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Low-activity cryptochrome 1 plays a role in promoting stem elongation and flower initiation of mature *Arabidopsis* under blue light associated with low phytochrome activity

Yun Kong and Youbin Zheng

Abstract: To explore whether cryptochrome contributes to stem elongation and flowering promoted by blue lights associated with low phytochrome activity, wild-type *Arabidopsis* was compared with its cryptochrome-deficient mutants and cryptochrome-overexpressing transgenic plants. Results indicated that the promotion effects were mainly related to low CRY1 activity, despite partial involvement of high-activity CRY2.

Key words: cryptochrome, phytochrome, *Arabidopsis*, mutants, stem elongation, flowering.

Résumé : Pour déterminer si le cryptochrome concourt à l'élongation de la tige et à la floraison que promeut un éclairage bleu et qu'on associe à une faible activité du phytochrome, les auteurs ont comparé la variété sauvage d'*Arabidopsis* aux variétés mutantes sans cryptochrome et à des cultivars transgéniques qui expriment celui-ci de façon excessive. Les résultats indiquent que l'accélération de la croissance découle essentiellement de la faible activité du CRY1, en dépit d'une intervention partielle du CRY2, beaucoup plus actif. [Traduit par la Rédaction]

Mots-clés : cryptochrome, phytochrome, *Arabidopsis*, mutants, élongation de la tige, floraison.

Introduction

In most previous studies, blue light (BL) treatments were set up through selective solar filters or broad-band light sources (e.g., blue fluorescent lamp). It is difficult to achieve pure BL with these BL treatments. Consequently, the impure BL contains low levels of other wave-length lights due to a broad light band (Bergstrand et al. 2014). Light emitting diode (LED) technology, however, can create narrow-band BL (i.e., pure BL). This provides a new tool to study plant responses to pure BL, i.e., blue LED (B), as well as impure BL, which can result from mixing B with low levels of other light spectra, such as red LED (R) and far-red LED (FR).

Our recent studies using LED lighting have demonstrated that BL-mediated plant elongation and flowering is affected by phytochrome activity (Kong et al. 2018, 2020b, 2020a). In these studies, plant elongation and flowering were promoted by pure BL (i.e., B) compared with R. However, the promotion effects of B were reversed by adding a low level of R to B, which resulted in an impure BL, BR, and similar or greater inhibitory

effects were observed under BR relative to R. When BR was mixed with a low level of FR (with a flux ratio of R/FR $\approx$ 1), which created another impure BL (i.e., BRF), the promotion effects of B on plant elongation and flowering were recovered by BRF, and similar promotion effects were obtained between BRF and B. The R/FR reversibility provided a strong proof on the involvement of phytochrome. Another proof came from the comparison of phytochrome photostationary state (PPS) values. The PPS value was no more than 0.6 for B (0.5) or BRF (0.6) but was higher than 0.7 for R (0.9) or BR (0.7). Normally, phytochrome activity positively correlates to PPS value, and for most species, plants demonstrate inactive phytochrome responses with the PPS value decreasing below 0.6 (Stutte 2009). Apparently, plant elongation and flowering were promoted by BL with lower PPS (i.e., B or BRF), but inhibited by BL with higher PPS (i.e., BR). Our recent study on wild *Arabidopsis* and its quintuple phytochrome mutant has also further confirmed the involvement of phytochrome in the BL-mediated plant elongation (Kong and Zheng 2020b).

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Despite the phytochrome action, the involvement of the BL photoreceptor cryptochrome also needs to be considered in the mediation of plant elongation and flowering. For example, the inhibition effect of BR, an impure BL with high PPS, on plant elongation and flowering cannot be fully explained by higher phytochrome activity only, because BR relative to R showed a greater inhibitory effect for some species despite having a lower PPS (Kong et al. 2018, 2020a). This indicates that active cryptochrome might have also contributed partly to the BR's inhibition effect on plant elongation and flowering, as active phytochrome is required for full expression of cryptochrome activity under BL (Ahmad and Cashmore 1997). However, it is unclear whether cryptochrome plays a role in the stem elongation and flowering promoted by BLs with low PPS (i.e., B and BRF). It has been indicated that phytochrome activity can modify cryptochrome action through an interaction between the two photoreceptor systems (Liu et al. 2016). Possibly, due to low PPS values, B or BRF might have reduced cryptochrome activity in plants; however, a direct proof is required to support the speculation about the involvement of low-activity cryptochrome in this process.

Two types of cryptochromes, cryptochrome 1 (CRY1) and cryptochrome 2 (CRY2), have been discovered in *Arabidopsis* to mediate plant elongation and flowering (Yu et al. 2010). The *cry1* mutant fails to inhibit hypocotyl elongation under BL (Ahmad et al. 1995), and transgenic *Arabidopsis* plants overexpressing CRY1 are hypersensitive to BL in terms of inhibitory hypocotyl elongation response (Lin et al. 1996). Studies on *cry2* mutant and transgenic plants overexpressing CRY2 indicate that CRY2 also contributes to BL-mediated inhibition of hypocotyl elongation, despite playing a relatively minor role than CRY1 (Lin et al. 1998). The *cry1cry2* double mutant shows a longer hypocotyl under BL than the *cry1* or *cry2* single mutant, suggesting a partially redundant function of the two cryptochromes in this response (Mockler et al. 1999). Similarly, the *cry1cry2* double mutant showed a greater delay in flowering than the wild-type or the *cry1* and *cry2* monogenic mutants under broad-band BL (Guo et al. 1998; Mockler et al. 1999). These observations suggest that CRY2 acts additively with CRY1 in promoting flowering initiation. However, only the de-etiolated seedlings were used in the above studies on stem elongation, and only the broad-band BL sources were used in the studies on both stem elongation and plant flowering. For LED lighting, it is unclear whether CRY1 and CRY2 contribute to stem elongation of mature plants and plant flowering response to BL with different PPS values.

The objective of this study was to examine whether cryptochromes (CRY1 and CRY2) contribute to BL-mediated stem elongation and flower initiation under R, B, BR, and BRF LEDs by comparing the phenotypic responses among wild-type, cryptochrome-deficient

mutant, and cryptochrome-overexpressing transgenic plants of *Arabidopsis*.

Materials and Methods

The experiment was performed in an environment-controlled growth chamber. Six genotypes of *Arabidopsis*, one wild-type (Col-0), three cryptochrome-deficient mutants (*cry1*, *cry2*, and *cry1cry2*) and two cryptochrome-overexpressing transgenic lines (CRY1-OX and CRY2-OX) were used for the experiment. Seeds were stratified at 4 °C for 3 d and then sown on agar which was on top of rockwool cubes in a hydroponic system as described by Kong and Zheng (2020b). The six genotypes were evenly and randomly distributed to different rows (i.e., four rows for each genotype and 12 rockwool cubes for each row) within each tray. The sown trays were moved to the growth chamber and placed under the light treatments. The fertigation method and the environmental conditions for growing the experimental plants were the same as described in Kong and Zheng (2020a).

The four light treatments were: (i) a pure red light emitted from a narrow-band LED at 660 nm (R); (ii) a pure BL emitted from another narrow-band LED at 455 nm (B); (iii) an impure BL created by a LED combination with a photon flux of 94% B and 6% R (BR); and (iv) another impure BL created by another LED combination with BR and 6 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ of FR at 735 nm (BRF). A photoperiod of 24 h was used for all light treatments. At the plant canopy level, a photosynthetic photon flux density was targeted at around 100 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for each light treatment. The PPS values of R, BR, BRF, and B were calculated as follows: 0.9, 0.7, 0.6, and 0.5, respectively. The setting up of the four light treatments and the calculation method of PPS values were the same as described in Kong and Zheng (2020a).

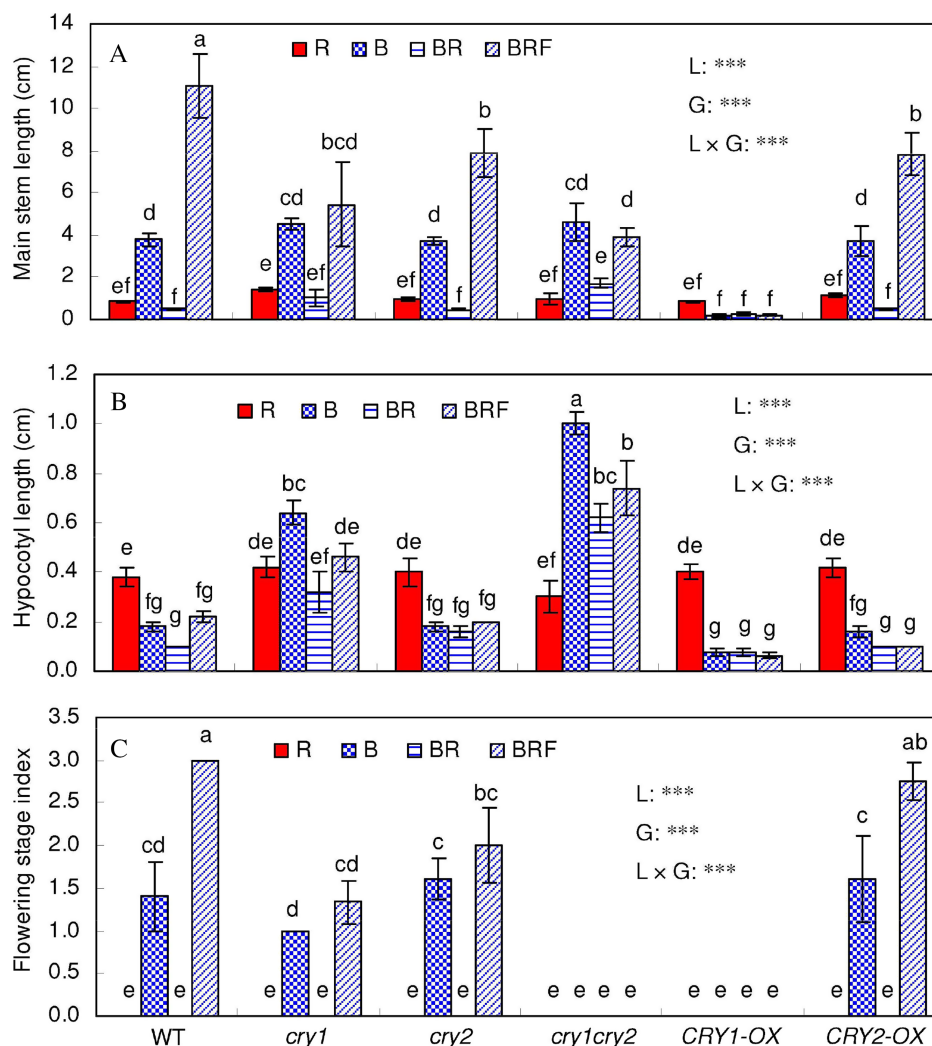
After 18-d lighting, 12 plants from each genotype per light treatment (i.e., three plants from each row within each tray) were randomly selected for plant morphology measurements. The measured plant traits included main stem length, hypocotyl length, and flowering index. The plant traits investigation and data analysis followed the same methods in our previous studies (Kong and Zheng 2020b).

Results and Discussion

The main stem elongation promoted by BLs with low PPS is related to low-activity CRY1

In the wild-type *Arabidopsis* plants, B and BRF increased main stem length compared with R and BR, and their promotion effect was eliminated by overexpression of CRY1 but not CRY2 (Fig. 1A). This suggests that the promotion effects of B and BRF on main stem elongation are mainly related to low activity of CRY1 rather than CRY2. A previous study on de-etiolated seedlings of *Arabidopsis* also indicates that of the two cryptochrome species CRY1 plays a main role in mediating inhibition of stem elongation (Lin et al. 1998). In the present study,

Fig. 1. Elongation growth and flowering in wild-type, cryptochrome-deficient mutants, and cryptochrome-overexpressing transgenic plants of *Arabidopsis* under different light treatments. For the X-axis labels: WT, wild-type; *cry1*, CRY1-deficient mutant; *cry2*, CRY2-deficient mutant; *cry1cry2*, both CRY1- and CRY2-deficient double mutant; *CRY1-OX*, CRY1-overexpressing transgenic plants; *CRY2-OX*, CRY2-overexpressing transgenic plants; R, pure red light; B, pure blue light; BR, impure blue light created by mixing B with low-level (6 %) R; and BRF, impure blue light created by mixing BR with low-level far-red light (red/far-red ≈ 1). For the flowering stage index in Fig. 1C, 0 = flower stalk invisible; 1 = flower stalk visible; 2 = flower petal visible; 3 = flower(s) opened. Symbols for light quality (L), plant genotype (G), or the interaction of light quality and plant genotype (L $\times$ G) followed by ns, *, **, or *** denote that treatment effects are not significant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively. Bars are means $\pm$ standard error ($n = 4$). Bars bearing the same letter are not significantly different at $P \leq 0.05$, according to Duncan's new multiple range test. [Colour online.]



although overexpression of CRY1 reduced main stem length of plants under B or BRF, it did not do so under BR, indicating that BR caused a higher CRY1 activity in wild *Arabidopsis* than B and BRF (Fig. 1A). The lower CRY1 activity under B and BRF than BR might be related to the lower phytochrome activity under the two BLs, as B and BRF had lower PPS values than BR. In other words, there is a crosstalk between cryptochrome and phytochrome (Su et al. 2017). For example, the co-action between CRY1 and phyB has been observed under suboptimal light conditions (Casal 2000). In this study, B and BRF had low PPS values (≤ 0.6), which can induce shade

response in plants and can be considered as suboptimal light conditions.

Although the promotion effects of B and BRF on main stem elongation are related to low activity of CRY1, the action of cryptochrome on this process seems to be different for B and BRF. In the present study, deficiency of either CRY1 or CRY2, or both, reduced the main stem elongation promoted by BRF, but not by B (Fig. 1A). This indicates that both CRY1 and CRY2 contributed partly and directly to BRF-promoted main stem elongation, but neither CRY1 nor CRY2 was directly involved in B-promoted main stem elongation relative to R. Despite

no direct involvement of cryptochromes, phytochrome activity can be directly affected by B, as phytochromes have a secondary peak of absorption in BL (Casal 2000). Also, it has been confirmed that either active phytochrome or cryptochrome can inhibit plant elongation by binding downstream transcription factors and (or) regulators (Leivar and Monte 2014; Wang and Lin 2020). Nevertheless, the detailed process of the involvement of low-activity cryptochrome in the B/BRF-promoted main stem elongation is unknown.

Moderate-intensity BLs with low PPS can activate CRY1 to inhibit hypocotyl elongation

Differing from main stem, hypocotyl elongation of wild-type *Arabidopsis* plants was similarly inhibited by B, BR, and BRF, compared with R, and overexpressing CRY1 or CRY2 did not increase the inhibitory effect of the three BLs (Fig. 1B). This suggests that the wild-type plants have a similarly high activity of cryptochrome during hypocotyl growth under B, BR, and BRF, despite their differences in PPS values. In this case, regardless of phytochrome activity, the cryptochrome was fully activated under the three BLs at an intensity of $100 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for hypocotyl elongation, but not for main stem elongation. Previous studies indicate that cryptochrome activity is positively related to BL intensity (Liu et al. 2016), and the same-intensity BL may trigger contrasting response in different organs in a single plant due to different threshold values (Yu et al. 2010).

Within the two cryptochrome species, CRY1 played a main role in mediating hypocotyl elongation under the three BLs (B, BR, and BRF). Deficiency of CRY1 eliminated and even reversed the inhibitory effect of the three BLs on hypocotyl elongation as observed in wild-type plants, however, deficiency of CRY2 did not (Fig. 1B). Despite a minimal effect of CRY2 on the inhibition of hypocotyl elongation, the inhibition effect of CRY1 can be strengthened by its interaction with CRY2. In the present study, the deficiency of both CRY1 and CRY2 modified the plant response under the three BLs to a larger degree than the deficiency of only CRY1. The roles of CRY1 and CRY2 and their interaction were also supported by a previous study on de-etiolated *Arabidopsis* seedlings under BL of $60 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ that a *cry2* mutant does not have elongated hypocotyl, but the *cry1cry2* mutant shows a longer hypocotyl than the *cry1* mutant (Mockler et al. 1999). Although the detailed process of interaction of CRY2 with CRY1 is unclear, the CRY1-CRY2 interactions have been detected in *Arabidopsis* (Lin and Todo 2005). For example, CRY1 and CRY2 not only relay light signals through distinct pathways but also share a common pathway (Liu et al. 2016).

Low-activity CRY1 and high-activity CRY 2 together contribute to flowering promotion by BLs with low PPS

In the wild-type plants, B and BRF promoted flowering compared with R, and their promotion effect was not

eliminated by the deficiency of either CRY1 or CRY2, but by the deficiency of both CRY1 and CRY2 (Fig. 1C). This suggests that CRY1 acts redundantly with CRY2 to regulate plant flowering under these conditions. Similar result on the action of the two cryptochromes has been found in a previous study on *Arabidopsis* under broad-band BL source (Mockler et al. 1999). It is worthwhile to note that in the present study, CRY1 and CRY2 acted redundantly to different degree under B and BRF: CRY1 and CRY2 had nearly overlapping function in B-promoted flowering, but they had only partially overlapped function in BRF-promoted flowering (Fig. 1C). The underlying mechanisms of the difference between B and BRF are unclear.

Although CRY1 and CRY2 have overlapping functions in regulating flowering, their involved activity is different in the same physiological process. In the present study, the promotion effect of B and BRF on flowering was eliminated by overexpression of CRY1 but was not changed by overexpression of CRY2 (Fig. 1C). This suggests that the promotion effect of B and BRF on flowering in the wild-type plants was related to low-activity CRY1 and high-activity CRY2. It is difficult to explain how CRY2 showed high activity if without abundant CRY2 protein in wild-type *Arabidopsis* plants under continuous B and BRF at a level of $100 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Normally, CRY2 protein is stable only under a low intensity of BL ($< 10 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), and gets degraded at higher intensity, especially under continuous illumination (Lin et al. 1998; Yu et al. 2007). However, a previous study suggests that under the narrow- vs. broad-band BL, CRY2 protein appears to be more stable and accumulates even at relatively high BL intensities (Ahmad et al. 2002). Possibly, in the present study, narrow-band BL from LED lighting contributed to the abundant CRY2 protein.

In summary, low-activity CRY1 plays a role in the stem elongation and flower initiation promoted by BL with low PPS values.

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