

Review

Molecular Mechanisms Underlying Floral Development Mediated by Blue Light and Other Integrated Signals: Research Findings and Perspectives

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Abstract

Blue light (BL) is a key environmental signal influencing plant flowering, yet its role in floral development beyond the transition phase remains underexplored. This review provides a comprehensive synthesis of current research on BL-mediated floral development, with a particular emphasis on horticultural crops grown in a controlled environment. Unlike prior reviews that focus primarily on floral induction, this article systematically examines BL's effects on later stages of flowering, including floral organ morphogenesis, sex expression, bud abortion, flower opening, scent emission, coloration, pollination, and senescence. Drawing on evidence from both model plants (e.g., *Arabidopsis thaliana*) and crop species, this review identifies key photoreceptors, hormonal regulators, and signaling components involved in BL responses. It also highlights species-specific and context-dependent outcomes of BL manipulation, proposes mechanistic hypotheses to explain conflicting findings, and outlines critical knowledge gaps. By integrating molecular, physiological, and environmental perspectives, this review offers a framework for optimizing BL applications to improve flowering traits and postharvest quality in horticultural production systems.

Keywords: floral development; photoreceptors; signal pathways; interaction factors; physiological mechanisms; future directions



Academic Editor: Yasuhito Sakuraba

Received: 26 August 2025

Revised: 10 October 2025

Accepted: 13 October 2025

Published: 15 October 2025

Citation: Kong, Y.; Zheng, Y. Molecular Mechanisms Underlying Floral Development Mediated by Blue Light and Other Integrated Signals: Research Findings and Perspectives. *Crops* **2025**, *5*, 72. <https://doi.org/10.3390/crops5050072>

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1. Introduction

Plant flowering, the transition from the vegetative to the reproductive phase, is a crucial process that determines reproductive success and significantly impacts the yield and commercial value of many horticultural crops [1,2]. Light is one of the most important environmental factors influencing plant flowering. Among different light wavelengths, blue light (BL; 400–500 nm) plays a significant role in regulating flowering. For example, BL has been shown to promote flowering as effectively as far-red (FR; 700–800 nm) light in both the model species *Arabidopsis thaliana* (hereafter *Arabidopsis*) and some agriculturally important crops [3,4].

In controlled-environment agriculture (CEA), BL can be precisely manipulated in terms of peak wavelength, intensity, duration, and its co-action with other wavelengths through LED lighting. Blue LEDs, in addition to FR LEDs, represent a promising light source for regulating plant flowering [5]. Moreover, blue LEDs are generally more affordable and accessible than FR LEDs, which helps reduce the overall costs of using LED lighting for flowering control [6]. Blue LEDs, either alone or combined with other wavelength(s),

have been increasingly used in CEA for various flowering regulation strategies, including night interruption lighting, day extension lighting, supplemental lighting, and sole-source lighting tailored to specific production purposes [5]. However, inconsistent results have been reported in previous studies about BL-mediated flowering. Therefore, an in-depth understanding of the relevant physiological mechanisms is necessary to optimize the application of BL for manipulating plant flowering in CEA systems [7].

Plant flowering is a complex process that can be divided into two seemingly distinct phases: floral transition (induction/initiation) and floral development [8–10]. After floral transition, the plant enters the floral development stage, which includes floral organ determination and morphogenesis, flower opening, and senescence. BL affects not only floral transition (the earlier phase) but also floral development (the later phase). For example, in *Delphinium* ‘Aurora Light Blue’, both the days to bolting and the days from bolting to flower opening were longer under blue LEDs compared to red (600–700 nm) LEDs when used for overnight lighting under natural short-day conditions [11]. However, environmental conditions that favor floral transition do not necessarily promote floral development. Moreover, BL-mediated floral development can be affected by factors such as light intensity, photoperiod, and other light wavelengths [5,11]. Consequently, BL exerts diverse effects across the entire process of floral development, much like its role in floral transition.

The molecular signaling mechanisms underlying BL-mediated floral transition and its interacting factors have been recently reviewed by Kong and Zheng [12,13]. However, information regarding BL-mediated floral development remains limited. In this review, we aim to provide an overview of current knowledge on the mechanisms of BL-mediated floral development not only in model plants but also in agricultural/horticultural crops. Given the scarcity of mechanistic studies directly focused on BL, we occasionally extend our discussion to other light signals to infer potential roles of BL, considering their shared downstream signaling pathway components. Additionally, we identify numerous knowledge gaps, and propose mechanistic hypotheses based on findings related to key regulators (such as hormones, sugars, and transcriptional factors, etc.) in floral development and their roles in other BL-mediated plant responses beyond floral development. Drawing on this information, we attempt to explain the contrasting results observed in previous studies of BL-mediated floral development and offer foundational insights for optimizing BL applications in CEA. Finally, we highlight future research directions and potential practical applications based on the identified gaps in knowledge.

2. Floral Organ Determination/Morphogenesis

Early floral development involves floral identity determination and organ morphogenesis, which together define sex expression and final flower size [14]. Environmental cues, such as BL, can influence these processes, affecting floral organ specification, growth, and the risk of floral bud abortion.

2.1. Flower Sex Expression

For monoecious plants such as certain members of the *Cucurbitaceae* family, which produce distinct male and female flowers on the same plant, BL can affect floral sex determination. In cucumber (*Cucumis sativus*), BL from LED lighting has been shown to increase the percentage of nodes bearing female flowers, compared to red, green (500–600 nm), or white light [15]. Similarly, in bitter melon (*Momordica charantia*), sole-source blue LED lighting increased both the total number of female flowers and the female flower-to-node ratio on main stems, relative to red LED treatment [16]. However, for squash (*Cucurbita moschata* Duch) seedlings, no significant difference in female flower number was observed

between blue and LED lighting [17]. Furthermore, RB-LEDs with a lower blue proportion (56% B) induced more female flowers and higher fruit yield compared with blue LEDs alone, red LEDs, and RB-LEDs with a higher blue proportion (71% B) [17]. Contrastingly, in cucumber, RB-LED lighting with a higher BL proportion (33% vs. 20%) enhanced female flower formation [18]. It is noteworthy that BL from blue LEDs exhibits low phytochrome photostationary state (PPS) values, potentially deactivating both phytochrome B (PHYB) and cryptochrome 1 (CRY1), whereas BL from RB-LEDs has high PPS values and may activate both PHYB and CRY1 [19]. So far, the information has been unavailable about how the two photoreceptors are involved in BL-mediated flower sex expression (Figure 1).

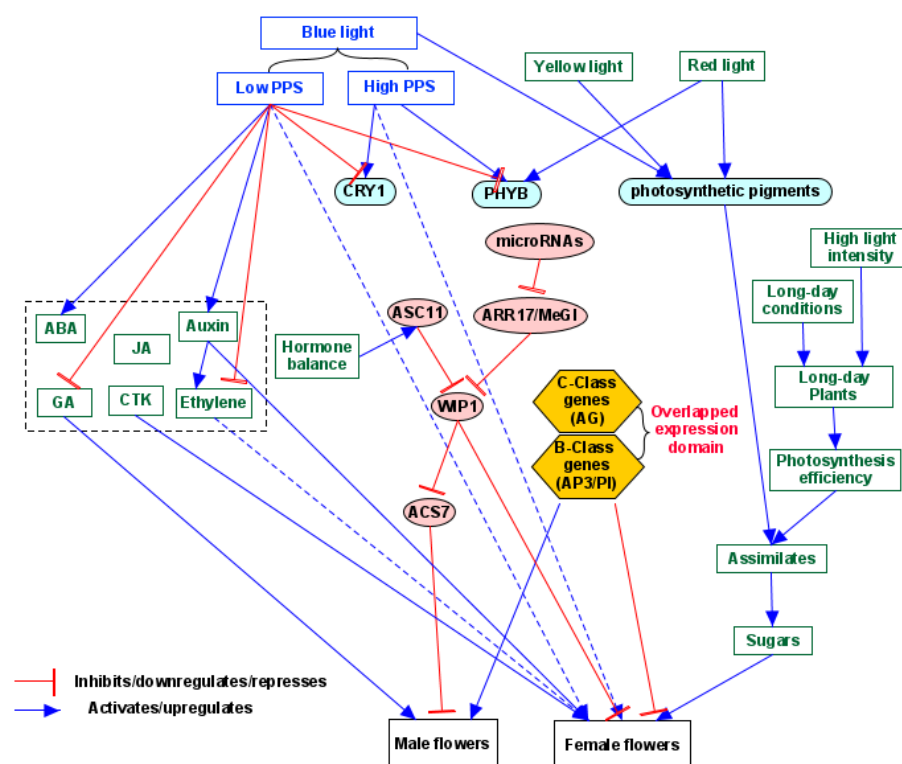


Figure 1. The physiological mechanisms underlying flower sex expression mediated by blue light, as well as other potentially integrated signals. PPS = phytochrome photostationary state; PHYB = phytochrome B; CRY1 = cryptochrome 1; AP3 = APETALA3; PI = PISTILLATA; ARR17 = ARABIDOPSIS RESPONSE REGULATOR 17; MeGI = MALE GROWTH INHIBITOR; ASC11 = AGAMOUS-LIKE SUPPRESSOR OF CYTOKININ 11; WIP1 = WOUND-INDUCED PROTEIN 1; ACS 7 = 1-aminocyclopropane-1-carboxylic acid synthase 7; AG = AGAMOUS; GA = gibberellin; ABA = abscisic acid; JA = jasmonic acid; CTK = cytokinin. In the diagram, the green rectangles are other signals that may integrate with blue light pathway; the blue rounded rectangles are photoreceptors or photosynthetic pigments; the pink ovals are transcription factors or other regulators; the yellow hexagons are key floral regulators. The dashed rectangles include a group of integrated signals. The dashed action lines indicate that the action can be affected by many factors, or the involved detailed action mechanism is still unclear.

Gibberellin (GA) plays a key role in BL-regulated sex expression in cucumber. In contrast, early studies identified ethylene as the primary hormone involved in sex determination and expression, promoting female flower occurrence in *Cucumis* and *Cucurbita* species [20]. Ethylene is often regarded as the fundamental “sex hormone” enhancing femaleness in monoecious cucumber [15,20]. However, BL-induced flower femaleness in cucumber is associated with the downregulation of genes involved in ethylene and GA biosynthesis and signaling, alongside the upregulation of abscisic acid (ABA) and auxin signaling genes [15,18]. These findings suggest that GA, together with coordinated interac-

tions among auxin, ABA, and Jasmonic acid (JA), rather than ethylene alone, mediate the sex response to BL.

BL-regulated sex expression in cucumber can be affected by endogenous signals beyond phytohormones. For instance, when part of the BL component in RB-LED (80%R:20%B) was replaced by yellow light peaking at 510 nm (80%R:10%B:10%Y), plants exhibited an increased number of female flowers, which correlated with higher sucrose content [21]. This finding highlights the significant role of sucrose metabolism in flower sex expression. Supporting this, photoperiod and light intensity have been shown to affect sex expression in cucumber. Photoperiod-sensitive varieties demonstrate enhanced photosynthesis efficiency and produce more female flowers under inductive photoperiods [22–24]. In long-day-sensitive cucumbers, high light intensity increased the number of female flowers, whereas shading favored female flower formation in short-day-sensitive varieties [24,25].

Despite advances in identifying endogenous signals, the molecular mechanisms linking BL to floral sex expression remain poorly understood. The extended ABCDE model describes how floral organs are specified by combinations of MADS-box genes, with B-class genes (*APETALA3*, *PISTILLATA*) overlapping with C-class *AGAMOUS* to control unisexual flower formation [26]. Sex-determination genes (SDGs) identified in several angiosperms, such as *AGAMOUS-LIKE SUPPRESSOR OF CYTOKININ 11* (*ASC11*) in melon (*Cucumis melo*), *ARABIDOPSIS RESPONSE REGULATOR 17* (*ARR17*) in poplar (*Populus*), and *MALE GROWTH INHIBITOR* (*MeGI*) in persimmon (*Diospyros lotus*), act through diverse genetic switches that ultimately suppress either male or female organ development [26–28]. These SDGs can also influence floral MADS-box genes, including B-class regulators, and are modulated by hormones such as CTKs and ethylene [27]. However, direct connections between BL-responsive photoreceptors (e.g., PHYB, CRY1) and these sex-determination networks have not yet been demonstrated, leaving the molecular basis of BL-mediated sex expression unresolved.

2.2. Floral Bud Abortion and Reversion

BL with high PPS values has minimal effects on flower bud abortion. For example, in roses (*Rosa*), sole-source lighting using BL from neon tubes did not affect flower abortion and supported normal floral organ development as efficiently as white light at comparable light intensities, despite slightly slower floral development and shorter peduncles [29]. Additionally, under sole-source broad-spectrum lighting with constant photosynthetic photon flux density, decreasing the proportion of BL from 18% to 2% did not influence flower abortion and floral development [30,31]. In these lighting conditions, the BL was either combined with or contained other light wavelengths characterized by high R:FR ratios, resulting in high PPS values that likely activate both PHYB and CRY1 [19]. However, whether CRY1 is involved in flower bud abortion mediated specifically by BL with high-PPS values remains unknown (Figure 2).

BL with low PPS values may act as a shade signal and potentially promote flower bud abortion, although direct evidence is lacking. Studies in roses and sweet pepper (*Capsicum annuum*) show that vegetative shade increases flower bud abortion [32,33]. Such shade is characterized not only by reduced light intensity but also by decreased PHY activity, particularly PHYB. While reduced PHYB activity caused by a low R:FR is known to trigger shade-induced flower bud abortion [34,35], the influence of BL with low PPS values remains unclear. Because pure BL from narrowband blue LEDs also produces a low PPS and can reduce PHYB activity, it may generate a signal similar to vegetative shade and likewise promote bud abortion. Whether blue LED light indeed causes a response comparable to low R:FR conditions has not yet been tested and remains an important direction for future research.

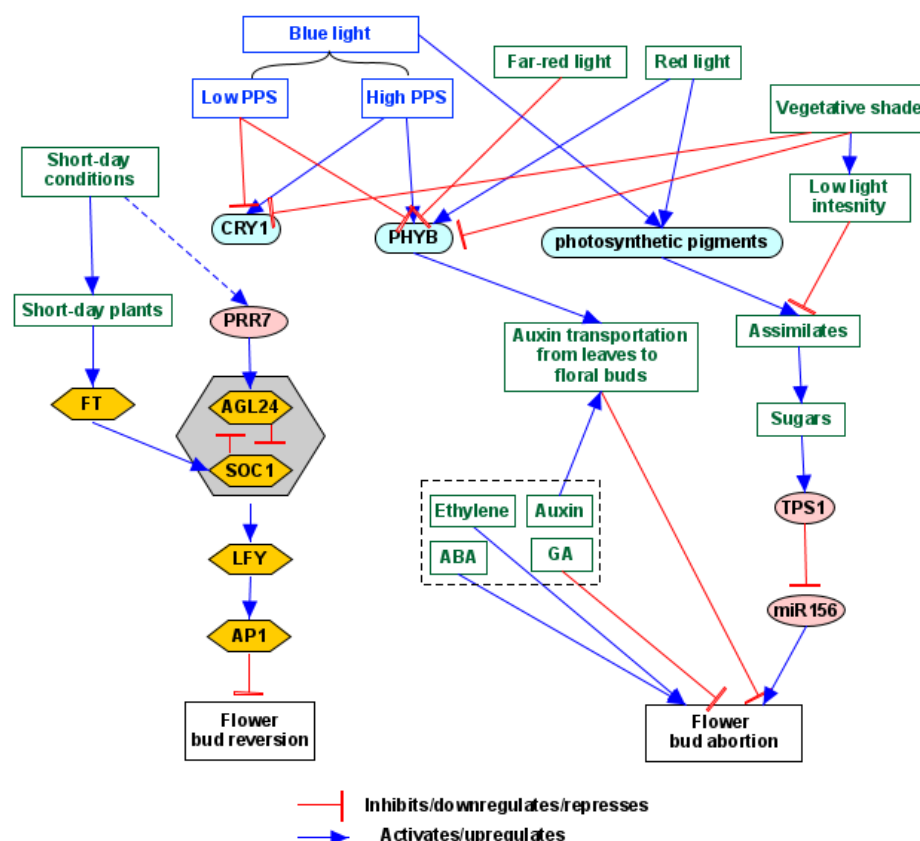


Figure 2. The physiological mechanisms underlying floral bud abortion and reversion mediated by blue light, as well as other potentially integrated signals. PPS = phytochrome photostationary state; PHYB = phytochrome B; CRY1 = cryptochrome 1; TPS1 = trehalose-6-P synthase 1; miR156 = microRNA156; FT = FLOWERING LOCUS T; PRR 7 = PSEUDO-RESPONSE REGULATOR 7; SOC1 = SUPPRESSOR OF OVEREXPRESSION OF CO 1; AGL24 = AGAMOUS-LIKE24; LFY = LEAFY; AP1 = APETALA1; GA = gibberellin; ABA = abscisic acid. In the diagram, the green rectangles are other signals that may integrate with blue light pathway; the blue rounded rectangles are photoreceptors or photosynthetic pigments; the pink ovals are transcription factors or other regulators; the yellow hexagons are key floral regulators. The dashed rectangles include a group of integrated signals. The dashed action lines indicate that the involved detailed action mechanism is still unclear.

BL may influence flower bud abortion by modulating hormone balances, but direct evidence remains limited. A study in *Hibiscus* suggests that PHY-regulated auxin transport from leaves to flower buds contributes to light-mediated bud abscission [36]. Auxin and ethylene act antagonistically: sustained auxin flow from leaves prevents abscission-layer formation, whereas high ethylene promotes abortion, and ethylene sensitivity depends partly on auxin levels [33,37,38]. Other hormones, such as ABA, often correlate positively with bud abortion, while GA has an opposite effect [33,39]. BL can alter auxin transport and hormone signaling in other developmental contexts, it is plausible that BL also affects the auxin–ethylene–ABA–GA network controlling flower bud abortion, but targeted studies are still needed to confirm this connection.

BL may regulate flower bud abortion through its effects on sugar accumulation. Besides auxin, sugar levels can also affect the sensitivity of flowers to ethylene [33]. A recent study on lotus (*Nelumbo nucifera*) has demonstrated that sugar signaling plays a central role in regulating flower bud abortion, with trehalose levels showing the greatest decline in the aborting flower buds [40]. A potential regulatory network centered on microRNA156 (miR156) was identified, where trehalose-6-P synthase 1 (TPS1), an enzyme required for trehalose synthesis, negatively regulates miR156 expression. Lotus plants overexpressing

TPS1 showed significantly decreased flower bud abortion rates under both normal and low-light conditions [40]. As an important component of photosynthetically active radiation, BL combined with red light can enhance photosynthesis and promote sugar accumulation, which may help reduce the incidence of flower bud abortion.

BL-mediated floral reversion appears to vary among plant species, which may be linked to the function of AGAMOUS-LIKE24 (AGL24). For example, in *Cannabis sativa* during floral transition stage, 4 h end-of-day BL treatment under short-day conditions inhibited floral development and promoted floral reversion [41]. In contrast, a similar BL treatment did not affect floral development in chrysanthemum (*Chrysanthemum × morifolium*) [42,43]. AGL24 is known to promote reversion of the floral meristem (FM) back to the inflorescence meristem (IM) [44,45], although it also functions as a floral activator during the floral transition [46]. Its activity is integrated into a regulatory network in which SUPPRESSOR OF OVEREXPRESSION OF CO 1 (SOC1) and AGL24 mutually activate each other and together induce *LEAFY* (*LFY*) expression [47]. *LFY* subsequently activates floral homeotic genes, including *APETALA1* (*AP1*), which specifies floral organ identity [48]. Once *AP1* is induced, it represses *AGL24* and *SOC1* to stabilize floral commitment and prevent FM reversion [44,45]. Thus, in *Arabidopsis*, positive feedback loops make floral initiation irreversible [47]. In contrast, in many other species, the absence of such stabilizing loops allows flower bud abortion or FM reversion to leaf production when inductive photoperiods are not maintained [47]. For example, when *Cannabis* plants were shifted from inductive to non-inductive photoperiods, leaves emerged on developing inflorescences [49], and a comparable reversion has been reported in chrysanthemums [47], despite its lack of responses to long-day BL treatment.

Long-day BL treatment does not affect floral reversion in chrysanthemum, possibly due to the unique role of AGL24 and the presence of a species-specific BL photoreceptor. In chrysanthemum plants, AGL24 is a crucial regulator of capitulum (i.e., a type of inflorescence) development in response to short-day conditions [47]. FLOWERING LOCUS T-LIKE 3 (FTL3) facilitates floral evocation but has a limited role in capitulum development. The transition from a naked IM to floral primordium formation represents a critical conversion point for successful anthesis in response to short days. Differing from *Arabidopsis*, SOC1 and AGL24 form a negative feedback loop in chrysanthemum. Notably, AGL24 expression is activated by PSEUDO-RESPONSE REGULATOR 7 (PRR7), which is detectable in the IM and individual floral primordia under short-day conditions, highlighting the importance of the PRR7–AGL24 module in the IM for continuous short-day signal perception, promoting capitulum development and successful anthesis in chrysanthemum [47]. Additionally, PHOTOLYASE/BLUE-LIGHT RECEPTOR 2 (PHR2), rather than CRY, responds to short days and interacts with CRYPTOCHROME-INTERACTING BASIC HELIX-LOOP-HELIX 1 (CIB1) to regulate flowering in chrysanthemum [50].

2.3. Floral Organ Morphogenesis/Growth

Floral organs, sepals, petals, stamens, and carpels, arise from founder cells on the floral meristem and develop in a centripetal sequence [14,51,52]. Their subsequent morphogenesis is driven by coordinated cell proliferation and expansion, which together determine organ size and shape [53,54].

BL-mediated flower stem length may be related to changes in cell proliferation and expansion (Figure 3), as the final size of a floral organ is largely determined by these growth processes [14]. The relative importance of cell proliferation vs. cell expansion in light-mediated flower stem growth differs between BL and other light wavelengths. For example, under background lighting from a metal halide (MH) lamp, localized blue LED radiation to the upper region of the peduncle of geranium (*Pelargonium × hortorum*) flowers

suppressed the peduncle elongation by reducing cell number rather than cell length [55]. In contrast, local FR light radiation increased peduncle cell length and consequently flower stem length. This study also suggests that primary light signal sensors governing peduncle elongation may be the peduncle cells themselves in geranium [55]. Notably, the involved photoreceptors may differ between blue and FR light; under the MH lamp background, both CRY1 and PHYB might be activated in local BL treatment, while PHYB was deactivated in local FR light treatment.

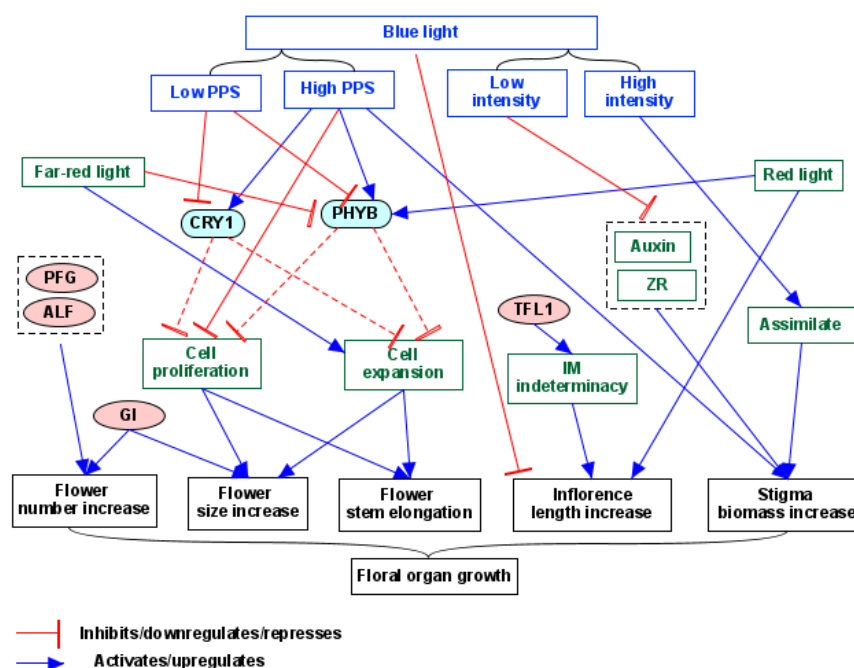


Figure 3. The physiological mechanisms underlying floral organ morphogenesis/growth mediated by blue light, as well as other potentially integrated signals. PPS = phytochrome photostationary state; PHYB = phytochrome B; CRY1 = cryptochrome 1; GI = GIGANTEA; PFG = PETUNIA FLOWERING GENE; ALF = ABERRANT LEAF AND FLOWER; TFL1 = TERMINAL FLOWER 1. IM = inflorescence meristem; ZR = zeatin riboside. In the diagram, the green rectangles are other signals that may integrate with blue light pathway; the blue rounded rectangles are photoreceptors; the pink ovals are transcription factors. The dashed rectangles include a group of integrated signals or transcription factors involved. The dashed action lines indicate that the action can be affected by many factors, or the involved detailed action mechanism is still unclear.

Accumulated evidence indicates that BL-mediated flower stem length is related to PHYB activity, which can be inferred from the PPS value. In calibrachoa (*Calibrachoa × hybrida*), sole-source lighting with blue LEDs (pure BL) or their combination with low-level red and FR LEDs (impure BL; R:FR = 1) similarly increased flower peduncle length compared to red LEDs, due to lower PPS values (<0.6); however, the promotional effect of impure BL gradually declined as PPS increased above 0.6 or the FR:R ratio decreased from 1 to 0 [56,57]. Similar promotional effect of blue vs. red LEDs on flower stem length has been observed in tulip (*Tulipa* spp.) [58] and strawberry (*Fragaria × ananassa*) [59] plants under sole-source lighting. In geranium, even a 4 h night interruption with blue vs. red LEDs reduced expression of PHYs and CRY1, although the increase in flower stalk length was only a trend and not statistically significant [60].

When associated with high PHYB activity, BL can reduce flower stem length or flower size through activation of CRY1. For rose under sole-source lighting, flower peduncles were shorter under impure BL compared to white light from non-LED lamps with a high R:FR ratio, due to a much higher BL percentage [29]. In saffron (*Crocus sativus*), sole-source RB-LED lighting reduced flower size compared with red LED treatment [61]. In St John's wort

(*Hypericum perforatum*), increasing the B% in RB-LEDs decreased flower diameter, as well as fresh and dry weight [62,63]. In *Lilium*, RB-LED lighting with the lowest BL proportion (ranging from 20% to 80% B) produced the largest flower [64]. For chrysanthemum under nighttime supplemental lighting with BL from a non-LED lamp, increasing BL intensity from 3.6 to 7.0 $\mu\text{mol m}^{-2} \text{s}^{-1}$ decreased flower size and dry mass [65].

It is unknown how the BL receptors deliver the light signal to affect foundation cell proliferation and expansion, and thus change floral organ size/growth. Recently, GI, as a regulator of BL-mediated flower initiation [12], has also been shown to play a positive role in flower bud growth in petunia (*Petunia × hybrida*) [66]. Plants with loss of GI1 function, grown under long-day conditions, show not only a reduction in the total number of floral buds, but also smaller flowers (a significant reduction in corolla diameter as well as in the tube length) than the wild type. The reduced total number of flower buds also indicates an upstream effect related to the flower-meristem-identity genes *PETUNIA FLOWERING GENE* (PFG) and *ABERRANT LEAF AND FLOWER* (ALF) [66–68]. Whether BL affects the above regulators and thus influences foundation cell proliferation and expansion to change floral organ size/growth needs to be confirmed in future studies.

BL has also been found to affect the growth of floral organs, such as stigma, differing its effects in different light intensities, which may be related to plant biomass accumulation and allocation, despite unclear molecular mechanisms. For example, in saffron, stigma growth response to sole-source blue LED lighting varies with light intensity. Under blue vs. red LED, stigma dry weight was increased at a higher light intensity, $\approx 150 \mu\text{mol m}^{-2} \text{s}^{-1}$ [69,70], but was reduced at a lower light intensity, $\approx 50 \mu\text{mol m}^{-2} \text{s}^{-1}$ [61]. Under the higher light intensity, blue vs. red LED increased photosynthesis, and promoted biomass allocation toward the corms and floral organs such as the stigma, rather than leaves [70]. Under the lower light intensity, blue vs. red LED reduced the auxin and zeatin riboside (ZR) levels in the mature corms [61], which may reduce the sink strength and thus decrease biomass allocation toward the corms.

Additionally, BL can affect inflorescence length, although the underlying molecular mechanisms remain unclear. In *Phalaenopsis* orchids, application of RB-LED lighting with varying proportions of BL to flower spikes did not influence the final spike length; however, flower spikes exposed to blue LED, or RB-LED lighting, were shorter than those grown under white light after 12 weeks of treatment [71]. Furthermore, under a white light background, enhanced blue vs. red light from LED lighting reduced spike length [72]. The specific contributions of blue and red light photoreceptors to spike elongation in *Phalaenopsis* orchids are still unknown, and the molecular pathways governing this process have yet to be elucidated. Inflorescence length, unlike flower stem length, depends on the main inflorescence meristem (IM) at the shoot apex, which determines whether the meristem terminates as a flower or remains indeterminate [73,74]. The activity of TERMINAL FLOWER 1 (TFL1) is critical for maintaining meristem indeterminacy [75]. The dynamic regulation of TFL1 activity governs the balance between indeterminate and determinate growth, thereby modulating plant architecture [76]. This TFL1-dependent regulation of inflorescence architecture is conserved across diverse species [76], including *Arabidopsis* [77], rice (*Oryza sativa*) [78], maize (*Zea mays*) [79], soybean (*Glycine max*) [80], and bean (*Phaseolus vulgaris*) [81]. Whether TFL1 plays a role in BL-mediated spike length in *Phalaenopsis* orchids remains to be investigated.

3. Flower Organ Maturation

Floral organ maturation, distinct from morphogenesis, is the stage when petals are gradually unfolded (i.e., flower opening) and flowers develop their characteristic colors and scents that attract pollinators and deter pests [14]. BL can influence this maturation process,

including flower opening and movement, scenting, and coloring, and thus reproductive success of flowers, although the detailed mechanisms remain unclear.

3.1. Flower Opening and Movement

3.1.1. Flower Opening

BL can inhibit flower opening in night-blooming species. For example, in *Oenothera lamarckiana*, an early study using a light filter demonstrated that wavelengths between 400 nm and 510 nm (primarily BL, along with part of green light) were effective in inhibiting flower opening by light [82]. It appears that specific BL receptors are involved in this process. Additionally, for flowers that open before dawn, the timing is generally governed by the length of the dark period [83]. This seems to be regulated by PHYTOCHROME INTERACTING FACTOR 4 (PIF4) and PIF5, both of which control the circadian clock [84]. It is plausible that in night-blooming species, the BL-inhibited flower opening may result from its photoreceptors' action on PIF4 and PIF5, thereby affecting the sensed dark length.

Flower opening with a diurnal rhythm can be regulated by BL as one of the light signals acting through the circadian clock (Figure 4), despite the unclear detailed mechanisms. For example, rose cut flowers exposed to BL opened faster than those exposed to red light or constant darkness, but slower than those exposed to white light, under a 12 h photoperiod [85]. It appears that multiple photoreceptors are involved in this process, as both CRYs and PHYs play roles in setting circadian rhythms [86]. These photoreceptors provide input signals to reset the circadian clock, partly by inhibiting CONSTITUTIVELY PHOTOMORPHOGENIC 1 (COP1), thereby regulating circadian rhythms [83,87]. It has been suggested that flowers, particularly petals, perceive light signals, including BL, to control flower opening [88]. However, the detailed signaling networks underlying the BL-mediated rhythmic flower opening remain unclear.

The effect of BL on the flower opening with a diurnal rhythm depends on photoperiod, light/dark cycle, light quality, and intensity. In *Eustoma grandiflorum*, under constant BL conditions, flower opening displayed circadian oscillations with a period of 25.6 h, similar to constant dark and 1 h longer than under constant red light [89]. Both red photoreceptors (e.g., PHYs) and BL photoreceptors (e.g., CRYs) appear to be involved in circadian rhythm entrainment. Under continuous co-irradiation with BL and red or white light, flowers opened and closed once, but subsequent oscillations ceased, suggesting that the endogenous clock's rhythm was disrupted or its signaling output interrupted. A synchronization of flower opening and closing rhythms to 24 h (16 h light/8 h dark; 16L/8D) and 20 h (12L/8D) light/dark cycles was observed under BL and red light. However, the synchronization was incomplete under 16 h light/dark cycles (8L/8D), and the flower oscillation period became 24 h under 12 h light/dark cycles (4L/8D). At 24 h light/dark cycles, the synchronization of flower opening rhythm involved two phases: an immediate, light-intensity-dependent response and a subsequent phase governed by the circadian clock. Increasing BL intensity from 25 to 100 W m⁻² ($\approx$ 63 to 250 μ mol m⁻² s⁻¹) accelerated flowers opening after illumination, while no such intensity-dependent effect was noted for red light [89], suggesting an important role for BL in light-intensity-dependent flower opening.

BL is known to influence plant hormone metabolism and signaling, yet its role in the hormonal control of flower opening remains largely speculative. Flower opening itself is regulated by several phytohormones, including ethylene, GA, auxins, ABA, and brassinolide (BR), whose effects vary among species [83,90–92]. BL has been shown in other developmental contexts to alter ethylene production, GA biosynthesis, and auxin transport [13,93], suggesting that BL could indirectly affect the hormonal networks governing petal expansion and unfolding. However, direct evidence linking BL-induced hormonal

changes to flower opening is not yet available, and targeted experiments are needed to clarify whether BL modifies these hormone pathways to control the timing or extent of flower opening.

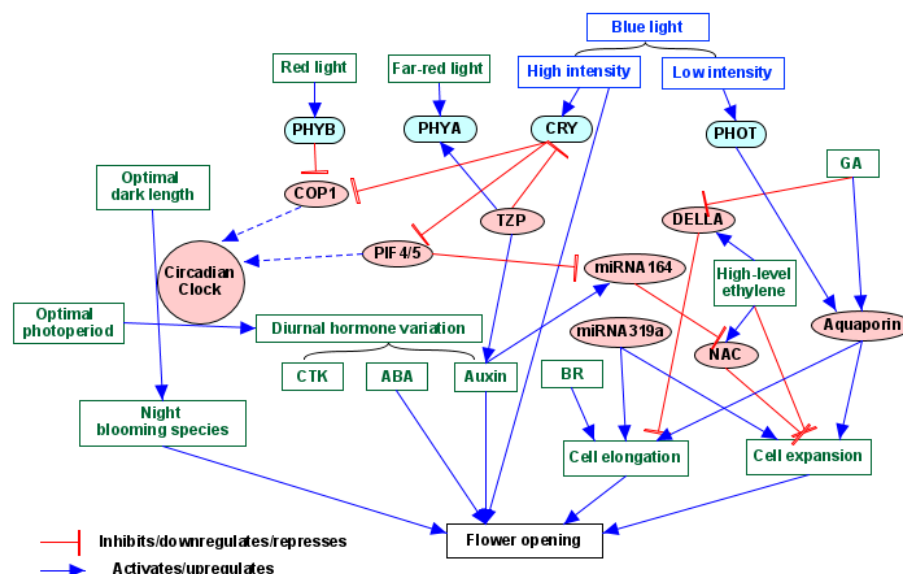


Figure 4. The physiological mechanisms underlying flower opening mediated by blue light, as well as other potentially integrated signals. PHY A/B = phytochrome A/B; CRY = cryptochrome; PHOT = phototropin; COP1 = CONSTITUTIVE PHOTOMORPHOGENIC1; PIF 4/5 = PHYTOCHROME-INTERACTING FACTOR 4/5; TZP = TANDEMZINC KNUCKLE/PLU3; miRNA 164/319a = microRNA 164/319a; NAC = NO APICAL MERISTEM (NAM), ARABIDOPSIS TRANSCRIPTION ACTIVATION FACTOR (ATAF), and CUP-SHAPED COTYLEDON (CUC); DELLA is a protein named after conserved amino acids: Asp-Glu-Leu-Leu-Ala; GA = gibberellin; ABA = abscisic acid; BR = brassinolide; CTK = cytokinin. In the diagram, the green rectangles are other signals that may integrate with blue light pathway; the blue rounded rectangles are photoreceptors; the pink ovals are transcription factors or other regulators. The dashed action lines indicate that the action can be affected by many factors, or the involved detailed action mechanism is still unclear.

BL may also influence flower hydraulic conductance and aquaporin activity to regulate flower opening, although direct evidence in flowers is still lacking. Flower opening depends on water influx and cell expansion, processes controlled in part by aquaporins, which facilitate water transport across membranes and contribute to organ-level hydraulic conductance [83,94]. In leaves, BL has been shown to enhance hydraulic conductance and increase aquaporin expression and activity through PHOT-mediated signal transduction [95–97]. These findings raise the possibility that BL could similarly modulate water movement and aquaporin function in flowers, thereby affecting petal expansion and opening, but this hypothesis remains to be experimentally tested.

Additionally, we hypothesized that BL modulates specific downstream components of its signaling pathway to regulate flower opening. Notably, TANDEMZINC KNUCKLE/PLU3 (TZP), a key factor within BL signaling networks, exhibits diurnally oscillating expression peaking in the morning and directly impacts auxin-related gene regulation [98,99]. This positions TZP as a critical mediator linking BL perception to hormonal control of growth processes involved in flower opening. BL also influences the stability of DELLA proteins, central repressors of flower cell elongation, by promoting their degradation, thereby facilitating petal expansion. This effect intersects with GA and ethylene signaling pathways known to govern DELLA protein levels [100–102]. By modulating DELLA stability, BL thus integrates light signals with phytohormone-mediated growth regulation. Furthermore, BL impacts the expression of multiple microRNAs, in-

cluding those such as miR319a and miR164, which indirectly regulate auxin signaling and transcription factors essential for petal morphology and flower opening (e.g., NAC family members regulated by miR164) [103–105]. These microRNAs provide an additional layer of post-transcriptional control linking BL perception to gene networks driving floral organ development. Therefore, the interaction of BL with TZP, DELLA protein stability, and microRNA expression highlights a complex regulatory network by which BL signaling exerts control over hormonal and transcriptional pathways critical for flower opening. Further research is necessary to elucidate the precise molecular mechanisms and temporal dynamics by which BL coordinates these downstream factors.

3.1.2. Flower Heliotropism

BL can provide the cue for floral heliotropism, a specialized phototropism in families such as *Asteraceae* and *Papaveraceae*, in which petals track the sun to raise flower temperature, thereby enhancing pollination and seed development [106]. An early field study on snow buttercup (*Ranunculus adoneus*) indicated that flowers could orient towards the sun when placed under boxes made entirely of blue-transmitting filters or in red-transmitting boxes with a single blue side facing the sun [106]. In contrast, the accuracy of solar orientation was significantly diminished in red-transmitting boxes and in red boxes with a single blue side facing away from the sun. However, a recent study on sunflowers (*Helianthus annuus*) found that depletion of either BL or red/FR light did not prevent the initiation or maintenance of heliotropism in the field [107]. Another recent investigation on *Arabidopsis* revealed that inflorescence phototropism is driven by photons in both the UV and blue spectral range (≤ 500 nm) and depends on multiple photoreceptor families [108]. The involved photoreceptors vary under different experimental conditions. Under controlled environments, UV RESISTANCE LOCUS 8 (UVR8) primarily mediates the phototropic response to narrowband UV-B radiation, while PHOTs regulate bending in response to low-intensity BL, and CRYs are the main photoreceptors at high-intensity BL (Figure 5). Additionally, PHOTs negatively regulate the action of CRYs at high BL intensities. Under natural field conditions, CRYs are the principal photoreceptors responsible for promoting the heliotropic movement of inflorescences under full sunlight [108]. Furthermore, PHYs such as PHYC, PHYD, and PHYE are also found to be involved in light-mediated floral heliotropism [109].

BL-mediated flower heliotropism may be related to its effects on elongation growth and phytohormone regulation, although direct evidence is still lacking. Flower heliotropism relies on differential stem elongation, with east-facing stem sides growing more during the day and west-facing sides elongating more at night, creating antiphasic growth patterns that drive solar tracking [107,110]. These growth asymmetries are closely linked to auxin and GA signaling, as auxin accumulates on the faster-elongating side of the stem and GA is required for maintaining proper elongation, often acting synergistically with auxin [109]. Since BL regulates both auxin distribution and GA levels to control cell elongation [19], it is reasonable to propose that BL contributes to heliotropic bending through its influence on hormone-mediated growth responses, though this connection remains to be experimentally demonstrated.

BL-mediated flower heliotropism appears to involve the integration of circadian and phototropism signaling. In young sunflowers, solar tracking is coordinated by circadian regulation of directional growth pathways, while phototropism-related genes are differentially expressed on opposite stem sides during heliotropic movement [110]. Recent studies show that a subset of phototropism-induced genes, particularly those linked to shade-avoidance growth, are strongly upregulated on the west side of stems at the onset of heliotropism [107]. These findings suggest that BL may influence flower heliotropism

through PHOT-mediated signaling in coordination with circadian regulation, although the precise molecular pathways remain to be elucidated.

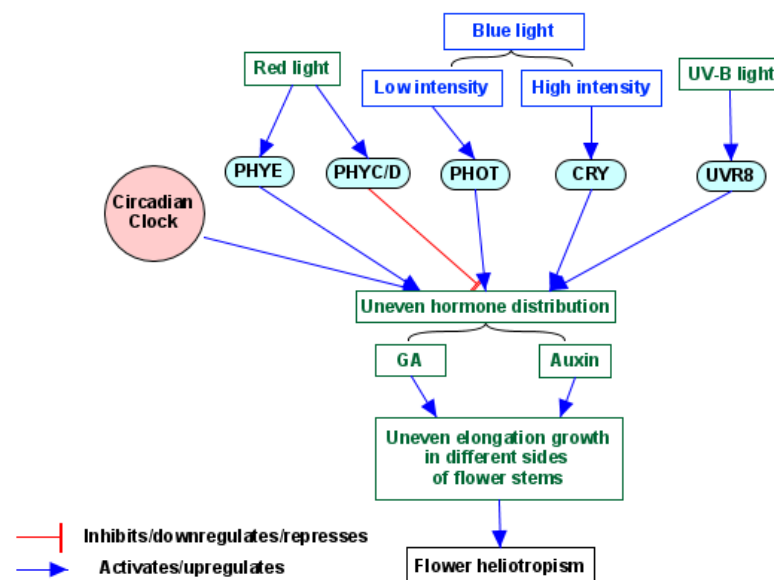


Figure 5. Physiological mechanisms underlying flower heliotropism mediated by blue light, as well as other potentially integrated signals. PHY E/C/D = phytochrome E/C/D; CRY = cryptochrome; PHOT = phototropin; UVR8 = UV RESISTANCE LOCUS 8; GA = gibberellin. In the diagram, the green rectangles are other signals that may integrate with blue light pathway; the blue rounded rectangles are photoreceptors; the pink circles are circadian clock.

3.2. Flower Scent Emitting

Floral scents, mainly composed of volatile organic compounds (VOCs) such as terpenoids, benzenoids/phenylpropanoids, and fatty acid derivatives, peak after flower opening to attract pollinators and provide defense functions [14,111,112]. BL can influence the timing and intensity of scent emission, potentially by coordinating VOC release with daily light cycles to optimize pollination success.

Although BL can influence VOCs and thus floral scent emission, its effects vary among plant species. In snapdragon (*Antirrhinum majus*), BL exposure significantly increased the production of key volatile compounds such as ocimene, myrcene, and methyl benzoate compared with red or green light [113,114]. In contrast, *Phalaenopsis* orchids showed different responses depending on genotypes: in *Phalaenopsis violacea*, monoterpene emission was lower under BL vs. white light, while other hybrids such as *Phalaenopsis* I-Hsin Venus 'KHM2212' and Meidarland Bellina Age 'LM128' also tended to release less scent under BL than full-spectrum light [115]. Similarly, in petunia, BL led to lower emission of phenylpropanoid/benzenoid volatiles compared with red or far-red light [116]. These findings indicate that BL can either enhance or suppress floral scent depending on the species and the specific volatile compounds involved.

BL regulates floral scent by activating CRY1 and downstream transcription factors that control VOC biosynthesis (Figure 6). In snapdragon, BL triggers AmCRY1, which interacts with AmMYB24 to activate ocimene synthetase (AmOCS), enhancing ocimene emission, and upregulates key genes for ocimene, myrcene, and methyl benzoate production, including OCS, myrcene synthetase (MYRS), and benzoic acid carboxyl methyl transferase (BAMT), CALMODULIN (CAM), and AmMYB63 [14,113,117]. In petunia, structural genes such as benzoic acid/salicylic acid carboxyl methyl transferase (BSMT), benzoyl-CoA:benzylalcohol/2-phenylethanol benzoyl transferase (BPBD), and cinnamate-CoA ligase 1 (CNL1), along with the

transcription factor ODORANT1 (ODO1), determine species-specific scent profiles, but their regulation by BL remains unknown [14,118].

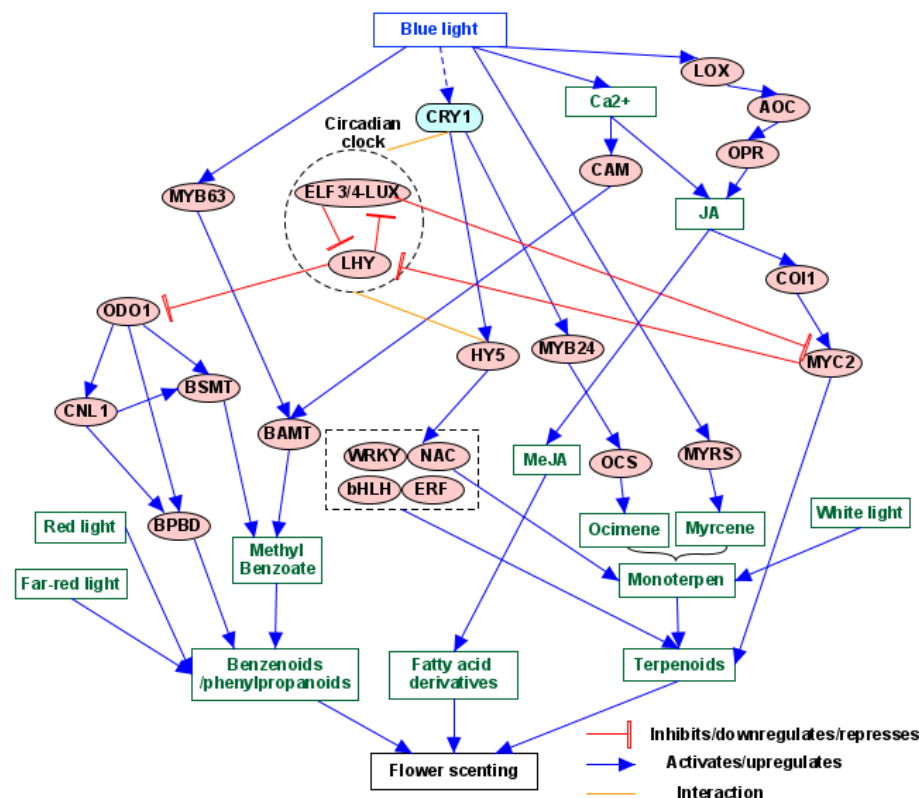


Figure 6. The physiological mechanisms underlying flower scent emission mediated by blue light, as well as other potentially integrated signals. CRY1 = cryptochrome 1; HY5 = ELONGATED HYPCOTYL5; MYBs are named after the v-Myb avian myeloblastosis viral oncogene homologs; LUX = LUX ARRHYTHMO; ELF3/4 = EARLY FLOWERING3/4; LHY = LATE ELONGATED HYPOCOTYL; OCS = ocimene synthetase; MYRS = myrcene synthetase; BMT = benzoic acid carboxyl methyl transferase; CAM = CALMODULIN; BSMT = benzoic acid/salicylic acid carboxyl methyl transferase; BPBD = benzoyl-CoA:benzylalcohol/2-phenylethanol benzoyl transferase; CNL1 = cinnamate-CoA ligase 1; ODO1 = ODORANT1; OPR = 12-oxo-phytodienoic acid reductase; AOC = allene oxide cyclase; LOX = lipoxygenase; COI1 = CORONATINE-INSENSITIVE 1; bHLH = BASIC HELIX-LOOP-HELIX; bZIP = BASIC LEUCINE ZIPPER; ERF = ETHYLENE RESPONSE FACTOR; NAC = NO APICAL MERISTEM (NAM), ARABIDOPSIS TRANSCRIPTION ACTIVATION FACTOR (ATAF), and CUP-SHAPED COTYLEDON (CUC); WRKY are transcription factors named after this signature sequence and their characteristic WRKY domain, which binds to W-box elements in gene promoters to regulate many plant processes; JA = jasmonic acid; MeJA = methyl jasmonate. In the diagram, the green rectangles are other signals that may integrate with blue light pathway; the blue rounded rectangles are photoreceptors; the pink ovals are transcription factors. The dashed action lines indicate that the action can be affected by many factors. The dashed circle includes the key circadian clock components involved. The dashed rectangle includes a group of transcription factors. The dashed action lines indicate that the action can be affected by many factors.

BL can also influence floral fragrance through calcium (Ca^{2+}) and JA signaling. In snapdragon, BL induced a net Ca^{2+} influx, suppressed by the Ca^{2+} channel blocker LaCl_3 , along with increased volatile emission and upregulation of key biosynthetic genes, indicating a role for Ca^{2+} signaling [113]. BL also enhanced the expression of JA-related genes, including those encoding enzymes for JA biosynthesis, 12-oxo-phytodienoic acid reductase (OPR), allene oxide cyclase (AOC), and lipoxygenase (LOX), and the JA receptor CORONATINE-INSENSITIVE 1 (COI1), implicating JA signaling in BL-induced VOC

production [113,114]. It suggests that BL activates Ca^{2+} and JA pathways to promote VOC biosynthesis, though the underlying regulatory mechanisms remain to be clarified.

The effects of BL on floral scent may partly involve interactions with the circadian clock, which regulates volatile emission in a light-dependent manner. In *Phalaenopsis* orchids, promoters of key monoterpene biosynthesis genes contain BL-responsive and circadian elements, and several light- and clock-related genes are expressed during anthesis [115]. In petunia, the clock gene *LATE ELONGATED HYPOCOTYL (LHY)* times the evening release of benzenoid/phenylpropanoid volatiles by repressing the master regulator ODORANT1 (ODO1), linking circadian control to scent emission [119–121]. The BASIC LEUCINE ZIPPER (bZIP) transcription factor ELONGATED HYPCOTYL5 (HY5), a central mediator of BL signaling, also integrates light and circadian pathways and may regulate terpene biosynthesis in orchids [122,123]. These findings suggest that BL influences floral scent partly through HY5–circadian clock interactions, although species-specific mechanisms remain to be clarified.

3.3. Flower Coloring

Flower color arises mainly from pigments such as carotenoids, anthocyanins, and betalains, whose spatial distribution determines floral hues and patterns [124,125]. Light, particularly BL, is a key environmental signal regulating pigment biosynthesis, but the molecular mechanisms underlying BL-mediated flower coloration remain poorly understood.

3.3.1. Anthocyanin/Flavonoid

As shown in Figure 7, BL can promote anthocyanin production and enhance flower coloration by upregulating the expression of structural genes in the anthocyanin biosynthetic pathway [126]. In gerbera (*Gerbera × hybrida*), BL is more effective than red light at inducing anthocyanin accumulation [127]. A study on chrysanthemum demonstrated that increasing BL component stimulated flavonoid synthesis [128]. In cherry blossom (*Prunus × yedoensis*), both blue and red LEDs influenced flower coloration, but the blue LED of 450 nm was most effective [129]. Furthermore, combined irradiation with both blue and red LEDs induced greater anthocyanin production than blue LED alone, indicating an interaction between the BL and red light receptors [129]. In petunia corolla, BL and red light showed similar promotive effects on chalcone synthase (CHS) expression and anthocyanin accumulation, whereas green light was slightly less effective [130]. An early study on petunia has revealed that at least three photoreceptors, which primarily sense blue light (CRY), red and FR light (PHY), and UV-B light (later identified as UVR8), are involved in regulating anthocyanin synthesis [126,131]. In *Arabidopsis*, red light induces dihydroflavonol 4-reductase (DFR), while BL upregulates CHS [132]. Differently, in gerbera ray florets, BL promotes gene expression of both *CHS* and *DFR*, and red light predominantly enhances *CHS* expression [127]. This indicates that both BL and red light receptors are involved in light regulation of flower pigmentation in gerbera.

The effect of BL on anthocyanin production and flower coloration may depend on light intensity, although direct evidence from BL-specific studies is limited. In petunia, the promotion of corolla pigmentation and *CHS* gene expression is photon-flux dependent, with continuous illumination at relatively high energy levels required to achieve maximum gene expression and pigmentation [133]. Beyond petals, leaves also contribute to the light regulation of petal pigmentation. For instance, In chrysanthemum ray florets, pigmentation depends on light intensity, and is primarily associated with the expression of seven structural genes in the anthocyanin biosynthetic pathway, including *CHS*, *DFR*, *F3H* (flavanone 3-hydroxylase), *F3'H* (flavonoid 3'-hydroxylase), *ANS* (anthocyanidin synthase), *3GT*

(anthocyanidin 3-O-glucosyltransferase), and 3MT (anthocyanin 3-O-methyltransferase), as well as some key regulatory genes such as *CmMYB* and *CmbHLH* [134,135].

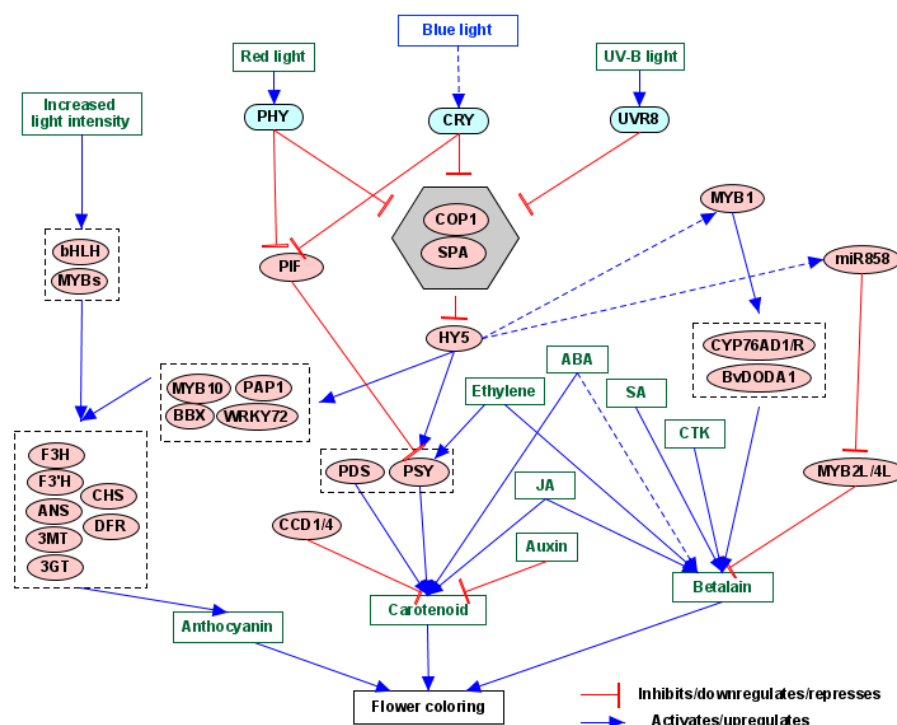


Figure 7. The physiological mechanisms underlying flower coloring mediated by blue light, as well as other potentially integrated signals. PHY = phytochrome; CRY = cryptochrome; UVR8 = UV RESISTANCE LOCUS 8; PIF = PHYTOCHROME-INTERACTING FACTOR; COP1/SPA = CONSTITUTIVE PHOTOMORPHOGENIC1/SUPPRESSOR OF PHYA-105; HY5 = ELONGATEDHYPOCOTYL5; BBX = B-BOX; bHLH = BASIC HELIX-LOOP-HELIX; MYBs are named after the v-Myb avian myeloblastosis viral oncogene homologs; MYB2L/4L = MYB2/4-LIKE; CYP76AD1/R = cytochrome P450 76AD1/R; BvDODA1 = beta vulgaris DOPA 4,5-dioxygenase 1; F3H = flavanone 3-hydroxylase, F3'H = flavonoid 3'-hydroxylase; ANS = anthocyanidin synthase; 3GT = anthocyanidin 3-O-glucosyltransferase; 3MT = anthocyanin 3-O-methyltransferase; DFR = dihydroflavonol 4-reductase; CHS = chalcone synthase; PSY = phytoene synthase; PDS = phytoene desaturase; CCD1/4 = carotenoid cleavage dioxygenase 1/4; PAP1 = PRODUCTION OF ANTHOCYANIN PIGMENT 1; WRKY72 = WRKY DNA-BINDING PROTEIN 72; miR858 = microRNA858; GA = gibberellin; JA = jasmonic acid; ABA = abscisic acid; SA = salicylic acid; CTK = cytokinin. In the diagram, the green rectangles are other signals that may integrate with blue light pathway; the blue rounded rectangles are photoreceptors; the pink ovals are transcription factors or other regulators. The dashed rectangles include a group of transcription factors. The dashed action lines indicate that the action can be affected by many factors, or the involved detailed action mechanism is still unclear.

BL-mediated anthocyanin production in flowers may be closely related to the regulation of the transcription factor HY5, as supported by evidence from fruit crops and *Arabidopsis*. In red pear (*Pyrus pyrifolia* × *Pyrus communis*), the BL signal transduction module CRY–COP1–HY5 plays a crucial role in anthocyanin biosynthesis and the resultant fruit skin coloration [136]. In ripening bilberry (*Vaccinium myrtillus*) fruits, BL effectively induces the accumulation of anthocyanin and delphinidin-based anthocyanins through CRY2/COP1, HY5, or ABA signaling pathways [137,138]. HY5 acts as a central modulator of light signaling by regulating gene expression necessary for anthocyanin production [125,139]. HY5 promotes anthocyanin accumulation by activating regulatory genes such as *PAP1* (PRODUCTION OF ANTHOCYANIN PIGMENT 1), *WRKY72* (WRKY DNA-BINDING PROTEIN 72), *MYB10*, and *BBX* (B-BOX) protein across various plant species [140–143]. Upon photoactivation, CRYs interact with COP1 and SUPPRESSOR

OF PHYA-105 (SPA) proteins to form the CRY–COP1–SPA complex, which enhances HY5 protein abundance [138,144,145]. Furthermore, activated PHYs can disrupt the COP1–SPA complex or inactivate its E3 ligase, thereby preventing HY5 degradation and sustaining anthocyanin biosynthesis [146–148].

3.3.2. Carotenoid

BL has been shown to positively affect carotenoid accumulation, although evidence from flower studies remains limited. In carnation flowers, BL maintained higher carotenoid levels in petals during vase life, but carotenoid concentrations decreased under red or white light [149]. Similar trends have been observed in non-floral tissues, where BL treatment increased carotenoid content in lettuce (*Lactuca sativa*) [150], pepper (*Capsicum annuum*) [151], and broccoli (*Brassica oleracea* var. *italica*) [152,153]. In *Citrus*, carotenoid accumulation was induced by BL treatment, but was not affected by red light treatment [154].

The molecular mechanisms underlying BL-mediated carotenoid accumulation in flowers remain unclear. Carotenoid accumulation in several yellow flowers and fruits is positively regulated by the expression of phytoene synthase (PSY) and phytoene desaturase (PDS), while it is negatively associated with the expression of carotenoid cleavage dioxygenase 1 (CCD1) or CCD4 [155,156]. Light signaling pathways are known to regulate carotenoid biosynthesis, with PIFs and HY5 playing antagonistic roles in controlling the expression of PSY and PDS [125]. Upon illumination, the degradation of negative regulators PIFs de-represses PSY gene expression, while HY5 activity is induced to promote PSY transcription [157]. In *Citrus* juice sacs, BL enhances carotenoid accumulation by upregulating *CitPSY* expression [154]. However, shading represses the expression of key carotenoid biosynthetic genes, including PSY and PDS, leading to reduced carotenoid levels [125,158].

BL-mediated carotenoid biosynthesis may also be regulated by phytohormones due to the interaction between light signaling and hormone pathways, although direct evidence from BL-specific studies is limited. Among phytohormones, ethylene, JA, and ABA have been shown to promote carotenoid accumulation in fruits by regulating fruit ripening, whereas auxin tends to inhibit carotenoid biosynthesis [155,159]. However, the mechanisms by which these phytohormones regulate carotenoid pathway gene expression remain poorly understood. Notably, ethylene promotes carotenoid biosynthesis by activating the expression of PSY, a key enzyme in the pathway [160,161]. Furthermore, an intricate crosstalk between light, ethylene, and auxin signaling pathways dynamically regulates carotenoid biosynthesis [125,162].

3.3.3. Betalain

BL generally plays a positive role in betalain production, despite no information on flower coloration. For instance, a positive effect of BL on the accumulation of this pigment was shown in *Amaranthus caudatus* seedlings [163], hairy roots of red beet (*Beta vulgaris*) [164], and calli of *Portulaca* [165], *Suaeda salsa* [166], and *Alternanthera brasiliana* [167]. These studies did not provide a mechanistic explanation except for the research on calli of *Suaeda salsa*, where the BL-increased betalain production relative to dark was attributed to enhanced activity of tyrosinase and increased expression of *dopa-4,5-dioxygenase* (DODA) gene [166]. However, in *Suaeda salsa* seedlings previously grown in the dark, BL illumination strongly depressed betacyanin content in the hypocotyl [168], where the BL-dependent degradation of the CRY2 protein decreased betacyanin content via inactivation of tyrosinase [169]. The differing impact of BL on betacyanin synthesis between calli and seedlings of *Suaeda salsa* likely results from distinct genetic regulatory pathways that operate differently at the whole-plant level vs. in tissue culture.

Although the detailed mechanisms underlying BL-mediated betalain production remain unclear, the light-induced betalain production is related to changes in hormone levels and the regulation of transcription factors and microRNAs. For example, UV-B has been shown to promote betalain accumulation by modifying the balance of hormones such as ethylene, ABA, JA, salicylic acid (SA), and CTK [170]. In *Beta vulgaris*, betalain accumulation is regulated by a MYB transcriptional regulator, BvMYB1, which directly activates key genes in the betalain biosynthetic pathway, including *cytochrome P450 76AD1/R* (CYP76AD1/R) and *beta vulgaris DOPA 4,5-dioxygenase 1* (BvDODA1) [171]. Additionally, the microRNA miR858 acts as a repressor of MYB4-LIKE (MYB4L) and MYB2-LIKE (MYB2L), releasing their suppression on the betalain accumulation [169,172]. However, whether these regulators are directly involved in BL-mediated betalain production remains to be elucidated through further research.

3.4. Flower Pollination and Fertilization

After pollen germination, the pollen tube grows toward the ovule, where it must rupture to release sperm cells for fertilization. A recent study indicates that BL irradiation induces pollen tube (PT) rupture in *Arabidopsis*, *Torenia* (*Torenia fournieri*), and tobacco (*Nicotiana benthamiana*) [173]. Additionally, Ca^{2+} influx was observed following BL exposure, accompanied by either PT rupture or a temporary halt in elongation. These findings offer insights into the interplay between PT integrity and Ca^{2+} influx at the PT tip, presenting a novel method to control PT bursts [173].

4. Flower Senescence

Flower longevity, a key factor for the postharvest quality of ornamental flowers and flower vegetables, is closely linked to the progression of senescence [174]. Flower senescence, a form of programmed cell death regulated by internal and external signals, including light, manifests as color change, fragrance loss, wilting, or tissue degradation in flowers and rapid sepal degreening in broccoli heads [90,153,175].

BL, when applied as postharvest sole-source lighting at low to moderate intensities ($15\text{--}150\ \mu\text{mol m}^{-2}\text{ s}^{-1}$), can delay flower senescence and consequently improve vase life or storage life, but its effectiveness varies depending on the photoperiod of the lighting [5]. For potted chrysanthemum, BL from fluorescent lamps (400–580 nm) delayed flower senescence and extended postharvest preservation time, compared to white, green (360–630 nm), red, or yellow (500–650 nm) light [176]. In carnation cut flowers, BL from LED lighting effectively delayed senescence and improved vase life, compared to red light or white light [149,177]. Similarly, for flower vegetables such as broccoli heads, blue + white LED treatment delayed the senescence and extended the product shelf life [153]. In *Alstroemeria* cut flowers, a daily BL duration of 12 h (within a range of 6–24 h daily) was most effective at prolonging vase life relative to no lighting treatment [178].

BL-delayed flower senescence is linked to specific biochemical changes in flowers (Figure 8). In carnation flowers exposed to BL, the increase of H_2O_2 and malondialdehyde (MDA) contents in petals was the lowest, while a higher membrane stability index was maintained [149]. Additionally, petals of BL-exposed flowers exhibited higher activities of antioxidant enzymes, including superoxide dismutase (SOD), peroxidase (POD), catalase (CAT), and ascorbate peroxidase (APX). Compared with flowers exposed to red or white light, BL-exposed flowers showed a delayed decline in petal carotenoid contents and elevated sugar concentrations [149]. Similarly, in broccoli heads, blue + white LED treatment maintained high levels of chlorophyll, sugar, carotenoid, and ascorbic acid [153]. During flower senescence, floral cells undergo biochemical and structural changes associated

with cell death [179,180]. BL may slow this process and thereby delay flower senescence, although the detailed mechanism involved remains unclear.

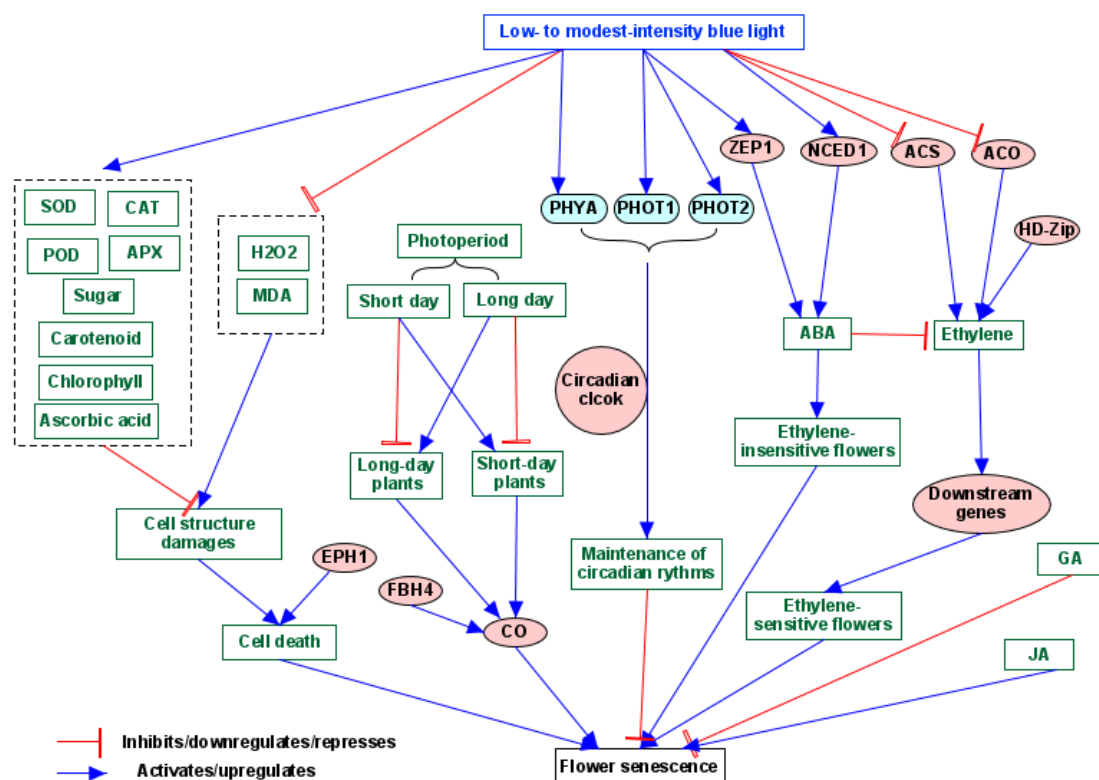


Figure 8. Physiological mechanisms underlying flower senescence mediated by blue light, as well as other potentially integrated signals. PHYA = phytochrome A; PHOT1/2 = phototropin 1/2; MDA = malondialdehyde; SOD = superoxide dismutase; POD = peroxidase; CAT = catalase; APX = ascorbate peroxidase; ZEP1 = zeaxanthin epoxidase 1; NCED1 = 9-cis-epoxycarotenoid dioxygenase 1; ACS = 1-aminocyclopropane-1-carboxylic acid synthase; ACO = 1-aminocyclopropane-1-carboxylic acid oxidase; HD-Zip = HOMEODOMAIN-LEUCINE ZIPPER; EPH1 = EPHEMERAL1; FBH4 = FLOWERING BHLH 4; CO = CONSTANS; GA = gibberellin; JA = jasmonic acid; ABA = abscisic acid. In the diagram, the green rectangles are other signals that may integrate with blue light pathway; the blue rounded rectangles are photoreceptors; the pink ovals are transcription factors or other regulators. The dashed rectangles include a group of integrated signals.

BL-delayed flower senescence is linked to changes in phytohormone signaling, particularly ethylene and ABA. In carnation, BL suppressed the expression of ethylene biosynthetic genes, *DcACS* and *DcACO* (1-aminocyclopropane-1-carboxylic acid oxidase), while enhancing ABA biosynthetic genes, *DcZEP1* (zeaxanthin epoxidase 1) and *DcNCED1* (9-cis-epoxycarotenoid dioxygenase 1) in petals [177], consistent with the roles of ethylene and ABA as key senescence promoters [179,181]. In ethylene-sensitive species such as carnation, BL-induced ABA accumulation may further suppress ethylene production through feedback regulation [182]. Other hormones, including CTKs, auxins, GA, and JAs, also affect flower senescence [90,183], but their roles in BL-mediated responses remain largely unexplored. Additionally, the integration of BL signaling with the key transcription factors in the regulatory pathways of ethylene-dependent and ethylene-independent petal senescence, such as HOMEODOMAIN-LEUCINE ZIPPER (HD-Zip) and EPHEMERAL1 (EPH1) [174,184–186], has yet to be clarified.

Several photoreceptors that perceive BL, including PHOTs and PHYA, may participate in BL-mediated flower senescence. In hibiscus (*Hibiscus rosa-sinensis*), PHOT1 transcript levels increased in petals during senescence [187], whereas in waterlily (*Nymphaea*

spp.), PHOT2 was downregulated as senescence progressed, suggesting weakened BL signaling [181]. Both PHOT1 and PHOT2 help maintain circadian rhythms under low BL [188], which may explain the effectiveness of low-intensity BL in delaying postharvest senescence. In *Mirabilis jalapa*, flower senescence follows a circadian rhythm mediated by the PHYA pathway [189], and in waterlily, PHYA expression increased during petal closure, potentially regulating senescence [181]. Possibly, BL delays flower senescence partly by coordinating PHYA and PHOT signaling with the circadian clock.

BL-delayed flower senescence can be influenced by photoperiod, as senescence is generally delayed in short-day plants under long-day conditions and in long-day plants under short-day conditions, opposite to floral transition [183]. In petunia, senescence is accompanied by increased levels of FLOWERING BHLH 4 (FBH4), a regulator of the photoperiodic pathway that promotes expression of CONSTANS (CO), a key integrator of photoperiodic flowering [185,190]. High CO activity is associated with early flowering and accelerated senescence, whereas low CO activity correlates with delayed senescence [183]. This suggests that CO, a shared downstream component of photoperiod and BL signaling, may underlie the photoperiod-dependent effects of BL on postharvest flower longevity.

5. Future Direction

Floral development is a crucial physiological process in plants, and its regulation is also important for the production of many crops [9,14]. Despite great advancements in studies about BL-mediated floral development, further relevant mechanism research to improve our scientific knowledge and manipulation technology in this field is still necessary in both model plants and agricultural crops.

Most mechanistic studies about BL manipulation in model plants have primarily focused on the floral transition phase, but relevant research on floral development remains comparatively limited. In some cases, the effectiveness of BL manipulation has been found, and even the relevant mechanisms have been explored in some horticultural crops, but corresponding information from model plants is scarce. For example, it has been found that postharvest sole-source lighting with BL is an effective environmental control method in improving the postharvest quality and extending the vase life of some floral crops [129,149,176–178]. BL thus appears to serve as a physical factor to improve some traits of postharvested flowers, although responses can vary with crop species, light duration, flower traits, and light spectra [5]. Given the relatively clearer understanding of the light signal pathway in model plants, these findings from horticultural crops may inspire targeted studies in model plants to elucidate the relevant mechanisms and refine BL-based light manipulation techniques.

Due to advancements in lighting technology for crop production, our knowledge about BL-mediated flowering in horticultural crops may also require updating. Earlier studies typically used impure BL from broad-band lighting sources for BL treatments; this BL often contained other light wavelengths and had a high R:FR ratio, which could activate PHYB and CRY1 in many cases [19]. However, modern narrow-band LED lighting provides purer BL with a low PPS value, likely inactivates PHYB and CRY1, and thereby induces shade-avoidance responses that affect flowering [19,56,191,192]. This distinction may partly explain the contrasting results reported on BL-mediated flowering between these two BL sources [5]. It also underscores the need to reevaluate BL's effect on the flowering process, especially floral development. For example, in roses, BL from broad-band lighting has been shown to exert minimal influence on flower bud abortion [29–31], whereas vegetative shade promotes bud abortion [32,33]. It is well established that vegetative shade is characterized by inactivated PHYB and CRY1 [193,194]. Therefore, pure BL from

LED lighting, acting as a shade signal, may increase flower bud abortion, a hypothesis warranting future investigation.

6. Conclusions

BL mediates floral development at different stages in this physiological process, from floral organ specification and growth to flower opening and flower senescence. Each stage involves distinct photoreceptors, signaling pathways, key pathway components, and interactions with other signaling factors, indicating a complex regulatory network underlying BL-mediated floral development. This complexity may partly explain the diverse flowering responses to BL manipulation. Consequently, it is important to consider all influencing factors when applying BL to regulate floral development. Further in-depth studies on the mechanisms of BL-mediated floral development are necessary, not only in model plants but also in horticultural species.

Author Contributions: Conceptualization, Y.K. and Y.Z.; methodology, Y.K.; investigation, Y.K.; writing—original draft preparation, Y.K.; writing—review and editing, Y.K. and Y.Z.; funding acquisition, Y.Z. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Data Availability Statement: Data are contained within the article.

Conflicts of Interest: The authors declare no conflicts of interest.

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