculated as $(X_{RB+B} - X_{RB}) / X_{RB}$, where X_{RB+B} is internode length or total dry weight of plants grown under blue-extended long day and X_{RB} is internode length or total dry weight of plants grown under short day.

increase was observed in cosmos compared to 36 % increase in diploid chrysanthemum (Fig. 11B). Similar increase in biomass with increased DLI were also reported in bedding plants (Faust et al., 2005).

Leaves of plants such as artemisia, stevia, and perilla are sources of specialized metabolites that have medicinal, aromatic, and culinary uses (Lu et al., 2017; Sadat Mirbehbahani et al., 2020; Myint et al., 2020). So, in these crops higher leaf biomass is desired compared to flowers. In this study, red-blue long day resulted in increased total dry weight (15 %) and higher leaf biomass in artemisia compared to red-blue short day (Figs. S7E and F), such increase in final yield is economically beneficial. In addition, there are explicit reports on the influence of light spectrum on the profiles of plant specialized metabolites grown under LED light systems. For instance, artemisia grown under blue light notably had higher content of two important bioactive compounds (artemisinin and artemisinic acid) responsible for antimalarial properties (Sankhuan et al., 2022). Similarly, in stevia long night interruption by red LED light sustained the vegetative growth that in turn linked to higher accumulation of steviol glycosides in the leaves (Ceunen et al., 2012). So, non-flowering responses of artemisia, stevia and perilla under red-blue long day and blue-extended long day is still seen as beneficial to grow these medicinal and therapeutic herbs under vertical farms with sole-source LED lighting (Mitchell and Sheibani, 2020; SharathKumar et al., 2020). Therefore, growing such medicinal crops in vertical farms offers a greater opportunity to produce plants with guaranteed quality that are rich with specific bioactive compounds. Taken together, these findings bring new opportunities to grow reliable high-value crops year round in emerging vertical farms, in which every environment factor including light spectrum is fully controlled to precisely regulate all plant growth and developmental process.

5. Conclusion

Several short-day species (artemisia - *Artemisia annua*, chrysanthemum - *Chrysanthemum seticuspe* and *Chrysanthemum morifolium*, cosmos - *Cosmos bipinnatus*, poinsettia - *Poinsettia pulcherrima* and wild tomato - *Solanum habrochaites*) showed normal flowering under blue-extended long days, although blue-extended long days resulted in flowering delay in cosmos, poinsettia, and wild tomato. For short-day plants that flowered under blue-extended long days with 15 % increased DLI, internode length was 6 to 48 % higher and total dry weight was 4 to 36 % higher, compared to short days. Therefore, we conclude that in short-day species, photoperiodic flowering under a dynamic light spectrum (11 h red-blue short day extended to a long day with 4 h blue light) is species dependent. Several short-day species

showed normal flowering under blue-extended long days, but this response is not universal for all short-day plants. Such dynamic LED lighting will be useful for developing species-specific light management programs for vertical farms. Furthermore, it opens the possibility to produce short-day plants by providing more hours of light through blue-extended long days without compromising their photoperiodic requirement for flowering.

This research highlights the potential of employing dynamic lighting, specifically 11 h of dichromatic red-blue light extended with 4 h of sole blue LED light, for year-round cultivation of short-day plants. This strategy can effectively bypass the short-day requirement when applied in indoor vertical farming setups that lack natural solar light. However, blue daylength extension in commercial greenhouse production where the short day consists of solar light does not lead to flowering in chrysanthemum (SharathKumar et al., 2021). Other broad-spectrum sources like high pressure sodium lamps (HPS), fluorescent, or white light warrants further investigation. Moreover, when incorporating blue extension, meticulous consideration of its interaction with natural sunlight or HPS lighting is essential.

CRediT authorship contribution statement

Malleshaiah SharathKumar: Conceptualization, Methodology, Investigation, Data curation, Visualization, Formal analysis, Writing – original draft. **Jingwen Luo:** Investigation, Data curation, Formal analysis. **Yu Xi:** Investigation, Data curation, Formal analysis. **Wim van Ieperen:** Writing – review & editing. **Leo F.M. Marcelis:** Resources, Project administration, Supervision, Writing – review & editing. **Ep Heuvelink:** Conceptualization, Methodology, Supervision, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.scienta.2023.112657.

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