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# Diverse Flowering Response to Blue Light Manipulation: Application of Electric Lighting in Controlled-Environment Plant Production

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**Abstract:** Blue light is an important light wavelength in regulating plant flowering. In a controlled environment (CE) plant production systems, blue light can be manipulated easily and even precisely through electric lighting, especially with the advancement of light-emitted diode (LED) technologies. However, the results of previous studies in the literature about blue-light-mediated flowering are inconsistent, which would limit its practical application in CE plant production while implying that an in-depth study of the relevant physiological mechanism is necessary in the future. This review consolidates and analyzes the diverse findings from previous studies on blue light-mediated plant flowering in varying high-value crops from ornamental plants to fruits, vegetables, and specialty crops. By synthesizing the contrasting results, we proposed the possible explanations and even the underlying mechanisms related to blue light intensity and exposure duration, its co-action with other light wavelengths, background environment conditions, and the involved photoreceptors. We have also identified the knowledge gaps based on these studies and outlined future directions for research and potential application in this promising field. This review provides valuable insights into the important and diverse role of blue light in plant flowering and offers a foundation for further investigations to optimize plant flowering through lighting technologies.

**Keywords:** high-value crops; light emitted diode; light intensity; light duration; light wavelengths; photoreceptors; physiological mechanisms; future directions

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## 1. Introduction

Flowering is a prerequisite physiological process for plants to produce blooms, fruits, and seeds; regulation (promotion or inhibition) of this process is necessary for change of harvesting time according to different production purposes [1]. The flowering process can be divided into two seemingly disparate phases: floral differentiation and floral development, and this process can be affected by environmental factors such as light [2].

Among the different light wavelengths, blue light (BL; 400–500 nm) has been shown to have a significant role in regulating various aspects of plant flowering. BL as an important photosynthetically active radiation (PAR) component can contribute to plant photosynthesis and thus provide a necessary carbon source for plant flowering. Also, BL can regulate the flowering process through its photoreceptors such as cryptochromes, through crosstalk with other photoreceptors such as phytochromes.

In controlled environments such as a greenhouse and vertical farm, BL can be more precisely manipulated through electric lighting, especially with the development of LED technology. Unlike traditional lighting, blue LEDs can provide narrow-band BL without containing other light wavelengths (i.e., pure BL), which can affect photoreceptors' activity differently from impure BL (i.e., normally including low-levels other wavelengths) from non-LED lighting [3]. Also, blue LEDs have become more and more efficient and inexpensive for commercial applications [4]. Consequently, LED technology makes it possible to

apply BL alone or in combination with other wavelengths to mediate plant growth and development (including flowering).

Like diverse plant elongation responses to BL as presented in our recent review [3], inconsistent results have also been reported on plant flowering response to the BL manipulation through electric lighting in the literature. This would affect its application in commercial plant production. Based on the existing literature as well as our research, this review summarizes and compares the relevant results, analyzes and explains the possible reasons, and identifies and suggests the knowledge gaps and future research directions. Also, this review focuses on the relevant application research rather than mechanistic research, in the controlled environment production of different crops, especially flowering plants.

## 2. Application of Electric Lighting to Manipulate BL in Ornamental Plant Flowering

Electric lighting has been increasingly used for controlled environment production of ornamental plants [5,6]. There are different ways to apply electric lighting in production such as night interruption lighting, day extension lighting, supplemental lighting, and sole-source lighting, for different production purposes.

### *2.1. Night Interruption Lighting*

Under short-day conditions, night interruption (NI) uses low-intensity (3–5 μmol $m^{-2}$ $s^{-1}$) lights from incandescent bulbs traditionally to break up a lengthy period of darkness, resulting in a long-day condition [7,8]. During short-day seasons, NI normally expedites the flowering of long-day plants, while inhibiting the flowering of short-day plants [7,8]. When BL is used for NI lighting, its effectiveness is dependent on lighting spectral (i.e., BL alone or its combination with other wavelengths), intensity, duration, as well as other factors such as daytime light conditions and plant genotype (Table 1).

**Table 1.** Effects of blue light manipulation through night interruption (NI) lighting on flowering and other traits of ornamental plants grown in a controlled environment.

| Plant Genotype | Lighting Treatments | Effects of Lighting Treatments on Plants | Reference(s) |
| --- | --- | --- | --- |
| Chrysanthemum (*Chrysanthemum* × *morifolium*) | 4 h NI lighting with blue LED at 10 μmol $m^{-2}$ $s^{-1}$ under 10 h short-day or 13 h long-day conditions created by daytime lighting with white LED at 180 μmol $m^{-2}$ $s^{-1}$ in a growth chamber. | The blue LED lighting did not inhibit flowering but promoted stem elongation, compared with no NI lighting.<br>The blue LED lighting caused plant flowering under either short-day or long-day conditions with similar flower number per plant, despite delayed flowering time and smaller flower size. | [9,10] |
| Chrysanthemum (*Chrysanthemum* × *morifolium*) | 4 h NI lighting with blue LED at 0.8 or 3.3 μmol $m^{-2}$ $s^{-1}$ under natural short-day inside a protected structure. | The blue LED lighting did not inhibit flowering, compared with no NI lighting. | [11] |
| Chrysanthemum (*Chrysanthemum* × *morifolium*) | 4 h NI lighting with blue LED at 39 μmol $m^{-2}$ $s^{-1}$ in a chamber under 12 h daytime lighting with white light at 150 μmol $m^{-2}$ $s^{-1}$.<br>4 h NI lighting with blue LEDs at 20 μmol $m^{-2}$ $s^{-1}$ in a chamber under 12 h daytime lighting with blue LED or RB-LED at 100 μmol $m^{-2}$ $s^{-1}$. | The NI lighting with blue LED at 39 μmol $m^{-2}$ $s^{-1}$ did not inhibit flowering under daytime lighting with white light, compared with no NI lighting; however, the blue LED lighting at 20 μmol $m^{-2}$ $s^{-1}$ strongly inhibited flowering under daytime lighting with blue LEDs rather than RB-LED. | [12] |
| Chrysanthemum (*Chrysanthemum* × *morifolium*) | 4 h NI lighting with blue LED at 10−40 μmol $m^{-2}$ $s^{-1}$ in growth chamber under sole-source daytime lighting with white light at 300 μmol $m^{-2}$ $s^{-1}$ PPFD for 10 h or 13 h daily. | The blue LED lighting at 40 μmol $m^{-2}$ $s^{-1}$ under 13 h photoperiod inhibited flowering, compared with no NI lighting under 10 h photoperiod.<br>The blue LED lighting at 10−30 μmol $m^{-2}$ $s^{-1}$ under 13 h photoperiod, or at 10−40 μmol $m^{-2}$ $s^{-1}$ under 10 h photoperiod delayed flowering time compared with no NI lighting under 10 h photoperiod.<br>For the lower-intensity (<40 μmol $m^{-2}$ $s^{-1}$) NI lighting, the flowering was gradually promoted with increasing PPFD from 10 to 30 μmol $m^{-2}$ $s^{-1}$ regardless of the daytime photoperiod. | [13] |

**Table 1.** *Cont.*

| Plant Genotype | Lighting Treatments | Effects of Lighting Treatments on Plants | Reference(s) |
|---|---|---|---|
| Chrysanthemum (*Chrysanthemum* × *morifolium*) | A total of 4 h NI lighting with 2 h blue LED first and then 2 h red LED or far-red LED (NI-B-R; or NI-B-FR), or a total of 4 h NI lighting with 2 h red LED or far-red LED first and then 2 h blue LED (NI-R-B; or NI-FR-B) at 10 μmol $m^{-2}$ $s^{-1}$ in an indoor condition with daytime lighting from white LED at 180 μmol $m^{-2}$ $s^{-1}$ for 10 h $d^{-1}$. | Flowering was observed in the NI-R-B rather than NI-B-R. However, both NI treatments (NI-B-FR and NI-FR-B) promoted flowering to a greater degree than NI-R-B. | [14] |
| Chrysanthemum (*Chrysanthemum* × *morifolium*), and marigold | 4 h NI lighting with blue LED at 1, 15, or 30 μmol $m^{-2}$ $s^{-1}$ under natural 9 h short-day condition in a greenhouse, | The blue LED lighting at 30 μmol $m^{-2}$ $s^{-1}$ rather than 1 or 15 μmol $m^{-2}$ $s^{-1}$ delayed flowering by 15–20 d while promoting stem elongation, compared with no NI lighting. | [15] |
| Chrysanthemum (*Chrysanthemum* × *morifolium*), cosmos (*Cosmos sulfureus*), dahlia (*Dahlia pinnata*), marigold (*Tagetes erecta*), dianthus (*Dianthus chinensis*), rudbeckia (*Rudbeckia hirta*) | 4 h NI lighting with blue LED at 1.5 μmol $m^{-2}$ $s^{-1}$ under natural 9 h short-day conditions in a greenhouse. | The blue LED lighting did not inhibit flowering in short-day plants including chrysanthemum, cosmos, dahlia, and marigold, and did not promote flowering in long-day plants such as dianthus and rudbeckia, compared with no NI lighting. | [16] |
| Chrysanthemum (*Chrysanthemum* × *morifolium*), cosmos (*Cosmos sulfureus*), dahlia (*Dahlia pinnata*,'Leanne' and 'Gallery Pablo'), marigold (*Tagetes erecta*); dianthus (*Dianthus chinensis*), and rudbeckia (*Rudbeckia hirta*) | 4 h NI lighting with a mixture of blue and far-red LEDs (BFR; 51% blue), or a mixture of blue and red LED (RB-LED; 48% blue) at 1.5 μmol $m^{-2}$ $s^{-1}$ under natural 9 h short-day condition in a greenhouse. | The BFR-LED lighting inhibited flowering in short-day plants, marigold, and dahlia 'Leanne', but not in chrysanthemum or dahlia 'Gallery Pablo' and promoted flowering in long-day plant, rudbeckia. The RB-LED lighting inhibited flowering in all short-day plants except chrysanthemum and promoted the flowering of most long-day plants tested. | [16,17] |
| Cyclamen (*Cyclamen persicum* Mill.) | 4 h NI lighting with blue LED, or RB-LED (50% Blue) at a PPFD of 4 μmol $m^{-2}$ $s^{-1}$ under natural 9 h short-day condition in a greenhouse. | The RB-LED lighting promoted flowering of this quantitative long-day genotype, compared with no NI lighting. | [18] |
| Geranium (*Pelargonium*× *hortorum*) | 4 h NI lighting with blue LEDs at 10 μmol $m^{-2}$ $s^{-1}$ in a chamber under daytime lighting with white LED at 180 μmol $m^{-2}$ $s^{-1}$ for 10 h daily. | The NI lighting promoted plant flower initiation by 5 days, and increased flower stalk length while increasing plant height and enlarging total leaf area. The NI lighting did not affect flowering plant percentage nor flower number per plant, compared with no NI lighting treatment. | [19] |
| Godetia (*Godetia* cvs.), petunia (*Petunia*×*hybrida* Vilm.), perilla (*Perilla ocymoides* L.), cosmos (*Cosmos bipinnatus* Cav.), yellow cosmos (*Cosmos sulphureus* Cav.), zinnia (*Zinnia elegans* Jacq.), and Japanese morning glory (*Pharbitis nil* Choisy) | 2 h NI lighting with blue LED at 8–10 μmol $m^{-2}$ $s^{-1}$ under short-day season (late autumn to early spring) in a greenhouse. | The blue LED lighting inhibited flowering only in perilla, a short-day plant, but not in other three long-day plant genotypes and four short-day genotypes, compared with no NI lighting. | [20] |
| Kalanchoe (*Kalanchoe blossfeldiana*) | 4 h NI lighting with blue LED at 10 μmol $m^{-2}$ $s^{-1}$ in an indoor condition with daytime lighting from white LEDs at a PPFD of 300 μmol $m^{-2}$ $s^{-1}$ for 10 h or 13 h. | The blue LED lighting caused plant flowering only under short day (10 h) rather than under long day (13 h) conditions. | [7] |
| Lisianthus (*Eustoma grandiflorum*) | 5 h NI lighting with blue LED at 5 μmol $m^{-2}$ $s^{-1}$ under natural short-day conditions (11–12.5 h $d^{-1}$) in a greenhouse. | The blue LED lighting caused earlier flowering in this long-day plant genotype, compared with no NI lighting, despite decreased cut flower length and stem length. | [21] |
| Petunia (*Petunia* × *atkinsiana*), rudbeckia (*Rudbeckia hirta*), and Tickseed (*Coreopsis grandiflora*) | 4 h NI lighting with blue LED at 3.3 μmol $m^{-2}$ $s^{-1}$ under natural 9 h short-day condition in a greenhouse. | The blue LED lighting did not promote flowering in long-day plants such as petunia, rudbeckia, and tickseed, compared with no NI lighting. | [22] |

Note: LED = light emitting diodes; RB = mixture of red and blue light; PPFD = photosynthetic photon flux density.

2.1.1. BL Alone

In some plant genotypes, low-intensity BL is not an effective NI light signal to regulate plant flowering. Under short-day conditions in the greenhouse, 4 h NI lighting with blue LED at 1.5 μmol $m^{-2}$ $s^{-1}$ was not perceived as a long day by the tested short-day plants including chrysanthemum, cosmos, dahlia, and marigold, and long-day plants such as dianthus and rudbeckia due to failing to regulate flowering in these plants [16]. Similarly, a 4 h NI lighting provided by blue LEDs at 3.3 μmol $m^{-2}$ $s^{-1}$ was not perceived as a long-day signal by the long-day plants such as petunia, rudbeckia, and tickseed in a greenhouse under natural short-day conditions because of no promotional effects on their flowering [22]. Also, a long-day treatment with 4 h NI lighting from blue LED at 10 μmol $m^{-2}$ $s^{-1}$ did not inhibit flowering in chrysanthemum, an obligate short-day plant, grown in a chamber [9,10]. Furthermore, in some short-day plants, chrysanthemum, dahlia, and African marigold, BL was not needed to interrupt the long night to inhibit flowering, but a moderate to high red/far-red (R: FR) ratio of light was most effective at interrupting the night [23].

In some other plant genotypes, but not for all, low-intensity blue LED light, like an incandescent light, can also be effective as an NI lighting source for regulating flowering. For example, a 4 h NI lighting provided by blue LEDs at 4 μmol $m^{-2}$ $s^{-1}$ promoted flowering in cyclamen, a quantitative long-day genotype, compared with the short-day treatment without NI lighting [18]. Another long-day plant, lisianthus flowered earlier under a 5 h NI lighting with blue LEDs at 5 μmol $m^{-2}$ $s^{-1}$ compared with ambient short-day conditions without an NI lighting [21]. However, among three long-day plant genotypes and five short-day genotypes growing in a greenhouse under natural short-day conditions, only perilla, a short-day plant, showed inhibited flowering by a 3 h NI lighting with blue LEDs at 8–10 μmol $m^{-2}$ $s^{-1}$ [20]. Possibly, the effective BL intensities for NI lighting varied with plant genotype, which has been supported by a study on some long-day plant genotypes [24].

It has been found that, unlike red light, BL can influence flowering only when delivered with sufficiently high intensities as NI lighting but is ineffective in regulating flowering at low intensities [6]. A 4 h NI lighting provided by blue LEDs at 0.8 or 3.3 μmol $m^{-2}$ $s^{-1}$ was not perceived as a long-day signal by chrysanthemum plants because of no inhibitory effects on the flowering [11]. Also, a 4 h NI lighting with blue LEDs at 10 μmol $m^{-2}$ $s^{-1}$ failed to inhibit the flowering of chrysanthemums [9,10]. However, 4 h NI lighting with blue LED at 30 μmol $m^{-2}$ $s^{-1}$ rather than a lower intensity (1 or 15 μmol $m^{-2}$ $s^{-1}$) delayed flowering in chrysanthemum as well as marigold in a greenhouse under short-day conditions [15].

In addition to NI lighting intensity, under short-day conditions, the effectiveness of BL for NI is also affected by daytime light quality. For chrysanthemum growing in a chamber, a 4 h NI lighting with blue LEDs did not inhibit flowering when daytime lighting was delivered by white light [12]. However, a 4 h NI lighting with blue LEDs strongly inhibited flowering, when daytime lighting was provided by blue LEDs rather than RB-LED [12]. Blue LED had a lower phytochrome photostationary state (PPS) than white light and RB-LED. It appeared that, as an NI lighting source, blue LED was not effective when daytime lighting created a high phytochrome activity in the plant. This suggested that light quality during the daytime affected the sensitivity to NI lighting at midnight. Possibly, at least two distinct phytochrome-mediated flowering regulation systems might exist during daytime and nighttime [25].

Besides NI lighting intensity and daytime light quality, flowering mediated by NI lighting with BL is also affected by daytime light duration (i.e., main photoperiod), showing an interaction between NI light intensity and daytime light duration. For chrysanthemum in a growth chamber, the flowering was completely inhibited by 4 h NI lighting with blue LED at 40 μmol $m^{-2}$ $s^{-1}$ under 13 h main photoperiod, but not by that at 10−30 μmol $m^{-2}$ $s^{-1}$ under 13 h main photoperiod nor by that at 10−40 μmol $m^{-2}$ $s^{-1}$ under 10 h main photoperiod [13]. However, for the lower-intensity (<40 μmol $m^{-2}$ $s^{-1}$) NI lighting, the flowering was gradually promoted with increasing lighting intensities from 10 to 30 μmol $m^{-2}$ $s^{-1}$ regardless of the main photoperiod, [13]. For NI lighting in this genotype, it appeared

that there was a complicated interaction between BL intensity and daytime duration to act on flowering.

Whether the effectiveness of BL for NI is affected by daytime light duration is also dependent upon plant genotypes even if they have the same photoperiodism. In kalanchoe, a qualitative short-day plant grown indoors, plants under 4 h NI lighting with blue LED flowered only under short day (10 h) rather than under long day (13 h) conditions [7]. However, in another qualitative short-day plant chrysanthemum grown under 4 h NI lighting with blue LED flowered in all plants under either short-day (10 h) or long-day (13 h) conditions [10].

Limited information is available on the effects of blue LED for NI on day-neutral plants. For geranium grown in a chamber under 10 h short-day conditions, a 4 h NI lighting with blue LEDs showed more pronounced effects on morphogenesis than on flowering [19]. Compared with short-day treatment, NI lighting with blue LED promoted plant flower initiation, and increased flower stalk length while increasing plant height and enlarging total leaf area, but did not affect flowering plant percentage nor flower number per plant [19].

#### 2.1.2. BL in Combination with Other Light Wavelength(s)

In addition to BL alone, a combination of BL with other light wavelength(s) can also be used for NI lighting, and its effectiveness at flowering regulation varies with NI light spectral quality and plant genotypes. For example, a 4 h NI lighting with a mixture of blue and far-red LEDs (51% blue) was perceived as a long-day signal by short-day plants, marigold and dahlia 'Leanne', but not by chrysanthemum or dahlia 'Gallery Pablo' and by a long-day plant, rudbeckia, under short-day conditions [16,17]. However, a 4 h NI lighting with a mixture of blue and red LEDs (RB-LED; 48% blue) promoted the flowering of most long-day plants tested [17]. Similarly, under short-day conditions, a 4 h NI lighting with RB-LED (50% Blue) was effective at promoting the flowering of cyclamen, a quantitative long-day genotype [18]. Also, 4 h NI with RB-LED (48% blue) was effective at inhibiting flowering by creating a long day for all short-day plants except chrysanthemum, suggesting varying sensitivity among plant genotypes [16].

When BL is applied with red light sequentially for NI lighting under short-day conditions, the effectiveness of BL for NI lighting is affected by its application time frame. For example, chrysanthemum plants grown indoors under short-day conditions were provided a total of 4 h NI lighting, using 2 h blue LEDs first and then 2 h red LEDs (NI-B-R), or 2 h red LEDs first and then 2 h blue LEDs (NI-R-B). Flowering was observed in the NI-R-B rather than NI-B-R. However, when blue LED is applied with far-red LED sequentially for NI lighting, both NI treatments (NI-B-FR and NI-FR-B) promoted flowering to a greater degree than NI-R-B [14]. Both blue and far-red LED had lower PPS values (<0.5) than red LED (>0.8), and could potentially cause inactive phytochrome responses in plants and reverse the effects of red LEDs [26,27]. It appeared that the effects of NI lighting using the combination of BL with other wavelengths on plant flowering might be related to the final phytochrome activity after NI lighting.

### *2.2. Day Extension Lighting*

In addition to NI lighting, day extension (DE) lighting can also create long day conditions through prolonging photoperiod to regulate plant flowering. Differing from NI lighting delivered in the middle of the night (from 10:00 pm to 2:00 am), DE lighting is normally started before the sun sets and kept on until the desired day length is achieved. In short-day conditions, BL alone or its combination with other wavelengths can be used for DE lighting (Table 2).

**Table 2.** Effects of blue light manipulation through day extension (DE) lighting on flowering and other traits of ornamental plants grown in a controlled environment.

| Plant Genotype | Lighting Treatments | Effects of Lighting Treatments on Plants | Reference(s) |
|---|---|---|---|
| Chrysanthemum (*Chrysanthemum* × *morifolium*) | Overnight or shortened-time (14 h $d^{-1}$) DE lighting with blue LED at about 20 μmol $m^{-2}$ $s^{-1}$ in high tunnels covered with shading nets. | Overnight DE lighting resulted in inhibition of flowering and had no significant effect on their growth, but failed to prevent flowering when DE lighting time was shortened to 14 h $d^{-1}$. | [28] |
| Chrysanthemum (*Chrysanthemum* × *morifolium*) | 4 h DE lighting treatment with blue LED of 10 μmol $m^{-2}$ $s^{-1}$ in a chamber under 9 h daytime lighting with white LED at a PPFD of 180 μmol $m^{-2}$ $s^{-1}$. | The blue LED lighting did not delay flowering time nor reduce flower number compared with no DE lighting, despite increased plant height, leaf number, and leaf area. | [10] |
| Chrysanthemum (*Chrysanthemum* × *morifolium*) | 4 h DE lighting with blue LED at about 70 μmol $m^{-2}$ $s^{-1}$ in a chamber under 12 h daytime lighting with white fluorescent light at 70 μmol $m^{-2}$ $s^{-1}$. | The blue LED lighting did not inhibit flowering compared with no DE lighting. | [29] |
| Chrysanthemum (*Chrysanthemum* × *morifolium*) | 4 h DE lighting or 13 h overnight lighting with blue LED at 100 μmol $m^{-2}$ $s^{-1}$ in a chamber under 11 h daytime lighting with RB-LED (20% B) at 100 μmol $m^{-2}$ $s^{-1}$. | The blue LED lighting did not inhibit flowering but did promote stem elongation compared to no DE lighting or no overnight lighting. | [30,31] |
| Chrysanthemum (*Chrysanthemum* × *morifolium*) | 4 h DE lighting with blue LED at 40 μmol $m^{-2}$ $s^{-1}$ under an 11 h short-day condition in a greenhouse with daytime solar light or in a growth chamber with daytime lighting from RB-LEDs (40% B) at a PPFD of 100 μmol $m^{-2}$ $s^{-1}$. | The blue LED lighting inhibited flowering of plants grown in a greenhouse, but not those in a growth chamber, despite an increased stem length in both greenhouse and chamber | [32] |
| Chrysanthemum (*Chrysanthemum* × *morifolium*) | 4 h DE lighting with blue LED at 60 μmol $m^{-2}$ $s^{-1}$ under an 11 h short-day indoor condition created by RB-LED, RBFR-LED or RBG-LED light at flux density of 180 μmol $m^{-2}$ $s^{-1}$. | The DE lighting with blue LED inhibited flowering when RBFR-LED rather than RBG-LED was used for the daytime lighting. | [33] |
| Coreopsis (*Coreopsis grandiflora*), snapdragon (*Antirrhinum majus*), petunia (*Petunia* × *atkinsiana*), and rudbeckia (*Rudbeckia hirta*) | 7 h DE lighting or 4 h NI lighting with blue LED at 5−30 μmol $m^{-2}$ $s^{-1}$ in a greenhouse under natural short-day conditions (9 h $d^{-1}$). | At a sufficiently high intensity, blue LED delivered as a 7 h DE lighting or 4 h NI lighting promoted the flowering of all four genotypes compared to no DE or NI lighting. The threshold intensity of BL was 5 μmol $m^{-2}$ $s^{-1}$ for coreopsis and snapdragon, and 15 μmol $m^{-2}$ $s^{-1}$ for petunia and rudbeckia. | [24] |
| Impatiens (*Impatiens hawkerihybrid*) | DE lighting with blue LED at 1052 μmol $m^{-2}$ $s^{-1}$, red LED at 955 μmol $m^{-2}$ $s^{-1}$, or RB-LED (20% B) at 867 μmol $m^{-2}$ $s^{-1}$ for 2 or 4 h daily in a greenhouse under short-day season. | Compared with blue LED alone, RB-LED delayed flowering when delivered as 2 h or 4 h DE lighting, despite increased the number of flower buds and open flowers when delivered as 4 h DE lighting.<br>Compared with blue LED alone, RB-LED reduced plant height, leaf area, and aboveground biomass, especially when delivered as 2 h DE lighting. | [34] |
| Kalanchoe (*Kalanchoe blossfeldiana*), perilla (*Perilla frutescens*), stevia (*Stevia rebaudiana*), artemisia (*Artemisia annua*), chrysanthemum (*Chrysanthemum morifolium*), cosmos (*Cosmos bipinnatus*), and poinsettia (*Poinsettia pulcherrima*) | 4 h DE lighting with blue LED at 40 μmol $m^{-2}$ $s^{-1}$ in an indoor environment under short (11 h) daytime lighting with RB-LED (40% B) at 100 μmol $m^{-2}$ $s^{-1}$. | The blue LED lighting inhibited flowering for kalanchoe, perilla, and stevia, but did not for artemisia, chrysanthemum, cosmos, or poinsettia compared to short-day treatment, despite a flowering delay in cosmos, and poinsettia among these short-day genotypes. | [35] |
| Okra [*Abelmoschus esculentus* (L.) Moench.] | 12 h DE lighting or 4 h NI lighting with blue LEDs at 4 μmol $m^{-2}$ $s^{-1}$ in an indoor condition under daytime lighting from fluorescent lamps at 200 μmol $m^{-2}$ $s^{-1}$ for 6−8 h $d^{-1}$. | The blue LEDs delayed flowering in this short-day genotype when delivered as 12 h DE lighting but did not when delivered as 4 h NI lighting, compared to short-day treatment with no DE or NI lighting. | [36] |

Note: LED = light emitting diodes; RB = mixture of red and blue light; RBFR = mixture of red, blue and far-red light; RBG = mixture of red, blue, and green light; PPFD = photosynthetic photon flux density.

2.2.1. BL Alone

Delivering BL as DE lighting or NI lighting may result in different flowering responses in some genotypes. For example, for okra, a short-day plant, grown indoors under short-day treatment, 4 μmol $m^{-2}$ $s^{-1}$ of blue LEDs delayed flowering when delivered as 12 h DE lighting but did not when delivered as 4 h NI lighting [36]. Possibly, in this genotype, the sensitivity of flowering response to BL was related to lighting amount (lighting duration × lighting intensity) rather than the ways of prolonged-photoperiod lighting (i.e., DE lighting or NI lighting). A similar dependence of BL effectiveness for flowering on the lighting amount was also found in another short-day plant under DE lighting. For chrysanthemums growing in high tunnels covered with shading nets, overnight DE lighting with blue LEDs at about 20 μmol $m^{-2}$ $s^{-1}$ inhibited flowering, but failed to prevent flowering when DE lighting time was shortened to 14 h $d^{-1}$ [28].

The dose–response relationship between prolonged-photoperiod lighting with BL and its effectiveness at flowering regulation has been also identified in some long-day plants. For coreopsis, snapdragon, petunia, and rudbeckia grown in a greenhouse under natural short-day conditions, at a sufficiently high intensity, blue LED delivered as a 7 h DE lighting or 4 h NI lighting promoted the flowering of all four genotypes compared to no DE or NI lighting [24]. The threshold (minimum) intensity of BL was 5 μmol $m^{-2}$ $s^{-1}$ for coreopsis and snapdragon, and 15 μmol $m^{-2}$ $s^{-1}$ for petunia and rudbeckia, which was higher than that of red + far-red light (2–3 μmol $m^{-2}$ $s^{-1}$) when delivered as prolonged-photoperiod lighting [24]. Possibly, BL receptors' function on flowering induction depends more on light intensity, compared with the photoreceptors of red + far-red light.

Differently, for chrysanthemums growing indoors under short-day daytime lighting, the flowering response to DE lighting with BL seems to be independent of BL amount (either light intensity or light duration), since DE lighting with blue LED that extends total photoperiod to longer than critical day length cannot inhibit flowering while promoting stem elongation, when delivered at a light intensity varying from 10 to 100 μmol $m^{-2}$ $s^{-1}$. For example, a 4 h DE lighting treatment with blue LED of 10 μmol $m^{-2}$ $s^{-1}$ after 9 h daytime lighting did not delay flowering time and reduce flower number compared with no DE lighting, despite increased plant height [10]. Also, a 4 h DE lighting with BL at about 70 μmol $m^{-2}$ $s^{-1}$ did not inhibit the flowering of chrysanthemum growing under 12 h daytime lighting [29]. Furthermore, a 4 h DE lighting or 13 h overnight lighting with blue LED at 100 μmol $m^{-2}$ $s^{-1}$ did not inhibit flowering but did promote stem elongation for plants growing under 11 h daytime lighting [30,31].

It appears that blue LED can potentially be used as a DE lighting source during short-day conditions for controlled environment production of cut chrysanthemum flowers to promote stem elongation with no inhibition of flowering. Chrysanthemums are quantitative short-day plants that flower uniformly when the critical day-length photoperiod is ≈13.5 h or less but fail to flower under longer photoperiods than the critical day length [31]. The grading standards for cut chrysanthemum on the world market require an elongated and unbranched plant shape and large-sized flowers [5]. Due to the required stem length specification in cut chrysanthemum production, artificially long days are maintained routinely for 2–3 weeks before the onset of short days [31]. Although the long-day treatment guarantees a sufficient stem length, it delays the transition to flowering in cut chrysanthemum [31]. In this case, DE lighting with blue LED may address this issue.

It is worthwhile to note that different flowering responses were found in chrysanthemums growing under electrical lighting and solar light during the daytime. Under short-day conditions, 4 h DE lighting with blue LED inhibited chrysanthemum flowering in a greenhouse with daytime solar light, but not in a growth chamber with daytime lighting from RB-LEDs (40% B), despite an increased stem length in both greenhouse and chamber [32]. This contrasting flowering response to DE lighting from blue LED might have resulted from different daytime spectral qualities, which was also observed for NI lighting mentioned before [12]. A recent indoor study indicated that the inclusion of FR light, but not a green light, in the daytime lighting was necessary for 4 h DE lighting with

blue LED to inhibit flowering in chrysanthemums [33]. It appeared that a high daytime phytochrome activity might have prevented chrysanthemum perception of subsequent BL as a long-day signal [33].

The flowering response in chrysanthemums to DE lighting with BL is not universal but varies with genotype even if they are short-day plants. For some short-day genotypes growing indoors under short-day daytime lighting with RB-LED (40% B), 4 h DE lighting with blue LED inhibited flowering for kalanchoe, perilla, and stevia, but not for artemisia, chrysanthemum, cosmos, or poinsettia compared to short day treatment despite a flowering delay in cosmos, and poinsettia [35]. Also, the plants under 4 h DE lighting with blue LED resulted in a 4% to 36% increase in total dry weight. It appeared that increasing growth rate under short-day conditions through DE lighting with BL, without compromising flowering and quality, was possible for some, but not all short-day genotypes.

#### 2.2.2. BL in Combination with Other Light Wavelengths

When delivered as DE lighting, a combination of BL with high-level (e.g., 80%) red light (i.e., RB-light) differs from BL alone in its effect on plant flowering and other traits. In a study on impatiens, a day-neutral plant, compared with blue LED alone, RB-LED delayed flowering when delivered as 2 h or 4 h DE lighting, despite an increased number of flower buds and open flowers when delivered as 4 h DE lighting [34]. Also, compared with blue LED alone, RB-LED reduced plant height, leaf area, and aboveground biomass, especially when delivered as 2 h DE lighting [34]. It appeared that DE lighting with RB-light and BL were perceived by plants as different photoperiod signals, which may be related to different involved key photoreceptors as well as their different activities.

When delivered as DE lighting, a combination of BL with low levels of other wavelength(s) (i.e., impure BL) and BL alone (i.e., pure BL) can affect plant flowering differently, despite varying sensitivity among plant genotypes. In one of our recent unpublished studies, we treated chrysanthemum (obligate short-day plant), geranium (day-neutral plant), calibrachoa (facultative long-day plant), and gerbera (facultative short-day plant) plants in a greenhouse using 4 h DE lighting with pure BL, i.e., blue LED (PPS = 0.47) or impure BL, i.e., a combination of blue, red, and FR LEDs (94% B; PPS = 0.66) during winter. In chrysanthemums, pure BL slightly delayed flowering time and increased flower bud number, and impure BL inhibited flower initiation, compared with no DE lighting. In calibrachoa, both DE lighting treatments promoted earlier flowering compared with no DE lighting, but impure BL had a greater promotion effect on the number of flower buds than pure BL. In geranium, both DE lighting treatments did not affect flowering initiation time, but increased flower bud size compared with no DE lighting treatment. In gerbera, both DE lighting treatments did not affect flowering initiation time or flower size compared with no DE lighting. It appeared that BL in combination with low levels of other light wavelengths might have changed phytochrome activity based on PPS values and thus shows different flowering responses for the same plant genotype.

### *2.3. Supplemental Lighting*

When the daytime light level is low, supplemental lighting (SL) is normally used for increasing light amount to compensate for insufficient photo-assimilates, while changing spectral quality and extending photoperiod if applied at nighttime. BL can be applied alone or combined with other light wavelength(s) as an SL source during daytime or nighttime in a greenhouse or indoor environment to regulate flowering as well as morphology in ornamental plants, based on production purposes (Table 3).

**Table 3.** Effects of blue light manipulation through supplemental lighting (SL) on flowering and other traits of ornamental plants grown in a controlled environment.

| Plant Genotype | Lighting Treatments | Effects of Lighting Treatments on Plants | Reference(s) |
|---|---|---|---|
| Chrysanthemum (*Chrysanthemum* × *morifolium*) | Pre-dark SL with blue LED at 10 μmol $m^{-2}$ $s^{-1}$ for 4 h in an indoor environment under 13 h daytime lighting with white LED at a PPFD of 180 μmol $m^{-2}$ $s^{-1}$. | The SL with blue LED promoted flowering and increased plant height, compared with no SL treatment. | [10] |
| Chrysanthemum (*Chrysanthemum* × *morifolium*) | Pre-dark SL with blue LED at 10−40 μmol $m^{-2}$ $s^{-1}$ for 4 h in an indoor environment under daytime lighting with white light at a PPFD of 300 μmol $m^{-2}$ $s^{-1}$ for 10 h or 13 h daily. | The blue LED light at 10−30 μmol $m^{-2}$ $s^{-1}$ did not affect flowering compared with no SL treatment under 10 h main photoperiod, but promoted flowering compared with no SL treatment under 13 h main photoperiod. Also, for blue LED lighting, the flowering was gradually promoted from 10 to 30 μmol $m^{-2}$ $s^{-1}$ PPFD and inhibited by 40 μmol $m^{-2}$ $s^{-1}$ PPFD regardless of the photoperiod. | [13] |
| Chrysanthemum (*Chrysanthemum* × *morifolium*) | Pre-dark SL with blue LED at 30 μmol $m^{-2}$ $s^{-1}$ for 4 h every 1−7 day in an indoor environment under daytime lighting with white light at a PPFD of 300 μmol $m^{-2}$ $s^{-1}$ for 10 h or 13 h daily. | Under 13 h main photoperiod, the number of flowers increased, and the flower buds appeared earlier as the proportion of SL days increased, despite the earliest flowering in no SL treatment under short-day (10 h) conditions. | [37] |
| Chrysanthemum (*Chrysanthemum* × *morifolium*, 'Manatee Iceberg' and 'Naples') | Trial 1: 15 h nighttime SL with BL from coloured fluorescent light * at 3.6 or 7.0 μmol $m^{-2}$ $s^{-1}$ in a greenhouse under 9 h ambient light during daytime.<br>Trial 2: 6 h nighttime SL with BL from coloured fluorescent light at 0.4−3.5 μmol $m^{-2}$ $s^{-1}$ in a greenhouse under 9 h ambient light during daytime. | In trial 1, nighttime SL with BL at 3.6 μmol $m^{-2}$ $s^{-1}$ did not affect flower initiation, but the BL at 7.0 μmol $m^{-2}$ $s^{-1}$ delayed flowering compared with no SL. Also, in both BL intensities, flower size, and dry mass were less than those in the short-day regimes. Increasing the dose of BL decreased flower dry mass in 'Naples' by 60% and in 'Manatee Iceberg' by 72%. Plants were shorter with less vegetative mass in the short-day regimes.<br>In trial 2, 6 h nighttime SL with BL at 0.4−3.5 μmol $m^{-2}$ $s^{-1}$ did not affect flower dry mass or vegetative dry mass compared with no SL treatment. | [38] |
| *Delphinium* | 12 h nighttime SL with blue LED, red LED of far-red LED light at 3 μmol $m^{-2}$ $s^{-1}$ in indoor conditions under 8 h daytime lighting with metal halide light at a PPFD of 214 μmol $m^{-2}$ $s^{-1}$. | The nighttime SL with blue LED promoted flowering compared with no SL but reduced the number of spikes, and total florets without affecting cut flower length. Compared with red LED, the promotional effect of blue LED on flowering was less in 'Aurora Light Blue' and was greater in 'Super Grand Blue'. Compared with far-red LED, the promotional effect of blue LED on flowering was less in both cultivars. | [39] |
| *Eustoma grandiflorum* | Overnight SL with blue LED at 8.8 μmol $m^{-2}$ $s^{-1}$, or far-red LED at 10 μmol $m^{-2}$ $s^{-1}$, in a phytotron under 8 h short-day natural light conditions. | For this long-day plant, flower budding was promoted by the nighttime SL with blue LED, compared with no SL, but the flower budding with blue LED was later than those with far-red LED. | [40] |
| Geranium (*Pelargonium* × *hortorum*) | SL using RB-LED with 45% B at 90 μmol $m^{-2}$ $s^{-1}$ for 16 h $d^{-1}$ in a greenhouse. | SL using RB-LED promoted early flowering and flower number, as well as canopy compactness, compared with HPS. | [41] |
| Gerbera (*Gerbera jamesonii*) | Daytime SL with RB-LED (15% B) or HPS at a PPFD of 56 μmol $m^{-2}$ $s^{-1}$ for 11.5 h daily in a greenhouse. | Plants under the SL with RB-LED had a 2% larger flower diameter in 'Acapulco', compared to those in HPS treatment, despite no differences in total or marketable flower numbers.<br>SL with the RB-LED resulted in 4% shorter and longer stems in 'Heatwave' and 'Terra Saffier', respectively; and 8% and 9% higher fresh weights for 'Acapulco' and 'Terra Saffier', respectively | [42] |
| Godetia (*Clarkia amoena*), snapdragon (*Antirrhinum majus*), and stock (*Matthiola incana*) | SL with blue LED, red LED, or LED combinations (B20R85FR15, and B20G50R45FR5), or HPS at a PPFD of 120 μmol $m^{-2}$ $s^{-1}$ (for 12 h daily for a month and then for 16 h daily to induce flower) in a greenhouse. | SL with B20R85FR15 resulted in earlier flowering by 10–15 days depending on genotypes compared with red LED and showed no difference from the blue LED and HPS. B20R85FR15, as well as blue LED and HPS, caused shorter cut flowers than red LED. B20G50R45FR5 slightly delayed flowering time relative to B20R85FR15 and promoted earlier flowering than red LED.<br>Stem caliper was up to 14% thinner for stock grown under SL with blue LED compared to the other treatments. Flower petal color was not commercially different between SL treatments. | [43] |

**Table 3.** *Cont.*

| Plant Genotype | Lighting Treatments | Effects of Lighting Treatments on Plants | Reference(s) |
|---|---|---|---|
| *Gypsophila paniculata* | 15 h nighttime SL with blue LED or far-red LED at 20−30 μmol $m^{-2}$ $s^{-1}$ under 9 h short-day natural light conditions. | For this long-day plant, the nighttime SL with blue LED did not promote flowering, but far-red LED did, compared with no SL | [44] |
| Kalanchoe (*Kalanchoe blossfeldiana*) | Pre-dark SL with blue LED at 10 μmol $m^{-2}$ $s^{-1}$ for 4 h in an indoor environment under 10 h or 13 h daytime lighting with white LEDs at a PPFD of 300 μmol $m^{-2}$ $s^{-1}$. | The SL with blue LED promoted flowering and enhanced plant growth regardless of photoperiod compared with no SL, with a greater promotional effect on flowering in the long day condition. | [7] |
| Kalanchoe (*Kalanchoe blossfeldiana*) | Daytime SL with blue LED at 100 μmol $m^{-2}$ $s^{-1}$ for 12 h $d^{-1}$ or nighttime SL with blue LED at 100 μmol $m^{-2}$ $s^{-1}$ for 7 h $d^{-1}$ in a greenhouse under short-day natural light conditions. | Daytime SL with blue LED accelerated the flowering equally for the early cultivar ('Cora') or more for the late cultivar ('Arena') compared with no SL, while there was no flowering under SL with red or green LED. Nighttime SL with blue LED at 100 μmol $m^{-2}$ $s^{-1}$ for 7 h $d^{-1}$ completely inhibited flowering similarly to other LEDs compared with no SL. | [45] |
| Marigold (*Tagetes patula*) | SL with low-blue RB-LED (25% B), high-blue RB-LED (50% B), or HPS light at 100 μmol $m^{-2}$ $s^{-1}$ for 24 h $d^{-1}$ in a greenhouse. | SL with low-blue RB-LED caused 15% more blooms than high-blue RB-LED, or HPS, although the latter two SL treatments also produced more blooms than no SL treatment. Also, low-blue RB-LED increased shoot growth compared with the HPS treatment, but high-blue RB-LED was not different from the HPS treatment. Plants in both RB-LED light treatments had greater petal pigment content than plants in the no-SL treatment. | [46] |
| Morning glory (*Pharbitis nil*) | Daytime SL using blue LEDs with various peak wavelengths from 400−495 nm at 100 μmol $m^{-2}$ $s^{-1}$ in an indoor environment under white lighting at 20 μmol $m^{-2}$ $s^{-1}$ for 13 h $d^{-1}$. | The blue LED of 450 nm was the most effective wavelength in promoting flowering among various peak wavelengths. | [47] |
| Orchid (*Phalaenopsis*) | Daytime SL with blue LED or red LED at 7 μmol $m^{-2}$ $s^{-1}$ (10% of total PPFD) in a growth chamber under white fluorescent lamps at 14 h photoperiod. | The blue LED did not differ in flowering time from no SL treatment. The blue LED delayed flowering, and caused a lower spiking ratio, and reduced spike length compared to red LED, despite resulting in similar chlorophyll concentrations and soluble sugar levels in the leaf. | [48] |
| Petunia (*Petunia* × *atkinsiana*) | Daytime SL with blue LED, red LED, or high-pressure sodium (HPS) light at 50 μmol $m^{-2}$ $s^{-1}$ for 16 h $d^{-1}$ in a greenhouse under plastic film transmitting and not transmitting FR light during the period from early to late spring with a natural irradiance of 1.35 and 2.33 mol $m^{-2}$ $h^{-1}$. | In early spring, BL promoted flowering and increased plant height, causing a more upright shoot orientation, compared to HPS light. In late spring, BL in an FR-deficient environment did not differ from red light on the response to plant flowering and stem elongation. | [49] |
| Petunia (*Petunia* × *hybrida*), calibrachoa (*Calibrachoa* × *hybrida*), geranium (*Pelargonium* × *hortorum*), and marigold (*Tagetes erecta*) | 2 h pre-dark SL treatments with RB-LED (10−75% B) at 70 μmol $m^{-2}$ $s^{-1}$ in indoor conditions under daytime lighting from broad-spectrum LED with photon flux ratio of 1UVA:27B:37G:36R:33FR at a PPFD of 200 μmol $m^{-2}$ $s^{-1}$ for 14 h $d^{-1}$. | SL treatments with RB-LED did not affect flowering nor plant elongation compared with SL treatment with daytime-spectrum LED, except for a small decrease in plant height for petunia. Also, plant responses did not differ among RB-LEDs with different BL proportions. | [50] |
| Poinsettia (*Euphorbia pulcherrima*) | Daytime SL with RB-LED (20% B) or HPS lamp (5% B) at a PPFD of 100 μmol $m^{-2}$ $s^{-1}$ for 10 h daily in greenhouse | The SL with RB-LED did not delay bract color formation, visible cyathia or flowering, but produced 20–34% shorter plants, and decreased leaf and bract area, chlorophyll content, and total dry matter accumulation, compared with HPS. | [51] |
| Rose *(Rosa* × *hybrida)* | SL with RB-LED (20% B) or HPS (5% B) lamp at a PPFD of 100 μmol $m^{-2}$ $s^{-1}$ for 20 h $d^{-1}$ in a greenhouse. | The SL with RB-LED did not affect the time to open flowers and the total dry mass production, despite causing floral initiation at a higher leaf number and enhancing more compact plants, compared with HPS. | [52] |
| Tulip (*Tulipa* spp.) | 4 h nighttime SL with BL or white light from coloured fluorescent light at 30 μmol $m^{-2}$ $s^{-1}$ in a greenhouse (for 2 h before sunrise and 2 h after sunset). | The nighttime SL with BL rather than white light induced earlier flowering and improved flowering uniformity compared with no SL, despite no effects on flower morphology. | [53] |

Note: LED = light emitting diodes; HPS = high-pressure sodium; BL = blue light; RB = mixture of red and blue light; PPFD = photosynthetic photon flux density. * Coloured fluorescent lights emit a colored light with peak wavelength in the region of bule, red, or green by changing chemical components in the lamp.

2.3.1. BL Alone

The effect of daytime SL with low-intensity BL on the flowering of long-day ornamental plants in a greenhouse is dependent on the natural light level and the presence of FR light. For example, for petunia grown in a greenhouse under plastic film transmitting or not transmitting FR light, daytime SL with blue LED at 50 μmol $m^{-2}$ $s^{-1}$ promoted flowering, compared to high-pressure sodium (HPS) light, during early spring when the natural irradiance was low; however, in late spring, when the natural irradiance was higher, the effect of blue LED in an FR-deficient environment was not different from red LED on plant flowering [49].

For some short-day plants grown indoors under long-day conditions, whether daytime SL with BL can promote flowering depends on plant genotypes, which may differ in dominant photoreceptors for controlling flowering. For orchids grown in growth chambers under white fluorescent lamps, daytime SL with blue LED did not differ in flowering time from no SL treatment and delayed flowering compared to SL with red LED [48]. In addition to a lower spiking ratio, SL with blue LED also reduced spike length, compared to SL with red LED [48]. It appeared that whether the spiking of orchid was improved by daytime SL might be dependent on the relative amount of active phytochrome. However, for seedlings of morning glory, grown indoors under white lighting, daytime SL with blue LEDs of 450 nm was the most effective at promoting flowering among various peak wavelengths from 400−495 nm, and the flowering responses to different peak wavelengths corresponded to the absorption spectrum of cryptochromes [47]. Possibly, in morning glory, the activated cryptochrome by the daytime SL with BL might have promoted flowering as a strong stimulus over the critical day length.

Daytime SL with BL for several hours before dark (pre-dark SL) can promote flowering and improve the aesthetic value of some short-day ornamental plants grown indoors. For kalanchoe, a 4 h pre-dark SL with blue LED promoted flowering and enhanced plant growth compared with no SL, with a greater promotional effect on flowering in the long- vs. short day (13 h vs. 10 h) condition [7]. In chrysanthemum grown indoors under 13 h photoperiod, a 4 h pre-dark SL with blue LED promoted flowering with increased plant height, compared with no SL [10]. It appeared that it was possible to apply pre-dark SL with blue LED as an alternative method to using blackout curtains in long-day seasons to induce flowering of short-day plants.

It is worthwhile to note that the effect of pre-dark SL with BL on the flowering of short-day plants is affected by daytime duration (or main photoperiod), SL intensity, as well as SL duration. For chrysanthemums grown indoors, a 4 h pre-dark SL with blue LED at 10−30 μmol $m^{-2}$ $s^{-1}$ did not affect flowering compared with no SL treatment under 10 h main photoperiod but promoted flowering compared with no SL treatment under 13 h main photoperiod [13]. Also, under the blue LED lighting treatments, the flowering was gradually promoted when the PPFD increased from 10 to 30 μmol $m^{-2}$ $s^{-1}$ but inhibited when the PPFD increased up to 40 μmol $m^{-2}$ $s^{-1}$ regardless of the photoperiod [13]. In addition, when blue LED light of 30 μmol $m^{-2}$ $s^{-1}$ was applied as 4 h pre-dark SL under 13 h main photoperiod at different intervals (from once every 7 days to once every day), the number of flowers increased and the flower buds appeared earlier as the proportion of SL days increased [37].

In short-day plants, daytime and nighttime SL with modest-intensity BL have different effects on flowering. For kalanchoe, grown in a greenhouse under short-day natural light conditions, daytime SL with blue LED at 100 μmol $m^{-2}$ $s^{-1}$ accelerated flowering compared with SL with red or green LED (no flowering), with an equal or greater promotional effect relative to no SL treatment, depending on cultivar [45]. However, when these LEDs were used as nighttime SL at the same intensity, the blue LED completely inhibited flowering similar to other LEDs, compared with no SL [45]. Possibly, nighttime SL with modest-intensity BL could be sensed as a photoperiod signal.

Like NI or DE lighting, nighttime SL with low-intensity BL is not sensed as a photoperiod signal to affect flowering in some short-day plants such as chrysanthemum. For

chrysanthemum in a greenhouse under short-day natural light conditions, 15 h nighttime SL with BL at 3.6 μmol $m^{-2}$ $s^{-1}$ did not affect flower initiation, but the BL at 7.0 μmol $m^{-2}$ $s^{-1}$ delayed flowering compared with no nighttime SL [38]. Also, the nighttime SL with BL at both intensities reduced flower size, and flower dry mass compared to no SL, with a greater decrease in flower dry mass at a higher BL intensity, [38]. In another trial on the genotype from the same group under the same daytime conditions, 6 h nighttime SL with BL at 0.4−3.5 μmol $m^{-2}$ $s^{-1}$ did not affect flower dry mass compared with no SL treatment. This indicated that for chrysanthemum long-day treatment through SL with BL at intensities < 3.5 μmol $m^{-2}$ $s^{-1}$ did not adversely affect the flowering process [38].

For some long-day ornamental plants grown under short-day conditions, nighttime SL with BL cannot necessarily promote flowering relative to no SL, and its promotional effect is less than far-red light. For *Eustoma grandiflorum*, grown in a phytotron under 8 h sunlight, flower budding was promoted by overnight SL with blue LED at 8.8 μmol $m^{-2}$ $s^{-1}$, compared with no SL, but the flower budding with blue LED was later than those with far-red LED at 10 μmol $m^{-2}$ $s^{-1}$ [40]. For *Gypsophila paniculata* under 9 h natural light conditions, 15 h nighttime SL with blue LED at 20−30 μmol $m^{-2}$ $s^{-1}$ did not promote flowering, but far-red LED did, compared with no SL [44]. Possibly, for these long-day plants, their flowering responses to nighttime SL with BL might require different threshold BL amount (intensity × duration), as mentioned before in prolonged-photoperiod lighting.

For some perennial ornamental plants insensitive to photoperiod, nighttime SL with BL can promote flowering relative to no SL, and its promotional effect relative to other wavelengths differs among plant genotypes. For tulips grown in a greenhouse under short-day season, 4 h nighttime SL with BL rather than white light from colored fluorescent lights induced earlier flowering and improved flowering uniformity compared with no SL, despite no effects on flower morphology [53]. For *Delphinium* grown indoors under 8 h short-day conditions, 12 h nighttime SL with blue LED light promoted flowering compared with no SL but reduced the number of spikes, and total florets without affecting cut flower length [39]. Although flowering was promoted by blue LED relative to no SL, its promotional effect relative to other LEDs varied among cultivars. Compared with red LED, the promotional effect of blue LED was less in 'Aurora Light Blue' and was greater in 'Super Grand Blue'. Compared with far-red LED, the promotional effect of blue LED was less in both cultivars [39].

#### 2.3.2. BL in Combination with Other Light Wavelengths

As an SL source in the greenhouse, a mixture of blue with red light (RB-light) with 15−20% BL has equivalent or better effects on flowering and other metrics compared with HPS (high-pressure sodium; normally 5% B). For potted poinsettia, with strict requirement of plant height in production, daytime SL with RB-LED (20% B) did not delay bract color formation, visible cyathia or flowering, but produced shorter plants, and decreased leaf and bract area, chlorophyll content, and total dry matter accumulation, compared with HPS lamps [51]. Similarly, for roses, SL with RB-LED (20% B) did not affect the time to open flowers and the total dry mass production, despite causing floral initiation at a higher leaf number and enhancing more compact plants, compared with HPS [52]. For gerbera, plants under daytime SL with RB-LED (15% B) had a larger flower diameter in 'Acapulco', compared to those in HPS treatment, despite no differences in total or marketable flower numbers [42]. Also, the SL with the RB-LED changed stem length and improved fresh biomass in some cultivars [42].

In greenhouse production, SL from RB light with higher BL proportions (>20%) can cause different effects on flowering and other metrics among different plant genotypes. For marigolds grown under SL, low-blue RB-LED (25% B) caused more blooms than high-blue RB-LED (50% B), or HPS, although the latter two SL treatments also produced more blooms than no SL treatment [46]. Also, the low-blue RB-LED increased shoot growth compared with the HPS treatment, but the high-blue RB-LED was not different from the HPS treatment. Plants in both RB-LED light treatments had greater petal pigment

content than plants in the no-SL treatment [46]. However, for potted geranium plants, SL with blue-rich RB-LED (45% B) promoted early flowering and flower number, as well as canopy compactness, compared with HPS [41]. In the future, it is necessary to explore the optimal BL percentages in RB light for SL in greenhouse production for some commercially important ornamental plants in terms of flowering as well as other metrics.

Unlike long-time (≥10 h daily) SL, short-time (2−4 h daily) pre-dark SL using RB-LED with varying BL percentages seems to have minimal effects on plant flowering and other traits. In a study conducted in our lab on four potted flowers, petunia, marigold, calibrachoa, and geranium grown indoors under 14 h daytime lighting from broad-spectrum LED, 2 h pre-dark SL treatments with RB-LED (10−75% B) did not affect flowering nor plant elongation compared with pre-dark SL treatment with daytime-spectrum LED, except for a small decrease in plant height for petunia [50]. Also, plant responses did not differ among RB-LEDs with different BL proportions. Possibly, the effects of BL proportions in RB-LED could also be related to SL duration.

In addition to RB-LED, a mixture of RB-LED with far-red (RBFR-LED), or both far-red and green LED (RBGFR-LED) can also be used as an SL source in greenhouse conditions. When the blue proportion in these LED combinations is optimal, they can cause a similar or better effect on plant flowering compared with blue LED or HPS. For three long-day specialty cut flowers, godetia, snapdragon, and stock, grown in a greenhouse under SL, RBFR-LED (17% B) resulted in earlier flowering by 10−15 days depending on genotypes compared with red LED and showed no difference from the blue LED and HPS [43]. However, RBFR-LED, as well as blue LED and HPS, caused shorter cut flowers than red LED. RBGFR-LED (17% B) slightly delayed flowering time relative to RBFR-LED and promoted earlier flowering than red LED. Stem caliper was thinner for stock grown under SL with blue LED compared to the other treatments. Flower petal color was not commercially different between SL treatments. It was recommended to utilize an SL fixture providing a spectrum similar to the RBFR-LED or RBGFR-LED [43].

### *2.4. Daytime Sole-Source Lighting*

For ornamental plants grown in an indoor environment excluding natural light, BL alone or a mixture with other light wavelength(s) can be used for daytime sole-source lighting to mediate the flowering initiation and development (Table 4). In addition to pre-harvest lighting, BL alone or a mixture with other light wavelength(s) can also be used as sole-source lighting for postharvest lighting to mediate flower development such as senescence.

**Table 4.** Effects of blue light manipulation through daytime sole-source lighting on flowering and other traits of ornamental plants grown in a controlled environment.

| Plant Genotype | Lighting Treatments | Effects of Lighting Treatments on Plants | Reference(s) |
|---|---|---|---|
| *Alstroemeria* 'Napoli' | Post-harvest sole-source lighting with BL at 15 μmol $m^{-2}$ $s^{-1}$ for 6−24 h daily. | Exposure duration of 12 h within the tested photoperiod ranges was most effective at improving vase life of the cut flowers relative to no lighting treatment.<br>The highest water uptake and total chlorophyll and the lowest ethylene were also obtained from the flowers exposed to 12 h of BL. | [54] |
| Campanula (*Campanula portenschlagiana*) | Daytime sole-source lighting with red LED (170 μmol $m^{-2}$ $s^{-1}$), blue LED (30 μmol $m^{-2}$ $s^{-1}$), and RB-LED (15% B; 100 μmol $m^{-2}$ $s^{-1}$) sequentially at three stages (dynamic lighting) or using RB-LED (15% B; 100 μmol $m^{-2}$ $s^{-1}$) with the same total DLI through the whole growth period (concurrent lighting). | The dynamic lighting did not differ in its effect on flowering time from the concurrent lighting, despite modified plant morphology such as promoted plant elongation. | [55] |

**Table 4.** *Cont.*

| Plant Genotype | Lighting Treatments | Effects of Lighting Treatments on Plants | Reference(s) |
|---|---|---|---|
| Carnation (*Dianthus caryophyllus* L.) | Post-harvest sole-source LED lighting with BL, red light, or white light at 150 μmol $m^{-2}$ $s^{-1}$ for 12 h $d^{-1}$ | BL delayed senescence and improved vase life of the cut flowers compared with red light, or white light. In BL-exposed flowers, the decline in petal carotenoid contents was delayed comparison to red-light- and white-light-exposed flowers. | [56,57] |
| Cherry blossom (*Prunus* × *yedoensis*) | Post-harvest sole-source lighting with blue LED, red LED, or both blue and red LED at 20−45 W $m^{-2}$ (≈96−216 μmol $m^{-2}$ $s^{-1}$) for five days. | For the cut shoots bearing flowers in bloom incubated in nutrient solution, both the blue and red LEDs were involved in blossom coloration, for which blue LED of 450 nm was most effective among the tested peak wavelengths (430, 450, or 470 nm). Red LED alone did not affect anthocyanin biosynthesis; however, irradiation with both blue and red LED induced greater anthocyanin production than with blue LED. | [58] |
| Chrysanthemum (*Chrysanthemum* × *morifolium*) | Daytime sole-source lighting with RB-LED (20% B) or blue LED at 100 μmol $m^{-2}$ $s^{-1}$ for 11 or 15 h $d^{-1}$. | RB-LED delayed flower initiation by 30 d at a photoperiod of 15 h, but not at a photoperiod of 11 h compared with blue LED for 11 h daily. However, regardless of photoperiod, plants under RB-LED had shorter stems and more leaf numbers than those under blue LED. | [30] |
| Chrysanthemum (*Chrysanthemum* × *morifolium*) | Post-harvest sole-source lighting with blue, white, green, yellow, or red light from coloured fluorescent lamp at 30 μmol $m^{-2}$ $s^{-1}$ for 10 h $d^{-1}$. | In these potted plants stored indoors, BL resulted in the greatest number of developed flower heads, the earliest opening and coloring of inflorescence buds, and the longest post-harvest preservation among all light treatments. Also, BL led to bigger flower heads than white and green light. | [59] |
| Cyclamen (*Cyclamen persicum* Mill.) | Daytime sole-source lighting with RB-LED (50% B) or blue LED at a PPFD of 83 μmol $m^{-2}$ $s^{-1}$ for 12 h $d^{-1}$ or 100 μmol $m^{-2}$ $s^{-1}$ for 10 h $d^{-1}$. | RB-LED improved flower induction, with the highest number of flower buds and open flowers under 10 h photoperiod, compared with blue LED, despite reduced peduncle length at 10 h photoperiod. | [60] |
| Dianthus (*Dianthus barbatus*), petunia (*Petunia* × *atkinsiana*), snapdragon (*Antirrhinum majus*); African marigold (*Tagetes erecta*), coleus (*Solenostemon scutellarioides*), zinnia (*Zinnia elegans*); geranium (*Pelargonium* × *hortorum*), and impatiens (*Impatiens walleriana*) | Daytime sole-source lighting at a PPFD of 180 μmol $m^{-2}$ $s^{-1}$ for 18 h $d^{-1}$ with RB-LEDs (25% to 33% B; or 20 to 60 μmol $m^{-2}$ $s^{-1}$ BL), or RBFR-LED (adding FR of 10−40 μmol $m^{-2}$ $s^{-1}$ to the above RB-LEDs). | Increased BL proportions in RB-LED from 25% to 33% did not affect subsequent flowering of annual bedding plants.<br>The addition of FR at ≥20 μmol $m^{-2}$ $s^{-1}$ to RB-LED accelerated the flowering of at least some long-day plants such as snapdragons, with little to no effect on elongation growth, but did not affect the flowering of day-neutral or short-day plants. | [61] |
| Duckweed (*Lemna paucicostata*) | Daytime sole-source lighting with BL at 2.5 W $m^{-2}$ (≈12 μmol $m^{-2}$ $s^{-1}$), or far-red light at 7.0 W $m^{-2}$ (≈32 μmol $m^{-2}$ $s^{-1}$), from coloured fluorescent lamps in indoor conditions under a short-day photoperiod (<13 h). | The daytime lighting with BL or far-red light failed to induce flowering in this short-day plant.<br>When the short-day photoperiod of BL or far-red light was terminated by a 15 min red light pulse, flowering recovered completely. Also, the inducing effect of red light was reversed by subsequent exposure to far-red light or BL | [62] |
| Gerbera (*Gerbera jamesonii*) | Daytime sole-source lighting at a PPFD of 165 μmol $m^{-2}$ $s^{-1}$ for 16 h daily with RB-LED (15% B), or mixtures of the RB-LED with UVB, UVA, green, or far-red light (at a level of 0.5, 9.6, 41, or 17 μmol $m^{-2}$ $s^{-1}$). | The flowering time after transplanting was not different among the different lighting treatments. | [63] |
| *Hippeastrum hybrid* | Daytime sole-source lighting from RB-LEDs with a higher or lower B% (90% or 10%) or white LED at 200 μmol $m^{-2}$ $s^{-1}$ for 14 h $d^{-1.}$ | Compared with white LED, RB-LED with a higher B% promoted early flowering initiation and extended flowering time, while RB-LED with a lower B% promoted vegetative plant growth but delayed flowering. | [64] |
| *Jasminum sambac* | Daytime sole-source lighting with blue or red LED at 18 μmol $m^{-2}$ $s^{-1}$ for 12 h $d^{-1}$. | The blue LED delayed flowering time and decreased the number of flower buds, compared with red light. | [65] |

**Table 4.** *Cont.*

| Plant Genotype | Lighting Treatments | Effects of Lighting Treatments on Plants | Reference(s) |
|---|---|---|---|
| Kalanchoe (*Kalanchoe blossfeldiana*) | Daytime sole-source lighting with blue LED, or other color (white, red, or green) LED at 90 μmol $m^{-2}$ $s^{-1}$ for 8 h $d^{-1}$ in indoor conditions. | The daytime lighting with blue LED delayed flowering in this short-day plant, compared with white, red, and green LEDs, with the earliest flowering occurring under red LED. | [45] |
| *Lilium* | Daytime sole-source lighting using RB-LED with 20–80% B at a total PPFD of 90 μmol $m^{-2}$ $s^{-1}$ for 14 h daily. | Plants were the tallest and had the largest flower under 20% BL, the longest vase life under 40% BL, the shortest growing cycle under 60% BL, and the largest leaf area and the most intense petal color under 80% BL. | [66] |
| Marigold (*Tagetes erecta* L.) and salvia (*Salvia splendens*) | Daytime sole-source lighting with blue LED, red LED, or white fluorescent light at a PPFD of 100 μmol $m^{-2}$ $s^{-1}$ for 16 h $d^{-1}$. | The blue LED reduced the number of flowers and increased stem length compared with fluorescent light. The blue LED caused similar flower numbers as red LED, but increased stem length. | [67] |
| Morning glory (*Pharbitis nil*) | Daytime sole-source lighting with blue, green, red, or white light from colored fluorescent light at 120 μmol $m^{-2}$ $s^{-1}$ for 16 h daily in indoor conditions. | The daytime lighting with BL induced flowering in this short-day plant, but not at all under green, red, or white light. | [68] |
| Morning glory (*Pharbitis nil*) | Daytime sole-source lighting with blue, red, or white light from coloured fluorescent light* at 120 μmol $m^{-2}$ $s^{-1}$ at temperatures of 18, 23, or 28 °C under a 12 h photoperiod. | The BL did not differ from red or white light in flowering at 18 °C, and promoted flowering at 23 °C or 28 °C, with a greater promotional effect at 23 °C, although stem elongation was inhibited under BL. | [68] |
| Morning glory (*Pharbitis nil*) | Daytime sole-source lighting using RB-light (20−85% B) from mixture of coloured fluorescent lights at 100 μmol $m^{-2}$ $s^{-1}$ for 13 h $d^{-1}$. | With BL proportions in the RB-lighting increasing from 20% to 85%, plant flowering was promoted but plant elongation was inhibited, showing sensitive response to BL proportions | [47] |
| Narcissus (*Narcissus pseudonarcissus*) | Daytime sole-source lighting with blue or red light from coloured fluorescent lamps at a low PPFD of 12.5 μmol $m^{-2}$ $s^{-1}$ for 6 h $d^{-1}$. | The bulbs forced under BL (393–580 nm) did not differ from red light in flowering date, or the number of flowers, despite having shorter, and more rigid shoots of lower weight with shorter leaves. | [69] |
| Petunia (*Petunia* × *atkinsiana*) | Daytime sole-source lighting at 140 μmol $m^{-2}$ $s^{-1}$ for 16 h $d^{-1}$ using RB-LEDs with a gradual increase in BL proportion from 0 to 100% (dynamic lighting), or using RB-LEDs with constant BL proportions, or HPS lamps (constant lighting) over 28 days. | The dynamic lighting using RB-LEDs resulted in the earliest flowering time despite having a lower number of flowers, compared with constant lighting using HPS lamp.<br>The dynamic lighting enhanced shoot dry weight, shoot length, and leaf area, compared to constant lighting with RB-LEDs or HPS lamps. | [70] |
| Petunia (*Petunia* × *atkinsiana*) | Post-harvest sole-source lighting with BL, red, white, or far-red light at 50 μmol $m^{-2}$ $s^{-1}$ for 24 h $d^{-1}$. | BL had little to no effect on volatile emission of cut flowers and sightly decreased benzaldehyde emission relative to white light. Unlike red or FR light, BL did not affect the emission of phenylacetaldehyde, 2-phenylethanol, benzyl alcohol, and benzyl benzoate. | [71] |
| Petunia (*Petunia* × *hybrida*), calibrachoa (*Calibrachoa* × *hybrida*), geranium (*Pelargonium* × *hortorum*), and marigold (*Tagetes erecta*) | Daytime sole-source lighting with blue or red LED at 100 μmol $m^{-2}$ $s^{-1}$ for either 24 h or 16 h daily. | The plants under blue LED showed an earlier flowering time than those under red LED, regardless of photoperiod. However, the magnitude of BL promotion was greater under 24 h than 16 h lighting in many cases. | [72] |
| Petunia (*Petunia* × *hybrida*), calibrachoa (*Calibrachoa* × *hybrida*), geranium (*Pelargonium* × *hortorum*), and marigold (*Tagetes erecta*) | Daytime sole-source lighting at 100 μmol $m^{-2}$ $s^{-1}$ for 24 h daily with blue LED, red LED, or unpure BLs (BRF0; BRF2; BRF4; and BRF6) created by mixing blue with low-level (6%) red, and further adding far-red light of 0, 2, 4, and 6 μmol $m^{-2}$ $s^{-1}$. | The daytime lighting with blue and BRF6 promoted flowering compared to R or BRF0, as demonstrated by an earlier flowering time for petunia and calibrachoa, and a greater flowering index, more visible flower buds, and more opened flowers for geranium and marigold. The promotion effect of impure blue light on these traits increased following the order of BRF0, BRF2, BRF4, and BRF6. | [26] |
| Petunia (*Petunia* × *hybrida*), calibrachoa (*Calibrachoa* × *hybrida*), geranium (*Pelargonium* × *hortorum*), and marigold (*Tagetes erecta*) | Daytime sole-source lighting at 100 μmol $m^{-2}$ $s^{-1}$ for 24 h daily with blue or red LED before transplanting and kept this lighting spectral or switched to red or blue LED after transplanting. | The transplants grown under blue LED flowered earlier after transplanting when switched to red LED compared with the transplants under red LED. | [73] |

**Table 4.** *Cont.*

| Plant Genotype | Lighting Treatments | Effects of Lighting Treatments on Plants | Reference(s) |
|---|---|---|---|
| Rose (*Rosa*× *hybrida*) | Daytime sole-source lighting with RB-LED (20% B) or HPS lamps (5% B), at 100 μmol $m^{-2}$ $s^{-1}$ for 20 h $d^{-1}$. | Compared to HPS, RB-LED did not affect flowering, despite decreased plant height, leaf area, and shoot biomass, and increased the dry weight proportion allocated to the leaves. | [52] |
| Tulip (*Tulipa* spp.) | Daytime sole-source lighting with blue or red LED at a PPFD of 200 μmol $m^{-2}$ $s^{-1}$ for 12 h daily. | The blue LED did not affect flowering time nor flower diameter, compared with red LED, despite increased flower length and fresh weight. | [74] |

Note: LED = light emitting diodes; HPS = high-pressure sodium; BL = blue light; DLI = daily light integral; RB = mixture of red and blue light; PPFD = photosynthetic photon flux density. * Coloured fluorescent lights emit a colored light with peak wavelength in the region of bule, red, or green by changing chemical components in the lamp.

#### 2.4.1. Pre-Harvest Lighting

(1) BL alone

For some short-day plants grown indoors, daytime sole-source lighting with BL for short-day hours (below critical day length) is less effective in inducing flowering than red, white, or green light. For duckweed, sole-source lighting with BL at as well as far-red light failed to induce flowering under a short-day photoperiod (<13 h), although these plants responded as a typical short-day plant in red and white light [62]. For kalanchoe, sole-source lighting with blue LED for 8 h $d^{-1}$ delayed flowering, compared with white, red, and green LEDs, with the earliest flowering occurring under red LED [45]. Possibly, the inhibitory action of BL or far-red light might be due to the lowering of phytochrome activity below those required to start the dark reactions that lead to flowering. This has been supported by the reverse flowering response to R/FR or R/BL in a study on duckweed [62].

In contrast, for some short-day plants grown indoors, daytime sole-source lighting with BL for long-day hours (above critical day length) is more effective in inducing flowering than red, white, or green light. When morning glory plants were exposed to sole-source lighting with blue, green, red, or white light at 120 μmol $m^{-2}$ $s^{-1}$ for 16 h daily, flowering occurred in BL, but not at all under green, red, or white light [68]. For morning glory plants under long-day conditions, active phytochromes seemed to have little effect on flower induction, but BL receptors, such as cryptochromes, might have played a key role in flowering initiation. It appeared that the duration of sole-source lighting with BL at low to modest intensities was not sensed by short-day plants as a day-length signal in terms of flowering initiation response.

In addition to short-day plants, the flowering of long-day plants and day-neutral plants grown indoors can also be promoted by daytime sole-source lighting with BL for long-day hours relative to red light. In our studies on petunia, calibrachoa, geranium, and marigold, daytime lighting for either 24 h or 16 h daily with blue LED promoted plant flowering (earlier flowering, a greater flowering index, and more visible flower buds and open flowers) compared with red LED [26,72]. Also, even when blue or red LED was applied only at the transplant stage and switched to other spectral lights at the post-transplanting stage, the promotional effect of blue LED relative to red LED was still observed in the afterward flowering of mature plants [73]. Through a series of studies, we have concluded that the promotional effect of blue LED on flowering relative to red LED is related to its low PPS, which can induce lower activity of phytochromes and CRY1, but higher activity of CRY2 and phototropins in plants [26,75–77]. Furthermore, the promotional effect of blue LED relative to red LED was greater under 24 h than 16 h lighting in many cases [72]. It appeared that plant flowering response to daytime sole-source lighting with BL could be positively affected by photoperiod (i.e., lighting duration) under long-day conditions.

Besides photoperiod, different plant genotypes can also contribute to the varying effect of daytime sole-source lighting with BL relative to red light on plant flowering, which has been observed in some perennial ornamental plants. For *Jasminum sambac*, sole-source lighting with blue LED delayed flowering time and decreased the number

of flower buds, compared with red light [65]. However, for tulips grown indoors under sole-source lighting, blue LED did not affect flowering time nor flower diameter, compared with red LED, despite increased flower length [74]. Also, for narcissus bulbs forced under sole-source lighting, BL did not differ from red light in its effects on flowering date or the number of flowers [69].

For the same plant genotype(s), the effect of daytime sole-source lighting with BL on flowering varies with reference light wavelength or growth temperature. In marigold and salvia, daytime lighting with blue LED reduced the number of flowers compared with fluorescent light; however, blue LED resulted in similar flower numbers as red LED [67]. For morning glory exposed to daytime sole-source lighting at temperatures of 18, 23, or 28 °C, BL did not differ from red or white light in its effects on flowering at 18 °C and promoted flowering at 23 °C or 28 °C, with a greater promotional effect at 23 °C [68].

(2) BL in combination with other wavelength(s)

BL can also be applied with red light (RB light) as daytime sole-source lighting in controlled environment production of ornamental plants. However, the effect of RB light (20−50% B) on flowering relative to BL alone depends on plant genotypes and photoperiod. In cyclamen under sole-source lighting for 12 or 10 h $d^{-1}$, RB-LED (50% B) improved flower induction, with the highest number of flower buds and open flowers under 10 h photoperiod, compared with blue LED [60]. For chrysanthemums, sole-source lighting with RB-LED (20% B) delayed flower initiation by 30 d at a photoperiod of 15 h, but not at a photoperiod of 11 h compared with blue LED for 11 h daily [30]. It appeared that BL-mediated plant flowering could be affected by its co-action with red light, due to a cross-talk between cryptochrome and phytochromes.

For some ornamental plants, a higher BL percentage in RB-lighting as sole-source lighting benefits plant flowering. In *Hippeastrum hybrid* under sole-source lighting for 14 h $d^{-1}$, compared with white LED, RB-LED with a higher B% (90%) promoted early flowering initiation and extended flowering time, while RB-LED with a lower B% (10%) delayed flowering [64]. For morning glory under sole-source lighting from RB-light for 13 h $d^{-1}$, with BL proportions in the RB-lighting increasing from 20% to 85%, plant flowering was promoted, showing a sensitive response to BL proportions [47]. It appeared that at least for these genotypes under the normal photoperiod, BL could effectively promote flowering with the co-action of red light.

It is worthwhile to note that for a certain plant genotype under RB-light as sole-source lighting, the optimal BL proportion for flowering is not necessarily also optimal for other plant traits. When sole-source lighting with RB-LEDs with varying BL percentages was applied to indoor cultivation of *Lilium*, plants were the tallest and had the largest flower under 20% BL, the longest vase life under 40% BL, the shortest growing cycle under 60% BL, and the largest leaf area and the most intense petal color under 80% BL [66]. So, the optimization of BL proportion in RB-LED lighting could be based on specific production purposes.

When BL percentages in sole-source lighting vary within a smaller range (e.g., 5−33%), it may have little effect on plant flowering for many ornamental plant genotypes; however, in this case, light spectral quality change may play a more important role in mediating flowering. In roses, compared to HPS lamps (5% B), sole-source lighting with RB-LED (20% B) did not affect flowering s [52]. For different types of ornamental transplants under sole-source lighting with RB-LEDs, increased BL proportions from 25% to 33% did not affect the subsequent flowering of annual bedding plants [61]. Differently, the addition of FR at ≥20 μmol $m^{-2}$ $s^{-1}$ to RB-LED accelerated the flowering of at least some long-day plants such as snapdragons, but did not affect the flowering of day-neutral or short-day plants [61]. However, in our recent study on gerbera transplants under sole-source lighting, when adding low-level UVB, UVA, green, or far-red light to RB-LED (15% B) and keeping the same total PPFD for all treatments, the flowering time after transplanting was not different among the different lighting treatments [63]. When the low levels of other light wavelengths were added to RB-LED, and the phytochrome activity was changed little (with

the PPS values varying 0.84−0.88). In this case, possibly, BL percentage still played a key role in flowering mediation.

When maintaining high BL proportions in sole-source lighting, mixtures of BL with different other light wavelengths even at low levels may trigger contrasting flowering responses. In our recent studies on petunia, calibrachoa, geranium, and marigold under sole-source lighting, adding a low level of red to blue LED light (94% B) delayed plant flowering time compared with blue LED alone [26,73]. However, further adding low levels of far-red LED light gradually increased its promotional effects on flower initiation and eventually showed a similar effect to blue LED. Similar promotional effects were found on flower size for calibrachoa [26,73]. It appeared that impure and pure BL might have contrasting effects on plant flowering, depending on the contaminated light wavelengths that cause varying phytochrome activity. BL associated with lower phytochrome activity could promote flowering, although there was a varying level of sensitivity among plant genotypes.

For plant genotypes sensitive to variations of BL proportions, it is possible to apply dynamic lighting with varying BL proportions during different growth stages to mediate flowering and morphology. For petunia seedlings grown under sole-source lighting, dynamic lighting using RB-LEDs with a gradual increase in BL proportion from 0 to 100% resulted in the earliest flowering time despite causing less flowers, compared with HPS lamp [70]. Also, the dynamic lighting enhanced shoot dry weight, shoot length, and leaf area, compared to RB-LEDs with constant BL proportions, or HPS lamps. It appeared that modifying BL percentages in RB-LED lighting during the seedling stage could be an efficacious alternative to standard lighting systems [70]. However, in our recent study on campanula under sole-source lighting, dynamic lighting with red LED, blue LED, and RB-LED sequentially at three stages did not differ in its effect on flowering time from concurrent lighting using RB-LED with the same total DLI through the whole growth period, despite modified plant morphology such as promoted plant elongation [55]. Possibly, flowering response to BL percentage was less sensitive for campanula than petunia.

#### 2.4.2. Post-Harvest Lighting

Improving the marketability of pot flowers and extending the vase life of cut flowers have practical significance for the development of the flower industry. In addition to controlling the other storage environment factors and post-harvest use of floral preservatives, recently, it has been found that post-harvest sole-source lighting with BL is an effective environmental controlling method in improving the postharvest quality and extending the vase life of some floral crops [56]. Although sole-source lighting with BL can be introduced as a physical factor to improve some traits of post-harvested flowers, the response can vary with crop types, light duration, flower traits, or light spectra.

Among different light wavelengths, low-intensity BL seems to be the most effective one for sole-source lighting during post-harvest storage of potted flowers in terms of flowering responses. For example, in potted chrysanthemums stored indoors, sole-source lighting at 30 μmol $m^{-2}$ $s^{-1}$ with BL resulted in the greatest number of developed flower heads, the earliest opening and coloring of inflorescence buds, and the longest post-harvest preservation among all lights (white, blue, green, yellow and red light) [59]. Also, BL led to bigger flower heads than white and green light [59].

For cut flowers, postharvest sole-source lighting with low- to modest-intensity BL can delay flower senescence and thus improve vase life relative to other light wavelengths or no lighting, but its improving effects vary with the photoperiod of the lighting. In cut flowers of carnation, postharvest LED lighting with BL at 150 μmol $m^{-2}$ $s^{-1}$ for 12 h $d^{-1}$ delayed senescence and improved vase life compared to red light and white light [56,57]. BL also delayed the decline in petal carotenoid contents in comparison to red or white light [56,57]. In *Alstroemeria* cut flowers under postharvest lighting with BL at 15 μmol $m^{-2}$ $s^{-1}$, a lighting duration of 12 h within the tested photoperiod ranges (6−24 h daily) was most effective at improving vase life relative to no lighting treatment [54]. The highest water

uptake and total chlorophyll and the lowest ethylene were also obtained from the flowers exposed to 12 h of BL [54].

Effects of postharvest sole-source lighting with BL on cut flowers vary with flower traits and background light. In cut flowers of petunia, postharvest lighting with BL had little to no effect on volatile emission, but slightly decreased benzaldehyde emission relative to white light [71]. Unlike red and FR light, BL treatments did not affect the emission of phenylacetaldehyde, 2-phenylethanol, benzyl alcohol, and benzyl benzoate [71]. However, postharvest lighting with BL was found to affect flower color effectively associated with increased anthocyanin, the main pigment of cherry blossoms, especially with a coaction of red light. In cherry blossom, when cut shoots bearing flowers in bloom were exposed to postharvest lighting for five days, both the blue and red LEDs were involved in cherry blossom coloration, but the blue LED of 450 nm was the most effective [58]. Also, irradiation with both blue and red LED induced greater anthocyanin production than irradiation with blue LED alone, indicating an association between the BL and red light receptors [58].

## 3. Application of Electric Lighting to Manipulate BL in Other Plants

For plants other than floral crops, such as tree fruits and fruit vegetables, although flowers are not harvested organs for the crops, flowering is a prerequisite physiological process for their production. For some vegetables (e.g., broccoli head, Chinese kale) and some medicinal crops (e.g., saffron, cannabis), flowers are also the main harvested organs. Even when vegetative parts are the main harvested organs, promotion or inhibition of flowering is necessary for shortening or prolonging the time of the cropping cycle according to different production purposes. In this case, the studies about BL manipulation through electric lighting to mediate the flowering of some fruit crops, vegetable crops, and specialty crops are also included in this review (Table 5).

**Table 5.** Effects of blue light manipulation through electric lighting on flowering and other traits of fruit crops, vegetable crops, and specialty crops grown in a controlled environment.

| Plant Genotype | Lighting Treatments | Effects of Lighting Treatments on Plants | Reference(s) |
|---|---|---|---|
| American skullcap (*Scutellaria lateriflora*), and Baikal skullcap (*Scutellaria baicalensis* Georgi) | Sole-source lighting with higher-BL broad-spectrum LED (0.2% UVA: 83.5% B: 7.9%G: 7.7%R: 0.6%FR) or lower-BL broad-spectrum LED (0.1% UVA:17.9% B: 39.1%G: 40%R: 2.9%FR) at 200 μmol $m^{-2}$ $s^{-1}$ for 16 h daily. | The higher-BL broad-spectrum LED resulted in earlier flowering, caused more compact plants, and increased flavone accumulation in leaves for *S. lateriflora* but decreased it in roots for *S. baicalensis* Georgi, compared with lower-BL broad-spectrum LED. | [78] |
| Bitter gourd (*Momordica charantia* L.) | Sole-source lighting with blue, red, or white LED at a PPFD of 50 μmol $m^{-2}$ $s^{-1}$ for 12 h daily. | Blue LED increased the total female flower number and female flower nod ratio on main stems in the seedlings grown indoors, compared with red LED.<br>Compared to white LED, blue LED improved photosynthetic performance and increased seedling stem diameter. | [79] |
| Blueberry (*Vaccinium corymbosum*, 'Misty', and 'Sharpblue') | Daytime sole-source lighting with blue LED, RB-LED (50% B) or red LED at 300−380 μmol $m^{-2}$ $s^{-1}$ for 14 h $d^{-1}$. | 'Misty' had the highest cumulative flower number under blue LED light, while 'Sharpblue' had the highest flower number under RB-LED light.<br>Blue LED light caused growth delay in 'Sharpblue' plants, but RB-LED light promoted desirable vegetative growth and continuous flowering.<br>Fruits grown under blue LED and RB-LED lights had higher soluble solids and fruits under RB-LED lights had greater fresh weight, compared with red LED. | [80] |
| Broccoli (*Brassica oleracea* var. *italica*) | Continuous sole-source lighting with blue LED in combination with white LED at 20 μmol $m^{-2}$ $s^{-1}$. | The LED treatment resulted in greater greenness and higher chlorophyll levels at 5 °C or 22 °C, and slower sugar loss rate and higher carotenoid content at 22 °C, compared with darkness. | [81] |

**Table 5.** *Cont.*

| Plant Genotype | Lighting Treatments | Effects of Lighting Treatments on Plants | Reference(s) |
|---|---|---|---|
| Cannabis (*Cannabis sativa* L.) | Sole-source lighting with blue LED, red LED, RB-LEDs (9% B or 67% B), or HPS at a PPFD of 250−400 μmol $m^{-2}$ $s^{-1}$ for 18 h $d^{-1}$ and then 12 h $d^{-1}$. | The blue LED had lower fresh inflorescence mass than HPS, as well as other LEDs,<br>The red LED and RB-LEDs had lower inflorescence mass than HPS.<br>The blue LED resulted in the highest Δ9-tetrahydrocannabinol (THC) concentration (10.2% m/m), yet the lowest THC concentration per plant (1.44 g/plant).<br>The blue LED increased cannabigerol (CBG) and terpene concentration, compared with other light treatments.<br>The blue LED had a lesser impact on cannabidiol (CBD) biosynthesis. | [82] |
| Cannabis (*Cannabis sativa* L.) | Sole-source lighting using RB-LED with 47% B or 18% B, white LED (26% B), or HPS (5% B) at a PPFD of 950 μmol $m^{-2}$ $s^{-1}$ for 12 h daily. | RB-LED increased inflorescence yields compared with HPS, or white LED.<br>White LED had the lowest yield.<br>RB-LED with 47% B and white LED increased the accumulation of cannabigerolic acid (CBGA), but reduced plant height, compared with HPS light. | [83] |
| Cannabis (*Cannabis sativa* L.) | Sole-source lighting with different BL proportions (the lowest was 4% from HPS, and increased to 9.8%, 10.4%, 16%, and 20% from white or white + red LEDs) at a PPFD of 900 μmol $m^{-2}$ $s^{-1}$ for 12 h daily. | As the BL proportions increased from 4% to 20%, dry flower yield decreased linearly by 12%, but there was no effect on CBD or THC concentration.<br>Yield under the white + red LED fixture (10.4% B) was 4.6% lower than the HPS on a per unit area basis but was 27% higher on a per dollar of electricity basis. | [84] |
| Chinese kale (*Brassica alboglabra* Bailey) | 10 days pre-harvest SL with blue LED at 50−150 μmol $m^{-2}$ $s^{-1}$ for 12 h daily in a greenhouse. | Blue LED improved the growth, yield, and quality, compared with no SL.<br>50 μmol $m^{-2}$ $s^{-1}$ performed the best among the tested SL intensity. | [85] |
| Chinese kale (*Brassica alboglabra* Bailey) | 10 days pre-harvest SL with blue LED at 50 μmol $m^{-2}$ $s^{-1}$ for 12 h daily in a greenhouse. | Blue LED reduced the weight loss of the flower stalk and maintained a higher antioxidant activity during storage, compared with no SL. Blue LED increased contents of vitamin C, soluble protein, free amino acids, and chlorophyll at harvest, compared with no SL. | [86] |
| Cucumber (*Cucumus sativus* L.) | SL with blue or red light from coloured fluorescent lights* at 30 μmol $m^{-2}$ $s^{-1}$ for 4 h daily (2 h before sunrise and 2 h after sunset) in a greenhouse. | BL did not affect flower initiation time compared with no SL and had a similar effect as red light.<br>Fruit number was reduced by BL, but increased by red light relative to no SL. | [87] |
| Cucumber (*Cucumus sativus* L.), tomato (*Solanum lycopersicum*), and sweet pepper (*Capsicum annuum* L.) | SL with blue LED at 15 μmol $m^{-2}$ $s^{-1}$ for 18 h $d^{-1}$ in greenhouses under HPS lamps at 90 μmol $m^{-2}$ $s^{-1}$ for 18 h $d^{-1}$. | SL with blue LED did not affect flower bud formation of tomato and sweet pepper transplants, compared with no LED SL.<br>SL with blue LED slightly enhanced flower bud formation of cucumber transplant and increased leaf area, fresh and dry weight, and photosynthetic pigment content of all vegetable transplants, compared with no LED SL. | [88] |
| Peach (*Prunus persica*, 'Ruiguang 27' and 'Jing Yu') | SL with blue, red or white light from coloured fluorescent lamps at 30 μmol $m^{-2}$ $s^{-1}$ for 4 h daily (2 h before sunrise and 2 h after sunset) in a greenhouse. | BL did not affect flower density of a 1-year-stem for both peach varieties in the next year,<br>Red or white light increased flower density of 1-year-stem in "Ruiguang 27" and "Jing Yu", respectively, compared with no SL.<br>BL is less effective at inhibiting new shoot elongation growth than white light.<br>BL and white light improved fruit size, compared to no SL. | [89] |
| Pepper (*Capsicum annuum* L.) | Sole-source lighting with blue, green or red LED at a PPFD of 180 μmol $m^{-2}$ $s^{-1}$ for 12 h $d^{-1}$. | The blue LED promoted early flowering compared with green or red LED.<br>The blue LED reduced plant height and total leaf area, and increased axillary bud and root growth, compared with red LED. | [90] |
| *Polygonum tinctorium* | Sole-source lighting with blue LED, red LED, or fluorescent light at 160 μmol $m^{-2}$ $s^{-1}$ for 12 h or 24 h daily. | The blue LED increased the flowering rate by six-fold, compared with fluorescent light.<br>None of the plants flowered with red LED treatment.<br>Indican content was greatly enhanced by blue LED light under 24 h continuous irradiation. | [91] |

**Table 5.** *Cont.*

| Plant Genotype | Lighting Treatments | Effects of Lighting Treatments on Plants | Reference(s) |
|---|---|---|---|
| Saffron (*Crocus sativus* L.) | Sole-source lighting with blue LED, red LED, or RB-LED with 25−75% B at 150 μmol $m^{-2}$ $s^{-1}$ for 11 h daily. | Blue LED accelerated flowering and increased flower number and stigma weight, compared to red LED or RB-LED.<br>Blue LED increased the production of high-quality daughter corms and altered biomass partitioning towards harvestable organs (corms and flowers).<br>The highest content of crocin (trans-crocetin ester), and picrocrocin as well as total carotenoids, anthocyanins, and flavonoids was detected in plants grown with blue LED. | [92,93] |
| Saffron (*Crocus sativus* L.) | Sole-source lighting with blue LED, red LED, or RB-LEDs with 33–67% B at 50 μmol $m^{-2}$ $s^{-1}$ for 12 h daily. | Red LED performed the best among the tested LEDs, demonstrated by advanced flowering, enhanced flower size and number, and improved stigma yield in terms of dry weight.<br>Red LED reduced corm biomass loss, accelerated apical bud growth, improved total crocin production, and the practical value ratio of saffron. | [94] |
| Saffron (*Crocus sativus* L.) | Sole-source lighting with broad-band LED (blue: red: FR light = 20%: 62%: 18%) at PPFD of 100 μmol $m^{-2}$ $s^{-1}$ for 10 h $d^{-1}$. | Within the range of total daily light integral (TDLI; TDLI = DLI × days = PPFD × photoperiod × days) from 79 to 166 mol $m^{-2}$, flower number, daily flowering proportion, stigma dry weight, and crocetin esters content were significantly correlated with TDLI.<br>Both the average flower number per corm and dried stigma yield were the highest under the 150 mol $m^{-2}$ TDLI treatment, which was 70% and 50% higher than that under the original natural light treatment, respectively. | [95] |
| Snow peas (*Pisum sativum* var. *saccharatum*) | SL with RB-LED (20% B) at a PPFD of 50−140 μmol $m^{-2}$ $s^{-1}$ for 16 h $d^{-1}$ in a greenhouse. | RB-LED did not affect flower initiation regardless of lighting intensities, compared with no SL.<br>RB-LED increased pod yield, promoted plant growth, and improved pod quality, compared with no SL. | [96] |
| Squash (*Cucurbita moschata* Duch) | Sole-source lighting using blue, red, or RB-LED (56% B or 71% B) at a PPFD of 150 μmol $m^{-2}$ $s^{-1}$ for 12 h daily. | The blue LED did not differ from the red LED in female flower number.<br>RB-LED (56% B) induced more female flowers, produced more fruits, and reduced chlorophyll content compared with blue LED as well as red LED and RB-LED (71% B).<br>RB-LED (56% B) caused more compact plants than blue or red LED. | [97] |
| St John's wort (*Hypericum perforatum)* | Sole-source lighting from blue LED, red LED, or RB-LEDs with 20−80% B at 150 μmol $m^{-2}$ $s^{-1}$ for 16 h daily. | Blue LED and increased B% in RB-LEDs decreased flowering shoot number, flower number, flower diameter, fresh and dry weight of flowers, and percentage of hypericin, pseudohypericin, and hyperforin in flowers, compared with red LED.<br>Blue LED caused lower fresh and dry weight, leaf area and number, and plant height.<br>Red LED had the greatest promotional effects not only on flowering but also on plant growth, as well as secondary metabolite accumulation. | [98,99] |
| Strawberry (*Fragaria* × *ananassa*, "Festival") | 3 h end-of-day SL with blue, white, red, and RB-LEDs inside a net house in Bangladesh during the winter season. | Blue LED was less effective than red LED at promoting reproductive growth in terms of days to first flower bud, flowering, fruit setting, and fruit harvesting, despite the best performance regarding vegetative growth among all LED treatments.<br>RB-LED treatment showed the best in all the parameters and produced the highest yield. | [100] |
| Strawberry (*Fragaria* × *ananassa*, 'Albion') | Daytime sole-source lighting from RB-LEDs with varying blue percentages from 5% to 17% or HPS at a PPFD of 120 μmol $m^{-2}$ $s^{-1}$ for 16 h $d^{-1}$. | The RB-LED lighting with 5% B was most effective in enhancing the number of inflorescences and thus fruit yield per plant, while increasing flowering stem length, as well as the number of runners and leaves per plant, compared with HPS light. | [101] |
| Strawberry (*Fragaria* × *ananassa*, 'Albion') | 2 h NI lighting, or 24 h or 10 h SL daily with blue + far-red (BFR) LEDs with different blue proportions (17% B, 50% B, and 83% B) in a greenhouse. | SL with BFR-LED with a higher blue proportion (83% B) increased flower bud induction, with a greater promotional effect under 24 h vs. 10-h photoperiod.<br>Transplants grown under BFR-LED with 83% B supplied as 2 h NI lighting produced the highest flower buds per plant among all treatments and promoted flower development outside the crown. | [102] |

**Table 5.** *Cont.*

| Plant Genotype | Lighting Treatments | Effects of Lighting Treatments on Plants | Reference(s) |
|---|---|---|---|
| Strawberry (*Fragaria* × *ananassa*, 'Elsanta') | Daytime sole-source lighting using blue LED, red LED, or fluorescence light at a PPFD of 100 μmol $m^{-2}$ $s^{-1}$ for 14 h $d^{-1}$. | Blue LED did not affect flowering time or flower number per plant, but enhanced fruit set by 25%, and thus caused a higher final yield (65 g/plant), as compared to fluorescence light or red LED (45 and 35 g/plant respectively.<br>Blue LED increased flower stem length for easy harvesting but did not affect main fruit quality traits. | [103] |
| Strawberry (*Fragaria* × *ananassa*, 'HS138') | Daytime sole-source lighting with blue LEDs, red LEDs, or white fluorescent lamps at a PPFD of 190 μmol $m^{-2}$ $s^{-1}$ for either 16 h $d^{-1}$ or 24 h $d^{-1}$. | The lighting with blue LEDs during the nursery period resulted in earlier flowering compared to red LEDs, with a greater effect under longer photoperiods.<br>Plants grown under 24 h lighting with blue LEDs had a shorter vegetative growth period and a higher fruit yield compared to those grown under white fluorescent lamps at a 16 h photoperiod. | [104] |
| Strawberry (*Fragaria* × *ananassa*, 'HS138') | Daytime sole-source lighting using blue LEDs with different peak wavelengths of 405, 450, or 470 nm or red LEDs of 630, 660, and 685 nm at a PPFD of 80 μmol $m^{-2}$ $s^{-1}$ for 24 h daily. | For the plants under lighting during the nursery period, the number of days to anthesis did not differ among the three blue LEDs, and all blue LED types stimulated more flowering compared to three red LEDs with different peak wavelengths except 685 nm.<br>There was no difference in daily fruit production relative to red light, but the use of BL during the nursery period accelerated harvesting due to the advancement in flowering. | [105] |
| Strawberry (*Fragaria* × *ananassa*, 'Pechka') | Nighttime SL with blue, green, or red LEDs at a PPFD of 80 μmol $m^{-2}$ $s^{-1}$ for 16 h $d^{-1}$ inside a greenhouse. | Plants under the blue LED produced the largest number of flower clusters and plants under the red LED produced the fewest.<br>The total weight of flower clusters including developed fruits per plant under the blue LED reached two times more than under the red LED in June.<br>The BL promoted the flowering and fruiting of each floret. | [106] |
| Strawberry (*Fragaria* × *ananassa*, 'Yellow Wonder' and 'Hawaii-4') | SL with blue LED at 100 μmol $m^{-2}$ $s^{-1}$ during the morning, night or both morning and night for 8 h daily; or SL with far-red light at 71 μmol $m^{-2}$ $s^{-1}$ for 24 h daily inside a growth chamber under electrical lighting with sunlight-mimicking LED at 200−300 μmol $m^{-2}$ $s^{-1}$ for 16 or 12 h $d^{-1}$. | Flower induction was most successful under 8 h nighttime SL with blue LED or 24 h SL with far-red LED. Both light treatments overruled the photoperiodic control of flowering, and boosted flowering, leading to a higher fruit yield, with minor effects on vegetative plant growth. | [107] |
| Tomato (*Solanum lycopersicum*) | Sole-source lighting using RB-LED with 25−75% B at a PPFD of 100−150 μmol $m^{-2}$ $s^{-1}$ for 16 h daily | RB-LED with <50% B (with BL intensity of 75 μmol $m^{-2}$ $s^{-1}$) performed the best to suppress spindly growth and promote flowering during seedling growth. | [108] |
| Tomato (*Solanum lycopersicum*) | Sole-source lighting with RBG- LED (5−30% blue, 10% green, 85−65% red light) at 250, 450, or 650 μmol $m^{-2}$ $s^{-1}$ for 16 h daily. | The optimal BL proportion was 15−20% for earlier flowering and around 15% for the growth of young tomato plants.<br>The optimal value shifted to a higher blue proportion if the growth light intensity was low. | [109] |
| Tomato (*Solanum lycopersicum*) and pepper (*Capsicum annuum* L.) | Sole-source lighting with blue LED, red LED, or RB-LED (33−67% blue) at a PPFD of 300 μmol $m^{-2}$ $s^{-1}$ for 16 h $d^{-1}$. | The blue LED delayed time to flowering compared with red LED.<br>RB-LED resulted in earlier first flower and fruit formation and higher fruit yield compared with blue LED. | [110] |

Note: LED = light emitting diodes; BL= blue light; SL = supplemental lighting; HPS = high-pressure sodium; RB = mixture of red and blue light; RBG = mixture of red, blue, and green light; PPFD = photosynthetic photon flux density. * Coloured fluorescent lights emit a colored light with peak wavelength in the region of bule, red, or green by changing chemical components in the lamp.

### 3.1. Fruit Crops

Most fruit crops, especially tree fruits, are rarely grown in controlled environments except for some berry fruits such as strawberries. Recently, there has been a worldwide rise in controlled environment production of berry fruits in greenhouses or vertical farms, where the use of electrical lighting is a common approach for promoting flower initiation and improved fruit yield [111]. Strawberry plants are one of the candidate berry fruit crops for controlled environment production because they are smaller in size and need lower necessary light intensity (100–300 μmol $m^{-2}$ $s^{-1}$) for cultivation [105]. In this case, it is feasible to manipulate the light environment to mediate flowering and fruiting for

strawberry production in controlled environments. However, for fruit-bearing crops such as strawberries, their flowering response to light varies with plant genotype and growth environment [111]. Therefore, it is necessary to consider these factors during the manipulation of BL to optimize light spectral composition to control flowering.

For strawberries grown indoors under sole-source lighting, flowering, and fruit response to BL varies with plant variety, photoperiod, and reference light. In everbearing strawberry 'HS138', sole-source lighting with blue LEDs for either 16 h $d^{-1}$ or 24 h $d^{-1}$ during the nursery period resulted in earlier flowering compared to red LEDs, with a greater effect under longer photoperiods [104]. Despite a shorter vegetative growth period, plants grown under 24 h lighting with blue LEDs had a higher fruit yield compared to those grown under white fluorescent lamps at a 16 h photoperiod [104]. In another study by the same research group, 24 h sole-source lighting was applied to the same genotype of strawberry plants during the nursery period [105]. The number of days to anthesis did not differ among blue LEDs with three different peak wavelengths, and all blue LED types stimulated more flowering compared to red LEDs with three different peak wavelengths except 685 nm. Although there was no difference in daily fruit production relative to red light, BL accelerated harvesting due to the advancement in flowering [105]. However, in June-bearing strawberry 'Elsanta', 14 h sole-source lighting with blue LED did not affect flowering time or flower number per plant, but enhanced fruit set and increased final yield, as compared to fluorescence light or red LED [103]. Moreover, blue LED increased flower stem length for easy harvesting but did not affect main fruit quality traits [103].

For strawberries grown under supplemental lighting (SL), flowering response to BL varies with plant variety, and environmental conditions, especially background light. In the everbearing strawberry 'Pechka' inside a greenhouse, nighttime SL with blue LED produced the largest number of flower clusters among blue, green, and red LEDs [106]. The blue LED increased the total weight of flower clusters (including developed fruits) per plant than the red LED in June because the BL promoted the flowering and fruiting of each floret [106]. For the day-neutral strawberry 'Yellow Wonder' and 'Hawaii-4' grown inside a growth chamber under daytime lighting with sunlight-mimicking LED, flower induction was most successful under nighttime SL with blue LED and under 24 h SL with far-red light [107]. Both light treatments overruled the photoperiodic control of flowering, and boosted flowering, leading to a higher fruit yield [107]. For the strawberry 'Festival' inside a net house in Bangladesh during the winter season, 3 h end-of-day SL with blue LED was less effective than red LED at promoting reproductive growth in terms of days to first flower bud, flowering, fruit setting, and fruit harvesting [100]. However, RB-LED treatment showed the best in all the parameters and produced the highest yield [100].

When the combination of BL and other wavelength(s) is used for strawberry production either as sole-source lighting, SL, or NI lighting, its effect on flowering varies with BL proportions in the lighting. For example, sole-source lighting from RB-LED lighting with 5% B (within the range from 5% to 17% B) was most effective in enhancing the number of inflorescences and t fruit yield per plant, while increasing flowering stem length compared with HPS light [101]. For transplants grown in a greenhouse, SL using blue + far-red (BFR) LEDs with a higher blue percentage (83% B) (within the range from 17% to 83% B) increased flower bud induction, with a greater promotional effect under 24 h vs. 10 h photoperiod [102]. Furthermore, transplants grown under BFR-LED with 83% B supplied as 2 h NI lighting produced the highest flower buds per plant among all treatments and promoted flower development outside the crown [102].

Limited information is available on other berry fruit crops. For blueberries grown under sole-source lighting, plant flowering, and growth response to BL varies with plant variety and light spectral. In two blueberry varieties grown under sole-source lighting with blue LED, RB-LED (50% B) or red LED, 'Misty' had the highest cumulative flower number under blue LED light, while 'Sharpblue' had the highest flower number under RB-LED light [80]. Blue LED light caused growth delay in 'Sharpblue' plants, but RB-LED light promoted desirable vegetative growth and continuous flowering. Fruits grown under

blue LED and RB-LED lights had higher soluble solids and fruits under RB-LED lights had greater fresh weight, compared with red LED [80].

For tree fruits, the relevant information is nearly unavailable since tree fruits are mainly produced in open fields rather than greenhouse. However, greenhouse production of tree fruits has developed rapidly in China since the 1990s, which triggered the research interests in the application of lighting such as nighttime SL to address low natural light issues during early-spring production. For example, the researchers from Beijing University of Agriculture studied the effect of SL with different colored fluorescent lights on greenhouse peaches, "Ruiguang 27" and "Jing Yu" (Figure 1) [89]. Daily 4 h SL at 30 μmol $m^{-2}$ $s^{-1}$ with BL did not affect flower density of 1-year-stem for both peach varieties in the next year, but red or white light increased this trait in "Ruiguang 27" and "Jing Yu", respectively, compared with no SL. Also, BL is less effective at inhibiting new shoot elongation growth than white light. However, similarly to white light, BL improved fruit size, compared to no SL [89].

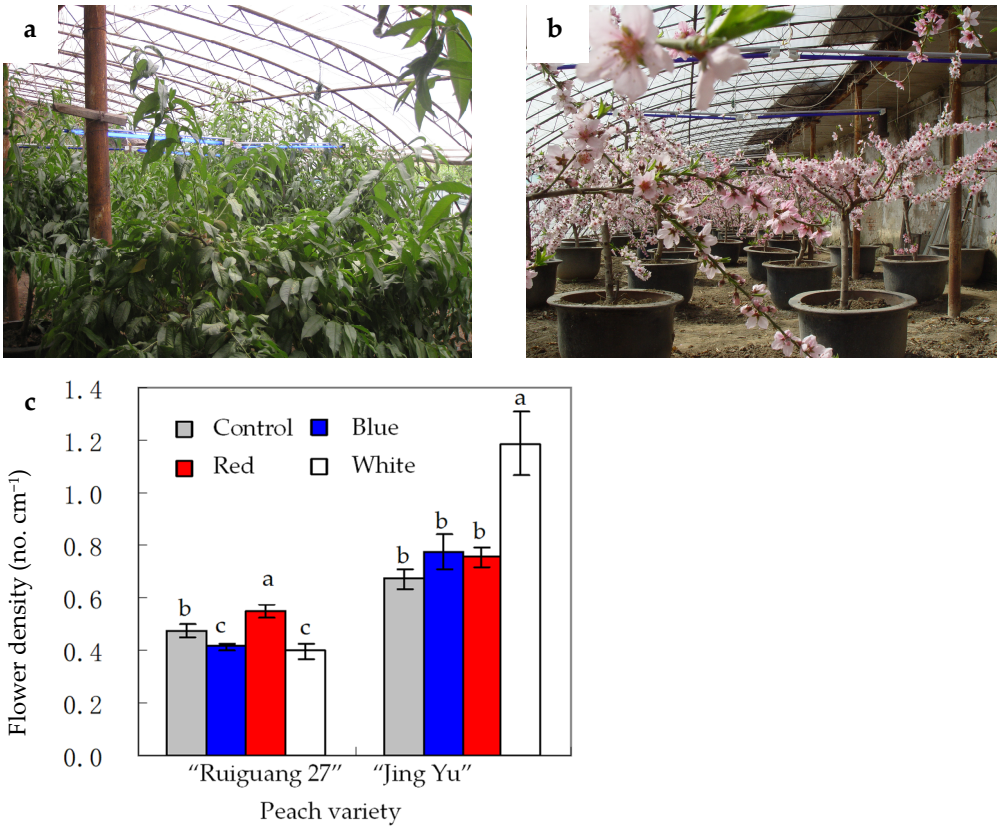


**Figure 1.** An example of the application of supplemental lighting with colored fluorescent light to greenhouse peach production in China [89]. (**a**) Plants from blue light treatment during fruit growth period; (**b**) Plants from blue light treatment during flowering period; (**c**) Flower density under supplement lighting with blue, red or white light, and no lighting as control. Flower density = flower number on one-year stem/length of one-year stem.

### *3.2. Vegetable Crops*

Flowering regulation plays an important role in the controlled environment production of vegetables, especially fruit vegetables. In fruit vegetables, strong and dwarf transplants with earlier flowers would not only benefit plant growth after transplanting but also promote early yield. For example, during the production of high-quality tomato seedlings in Japan, in addition to controlling the stem length, the node position of the first flower truss is also crucial due to the requirement to suppress stem elongation and promote flowering simultaneously [108]. Besides fruit vegetables, the crop yield and quality of vegetables

with flowers as the main edible organs (such as broccoli and Chinese kale) are directly determined by their flowering process. For the above vegetables, BL manipulation can affect plant flowering (such as sex expression and flower initiation) and thus crop yield and quality.

Sole-source lighting with BL or its combination with red light can affect flower sex expression by increasing female flower ratios in some fruit vegetables depending on plant genotypes. For bitter gourd seedlings, sole-source lighting with blue LED increased the total female flower number and female flower nod ratio on main stems, compared with red LED [79]. For squash seedlings, sole-source lighting with blue LED did not differ from the red LED in female flower numbers [97]. However, RB-LED with a lower blue proportion (56% B) induced more female flowers and produced more fruits compared with blue LED as well as red LED and RB-LED with a higher blue proportion (71% B) [97].

For indoor production of fruit vegetable transplants under sole-source lighting, plant flowering response to BL relative to red light varies with plant genotype, and RB-LED is a more reliable light source than blue LED alone. In pepper, sole-source lighting with blue LED promoted early flowering compared with green or red LED [90]. Another study on tomato and pepper indicated that sole-source lighting with blue LED delayed time to flowering compared with red LED [110]. However, RB-LED (33−67% B) resulted in earlier first flower and fruit formation and higher fruit yield compared with blue LED [110]. In tomatoes, sole-source lighting using RB-LED with less than 50% B (with BL intensity of 75 μmol $m^{-2}$ $s^{-1}$) was recommended to promote flowering while suppressing spindly growth during seedling growth [108].

In addition to RB-LED, RBG-LED can also be applied to the indoor production of fruit vegetables under sole-source lighting; however, the optimal blue proportions for flowering differ from those for growth. For tomatoes grown indoors under sole-source lighting with RBG- LED at varying light intensities, the optimal BL proportion was 15−20% for earlier flowering and around 15% for the growth of young plants [109]. However, the optimal value shifted to a higher blue proportion if the growth light intensity was low, suggesting the dependence of the optimal BL proportion on the light intensity as well [109].

During greenhouse production of fruit vegetables, supplemental lighting (SL) with low- to modest-intensity BL alone or its combination with red light has minimal effect on flowering, despite with significant effect on other metrics. For cucumber, tomato, and sweet pepper transplants growing in greenhouses under HPS lamps, SL with blue LED at 15 μmol $m^{-2}$ $s^{-1}$ did not affect flower bud formation of tomato and sweet pepper transplants, compared with no LED SL, although the SL with blue LED slightly enhanced flower bud formation of cucumber transplant and increased leaf area, fresh and dry weight, and photosynthetic pigment content of all vegetable transplants [88]. In contrast, for cucumber grown in a greenhouse under SL at 30 μmol $m^{-2}$ $s^{-1}$, BL did not affect flower initiation time compared with no SL, with a similar effect as red light [87]. Differing from red light, BL relative to no SL reduced fruit number, which was increased by red light [87]. In our study on podded peas grown in a greenhouse under SL at a PPFD of 50−140 μmol $m^{-2}$ $s^{-1}$, RB-LED (20% B) did not affect flower initiation regardless of lighting intensities, compared with no SL, despite increased pod yield, promoted plant growth, and improved pod quality [96]. Possibly, the effect of low- to modest-intensity BL from SL on the flowering of these plants was covered by background lighting or natural light.

In Chinese kale, a vegetable with its flower stalk as the main edible part, it was found that short-term pre-harvest SL with BL could be a promising strategy to enhance growth, yield, and both at-harvest and post-harvest quality of the flower stalks of this vegetable [86]. A 10-day pre-harvest SL with blue LED for 12 h daily improved the growth, yield, and quality of Chinese kale in the greenhouse relative to no SL, and 50 μmol $m^{-2}$ $s^{-1}$ was recommended as an optimal SL intensity [85]. In another study from the same research group, at the optimized intensity, short-term pre-harvest SL with blue LED reduced the weight loss of the flower stalk and maintained a higher antioxidant activity during storage

compared with no SL [86]. Meanwhile, SL with blue LED resulted in higher contents of vitamin C, soluble protein, free amino acids, and chlorophyll at harvest.

Broccoli head, a tight cluster of unopened flower buds, despite having high nutritional value, can senesce quickly after harvest causing product quality deterioration, with a visible decreasing green color in sepals. It has been found that continuous sole-source lighting with blue LED in combination with white LED at a low intensity (20 μmol $m^{-2}$ $s^{-1}$) extended the shelf life of broccoli heads, demonstrated by greater greenness and higher chlorophyll levels at 5 °C or 22 °C, and slower sugar loss rate and higher carotenoid content at 22 °C, compared with darkness [81]. The LED treatment would be a feasible and low-cost technology to extend the postharvest storage of whole broccoli heads [81].

### *3.3. Specialty Crops*

Some medicinal plants such as saffron, cannabis, and St. John's wort have their flowers as the primary harvested organs. For these medicinal plants, regulation of the flowering process through lighting technology can directly affect their harvesting time and crop yield. For example, saffron flower number and stigma yield are negatively affected by low light conditions such as cloudy or rainy weather [95]. Also, the level of secondary metabolites in saffron is affected by environmental factors such as light [92]. For indoor cultivation of saffron, it is possible to improve flower quality and yield through the manipulation of light, including BL [94].

For other medicinal plants, although flowers are not the main harvested organs, earlier flowering through light adjustment can shorten the cropping cycle and increase total biomass unit area and time, thus potentially increasing the yield of biologically active compounds for medicinal use. The accumulation of medicinal compounds can be also affected by light stimuli [99]. To meet the high demand for superior quality medicinal plants, controlled environment production systems with electrical lighting systems can be advantageous. However, before implementing such systems, it is essential to determine the specific light spectrum, such as the proportion of BL required for each plant genotype [99].

Saffron is a flowering specialty plant renowned for its expensive dried stigma, and this highly valued product holds significant importance in culinary, industrial, and medical applications [92,94]. Saffron quality is determined by the content of three apocarotenoids, including crocin, picrocrocin, and safranal [92]. The effects of BL on saffron flowering and other metrics vary with lighting amount. Sole-source lighting with blue LED at 150 μmol $m^{-2}$ $s^{-1}$ for 11 h daily accelerated saffron flowering, increased flower number and stigma weight, and improved biomass partitioning to flowers, compared to red LED or RB-LED [92,93]. Besides improved flowering properties, the highest content of phytochemicals such as crocin and picrocrocin was detected in plants grown with blue LED. Therefore, in this study, blue LED performed the best in terms of the quantity and quality of saffron products under controlled environments [92]. On the contrary, for saffron plants grown under sole-source lighting at 50 μmol $m^{-2}$ $s^{-1}$ for 12 h daily, blue LED performed worse than red LED, demonstrated by delayed flowering, reduced flower size and number, and decreased yield of dry stigma [94]. Possibly, the contrasting response to BL was due to an interaction of light spectral with light amount, which was proven to be an important affecting factor. A study under sole-source lighting with RBFR-LED (20% B) indicated that when total daily light integral (TDLI; TDLI = DLI × days = PPFD × photoperiod × days) varied from 79 to 166 mol $m^{-2}$ due to different lighting days, flower number, daily flowering proportion, stigma dry weight, and crocetin esters content were significantly correlated with TDLI, and the 150 mol $m^{-2}$ of TDLI was the most favorable condition for flower number and stigma quality of saffron [95].

Cannabis is a medicinal plant treasured for its secondary metabolites, especially cannabinoids, the unique biologically active compounds in the plant that are considered to be affected by light spectra [83]. For cannabis grown indoors under sole-source lighting, a combination of BL with other wavelength(s) performs better than BL alone in terms of inflorescence yield, but the optimal BL proportions vary with the combined light wave-

length(s) with BL. For example, when delivered as sole-source lighting, the blue LED had lower fresh inflorescence mass than HPS, as well as other LEDs such as red LED or RB-LEDs (9% B or 67% B) despite increased Δ9-tetrahydrocannabinol (THC) concentration in terms of dry mass, and cannabigerol (CBG) and terpene concentration [82]. Differently, in another study on cannabis under sole-source lighting, RB-LED with 47% B or 18% B increased inflorescence yields compared with HPS (5% B), or white LED (26% B) [83]. Also, blue-rich light such as RB-LED with 47% B and white LED increased the accumulation of cannabigerolic acid (CBGA), the primary cannabinoid and a precursor for most other cannabinoids, but reduced plant height, compared with HPS light [83]. It appeared that full-spectrum light did not necessarily improve inflorescence yield compared with RB-LED light, and manipulating BL proportions in LED lighting could fine-tune cannabis and cannabinoid production. However, contrasting results were achieved in another study on cannabis under sole-source lighting with different BL proportions (the lowest was 4% from HPS, and increased to 9.8%, 10.4%, 16%, and 20% from white or white + red LEDs) [84]. As the BL proportions increased from 4% to 20%, dry flower yield decreased linearly by 12%, but there was no effect on CBD or THC concentration. Although the white + red LED fixture (10.4% B) caused a lower yield than the HPS, it was more economically efficient due to the higher efficacy of the lighting fixtures [84].

*Hypericum perforatum*, commonly known as St John's wort, is a medicinal plant with flowers as the main source for the accumulation of secondary metabolites [98,99]. The three important active compounds in St. John's wort, including hypericin, pseudohypericin, and hyperforin, are effective in treating some diseases, especially mild to moderate depression. For *Hypericum perforatum* plants grown indoors under sole-source lighting, BL or RB-light performs worse than red light in terms of plant flowering and other metrics. For example, when plantlets were grown under sole-source lighting, blue LED or increased B% from 20% to 80% in RB-LEDs had a deterrent effect on flowering, demonstrated by decreased flowering shoot number, flower number, flower diameter, fresh and dry weight of flowers, and percentage of hypericin, pseudohypericin, and hyperforin in flowers, compared with red LED [98,99]. Also, blue LED reduced plant growth relative to red LED. On the contrary, without the presence of BL, i.e., red LED had the greatest promotional effects not only on flowering but also on plant growth, as well as secondary metabolite accumulation [98,99].

*Scutellaria lateriflora* (American skullcap) and *Scutellaria baicalensis* Georgi (Baikal skullcap) are two ethnobotanical medicinal plants used to treat gastrointestinal, respiratory, and inflammatory disorders, in addition to demonstrated anti-cancer properties [78]. The predominant bioactive compounds produced in these genotypes are unique 4-deoxyflavones, in the roots of *S. baicalensis* and leaves of *S. lateriflora* [78]. For these skullcap plants grown indoors under sole-source lighting with a broad spectrum, higher BL proportions benefit flowering and morphology, but its effects on other metrics vary with plant genotype. For example, sole-source lighting with higher-BL broad-spectrum LED (84% B) resulted in earlier flowering, caused more compact plants, and increased flavone accumulation in leaves for *S. lateriflora* but decreased it in roots for *S. baicalensis* Georgi, compared with lower-BL broad-spectrum LED (18% B) [78].

*Polygonum tinctorium* is not only a medicinal plant, but also an important industrial crop producing indigo blue dyes, and indican is an important substance as a precursor of indigo [91]. The indigo plant has been a useful material for traditional herbal medicine in Japan to exhibit anti-oxidant, anti-allergic effect, anti-cancer, and anti-inflammatory activities [91]. For indigo plants grown indoors under sole-source lighting, the blue LED appears to be a good light source in terms of both flowering response and other metrics. For example, sole-source lighting with blue LED increased the flowering rate of indigo plants by six-fold, compared with fluorescent light, while none of the plants flowered with red LED treatment [91]. Indican content was greatly enhanced by blue LED light under 24 h continuous irradiation. It appeared that blue LED light could provide a feasible strategy for artificially regulating plant flowering and indican synthesis in *P. tinctorium*.

## 4. Future Direction

### *4.1. Strengthing the Relevant Foundation Research*

There is a common opinion that BL can promote the flowering of long-day plants and inhibit the flowering of short-day plants [4]. However, from the aforementioned research, it is easy to find that BL-mediated flowering is affected by many factors. This brings challenges in the application of BL in practical production while also indicating that BL-mediated flowering is a complicated physiological process. It is necessary to conduct the relevant basic research for optimization and development of effective ways of manipulating BL through electric lighting to mediate plant flowering. Despite many studies on *Arabidopsis* in this field, limited information is available on horticultural plants. For example, in chrysanthemums under short-day conditions, what is the mechanism behind the phenomena observed in recent studies that prolonged-photoperiod lighting with pure BL (e.g., blue LED light) cannot inhibit flower initiation [9,10,29–31,35]? Also, differing from a complete flowering inhibition for chrysanthemum plants under long-day conditions, why can pre-dark SL with pure BL for hours promote flowering of these plants in LD conditions? It appears that pure BL is not sensed by chrysanthemum plants as a photoperiodism light signal. A recent study by a Korean group has revealed a co-regulation of photosynthetic carbon assimilation and differential photoreceptors in this process, supported by a high expression of CRY1 and PHYA, a low expression of PHYB, and high carbohydrate accumulation [13]. The high expression of CRY1 under pure BL contrasts with our observation on flowering response in *Arabidopsis* cry mutant and overexpressing plants, where pure BL decreased CRY1 activity and increased CRY2 activity [77]. If there is a high expression of CRY1 in chrysanthemum plants, it is difficult to understand why, unlike pure BL, the high-PPS impure BL, created in our recent study by adding low-level R and FR LED to blue LED (R: FR= 3:1; PPS = 0.66) completely inhibit the flower initiation. Based on our studies on *Arabidopsis*, the high-PPS impure BL was supposed to increase CRY1 activity [77].

### *4.2. Broadening the Field of Application Research*

The research about the application of electric lighting to manipulate BL for flowering regulation has been conducted on controlled-environment production of more and more types of crops (from ornamental plants to fruits, vegetables, and specialty crops), especially with the rise of vertical farming. Despite the limited relevant research on controlled environment production of field crops such as soybean and rice, increasing efforts have been started to put on speed breeding of some field crops in this way. Plant breeding plays a key role in agricultural production, but the process of developing suitable cultivars is time-consuming, partly because of the long generation times of crops. Recently, using a controlled environment for speed breeding has been introduced for long-day crops, but a similar protocol for short-day crops is lacking to date. In this case, German researchers developed a speed breeding protocol through the application of LED lighting with optimized spectral quality to promote flowering and thus increase breeding efficiency in some short-day crops, soybean, rice, and amaranth [112]. In their research, using LED lighting with a BL-enriched, and FR-deprived light spectrum at a 10 h photoperiod facilitated the growth of short and sturdy soybean plants that flowered about 23 days after sowing and matured within 77 days, thus allowing up to five generations per year. In rice and amaranth, flowering was achieved about 60 and 35 days after sowing, respectively. The developed protocol enables several generations per year using crop-specific LED-based lighting regimes, without the need for tissue culture tools such as embryo rescue. Moreover, this approach can be readily applied to a multi-story 96-cell tray-based system to integrate speed breeding with genomics toward a higher improvement rate in breeding [112].

## 5. Conclusions

Recent developments in LED technologies have made it easier to manipulate BL in a controlled environment. In this review, we have summarized the feasible ways to ma-

nipulate BL to mediate plant flowering through electric lighting such as night interruption lighting, day extension, supplemental lighting, and daytime sole-source lighting. Also, we have compared the effects of BL alone or its combination with other light wavelengths on plant flowering to those of no lighting treatment or other lighting sources. Furthermore, we have identified the possible factors resulting in inconsistent results of previous studies, including BL intensities and durations, background or previous environment conditions, and plant genotypes. This would not only provide useful information for growers to accurately and effectively manipulate BL to control flowering in production but also to identify the knowledge gaps for researchers to conduct relevant fundamental studies due to a complicated signal network involved in BL-mediated plant flowering response. In this review, we have included varying high-value crops from ornamental plants to fruits, vegetables, and specialty crops during either the pre-harvest or post-harvest stage, which would be potentially helpful for different crop growers.

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