

Flowering response to blue light and its molecular mechanisms in *Arabidopsis* and horticultural plants

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Abstract: Using light-emitting diodes (LEDs) in plant factories and protected horticulture is expected to decrease energy costs and environmental burden. Because LEDs emit monochromatic light, detailed knowledge of plant responses to light quality is essential for efficient and appropriate utilization of LEDs in horticultural production. Timing of flowering is important in cut flower and fruit/vegetable production, and it is often affected by light quality. Red/far-red light is well known to be effective in flowering, and there is abundant knowledge about the effects of red/far-red ratio on flowering of horticultural plants as well as of the model plant *Arabidopsis thaliana*. However, studies have not focused on the effects of blue light on flowering. Therefore, this review describes the progress in the promotion of flowering by blue light and its molecular mechanisms in *Arabidopsis* and horticultural plants.

1. Introduction

The utilization of light-emitting diodes (LEDs) is increasing because of their technological improvements and reduction in prices. Because LEDs emit monochromatic light, studying the effects of light quality on plant growth has become important for efficient utilization of LEDs in horticultural production. Plant factories are a promising system of horticultural production where the completely artificial environment may lead to efficient photosynthesis, year-round production unaffected by climate, farming without insecticides, and effective utilization of resources such as water (Kozai, 2013). However, plant factories consume large amounts of energy for lighting and air conditioning, which may result in global warming and high fuel costs and electricity bills. Using LEDs, which consume less electricity and have a long life, may reduce energy consumption and production costs. LEDs emit little thermal irradiation and can be used in close proximity with plants, making them suitable for multistage production to increase unit production (Goto, 2012).

LEDs are also expected to be useful in lighting culture, where flowering time is controlled by night-time lighting for cut flower production in greenhouses, because incandescent lamps, which have been commonly used for long-day treatments, are characterized by high energy consumption and short life. *Chrysanthemum morifolium* (hereby referred to as chrysanthemum), the most commonly used

cut flower in Japan, is a short-day plant; it is produced year-round by lighting culture, repressing flowering by long-day treatments. Long-day cut flowers can also be produced under short-day conditions during autumn and winter by long-day treatments to promote flowering.

The effects of monochromatic light quality on plant growth, morphogenesis, and metabolism need to be investigated for the development of horticultural production using LEDs. Blue, red, and far-red lights are already known to be effective in plant morphogenesis and flowering, and molecular mechanisms underlying the regulation of flowering by each light color have been proposed in studies using the model plant *Arabidopsis thaliana*, which is a long-day plant. Far-red light or a low red/far-red ratio, which promotes flowering in *Arabidopsis*, reportedly promotes flowering in long-day cut flowers such as *Eustoma grandiflorum* and *Gypsophila paniculata* (baby's breath) (Yamada *et al.*, 2008, 2009; Nishidate *et al.*, 2012). However, studies have not focused on the effects of blue light on flowering; blue light could also be important in timing of flowering. Therefore, this review describes flowering response to blue light and its molecular mechanisms in *Arabidopsis* and horticultural plants with the aim of advancing research on the utilization of LEDs in horticultural production.

2. Flowering response to light quality and its molecular mechanisms

Flowering is triggered upon the expression of *flowering locus T (FT)*, which is a key flowering integrator, in

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the phloem of leaves induced by CONSTANS (CO) under long-day conditions in the photoperiodic flowering pathway proposed for *Arabidopsis* (An *et al.*, 2004). CO expression is regulated downstream of the circadian clock, and CO mRNA is expressed during the dark period under short-day conditions and during the light period (late afternoon) under long-day conditions (Suárez-López *et al.*, 2001). Because CO protein translated from CO mRNA is degraded through ubiquitination by an E3 ubiquitin ligase, CONSTITUTIVE PHOTOMORPHOGENESIS 1 (COP1), during the dark period, the expression of *FT* and consequent induction of flowering are not triggered under short-day conditions (Jang *et al.* 2008; Liu *et al.* 2008 b).

In *Arabidopsis*, flowering is promoted under long-day conditions with blue and far-red lights but not with red light (Eskins, 1992). Blue light may induce *FT* expression by stabilizing CO, as described below. Far-red and blue light signaling through phytochrome A and through CRYPTOCHROME 1 (CRY1) and CRY2, respectively, stabilize CO protein by an antagonistic function to red light signaling through phytochrome B that induces CO degradation (Mockler *et al.*, 1999, 2003; Valverde *et al.*, 2004). As a result, the accumulation of CO protein increases during the light period (late afternoon), and the expression of *FT* and consequent induction of flowering are triggered under long-day conditions.

FT protein expressed in leaf phloem moves to the apical meristem through sieve tubes (Corbesier *et al.*, 2007) and activates floral identity genes such as *APETALA1* and *FRUITFUL* by interacting with FLOWERING LOCUS D (FD), a bZIP transcription factor (Abe *et al.*, 2005; Wigge *et al.*, 2005). In addition, FT activates *SUPPRESSOR OF OVEREXPRESSION OF CONSTANS 1* (*SOC1*) to promote flowering (Yoo *et al.*, 2005).

3. Molecular mechanism underlying the promotion of flowering mediated by blue light signaling via FKF1

Flavin-Binding Kelch repeat F-box 1 (FKF1), which has flavin mononucleotide as a chromophore, and GIGANTEA (GI) mediate CO transcription in the photoperiodic flowering pathway (Fig. 1) (Nelson *et al.*, 2000; Imaizumi *et al.*, 2003; Martin-Tryon *et al.*, 2007). They are important for the promotion of flowering because in the CO promoter region, FKF1 forms a complex with GI in a blue light-dependent manner, induces the degradation of CYCLING DOF FACTOR 1 (CDF1) to repress CO transcription, and promotes CO transcription (Fig. 2) (Imaizumi *et al.*, 2005; Sawa *et al.*, 2007). In detail, the F-BOX domain of FKF1 interacts with *Arabidopsis* Skp1-like proteins to form the E3 ubiquitin ligase complex, and this complex induces CDF1 degradation by ubiquitination (Yasuhara *et al.*, 2004; Imaizumi *et al.*, 2005; Sawa *et al.*, 2007). *Arabidopsis* has multiple CDF family proteins, which redundantly repress CO, and the degradation of another CDF family protein CDF2 is also induced by the interaction of FKF1 with GI in a blue light-dependent manner (Fornara *et al.*, 2009).

In addition, FKF1, GI, and CDF1 are proposed to regu-

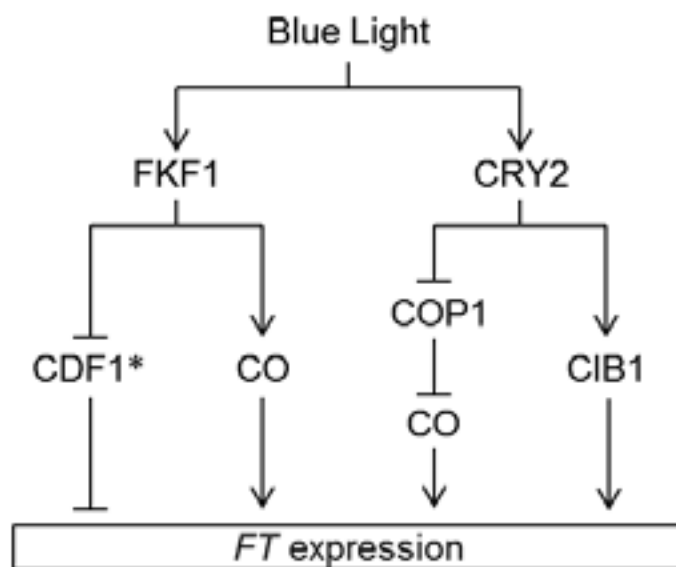


Fig. 1 - Proposed model for the induction of *FT* expression by blue light through two photoreceptors (Jang *et al.*, 2008; Liu *et al.*, 2008 a, b; Sawa and Kay, 2011; Zuo *et al.*, 2011; Song *et al.*, 2012). FKF1 stabilizes CO protein to activate *FT* expression in a blue light-dependent manner. CRY2 activates CIB1 as a transcription factor to induce *FT* expression and inhibits COP1, inducing the degradation of CO protein during the light period in a blue light-dependent manner. *See figure 2.

late *FT* transcription in the same manner as CO transcription regulation (Sawa and Kay, 2011; Song *et al.*, 2012). Furthermore, FKF1 stabilizes CO by interaction of the LOV domain of FKF1 with CO protein, which is enhanced by blue light (Song *et al.*, 2012). Thus, FKF1 transduces blue light signals to promote flowering in a complex manner.

4. Molecular mechanism underlying the promotion of flowering mediated by blue light signaling via CRY2

CRY is a blue/UVA photoreceptor in plants (Cashmore *et al.*, 1999). In *Arabidopsis*, the expression and function of CRY2 in vascular bundles regulates flowering (Endo *et al.*, 2007). COP1 controls the accumulation of GI and CO proteins, that is, COP1-mediated degradation of GI and CO proteins during the dark period is repressed by CRY2 during the light period to promote flowering (Fig. 1) (Jang *et al.*, 2008; Liu *et al.*, 2008 b; Yu *et al.*, 2008). COP1-mediated degradation of CO is repressed by blue light-dependent interactions between CRY2, COP1, and SUPPRESSOR OF PHYA-105 1 (SPA1) (Zuo *et al.*, 2011).

CRYPTOCHROME-INTERACTING BASIC-HELIX-LOOP-HELIX 1 (CIB1) has been isolated as an interacting factor of CRY2, and its interaction with CRY2 is promoted by blue light. CIB1 induces *FT* transcription to promote CRY2-dependent floral initiation (Liu *et al.*, 2008 a). CIB1 is believed to bind to E-box (CANNTG) elements in the promoter region of *FT* and stimulate *FT* mRNA expression (Liu *et al.*, 2008 a). CIB family proteins, containing CIB1, form heterodimers, and notably, in comparison with homodimers, some of these heterodimers have higher binding

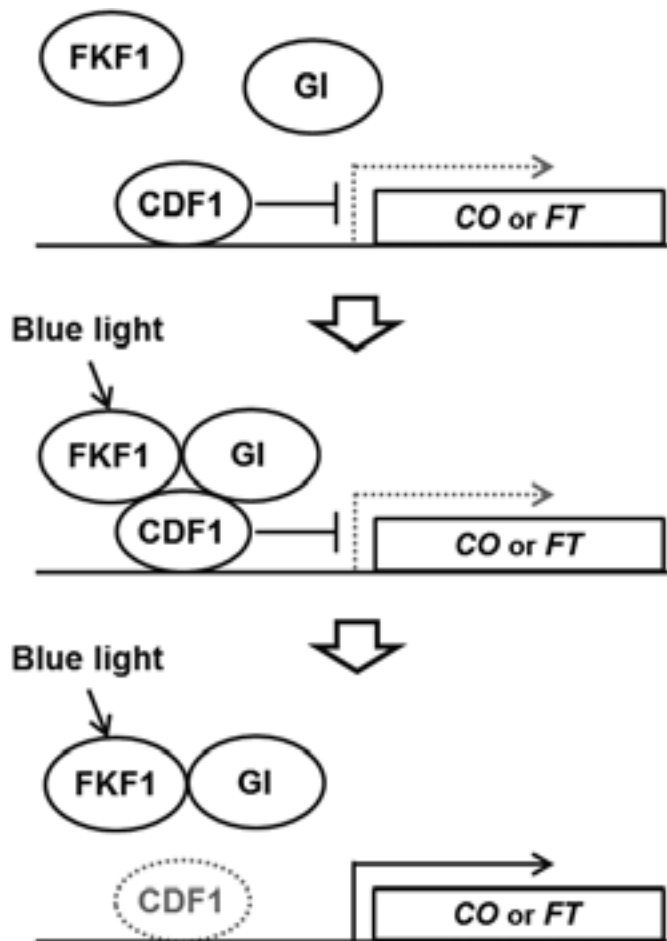


Fig. 2 - Proposed model for the induction of *CO* and *FT* expression by blue light through FKF1 (Yasuhara *et al.*, 2004; Imaizumi *et al.*, 2005; Sawa *et al.*, 2007; Sawa and Kay, 2011; Song *et al.*, 2012). CDF1 represses *CO* and *FT* expression under short-day conditions. FKF1 forms a complex with GI and CDF1 on *CO* and *FT* promoters in a blue light-dependent manner in the late afternoon under long-day conditions, and then induces the degradation of CDF1 protein by ubiquitination. As a result, the expression of *CO* and *FT* are induced because of the absence of CDF1.

affinity to E-box elements. This suggests the importance of the interaction between CIB proteins and E-box elements in the induction of *FT* expression (Liu *et al.*, 2013 b).

Although the interaction of CRY2 with CIB1 plays a role in *FT* expression in response to blue light, the stabilization of CIB1 protein may be controlled by other blue light photoreceptors such as ZEITLUPE (ZTL) and LOV KELCH PROTEIN 2 (LKP2). ZTL and LKP2, belonging to the LOV domain of blue light receptors containing FKF1, are required for suppressing the degradation of CIB1 protein by blue light (Liu *et al.*, 2013 a).

5. Flowering response to blue light in long-day horticultural plants

In some long-day horticultural plants, similar in behavior to *Arabidopsis*, the promotion of flowering by blue

light under long-day conditions has been reported. Flowering is promoted by inducing the expression of *FBP28*, a petunia homolog of the flowering accelerator *SOC1* in *Petunia*, an important potted and bedding plant (Fukuda *et al.*, 2011). The flowering of a popular cut flower *E. grandiflorum* can be promoted under short-day conditions by a night break with blue light as well as with far-red light or a low red/far-red ratio (Yamada *et al.*, 2011). The effect of light quality on flowering has also been investigated in long-day fruit/vegetable production. Ever-bearing strawberry cultivars (*Fragaria x ananassa*) are long-day plants in contrast with June-bearing strawberry cultivars, which are short-day plants. Similar to *Arabidopsis*, the flowering of ever-bearing strawberry cultivars is promoted by long-day treatments with blue as well as far-red light (Nishiyama and Kanahama, 2009; Yoshida *et al.*, 2012).

These reports indicate that the flowering of various long-day horticultural plants is promoted under long-day conditions with blue light. However, flowering is not promoted by long-day treatments with blue light, but it is promoted with far-red light in *G. paniculata* 'Bristol Fairy,' which is a popular cut flower frequently used in flower arrangements (Hori *et al.*, 2011; Nishidate *et al.*, 2012). In a study conducted by Hori *et al.* (2011), flowering in *Arabidopsis* was reportedly induced with *SOC1* expression by long-day treatments with far-red light, whereas it was induced with both *FT* and *SOC1* expression by long-day treatments with blue light. In contrast, although flowering in *G. paniculata* 'Bristol Fairy' was induced with the expression of the *SOC1* homolog of *G. paniculata* (*GpSOC1*) by long-day treatments with far-red light, flowering was not induced because of the low expression of the *FT* homolog of *G. paniculata* (*GpFT*) and *GpSOC1* by long-day treatments with blue light. To the best of our knowledge, there has been no report of blue light receptors FKF1 and CRY in these horticultural plants. Further studies are needed to understand the molecular mechanisms underlying the diversity in flowering response to blue light.

6. Flowering response to blue light in short-day and day-neutral horticultural plants

In short-day horticultural plants, flowering is usually repressed by a night break with red light under short-day conditions; there are only a few studies on flowering response to blue light in short-day horticultural plants. In chrysanthemum, a major short-day cut flower, flowering is repressed by a 4-h night break with blue light or far-red light under short-day (12 h) conditions with blue light (Higuchi *et al.*, 2012). However, flowering of chrysanthemum is not repressed by 4-h end-of-day irradiation with blue light under 11-h photoperiods with mixed red and blue lights (Jeong *et al.*, 2014). These studies suggest that in chrysanthemum, blue light affects flowering under some limited conditions, but red light plays a major role in the repression of flowering.

Solanum lycopersicum (tomato), the most important fruit/vegetable, is well known as a day-neutral plant. Tomato plants flower after vegetative growth regardless of photoperiods, and their flowering is believed to be unaffected by photoperiods. However, the node position of the first flower truss under a lower blue/red ratio has been reported to be lower than that under a higher blue/red ratio (Nanya *et al.*, 2012); the constitutive expression of the *CRY2* homolog of tomato *LeCRY2* delays flowering (Giliberto *et al.*, 2005), suggesting that blue light represses flowering in tomato plants. It is important to investigate the tomato homologs of genes that play roles in light signaling in the photoperiodic flowering pathway because the *FT* homolog of tomato *SFT* is a flowering activator, and heterozygosity for loss-of-function alleles of *SFT* increases the yield (Krieger *et al.*, 2010).

7. Concluding remarks

Similar to *Arabidopsis*, blue as well as far-red light-dependent promotion of flowering in long-day horticultural plants has been reported. On the other hand, flowering was not promoted by blue light, but by far-red light in a cultivar of another long-day plant, *G. paniculata*. This diversity in flowering response to blue light is notable, and gaining knowledge about it is important for promoting the utilization of LEDs in plant factories and lighting culture.

The flowering of *Arabidopsis* is promoted by blue light in a complex manner through FKF1 and CRY. There is a paucity of information on the molecular mechanisms underlying blue light signaling in the promotion of flowering in horticultural plants, although there are few studies on the relationship between flowering and expression of flowering-related genes under long-day conditions with blue light. Gaining knowledge at the molecular level about blue light signaling in long-day and day-neutral horticultural plants would contribute to the introduction of novel traits in molecular breeding.

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