



Coordinative regulation of plants growth and development by light and circadian clock

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Abstract The circadian clock, known as an endogenous timekeeping system, can integrate various cues to regulate plant physiological functions for adapting to the changing environment and thus ensure optimal plant growth. The synchronization of internal clock with external environmental information needs a process termed entrainment, and light is one of the predominant entraining signals for the plant circadian clock. Photoreceptors can detect and transmit light information to the clock core oscillator through transcriptional or post-transcriptional interactions with core-clock components to sustain circadian rhythms and regulate a myriad of downstream responses, including photomorphogenesis and photoperiodic flowering which are key links in the process of growth and development. Here we summarize the current understanding of the molecular network of the circadian clock and how light information is integrated into the circadian system, especially focus on how the circadian clock and light signals coordinately regulate the common downstream outputs. We discuss the functions of the clock and light signals in regulating photoperiodic flowering among various crop species.

Keywords Circadian clock, Light signaling, Photomorphogenesis, Flowering time

INTRODUCTION

As sessile organisms, plants have to adjust their growth, physiology, and developmental transitions to the cyclic changed environment cues. The circadian clocks, endogenous timekeeping mechanisms, can help plants to sense the diel changes of environmental cues, enabling them to predict and synchronize multiple physiological and developmental responses with environmental changes. The correct match between the internal oscillators and the external conditions can gain growth advantages for high plants.

The plant circadian systems are mainly composed of the input pathways that transmit environmental signals, the central oscillator that receives input signals and

generates rhythmic output signals, and the output pathways that regulate multiple physiological processes (Harmer 2009). The synchronization of internal clock with environmental signals or internal cues needs a process termed entrainment. Many entraining factors have been discovered, such as sugar signals have been found to modulate circadian clock and affect root meristem cell proliferation (Li et al. 2019; Wang et al. 2020). Notably, light is one of the predominant external entraining stimuli for the plant circadian clock, which also has a significant impact on plant growth and development independent of clock (Kaczorowski and Quail 2003). Photoreceptors can detect and transmit light information to the central circadian oscillator at transcriptional and post-transcriptional level (Oakenfull and Davis 2017). Although the complex regulatory network between clock and light has been widely

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studied in recent years, the mechanism underlying entrainment of the light-mediated clock is still not very clear. Nevertheless, the regulation mechanisms of clock coordination light signals on multiple downstream output pathways have been further disclosed, especially in photomorphogenesis, photoperiodic control of flowering.

Here, we summarize the proposed circadian clock network and how light information is integrated into the circadian system, and focus on how the circadian clock regulates the downstream outputs by coordinating light signals in *Arabidopsis*. Moreover, we discuss the functions of the clock and light signals in photoperiodic flowering of different crop species.

MOLECULAR NETWORK OF *ARABIDOPSIS* CORE-CLOCK OSCILLATOR

The circadian clock is considered as an internal 24 h pacemaker to help plants to anticipate daily changes in the environment. And the core circadian clock consists of a set of transcriptional–translational feedback loops (TTFLs) (Fig. 1). These TTFLs start at dawn by the expression of *CCA1* (*CIRCADIAN CLOCK ASSOCIATED 1*) and *LHY* (*LATE ELONGATED HYPOCOTYL*) in early morning, which encode MYB-like transcription factors (Schaffer et al. 1998; Wang and Tobin 1998). Then *PRR* (*PSEUDO-RESPONSE REGULATOR*) genes are expressed sequentially from dawn to dusk with the *PRR9* transcript peaking after *CCA1/LHY*, and followed by an order

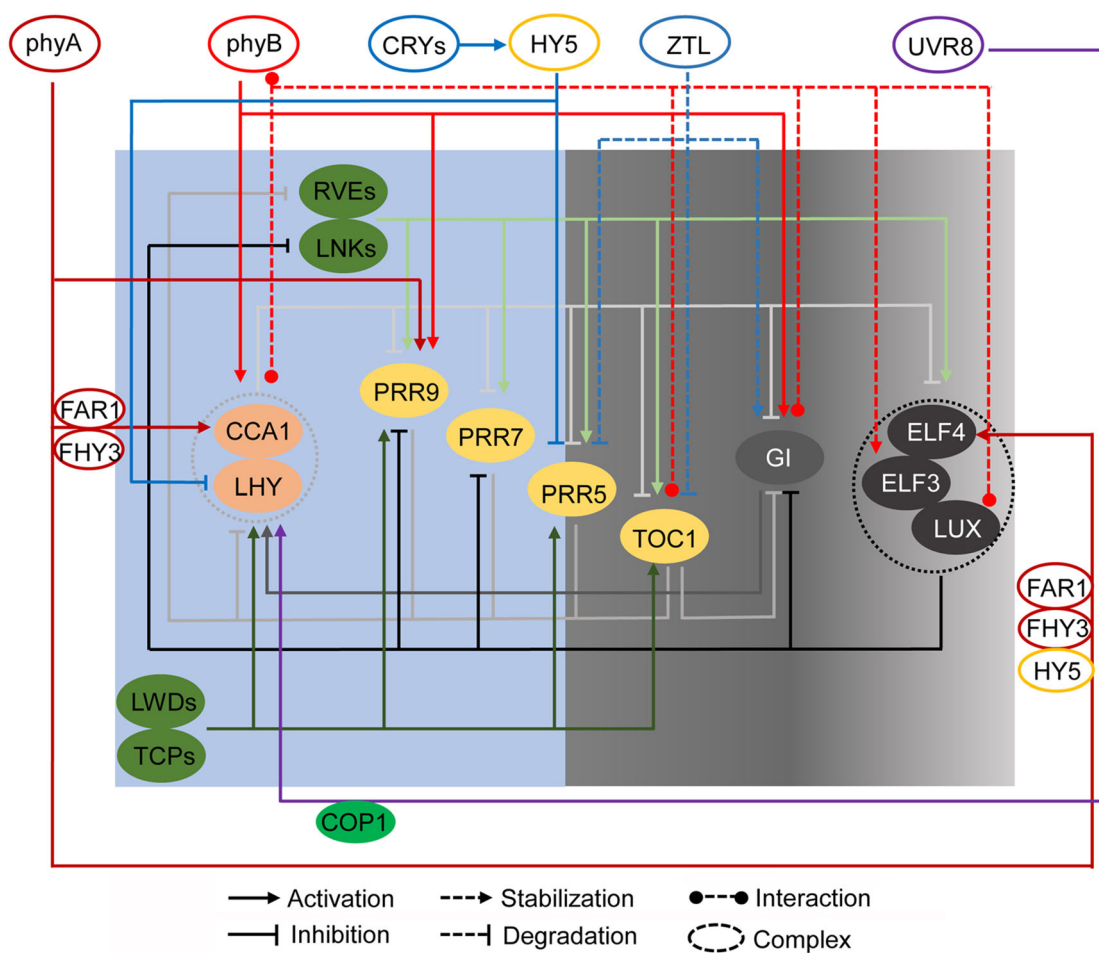


Fig. 1 A proposed model of the integration of light signaling pathways with circadian clock network in *Arabidopsis*. In day time, *CCA1/LHY* can repress the expression of *PRRs*, *GI* and the members of the *EC* complex in the morning, while *PRRs* bind to the promoters of *CCA1/LHY* and *RVE8* to repress their expression. In the evening, *EC* complex represses the expression of *PRR9*, *PRR7*, *GI*, and *LNKs*. *GI* can induce the transcription of *CCA1* and *LHY* and interact with the F-box protein *ZTL* in a blue-light enhanced manner. The accumulated *ZTL* protein subsequently promotes *TOC1* and *PRR5* degradation. *LWDs* can interact with *TCPs* to activate the transcription of *CCA1*, *PRR9*, *PRR5*, and *TOC1*. *RVEs* can activate the expression of *PRRs* and *EC*, and *RVE8* associates with *LNKs* to directly activate the expression of *TOC1* and *PRR5*. Moreover, the five photoreceptors transmit light information into the core oscillator through transcriptional and post-transcriptional regulation of circadian clock components

of *PRR7*, *PRR5*, *PRR3*, and *TOC1* (*TIMING OF CAB EXPRESSION 1*) (Makino et al. 2001; Mizuno and Nakamichi 2005). Finally, mRNA levels of *GI* (*GIGANTEA*), *ELF3* (*EARLY FLOWERING 3*), *ELF4*, and *LUX* (*LUX ARRHYTHMO*) are observed to dramatically rise around evening and night. The proteins encoded by *ELF3*, *ELF4*, and *LUX* physically interact to form a transcriptional regulatory complex known as the EC (Evening Complex) (Nusinow et al. 2011). These transcription factors tend to repress genes expressed earlier in the day. *TOC1* binds to the promoters of *CCA1* and *LHY* and represses their evening expression directly through a conserved CCT domain (Huang et al. 2012). *PRR9*, 7, and 5 can also bind to the promoters of *CCA1* and *LHY* directly to repress their expression which is similar to *TOC1* (Nakamichi et al. 2010, 2012). Besides, *PRR9/7/5* have been shown to associate with the TPL family of proteins through their EAR motif to repress *CCA1* and *LHY* expression through regulating the activity of histone deacetylase (Wang et al. 2013). *CCA1/LHY* are themselves primary transcriptional repressors and form homo- or hetero-dimers which bind to the evening element (EE) of many clock genes, such as the *PRRs*, *GI* and the members of the *EC* (Kamioka et al. 2016). *EC* repress the expression of *PRR9* and *PRR7* from dusk (Oakenfull and Davis 2017). The above is the central negative feedback loop. *GI*, as the central component of the clock, is different from others. It interacts with the F-box protein *ZTL* (*ZEITLUPE*) in a blue-light enhanced manner and helps sustain and modulate *ZTL* rhythmic accumulation, and *ZTL-GI* complex dissociate in the dark and then *ZTL* promotes *TOC1* and *PRR5* degradation (Kim et al. 2007). *GI* induces the transcription of *CCA1* and *LHY*, by contrast the expression of *GI* is regulated by the *CCA1/LHY*, *TOC1* and *EC* negatively (Huang et al. 2012; Mizuno et al. 2014), thereby forming another TTFL.

The positive arms of the clock oscillator are composed of three groups of proteins: *LWD1* (*LIGHT-REGULATED WD 1*) and *LWD2* functioning in the morning, *LNK1* to 4 (*NIGHT LIGHT-INDUCIBLE AND CLOCK-REGULATED 1*) together with *RVE4* (*REVEILLE 4*), *RVE6* and *RVE8* acting at midday. *LWD1* can interact with *TCP20* (*TEOSINTE BRANCHED 1-CYCLOIDEA-PCF 20*) and *TCP22* to activate the transcription of *CCA1* (Wu et al. 2016). In addition, *LWD1/LWD2* also promote the expression of *PRR9*, *PRR5*, and *TOC1* (Wang et al. 2011). *RVE4*, *RVE6*, and *RVE8*, have been reported to activate the expression of *PRRs* and *EC* genes (Rawat et al. 2011). In this scenario, *RVE8* associates with *LNK1* and *LNK2* and bind the promoters of *TOC1* and *PRR5* to activate their expression (Xie et al. 2014). *RVE8* expression is repressed by *PRRs* and promoters of the *LNK* genes

have been shown to be bound by the EC component *LUX* (Mizuno et al. 2014).

Light signaling entrains circadian clock via photoreceptors

Light is an essential environmental factor that provides energy and shapes plants grow and develop, through involving in many biological processes, such as seed germination, leaf expansion, seedling de-etiolation, flowering, senescence, and so on. Plants have various photoreceptors to absorb light which can help plants to monitor different light information. Photoreceptors in *Arabidopsis* include phytochromes, cryptochromes, the ZTL family, phototropins, and *UVR8* (*UV RESISTANCE LOCUS 8*). All families of photoreceptors, except phototropins, have been reported to participate in the light entrainment process of the circadian clock and help to set its pace (Litthauer et al. 2015).

Phytochromes have a wide spectrum of light absorption response including red (R) and far red (FR), and to a less degree blue (B) wavelengths (Bae and Choi 2008). In *Arabidopsis*, this family of photoreceptors has five members, from *phyA* to *phyE*. Moreover, there are two types of phytochromes, type I is light-labile, type II is light-stable. *phyA* is highly enriched in the dark and is degraded rapidly once exposure to light which belongs to type I while the other four members of this family belong to the latter (Franklin and Quail 2010). Specifically, *phyA* is considered to be the main FR sensor and has also been shown to participate in the blue-light signaling cascade, while *phyB-phyE* are the dominant regulators responding to red light (Wang and Wang 2015). In the dark, phytochromes are mostly localized in the cytoplasm and can shuttle to the nucleus with pulses of different light qualities (Nagatani 2004). However, the mechanisms of *phyA* and *phyB-E* movement towards the nucleus are different. *phyA* relies on *FHY1* (*FAR-RED ELONGATED HYPOCOTYL 1*) and *FHL* (*FHY1-LIKE*) proteins, *FHY1/FHL* interact with active form PFr *phyA* in the cytoplasm and transport it into the nucleus rapidly, and once in the nucleus, *phyA* will be photodegraded or become inactive form Pr *phyA* and *FHY1/FHL* are recycled back to the cytosol (Rausenberger et al. 2011). However, *phyB-phyE* are located in the nucleus originally by NLS (nuclear-localization signals) at the C-terminal of the proteins (Chen et al. 2005). At the molecular level, phytochromes regulate transcription by forming a complex with *PIFs* (*PHYTOCHROME INTERACTING FACTORS*), a family of basic helix-loop-helix transcription factors. Besides *PIFs*, phytochromes can also regulate positively acting transcription factors

like *HY5* (*ELONGATED HYPOCOTYL 5*) to facilitate photomorphogenesis.

Phytochromes have been proved to own multiple connections to the core oscillator at the transcriptional and post-transcriptional level (Fig. 1). *phyA* mutants have longer periods than that of wild-types in low-fluence red or blue light, and *phyA* is necessary for resetting the clock mediated by far-red light. *phyB* mutants show longer periods under high-fluence red light, and *phyB* has been shown to be involved in red light resetting clock (Devlin and Kay 2000; Yanovsky et al. 2001). *phyC-E* have also been considered to be involved in the red-light signal input to the clock (Devlin and Kay 2000). Previous studies have proposed that *phyB* preferentially binds to G-box elements and regulates the expression of *GI* and *PRR9* (Jung et al. 2016). *phyA*, lacking a known DNA-binding domain, also has the ability to associate with chromatin. FAR1 (FAR-RED IMPAIRED RESPONSE 1) and FHY3 (FAR-RED ELONGATED HYPOCOTYL 3) are two transcription factors of the *phyA* signaling pathway, which also could be involved in red-light input to the clock (Allen et al. 2006). It has been reported that FAR1 and FHY3 are necessary for the amplitude and rhythmic expression of *ELF4* (Li et al. 2011). FAR1, FHY3, and HY5 associate with the *ELF4* promoter to induce its expression, and the binding of CCA1 and LHY to that complex on *ELF4* locus represses their ability to activate transcription (Li et al. 2011). The activation of *ELF4* transcription, mediated by FAR1, FHY3, and HY5 which are regulators of the *phyA* signaling, represents a light input pathway to the clock (Gangappa and Botto 2016; Li et al. 2011). FHY3 and FAR1 can also active *CCA1* expression through directly binding to its promoter, while PIF5 inhibits *CCA1* expression directly. Moreover, PIF5 and TOC1 can repress FHY3 and FAR1 activation on *CCA1* expression through interacting with them (Liu et al. 2020). The key elements of the light input networks and the central oscillator form multiple interlocked feedforward loops to generate the appropriate time expression pattern for the clock genes (Liu et al. 2020). At the post-transcriptional level, studies have shown that *phyB* may interact with ELF3, LUX, CCA1, LHY, TOC1, and GI (Yeom et al. 2014). But the output of the interaction between *phyB* and circadian components remains unclear.

Unlike phytochromes are unique in higher plants, cryptochromes are evolutionarily conserved in many different organisms, from bacteria to human. CRY1 (CRYPTOCHROME 1) and CRY2 have been extensively characterized in *Arabidopsis* (Kleine et al. 2003). CRY1 and CRY2 mainly act as blue-light photoreceptors, but they can sense a wider spectrum of wavelengths (Liu et al. 2016a). CRY2 is rapidly down-regulated when

exposed to blue light, so it functions under low-fluence irradiances. Whereas CRY1 is more stable and functions at higher intensities of blue light (Lin et al. 1998). Photoexcited cryptochromes mediate their biological function via protein modifications and protein–protein interactions (Liu et al. 2016a). Under continuous blue light, *cry1 cry2* double mutant shows a longer circadian period than that of single mutant, suggesting that they are functional redundant in regulating blue light into the circadian clock (Devlin and Kay 2000). And *cry1cry2* mutants have also been found to be involved in far-red signaling, suggesting that there is a crosstalk between the signaling pathways sensing these different wavelengths (Yanovsky et al. 2001). However, the mechanisms of CRY mediated clock entrainment are still unclosed. *HY5* and its homolog *HYH* (*HY5-HOMOLOG*), which are transcription factors that function as molecular hub in the transduction of light signals, have been reported as key signal integrators linking the blue-light perception to the clock (Hajdu et al. 2018). The accumulations of *HY5* mRNA and protein are more easily induced by blue light, helping it regulate the binding with the clock gene promoters, among them, *HY5* regulates *PRR5*, *LUX*, and *BOA* (*BROTHER OF LUX ARRHYTHMO*) expression directly and is conjectured to modulate *CCA1* at post-transcriptional level (Hajdu et al. 2018).

Blue light perceptions also include the ZTL family, which is composed of three members: ZTL, FKf1 (FLAVIN-BINDING, KELCH REPEAT, F-BOX 1), and LKP2 (LOV KELCH PROTEIN 2). These photoreceptors have a Kelch repeat domain which mediates protein–protein interactions, and an F-box domain that allows them to function as part of the E3 ubiquitin ligase SCF (Skp–Cullin–F-box) complex which directly controls light-mediated protein degradation (Ito et al. 2012). The ZTL family has a profound impact on the photoperiodic control of floral transition, circadian oscillator regulation, and hypocotyl elongation by regulating the essential proteins accumulation in each network (Ito et al. 2012). *ztl* mutant plants show long period or arrhythmic phenotypes, while *lkp2* and *fkf1* mutants exhibit no significant difference from wild-type, suggesting that ZTL plays a major role in regulating circadian oscillations in this family (Baudry et al. 2010). The interaction between ZTL and GI can be significantly enhanced under blue light, and both proteins are mutually stable in light-dependent manner (Kim et al. 2013). GI and HSP90 can form a ternary chaperone complex with ZTL to stabilize the activity of ZTL and promote the maturation and folding of ZTL (Cha et al. 2017). Besides, GI can recruit UBP12 (UBIQUITIN-SPECIFIC PROTEASE 12) and UBP13, which are two de-ubiquitylases, to the

ZTL–GI complex, contributing to the stability and accumulation of ZTL at the end of the light period (Lee et al. 2019). At night, the ZTL–GI complexes eventually dissociate, and free ZTL triggers PRR5 and TOC1 proteasomal-mediated degradation through forming SCF complex, and FKF1 and LKP1 are redundant with ZTL in promoting TOC1 and PRR5 degradation (Kim et al. 2007). Remarkably, the light-dependent regulation of ZTL on TOC1 and PRR5 proteins accumulation transmits light signals into the circadian clock and affects its pace directly. Besides, ZTL can also sequester GI into the cytoplasm to regulate circadian rhythms, but it is unclear whether FKF1 or LKP2 have similar functions (Kim et al. 2013).

UV-B (Ultraviolet B) light is different from visible light, but it is also important in regulating plant growth and development. UV-B light can represent a stress factor, inducing DNA damage and impacting on development and growth, but the same wavelengths can promote photomorphogenesis at low intensities (Favory et al. 2009). The sensor of UV-B light is UVR8, which does not need a chromophore to convert the received photons into a biochemical signal (Rizzini et al. 2011). UV-B light pulses can induce transcription of several core-clock genes such as *CCA1/LHY*, dependent on UVR8 and COP1, but independent on HY5 and HYH. However, the level of transcriptional induction depends on the time of pulse applied, indicating that this response might be gated by the circadian clock, and a feedback regulation loop is formed between UV-B light perception and the circadian clock function (Feher et al. 2011).

Circadian clock regulates photoperiodic hypocotyl growth by integrating with light and temperature signals

It has been shown that exogenous light signal cooperates with endogenous clock to determine a daily and rhythmic growth of hypocotyls in *Arabidopsis*. In this process, PIFs are regarded as hubs (Leivar and Monte 2014). PIFs promote hypocotyl elongation mainly at the end of the night. Among them, PIF4 and PIF5 are well studied, and the transcription of *PIF4* and *PIF5* are controlled by circadian clock. Meanwhile, PIF4 and PIF5 proteins can be degraded by light-activated phytochromes signals during the day. Hence the regulation of PIF4/5 at transcriptional by clock and post-transcriptional levels by light signals contributes to regulate rhythmic hypocotyl growth in light/dark diurnal cycles (Nozue et al. 2007). A lot of studies have shown that core-clock components regulate the photoperiodic response of hypocotyl growth via cooperating with light

signaling pathway, especially through PIF4 and PIF5 (Fig. 2).

As clock-defective mutant, *cca1 lhy* seedlings display shorter hypocotyl, irrespective of the photoperiod conditions, which might be due to the according alteration of *PIF4* and *PIF5* expression patterns under different photoperiods (Niwa et al. 2009). *cca1* or *lhy* single mutant also displays short hypocotyl under red light compared with wild type, with the down expression of *PIF4* (Sun et al. 2019). The interaction between CCA1 and ELF3 also control the hypocotyl growth, *elf3-1 CCA1-OX* seedlings have similar hypocotyl length to *CCA1-OX* and longer hypocotyl than *elf3-1* plants under short-day (SD) condition, while in long day (LD) condition, the hypocotyls of *elf3-1 CCA1-OX* are slightly longer than *CCA1-OX* and much longer than *elf3-1* mutant. Intriguingly, although these three mutants have different length of hypocotyl, the *PIF4* and *PIF5* expression levels almost increase to the same level during the night in both SD and LD, indicating there are other factors involved in their different hypocotyl elongation regulation (Lu et al. 2012). PRR9, PRR7, PRR5, and PIFs can bind to the promoter of a common target gene *CDF5*, and the expression of *CDF5* is repressed by PRRs from morning to dusk, while PIFs can induce its transcription at pre-dawn when it promotes hypocotyl elongation under SD diurnal condition (Martin et al. 2018). In addition, *toc1* mutant has long hypocotyl in SD conditions, in which PIF3 is required for this phenotype because loss-of-function of *PIF3* in *toc1* background could rescue the long hypocotyls of *toc1* mutant. Further data show that TOC1 represses PIF3's transcriptional activation activity by interacting with it in nucleus to regulate growth-related common target genes under SD conditions (Soy et al. 2016). Besides, at the transcriptional level, PRRs can repress the expression of *PIF4/5* by directly binding to their promoters to regulate plant growth (Liu et al. 2016b, 2020b). Notably, the day length information changes the expression patterns of PRRs and EC complex at both transcriptional and translational levels, thus PRRs together with EC to modulate photoperiodic control of hypocotyl growth via repressing the transcription of *PIF4* and *PIF5* at specific time of the day (Li et al. 2020b).

The interaction between ELF3 and PHYB links the circadian clock and photoreceptors in regulating hypocotyl elongation, consistent with the *elf3* mutants display long hypocotyl and are defective in light perception or light-mediated signal transduction. Also, ELF4–ELF3–LUX complex regulated by light and clock, represses the transcription of *PIF4* and *PIF5* during early night by binding to their promoters (Nusinow et al. 2011). Moreover, ELF3 protein itself also can regulate plant

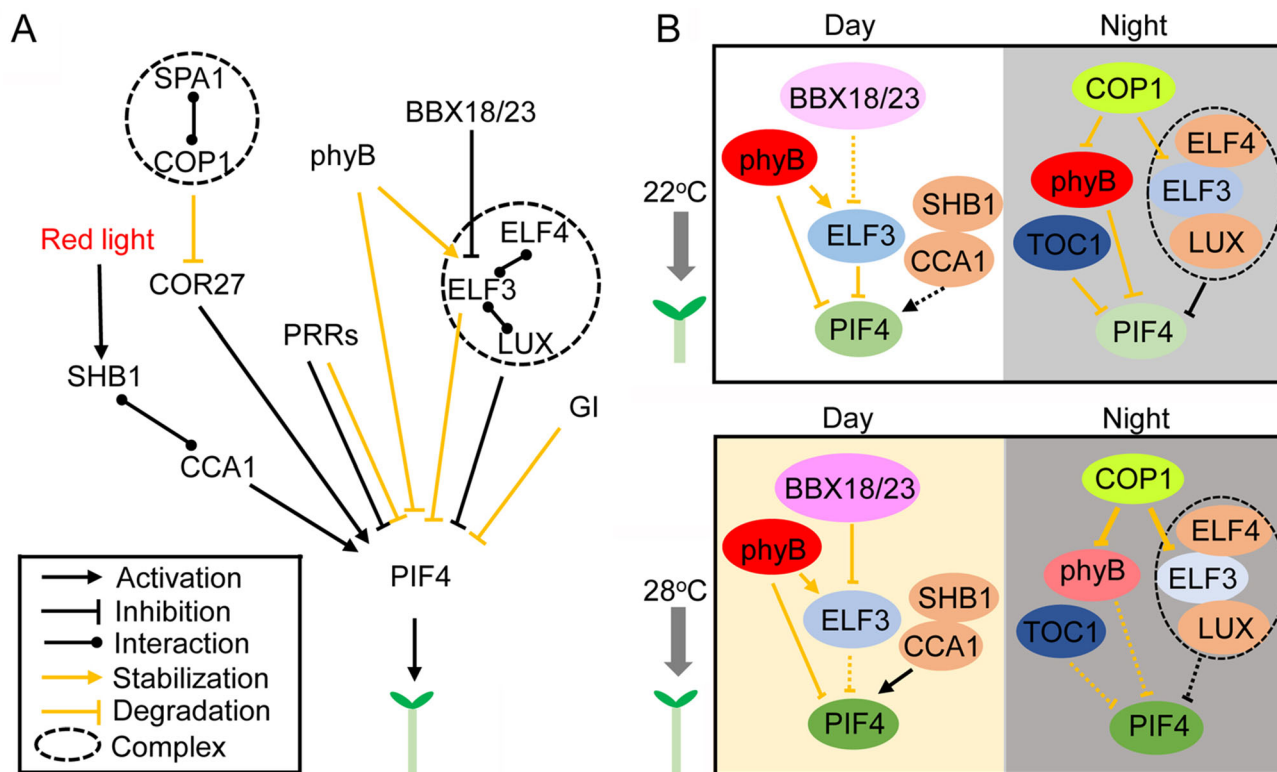


Fig. 2 Coordinative regulation of hypocotyl growth by light signals and clock components in *Arabidopsis*. **a** A simplified model of hypocotyl growth regulated by light signals and circadian clock. **b** In warmer day, BBX18/23 proteins can be promoted to accumulation, which weakens the degradation of PIF4 by ELF3 in the morning. And CCA1 together with SHB1 can promote the transcriptional activation of *PIF4* which can be induced in the warmer temperature. In warmer night, COP1 protein will be more accumulated, which can further degrade ELF3 and PHYB proteins, thus reducing the transcription inhibition or protein degradation of PIF4, respectively. Besides, warmer temperature could also diminish the interaction between TOC1 and PIF4

growth by physically interacting with PIF4 protein to suppress its DNA-binding activity (Nieto et al. 2015). Furthermore, ELF3 protein levels could be reduced by COP1-mediated degradation via an adaptor BBX19, thus the depletion of ELF3 results in less formation of Evening Complex and allows higher expression of *PIF4* and *PIF5* in the early evening, thus promoting the hypocotyl elongation (Wang et al. 2015). *gi* mutants display long hypocotyl, present a reduced sensitivity to red light and interact with phyB, indicating an involvement in photomorphogenesis (Huq et al. 2000). A few studies have reported the relationship between GI and ELF4 in controlling hypocotyl growth under different photoperiod through affecting *PIF4* expression (Kim et al. 2012). However, *elf3 gi* double mutant shows longer hypocotyl than both *elf3* and *gi* single mutant under SD and LD conditions, indicating an additive regulation in hypocotyl growth. GI not only affect PIFs expression at transcriptional level, but also control PIF activity at multiple aspects, such as PIFs protein stability, PIFs degradation and the ability of PIF access to their target chromatin to gate growth (Nohales et al.

2019). In addition, *ztl* mutants also display hypersensitivity to different fluence rates of red light, and *ZTL* overexpression seedlings exhibit elongated hypocotyl under red or blue light, further data show that the *ZTL* protein levels and hypocotyl length exist positive correlation in different fluence rates of red light, the inner mechanism need to be further investigated (Somers et al. 2004). Besides of the well-known clock component, the recently characterized clock-associated proteins such as COR27 (COLD-REGULATED GENE27) has also been shown to integrate circadian clock with light signals to control hypocotyl elongation by physically interacting with HY5 and upregulating the transcription of *PIF4* and *PIF4*-controlled genes (Zhu et al. 2020).

High temperature usually results in significant change in plant architecture such as hypocotyl elongation which is mediated by PIF4 (Quint et al. 2016). Extensive studies have been reported that some of core-clock components involve in thermomorphogenesis process via PIF4. Circadian clock regulator ELF3, a key component of temperature sensing, modulates elongation growth response to temperature by binding to the

PIF4 promoter (Mizuno et al. 2014). BBX18 and BBX23 negatively regulate ELF3 protein pool via interacting with ELF3, leading to upregulation of PIF4 to further regulate thermomorphogenesis in *Arabidopsis* (Ding et al. 2018). A prion-like domain (PrD) within ELF3 acts as a thermosensor is reported recently, the ability of thermal response is related to the length of polyQ repeat, and ELF4 can stabilize ELF3 protein by binding to the region of ELF3 protein adjacent to the PrD at high temperature, thus reducing its temperature response in elongation growth (Jung et al. 2020). TOC1 inhibits thermomorphogenesis specifically in the evening, further study demonstrates that TOC1 binds together with PIF4 at G-box motifs in their common targets' promoters, while TOC1 suppresses the thermomorphogenesis process by interacting with PIF4 and repressing its activation activity other than interfering with its DNA-binding activity (Zhu et al. 2016). Besides of ELF3 and TOC1 in temperature signaling, *CCA1* and *LHY*, which are highly expressed in the morning, could activate red-light induced *PIF4* expression by recruiting SHB1 (SHORT HYPOCOTYL UNDER BLUE 1). After dawn, with the light intensity and ambient temperature increasing, the interaction between SHB1 and *CCA1* could maintain the expression of PIF4 to better adapt to these conditions, thus enhancing plant thermos-responses to grow better (Sun et al. 2019). Collectively, it is conceivable that there are multiple intercrossed pathways mediate the coordination between circadian clock and light or temperature signals, which jointly profile the growth dynamics in response to day length change to ensure the proper growth rate.

Circadian clock and light signals coordinately determine the photoperiodic flowering time in *Arabidopsis*

The key to success of plant reproduction is timing the floral transition properly. Plants sense changes of the external environment constantly to adjust their own growth state, among which the environmental changes caused by day length are the most intuitional factors for plants to perceive the surrounding environment. In other words, the light information generated by photoperiod can be integrated into the circadian clock, which triggers plants to flower at the proper season. Studies have shown that clock components ELF3 and GI are the key factors in the synchronization of the endogenous cellular mechanism with the external environment signals. If these two genes are deleted, clock-mediated photoperiod-responsive growth will be lost completely, which indicates that ELF3 and GI cooperate in the transmission of photoperiod signals to

the central oscillator (Anwer et al. 2020). It is well-known that CO (CONSTANS) and FT (FLOWERING LOCUS T) are the core integrators in the photoperiod regulated flowering pathway, which are modulated by circadian clock (Samach et al. 2000). Meanwhile, CO functions as transcriptional activator to induce the expression of *FT* in long days (Song et al. 2015). Therefore, the key mechanism of photoperiod flowering in *Arabidopsis* is that the circadian components coordinate with photoperiod information to regulate CO function (Fig. 3).

Transcriptional and post-translational regulations of CO are both crucial in determining flowering time. In the morning, CDF (CYCLING DOF FACTOR) protein family can inhibit the transcription level of *CO* by binding to the *CO* promoter (Fornara et al. 2009). The expression level of *CDF* is directly modulated by the circadian clock. Besides, *CCA1* and *LHY* could induce the transcription of *CDF* in the morning, while *PRR9*, *PRR7*, and *PRR5* inhibit its transcription in the afternoon (Nakamichi et al. 2012). Meanwhile, *FKF1* can form a complex with *GI* to degrade CDF and release its inhibition of *CO* in the long-day afternoon (Sawa et al. 2007; Fornara et al. 2009). In short days, the peak time of *FKF1* and *GI* is different in the dark, so only a small amount of complex is formed, and it is negligible for the degradation of CDF (Sawa et al. 2007). *Arabidopsis* CO protein is also subjected to complicated regulation at post-transcriptional level. *PRR* proteins can stabilize CO protein via interacting with it at specific time of the day (Hayama et al. 2017). In addition, a ZTL/*FKF1*/ *GI*-dependent mechanism has also been reported, which regulates the stability of CO protein directly throughout the day, and ZTL mediates the degradation of CO in the morning by directly binding to it (Song et al. 2014). *GI* preferentially interacts with ZTL when it is expressed and inactivates ZTL function, leading to sequestration of CO from ZTL (Hwang et al. 2019). In addition, *FKF1* and *GI* form an active protein complex to stabilize CO in the afternoon (Song et al. 2015).

Light signaling components, such as two phytochromes, *phyA* and *phyB*, also can modulate the CO protein stability antagonistically, as *phyB* can destabilize CO protein through red light, while *phyA* stabilizes CO protein through far-red light (Valverde et al. 2004). In the morning, *HOS1* (HIGH EXPRESSION OF OSMOTICALLY RESPONSIVE GENES1) has been reported to interact with CO to involve its red light-mediated degradation (Lazaro et al. 2015). Interestingly, *phyB* interacts with *HOS1* and CO protein simultaneously, suggesting that they might exist in a three-protein complex coordinating the correct photoperiodic response (Lazaro et al. 2015). Additionally, *PHL*

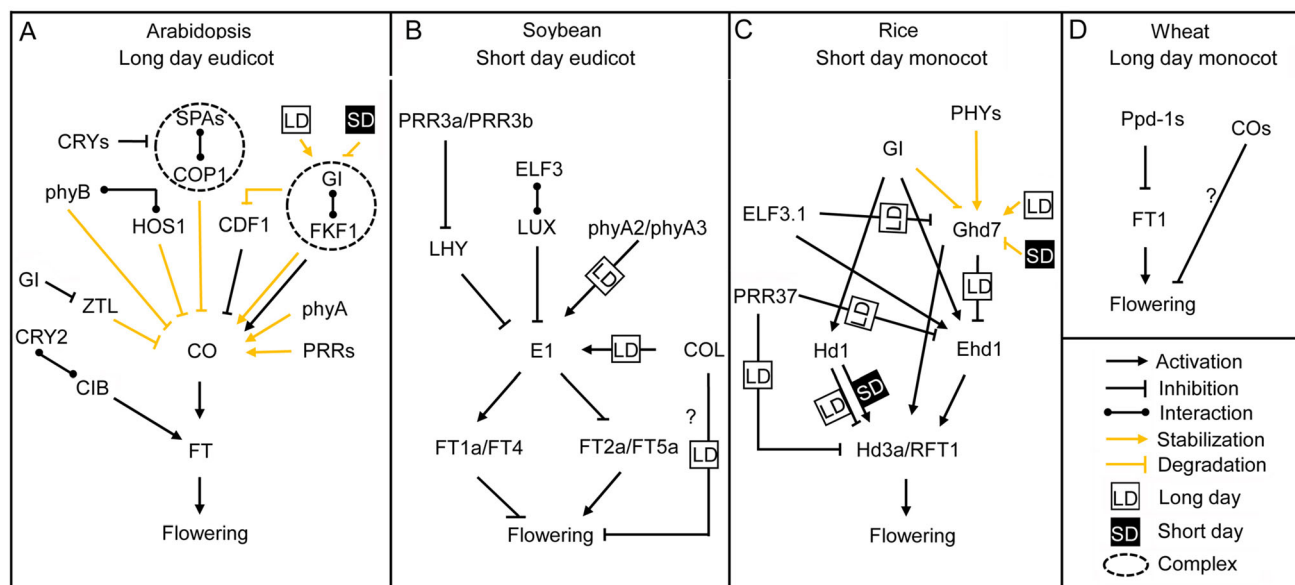


Fig. 3 Diagrams showing the photoperiodic flowering regulated by light signals and circadian clock in several typical plants. **a** In *Arabidopsis*, a facultative long-day plants, *CO* and *FT* function as central components for photoperiodic flowering, regulated by clock components and light signals transcriptionally and post-transcriptionally. **b** In SD plants soybean, *E1* has been identified as the main pathway to regulate photoperiodic flowering, which is regulated by light signal and circadian clock, and regulate *GmFTs* with different functions. **c** *CO-FT* signaling module is conserved in rice, a SD monocot, but *Hd1*, a homology of *CO*, has opposite effects on flowering time regulation under LD and SD. In addition, rice has evolved a few unique components and pathways to control heading date, such as *Ehd1* and *Ghd7*. **d** In LD monocot wheat, PRR proteins are required for photoperiod sensitivity, and other mechanisms need to be further studied

(PHYTOCHROME-DEPENDENT LATE-FLOWERING) plays an important role in phyB dependent flowering regulation mainly by antagonizing phyB's inhibition of flowering (Endo et al. 2013). However, the mechanisms of phyA stabilizes CO in the afternoon is still unknown, probably due to the disruption of COP1–SPA complex function by phyA (Sheerin et al. 2015). COP1 can reduce CO protein level by interacting and ubiquitinating it in the darkness. However, blue-light photoreceptors, CRY1 and CRY2 attenuate activity of SPA1 (SUPPRESSOR OF PHYTOCHROME1-105 1), which is responsible for positive regulation of the E3 ubiquitin ligase COP1, stabilizing CO protein in a light-dependent manner throughout the day (Liu et al. 2008b). Besides, blue-light activated CRY2 interacts with CIB (CRY-INTERACTING BASIC HELIXLOOP-HELIX), which function as transcriptional activators of *FT*, activating the transcription factor *FT* directly to promote flowering (Liu et al. 2008a). Together, it is imaginable that circadian clock and light signaling coordinately determine the photoperiodic flowering time, mainly integrated by CO at both transcriptional and post-transcriptional levels.

Circadian clock and light signals coordinate to regulate photoperiodic flowering in crops

Besides of *Arabidopsis*, the regulatory mechanisms of flowering time in major crops including soybean have been extensively studied in recent years. Soybean is a facultative short-day plant, its flowering can be promoted by the shortened day length via *E1* mediated photoperiodic pathway (Fig. 3). *E1*, encodes a legume specific transcription factor which is distantly related to *Arabidopsis* TEMPRANILL protein family (Matias-Hernandez et al. 2014). *E1* represses the transcription of *GmFT2a* and *GmFT5a*, the two soybean florigen genes, but in part get involves into the induction of *GmFT1a* and *GmFT4* to promote vegetative growth while to inhibit flowering. Meanwhile, photoreceptors *GmphyA3* and *GmphyA2*, homologs of *phyA*, can induce the expression of *E1* under LD. Moreover, blue-light receptor *GmCRY1a*, but not *GmCRY2a*, exhibits a strong activity in promoting floral initiation. *GmCIL10* (*CIB1-Like10*), similar to *CIB1* accelerates flowering under both LDs and SDs in transgenic *Arabidopsis*, suggesting that CIBs dependent regulation of flowering time is evolutionarily conserved in soybean (Yang et al. 2015). In addition, there are three homologs of *G1* in soybean, *GmG11*, *GmG12*, and *GmG13*, and yeast two hybrid assays

showed GmFKF1 and GmFKF2, orthologs of *Arabidopsis* FKF1, can interact with GmGI1/2 and the CDF1 ortholog GmCDF1, suggesting that *GmGI* might play a significant role in controlling soybean flowering time (Li et al. 2013). GmELF3, an ortholog of clock component ELF3 also play a critical role in promoting flowering via physically interacting with GmLUX2 to directly repress *E1* expression (Fang et al. 2020). Instead, another soybean clock component, *GmPRR3a*, and *GmPRR3b*, orthologs of *Arabidopsis* PRR3, can indirectly induce *E1* expression but repress *GmFT2a* and *GmFT5a* expression (Li et al. 2020a; Lu et al. 2020). Remarkably, soybean genome contains 26 *COL* (*CONSTANS-LIKE*) genes that can delay flowering in LD likely acting as activators of *E1* expression (Wu et al. 2019).

Rice is one of the representative short-day monocots and its flowering time (heading date) regulatory network has also been widely studied. There are three phytochrome genes in rice, named *OsPHYA* (*OsPHYTOCHROME A*), *OsPHYB*, and *OsPHYC* respectively. *OsPHYA* delays heading date under LD condition but accelerates it under SD condition (Lee et al. 2016). Interestingly, the role of *OsPHYB* in heading date is not affected by day length, while *OsPHYC* majorly modulates heading date under LD condition (Wei et al. 2020b). In addition, the heading date of *osphyA osphyb* double mutant or *osphyA osphyb osphyc* triple mutant is not affected by day length, suggesting that they are essential for regulating photoperiodic flowering time in rice (Takano et al. 2009). OsFKF1, a homolog of *Arabidopsis* FKF1, can interact with OsGI and CDF1 to modulate heading date independent of photoperiod in rice (Han et al. 2015), while the role of OsZTL1 in rice heading date is still unclear. *Hd3a* (*Heading date 3a*) encodes the rice florigen and its expression can be induced by SD but inhibited by LD conditions (Tamaki et al. 2007). Similar to *Arabidopsis*, the day length-dependent *Hd3a* expression requires *Hd1*, a rice orthologue of *CO*. Intriguingly, rice *Hd1* promotes heading date under SD but inhibits it under LD condition (Wei et al. 2020b). In addition to the conserved *Hd1–Hd3a* pathway, rice also has unique components and pathways to regulate photoperiodic flowering (Fig. 3). *Ehd1* (*Early heading date 1*) encodes a B-type response regulator that promotes heading date through the induction of *RFT1* (*Rice FT-like 1*)/*Hd3a* in both SD and LD conditions (Komiya et al. 2008). *Ehd1* expression can be promoted by OsGI in SD condition (Hayama et al. 2003), but in LD conditions can be repressed by Ghd7 (Grain number, plant height and heading date 7) and OsPRR37 (Gao et al. 2014). In addition, OsPRR37 also can repress *Hd3a* expression in LD conditions to function as a floral repressor (Koo et al. 2013). Moreover, OsGI interacts with Ghd7 to facilitate

its degradation, whereas OsPHYA and OsPHYB can antagonize with OsGI to interact with Ghd7, thus stabilize Ghd7 (Zheng et al. 2019). Notably, Ghd7 protein cannot be efficiently accumulated under SD condition, which may represent an uncover mechanism of recognition of day length. Meanwhile, OsELF3.1 activates *Ehd1* but suppresses *Ghd7* expression to promote heading date under SD conditions (Zhao et al. 2012). Hence, *Ehd1* and Ghd7, together with their regulatory factors, compose unique photoperiod-dependent heading date pathways in rice.

Although temperate maize is an autonomous day-neutral plant, it is domesticated from an obligate short-day plant teosinte. Recently, a few components in the photoperiodic flowering pathway were characterized in maize. *CONZ1* (*CONSTANS OF ZEA MAYS 1*) has been considered as the homolog of *CO* and *OsHd1*, and its expression patterns are significantly different in long and short days, suggesting that maize can recognize photoperiod changes and respond to the differential expression of *CONZ1*, but the specific flowering mechanisms need to be more studied (Miller et al. 2008). *ZmCCT* encodes a CCT-domain transcription factor which functions as flowering repressor in LD condition, and its mutation showed early flowering phenotype and has thus been selected for maize cultivars at higher latitudes (Hung et al. 2012). In addition, *ZmCCT*, together with *ZmCCA1*, was also shown as the important link to connect photoperiod and stress tolerance response in LD condition (Ku et al. 2016). *ZCN7* and *ZCN8* (*ZEA CENTRORADIALIS 8*) have been identified as the strongest candidate genes for maize florigen (Meng et al. 2011; Mascheretti et al. 2015). *ZCN8* together with, *ZCN12* can directly affect the flowering time of maize, which is necessary for adaptation to temperate climates (Castelletti et al. 2020). There are two *GI* homologs in maize which has been reported to be involved in photoperiodic flowering (Miller et al. 2008). Intriguingly, maize *gi1* mutants show early flowering phenotypes only in LD conditions, which is likely due to the up-regulation of floral activator gene *ZCN8* and flowering regulatory gene *CONZ1* (Bendix et al. 2013). *ZmPHYC1* and *ZmPHYC2* are two characterized phytochromes in maize, among which *ZmPHYC1* is regulated by circadian clock at the transcriptional level. Double knockout mutants of *ZmPHYC1* and *ZmPHYC2* exhibit moderate early flowering phenotypes under LD conditions, which can be used as molecular breeding targets for maize varieties adapted to different local environments (Li et al. 2020c).

In wheat, the flowering time is considered as predominantly determined by vernalization, nevertheless, photoperiod sensitivity also influences the wheat

heading date in which *Ppd-1* (*Photoperiod-1*) genes, members of PRR gene family in wheat, act as key regulators of this process (Beales et al. 2007). In total, there are three *Ppd-1* genes in hexaploid wheat, *Ppd-D1*, *Ppd-A1*, and *Ppd-B1*, which act jointly to repress flowering though repressing *TaFT1* expression directly or indirectly (Seki et al. 2011). Moreover, the mutants of *TaTOC1s* have shown to promote flowering initiation (Zhao et al. 2016). *TaG11*, an ortholog of *GI* in *Arabidopsis*, is involved in the regulation of photoperiodic flowering (Zhao et al. 2005). *TaLWD1L-A*, which can be affected by circadian clock-related genes, regulated the expression of the *TaFT1* indirectly by affecting the expression of photoperiod-related genes *TaPpd-1* and *TaGI* and its overexpression in transgenic wheat has shown an obvious early flowering phenotype (Hu et al. 2020). Moreover, PHYC in wheat is also required for flowering acceleration under inductive LD, which is mediated by *Ppd-1* and its downstream target *TaFT1* (Chen et al. 2014). Taken together, it is conceivable that clock-associated genes also play crucial roles in the flowering time determination in wheat.

CONCLUSION AND PERSPECTIVE

Light signals and circadian clock are required for the normal growth and development of plants. As an endogenous time regulator, the circadian clock can make the maximum profit for plant growth when the internal regulations match the external environments. And light has been reported as one of the key entrainment factors of the internal oscillator. Although there are still many uncharacterized molecular links and networks, the crosstalk between circadian clock and light signals has been preliminarily established. Not only the photoreceptors, but also the downstream signaling molecules of light signaling, such as PIFs, HY5, and COP1, can transmit light information to the core oscillator through transcriptional or post-transcriptional regulation, and coordinately regulate the growth and development of plants with circadian components (Fig. 1). The mechanisms of photoperiodic flowering are more complex in rice, a SD monocot. Although *CO-FT* signaling module is conserved in rice, it has opposite effects on flowering regulation under LD and SD. In addition, rice has evolved a few unique components and pathways to control heading date, such as *Ehd1* and *Ghd7*. How rice circadian clock senses and responds to photoperiod is an urgent problem to be solved, which may be needed to further explore the interaction among light signals, internal oscillator, and flowering factors. LD monocots, such as wheat, PRR proteins are required for

photoperiod sensitivity, and other mechanisms need to be further studied. In the future, more genetic locus or QTLs involved in the regulation of photoperiodic flowering in crops need to be identified, which may facilitate to explain the discrepancy of the photoperiodic flowering time mechanisms between long-day plants and short-day plants. Moreover, the comprehensive functions of clock components and photoreceptors need to be further explored especially in staple crops. Recently, circadian clock regulation stress responses have been studied, in which salt-induced *OPRR73* expression confers salt tolerance by recruiting HDAC10 to inhibit *OsHKT2; 1* transcriptional level, but whether the synergistic regulation of light signal awaits to be further examined (Wei et al. 2020a). Undoubtedly, circadian clock and light signals play the central roles to synchronize plants with the external environments for achieving optimal growth. Thus, the fully exploration of their coordinative manner will eventually benefit plant molecular design breeding for the optimum local or regional adaption.

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Declarations

Conflict of interest No potential conflicts of interest were disclosed.

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