



# Transcriptomics: Molecular Mechanism of the Control of the Flowering in Plants and Gene Regulatory Network Models for Control of Flowering

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## ABSTRACT

Plants are dynamic systems able to continuously adapt to changing environmental conditions, showing a remarkable phenotypic plasticity as from transition from germination to vegetative growth then to reproductive development (flowering). This review provides insight into regulatory mechanisms for phytochrome-mediated light signalling pathway; and the roles of phytochromes and their downstream signalling components, molecular mechanisms light-perceiving photoreceptors and other positive and negative regulators of light signalling as well as interactions between these components during plant growth and development. In this review, molecular mechanisms and the gene regulatory network for the control of flowering were reviewed. Light is one of the most important factors regulating plant growth and development (photo-morphogenesis) that control plant development, from seed germination to flowering and senescence. Plants transition from vegetative growth to reproductive development (flowering) is controlled by result of responses to various endogenous (molecular) and exogenous (environmental) signals that later integrate to result in flowering. Multiple genetically defined novel pathways have been identified that control flowering. Furthermore, these include the photoperiod, vernalization, autonomous and gibberellin (GA) pathways and are increasingly being identified, including hormonal signals to control floral transition.

## 1. INTRODUCTION

Some plants rely on light signals to determine when to switch from the vegetative to the flowering stage of plant development (Yano et al., 2000; Izawa, 2020). This type of photomorphogenesis is known as photoperiodism and involves using red photoreceptors (phytochromes) to determine the daylength (Yano et al., 2000; Izawa, 2020). Typically, plants are responsive to wavelengths of light in the blue, red and far-red regions of the spectrum through the action of several different photosensory systems (Taiz, L., et al. 2015). The photoreceptors for red and far-red wavelengths are known as phytochromes (660–730 nm) (Taiz, L., et al. 2015). There are at least 5 members of the phytochrome family of photoreceptors. There are several blue light photoreceptors known as cryptochromes (Taiz et al. 2015; Yu et al. 2010; Jenkins, Gareth I., 2017). The combination of phytochromes and cryptochromes mediate growth and the flowering of plants in response to red light, far-red light, and blue light (Izawa, 2020; Taiz et al. 2015; Yu et al. 2010; Jenkins, Gareth I., 2017). As a result, photoperiodic plants only start making flowers when the days have reached a "critical daylength," allowing these plants to initiate their flowering period according to the time of year. For example, "long day" plants need long days to start flowering, and "short day" plants need to experience short days before they will start making flowers (Yano et al., 2000; Izawa, 2020). Plants respond to environmental cues such as photoperiod, temperature and nutrient deficiency, as well as endogenous/developmental cues such as circadian clock phases, age information including juvenile and adult phases, and programmed organ differentiation.

Molecular genetic studies using *Arabidopsis thaliana* as a model system have overwhelmingly revealed many important molecular mechanisms underlying the control of various biological events, including floral induction in plants (Romera et al., 2020). This review focus on molecular mechanisms of the control of flowering.

## 2. Molecular Mechanisms of the Control of Flowering

In higher plants, flowering time is tightly manipulated by interactions among several internal elements and diverse external factors. To maximize reproductive success, plants must form flowers under the most suitable environmental conditions. The timing of flowering affects total yields as well as fruit quality (Cho, 2016, Izawa, 2020).

Molecular genetic studies using *Arabidopsis thaliana* as a model system have overwhelmingly revealed many important molecular mechanisms underlying the control of various biological events, including floral induction in plants (table 1). The major genetic and epigenetic pathways of control of flowering have been influenced by crosstalk of various environmental factors/stress such as photoperiod, vernalization (temperature), availability of water and nutrients in the soil, exogenous chemical compounds, microbes, pollinator availability, autonomous and hormonal pathways as shown in figure 1 (Simpson and Dean, 2002, Izawa, 2020). Understanding the regulatory mechanisms by which these factors modulate flowering time is very helpful when developing management strategies for plant production (Cho, 2016; Izawa, 2020).

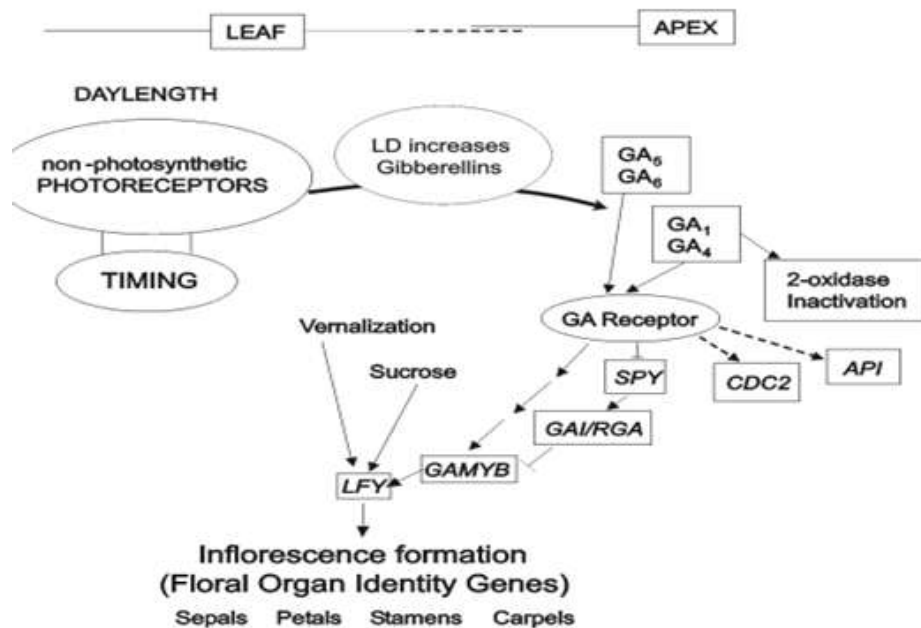


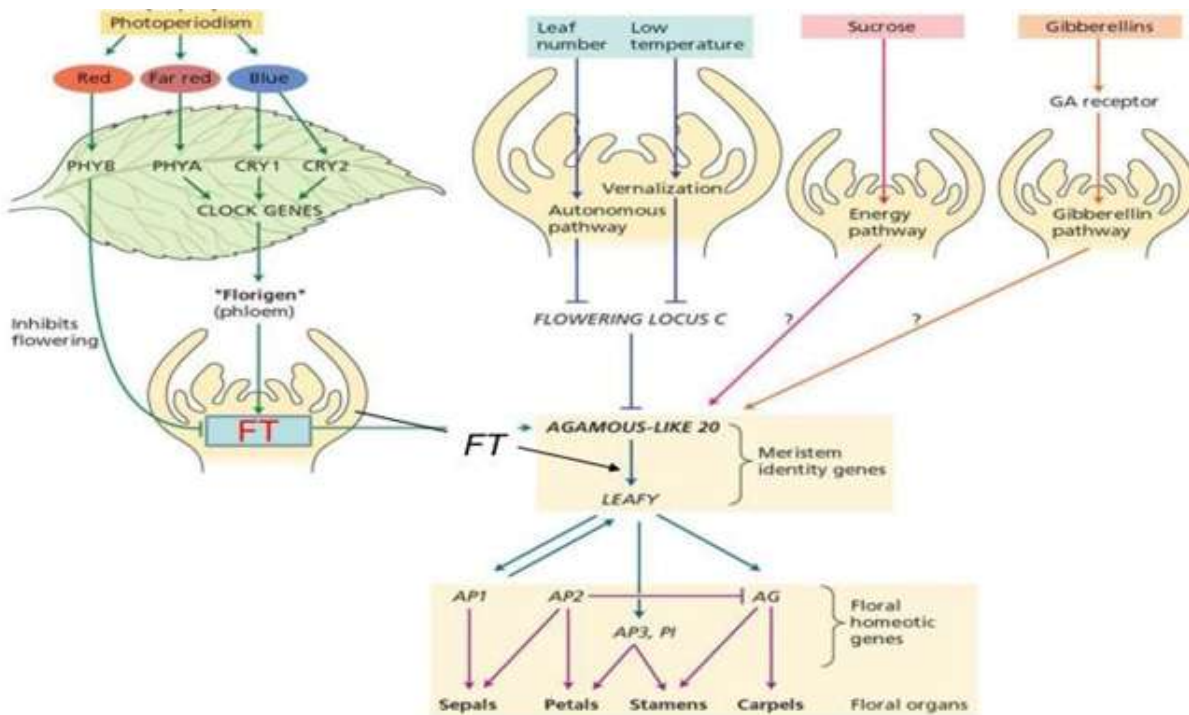
Figure 1. A model for the pathway from day length perception via gibberellins to flowering and related molecular changes. The various genes listed are: AP1, *Apetala 1*; CDC2, a serine/threonine protein kinase; GAMYB, a GA-regulated Myb transcription factor; GAI/RGA, GA-insensitivity genes; LFY, *Leafy*; and SPY, *Spindly* (Kim et al., 2007).

**Table 1. Function of orthologous genes related to flowering-time regulation between rice and *Arabidopsis thaliana***

Rice gene	Functions in rice	Arabidopsis gene	Functions in Arabidopsis	References
<i>Hd3a/RFT1</i>	Florigen	<i>FT/TSF</i>	Florigen	Kojima <i>et al.</i> , 2002; Komiya <i>et al.</i> , 2008
<i>OsMADS50</i>	Floral promoter under long-days Floral promoter upstream of <i>Ehd1</i>	<i>SOC</i>	Floral promoter as a <i>FLC</i> target	Lee <i>et al.</i> , 2004; Ryu <i>et al.</i> , 2009
<i>OsGI</i>	Clock component Blue light signaling <i>Ehd1</i> as a major target in floral regulation	<i>GI</i>	Clock component Integrator (transmitter) for multiple stimuli <i>CO</i> as a major target in floral regulation	Izawa <i>et al.</i> , 2011
<i>Hd1</i>	Floral promoter under short days Floral repressors under long days	<i>CO</i>	Floral promoter under long-days	Yano <i>et al.</i> , 2000
<i>miR156-SPL</i>	Tiller number control Panicle size control	<i>miR156-SPL</i>	Age-dependent floral promoter Stress responses Temperature-dependent floral promoter	Jiao <i>et al.</i> , 2010; Xie <i>et al.</i> , 2012; Wang <i>et al.</i> , 2015; Zheng <i>et al.</i> , 2019
<i>OsMADS51</i>	Floral promoter upstream of <i>Ehd1</i>	<i>FLC</i>	Major floral repressor for vernalization	Kim <i>et al.</i> , 2007; Ruelens <i>et al.</i> , 2013
<i>OsMADS22/47/55</i>	Negative regulator for BR signaling	<i>SVP</i>	Temperature-related floral promoter	Lee <i>et al.</i> , 2010, 2008a,b
<i>Ehd1</i>	Major floral promoter under short days	No ortholog	Cytokinin-related B type-RR may be related	Doi <i>et al.</i> , 2004
<i>Ghd7</i>	Major floral repressor under long days	No ortholog		Xue <i>et al.</i> , 2008; Itoh <i>et al.</i> , 2010

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**2.1. Molecular Mechanisms for Multiple Flowering Control**



**Figure 2. Molecular mechanism of plant multiple flowering time control and the transition to flowering involves multiple factors and pathways.**

### 2.1.1 The Role of AGAMOUS in Specifying Determinacy

In Arabidopsis, the specification of a determinate floral meristem depends on expression of the AGAMOUS (AG) MADS domain-containing transcription factor (figure 2); AG genes are floral homeotic genes determining for stamens and carpel identity of floral organs. WUS and LFY proteins together can activate AG expression, and both have been shown to bind directly to sequences in the AG promoter (Takeshi Izawa, 2020; Lenhard et al. 2001; Lohmann et al. 2001).

In plants requiring vernalization (figure 3), FLC chromatin is acetylated in a non-vernalized state, resulting in active transcription (Takeshi Izawa, 2020). The first step to negate the effects of FLC is the transcriptional repression of its RNA by COOLAIR, the antisense transcript of FLC during early exposure to cold. Another noncoding RNA called COLDAIR is transcribed

from the first intron of FLC and also plays a major role in downregulating FLC transcript levels. Upon initiation of vernalization (late cold), VIN3 methylates lysine residues of histone H3. This vernalized state is maintained by VRN1 and VRN2 upon vernalization, even after the temperatures become warmer (figure 3) (Takeshi Izawa, 2020).

The autonomous pathway regulators FLD and FVE also function by controlling methylation of lysine residues of histone H3. The RNA binding elements Cst64 and Cst77 and the autonomous pathway regulators FPA, FCA, and FY all regulate FLC transcript levels (figure 4). Levels of FLC RNA (black) are plotted against different stages of cold and compared to levels of COOLAIR RNA (red), COLDAIR RNA (green), and VIN3 protein (orange) (figure 4) (Takeshi Izawa, 2020; Lenhard et al. 2001; Lohmann et al. 2001).

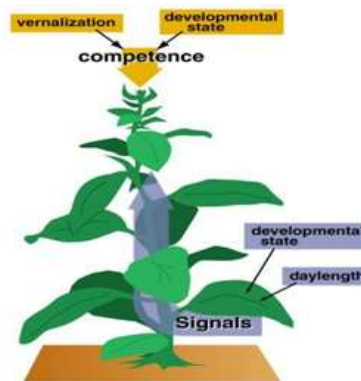


Figure 3. Regulation of Flowering and development under Vernalization in Arabidopsis. Besides the photoperiod-dependent regulation, floral transition is under controls of many other cues.

#### Flowering time regulation in Arabidopsis

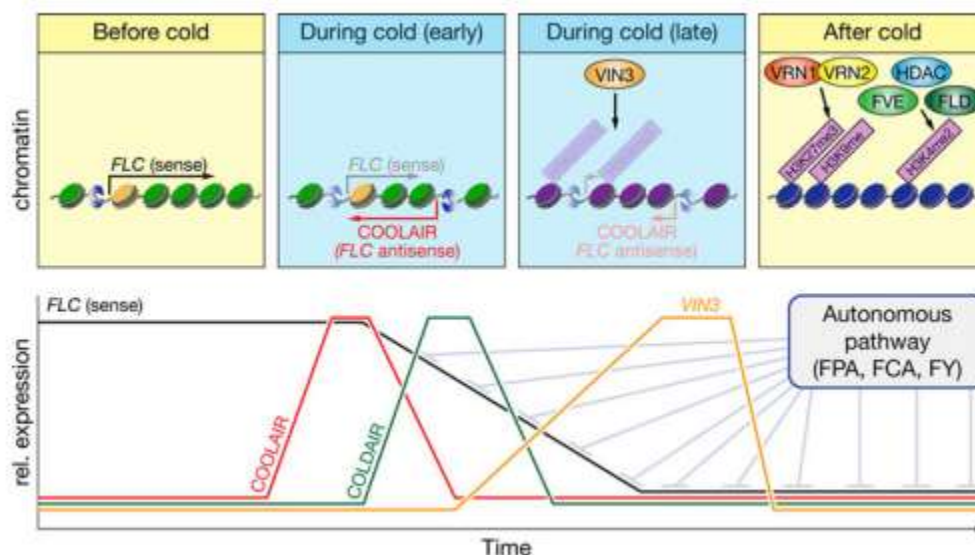


Figure 4. Regulation of FLC (flowering time regulation in Arabidopsis).

## 2.2. Hormonal control of flowering

What is going on with the hormonal control of flowering in plants? (Takeshi Izawa, 2020). Hormonal control of flowering in *A. thaliana* is represented by transcriptional regulation of related flowering-time genes (Takeshi Izawa, 2020). It is of note that gibberellin (GA) is required for floral transitions under non-inductive short-day conditions in *A. thaliana* (figure 5); for more details regarding the roles of ethylene, see Achard et al. (2007); for jasmonate (JA), see Zhai et al. (2015); for GA, see Hyun et al. (2017); for brassinosteroid (BR), see Li et al. (2018); and for GA and the circadian clock, see Nohales and Kay (2019).

438 Takeshi Izawa

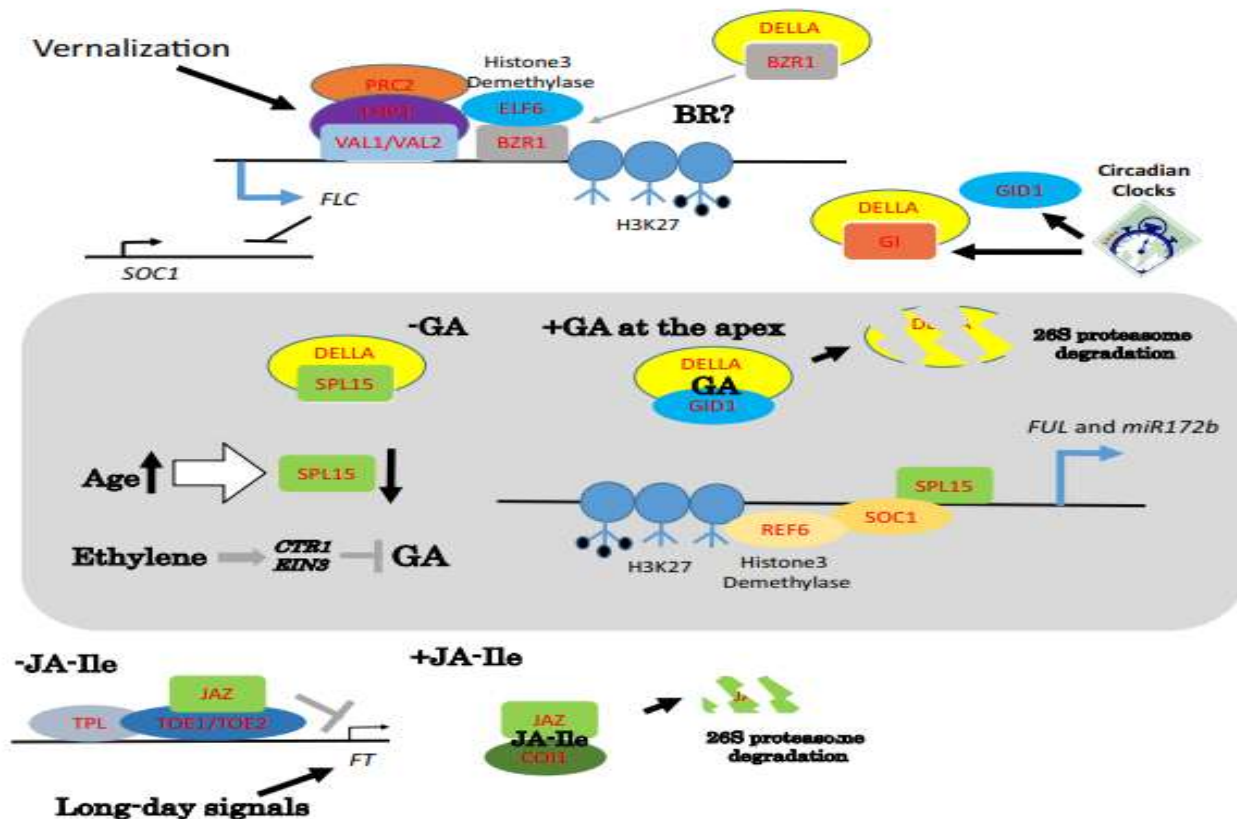


Figure 5. Hormonal control of flowering in *Arabidopsis thaliana* (Takeshi Izawa, 2020).

### 2.2.1 JASMONATE AND FLOWERING

Another phytohormone, jasmonate (JA), is known to function as a key immune signal for various plant diseases, and to be involved in a wide range of developmental processes, including flowering time in *A. thaliana* (Takeshi Izawa, 2020). FT is repressed by AP2-like transcription factors including TARGET OF EAT1 (TOE1) and TOE2, which can interact with a subset of JA-ZIM domain (JAZ) proteins (Takeshi Izawa, 2020). Under stress conditions, JA promotes CORONATINE INSENSITIVE 1 (COI1)-dependent degradation of JAZs. Degradation of JAZ repressors enables TOEs to repress FT expression, which in turn delays flowering (Zhai et al., 2015; Browse and Wallis, 2019).

In addition, DELLA proteins can interact with JAZs and reduce inhibition of their key target MYC2 (figure 5) (Browse and Wallis, 2019; Takeshi Izawa,

2020). Therefore, DELLA protein can enhance the activity of TOE1 and TOE2 indirectly via sequestration of JAZ. As a result, DELLA degradation by GAs frees multiple repression sites in the FT promoter (Takeshi Izawa, 2020). This relationship establishes a genetic link between GA and JA signaling to control flowering time in *A. thaliana* (Browse and Wallis, 2019, Zhai et al., 2015).

### 2.2.2 BR AND FLOWERING

BRs, a group of steroid hormones, are known to play important roles in plant development and growth, including flowering-time control (figure 5) (Takeshi Izawa, 2020). More recent analyses revealed that BRs inhibit floral transitions by recruiting proteins such as histone 3 lysine-27 demethylase, ELF6, BZR1 and BES1- INTERACTING MYC-like to a BR-responsive element in the first intron of FLC and related MADS box

genes; this disrupts Polycomb silencing at FLC, leading to FLC activation in rapid-cycler strains of *A. thaliana* (Li et al., 2018, Li and He, 2020).

### 2.2.3 DELLA AND FLOWERING

As mentioned above, DELLAs are key floral transition regulators, particularly in *A. thaliana* (figure 5) (Takeshi Izawa, 2020). DELLAs regulate the expression of several genes and mediate almost all phytohormonal signaling pathways, thereby controlling various developmental and environmental responses in plants, including floral induction (Daviere and Achard, 2016).

### 2.3 FD AND FLOWERING

The florigen protein has been hypothesized to form a transactivating complex termed florigen activation complex (FAC) with 14-3-3 and the bZIP protein FD. This occurs at the shoot apex, where it controls downstream genes to form inflorescence and flower meristems (Taoka et al., 2011; Tsuji et al., 2013). In a recent report, 135 genes were identified to be target genes of FD at the apex using Chromatin Immuno Precipitation and RNA-sequencing approaches in *A. thaliana* (Collani et al., 2019). Interestingly, Gene Ontology classification of the

genes revealed significant enrichment in biological processes such as “flower development,” “maintenance of inflorescence meristem identification” and “response to hormone.” Furthermore, both FD and a FD paralog, FDP, regulate genes involved in responses to ABA to control ABA sensitivity (Collani et al., 2019, Romera-Branchat et al., 2020).

### 2.4 The control of flowering time by environmental factors

The timing of flowering is determined by endogenous genetic components as well as various environmental factors, such as day length, ambient temperature, nutrient, exogenously applied hormones and stress. The genetic elements and molecular mechanisms that rule this process have been examined in the long-day-flowering plant *Arabidopsis thaliana* (figure 7) and short-day flowering rice (figure 6) (*Oryza sativa*) (Cho et al., 2016/2017) In response to such stresses or stimuli, plants either begin flowering to produce seeds for the next generation or else delay flowering by slowing their metabolism. These responses vary depending upon the dose of the stimulus, the plant developmental stage, or even the cultivar that is used (Cho et al., 2016/2017).

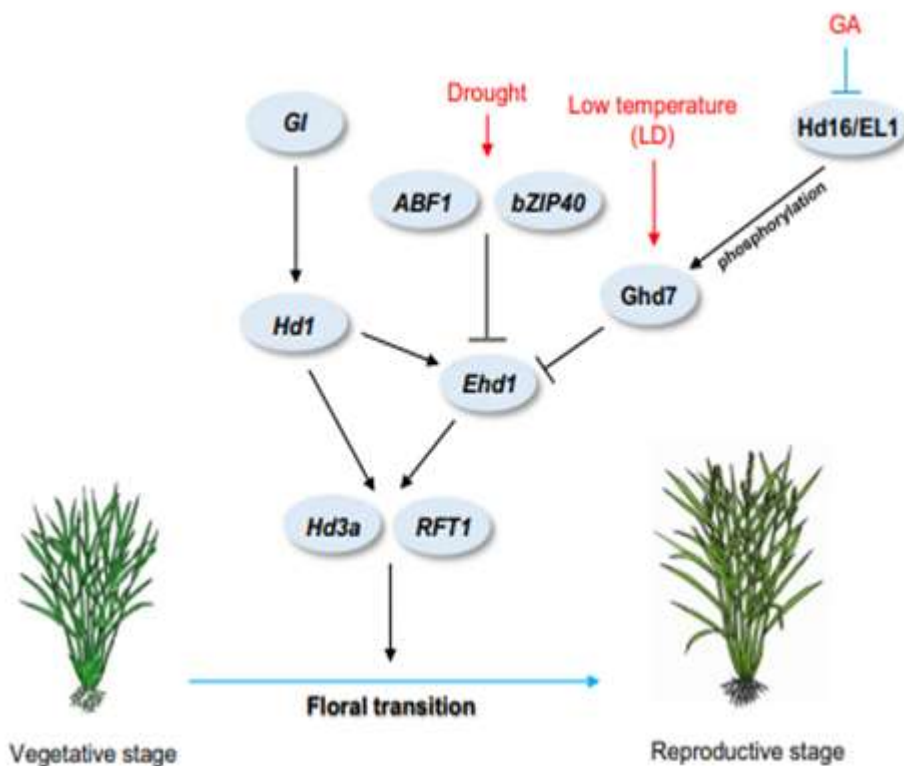


Figure 6. Overview of flowering time regulation by environmental factors in rice (Cho et al., 2017)

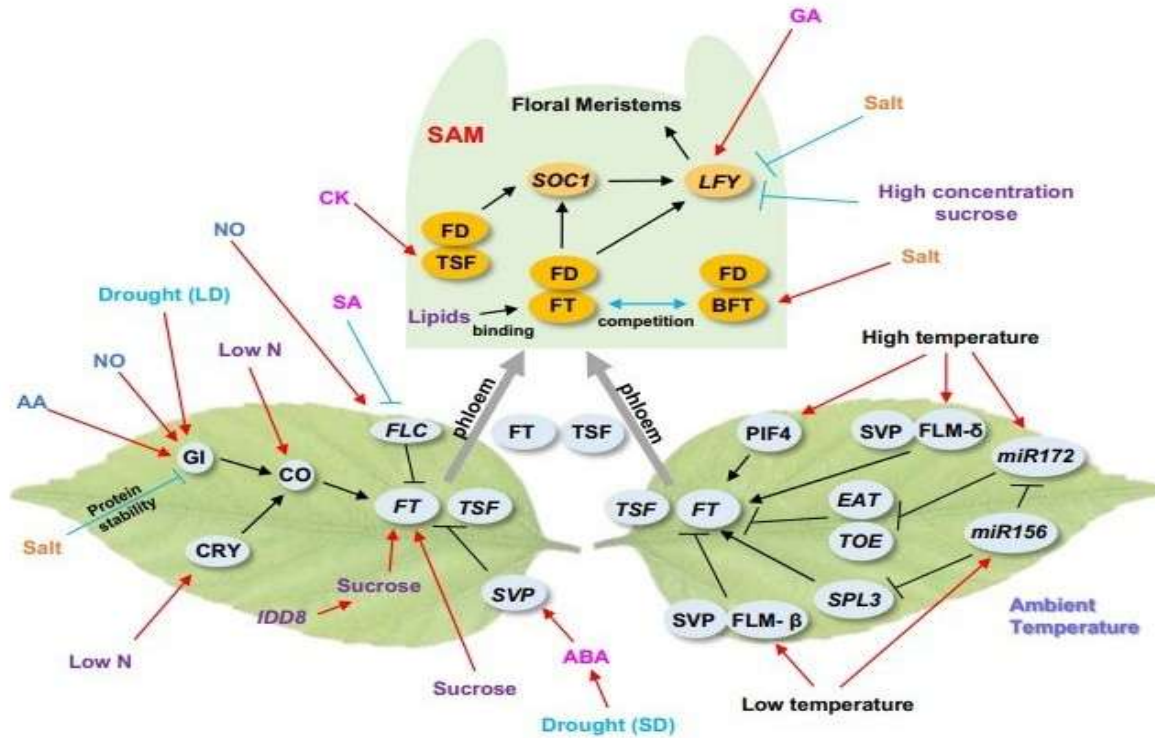


Figure 7. Various environmental factors and flowering time in *A. thaliana*.

2.5 Molecular and epigenetic Mechanisms of Floral Control

Gene regulatory networks that control vital floral organ developmental processes in plants are central to this process are the floral organ identity genes (figure 8 and 9), which encode members of the family of MADS-domain transcription factors (Thomas Jack, 2004, Stewart, 2016).

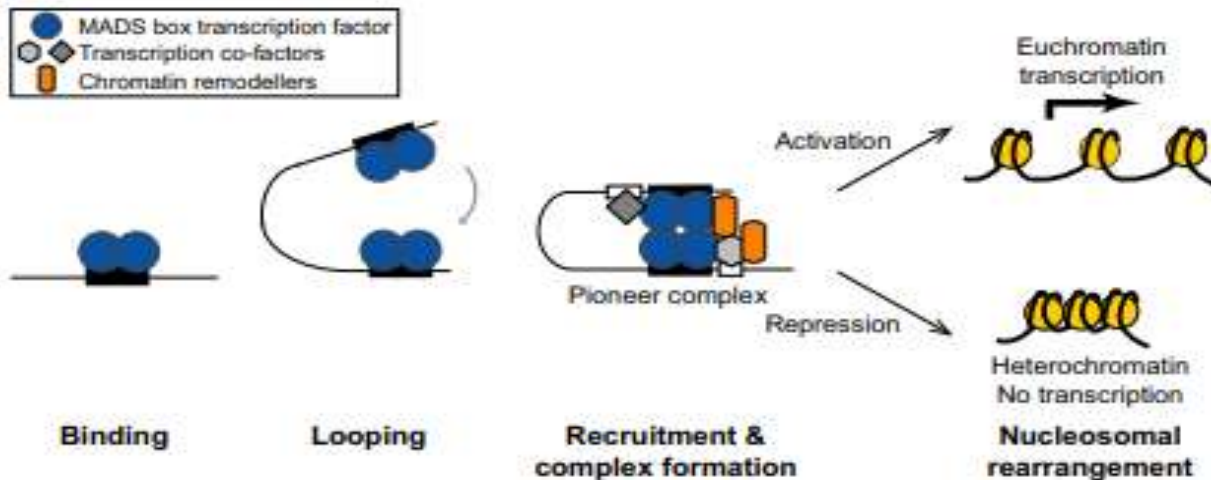
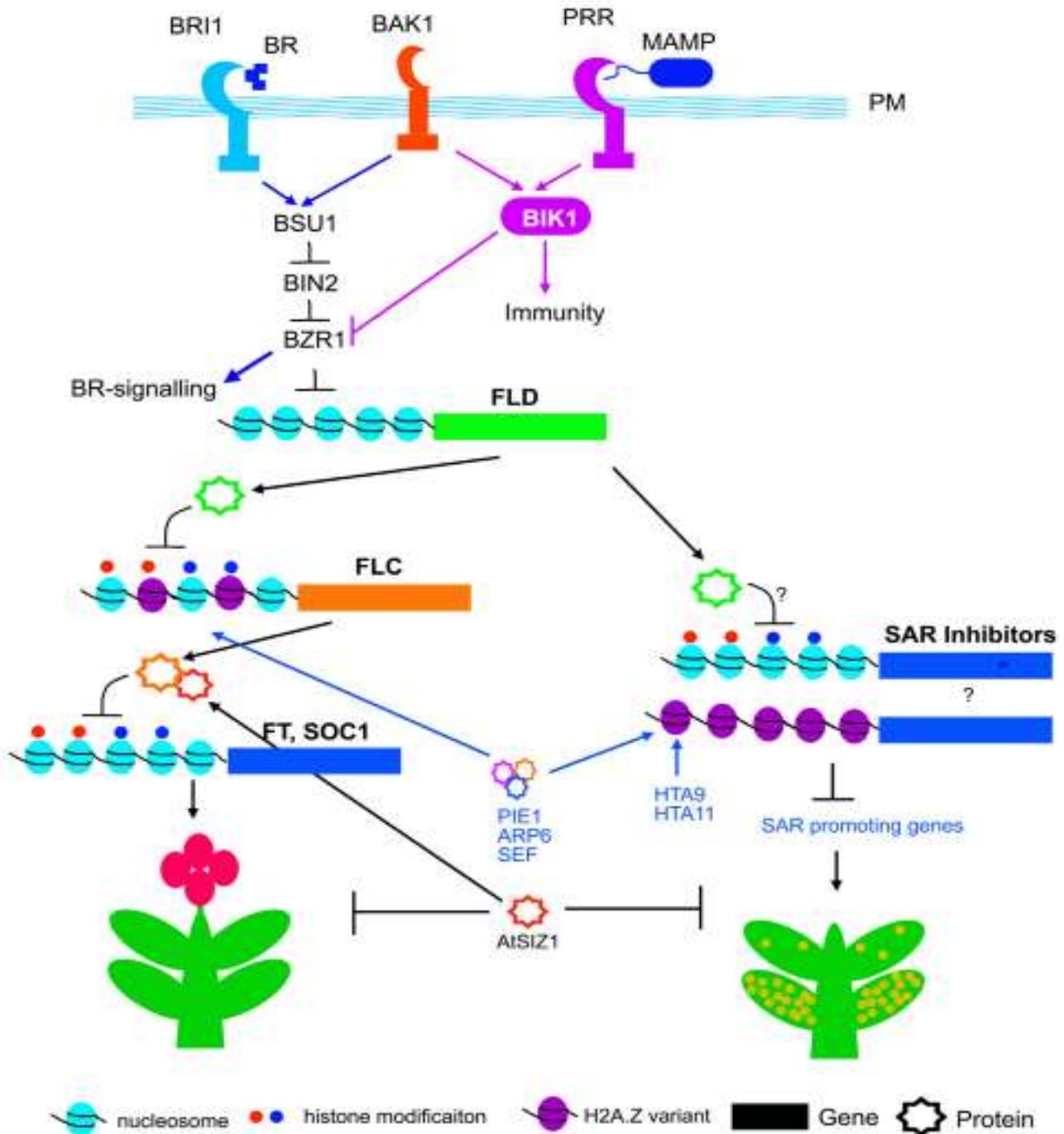


Figure 8. Working model for the activities of floral organ identity factor complexes. From left to right: two MADS-domain transcription factors dimerize and bind to a CARG-box sequence (black rectangles); through the interaction between two DNA-bound MADS-domain protein dimers, DNA looping occurs; the MADS-domain transcription factors recruit transcriptional co-factors to additional cis-regulatory elements (white rectangles) as well as chromatin remodellers possibly forming a 'pioneer complex'; the transcription factor complex can then alter chromatin accessibility, resulting in the formation of euchromatin or heterochromatin and in the activation and repression of gene expression, respectively (Thomas Jack, 2004, Stewart, 2016).



**Figure 9. Genetic and epigenetic control of flowering and SAR (Stewart, 2016).**

Plasma membrane (PM) resident BAK1 associates with both BRI1 and PRRs (pattern recognition receptors) which are required for BR and PTI signaling respectively (Stewart, 2016). BSU1 phosphatase is activated by BRI1 and BAK1. BSU1 dephosphorylates and inactivates BIN2, and thereby activates BZR1 and BR signaling (figure 9) (Stewart, 2016). BZR1 negatively regulates FLD expression. Activation of PTI activates BIK1, which suppresses BZR1 and thereby may promote expression of FLD. FLD transcriptionally suppresses FLC, the floral repressor. FLC protein is stabilized through interaction with AtSIZ1. AtSIZ1 functions as a negative regulator for

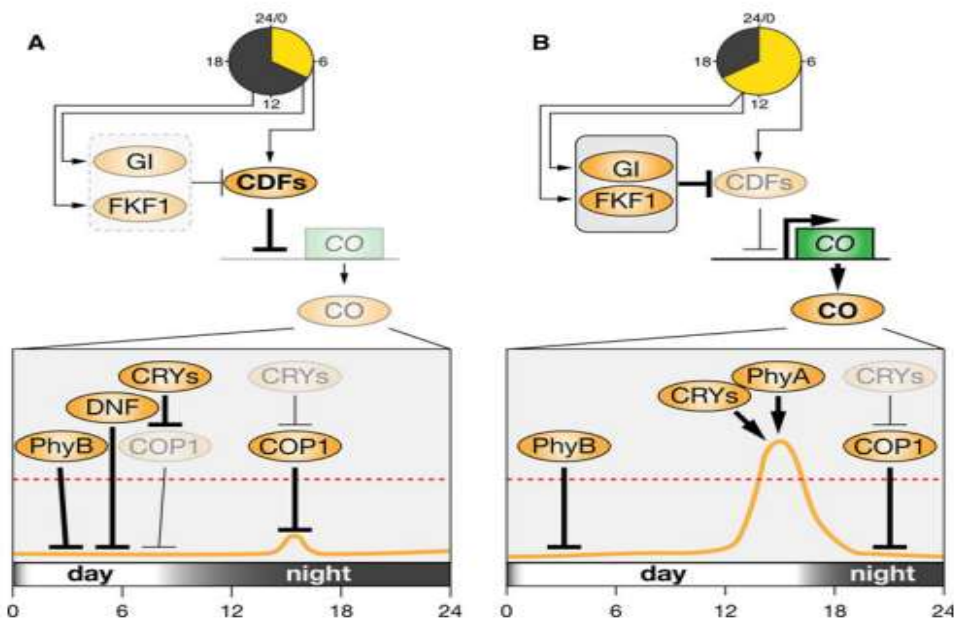
both flowering and SAR. The PIE1, ARP6 and SEF complex, and HTA9, HTA11 promote histone variant incorporation and biosynthesis, and thus promote transcription of FLC and unknown SAR suppressors (Bandy ZZ and Nandi AK, 2015; Stewart, 2016).

## 2.6 Molecular Mechanisms for Multiple Floral Inductive Pathway Control

Many long-day pathway genes encode proteins involved in light perception (e.g., PHYTOCHROME A and CRYPTOCHROME2) or components of the circadian

clock (e.g., GIGANTEA and ELF3) (Hayama et al., 2017). The light and clock components ultimately lead to the activation of CONSTANS (CO) as shown in figure 10

A & B). Overexpression of CO results in very early flowering (Yano et al., 2000).



**Figure 10. A, B Regulation of CONSTANS at a transcriptional and protein level.**

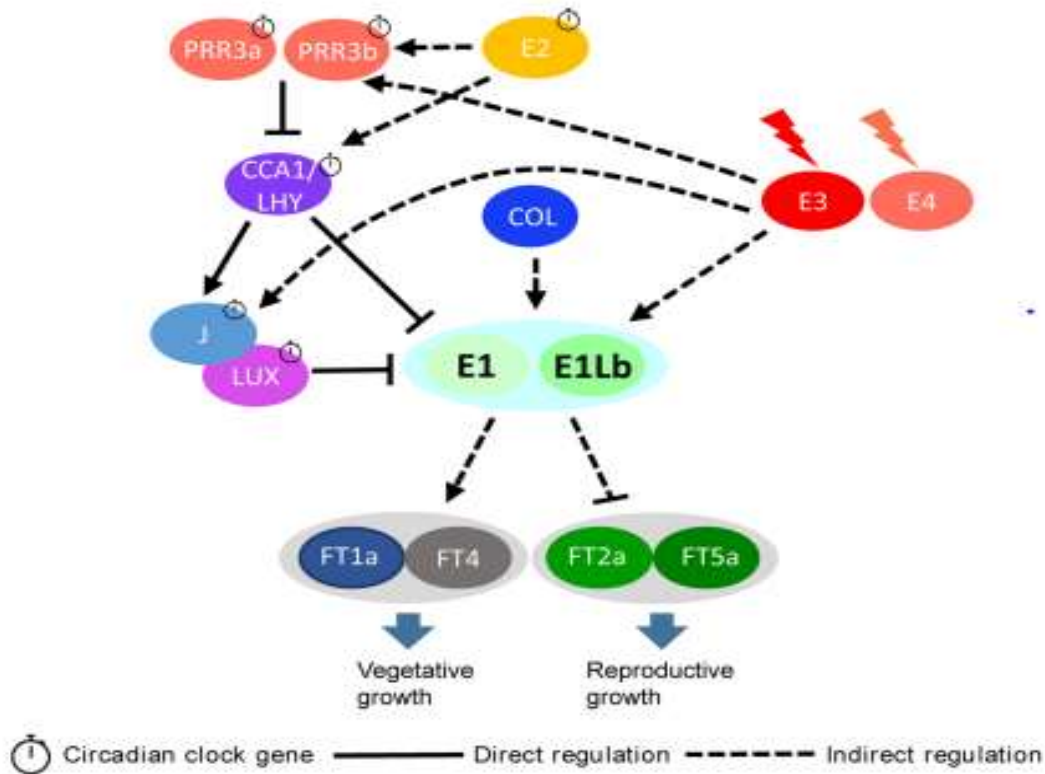
A) In short days, FKF1 and GI proteins peak at different times and hence are not able to efficiently repress CDF1, A transcriptional inhibitor of CO. CO protein levels are very low to start with in SD as indicated by the graph. PHYB plays a vital role in maintaining this low level of CO in the early hours of the day. Another protein, DNF, is important for maintaining low levels of CO between 4 and 7 h after dawn. Active CRY protein represses COP1, A ubiquitin ligase that marks CO for degradation. In the dark, the inactive CRY is no longer able to repress COP1 resulting in almost no CO protein being present. B) In long days, both FKF1 and GI peak at approximately 13 h after dawn, resulting in active repression of CDF1, and thereby, CO transcription. The protein levels are regulated by PHYB in the early morning hours, while active CRY and PHYA repress PHYB during the rest of the day (Hayama et al., 2017; Yano et al., 2000). Active CRY protein also binds to and inhibits transport of COP1 into the nucleus, hence preventing it from efficiently ubiquitinating the CO protein. Genes are represented in green, and proteins in orange. Dull colors represent inactive genes/ proteins, while bold colors indicate active genes/proteins. Dashed box shows weak complex formation, and the grey box shows efficient complex formation. The clock is a 24 h clock. The graph represents expression of CO protein through the day (SD/LD), with the day length represented on the x-axis (Hayama et al., 2017; Yano et al., 2000).

## 2.7 Molecular mechanisms for the photoperiodic and circadian regulation of flowering

### 2.7.1 Circadian clock genes control flowering time in soybean

Molecular mechanisms for the photoperiodic and circadian regulation of flowering in soybean (Lin et al., 2021). The circadian clock is an endogenous timekeeping mechanism that synchronizes biological processes with daily and seasonal cues (Greenham and McClung, 2015). In *Arabidopsis*, the circadian clock consists of two important components (figure 11): morning-expressed genes such as LHY/ CCA1 and

PRR7/9, and evening phased genes including TOC1, GI, and the evening complex genes (ELF4/ELF3/ LUX) (Lin et al., 2021; Oakenfull and Davis, 2017; Lu et al., 2020). Under 16 h/8 h LD cycles, PRR3a/PRR3b transcripts reach peak levels at zeitgeber time ZT8 and minimum levels at ZT0 (Li et al., 2020; Wang et al., 2020a), which represents a difference in phase of approximately 4 h relative to *Arabidopsis* PRR3 (Para et al., 2007). PRR3a/PRR3b bind to the promoter regions of four LHY/ CCA1 orthologs to inhibit their expression (Lu et al., 2020; Figure 1). LHY/ CCA1 orthologs bind directly to the promoter region of J to induce its expression (Li et al., 2020).

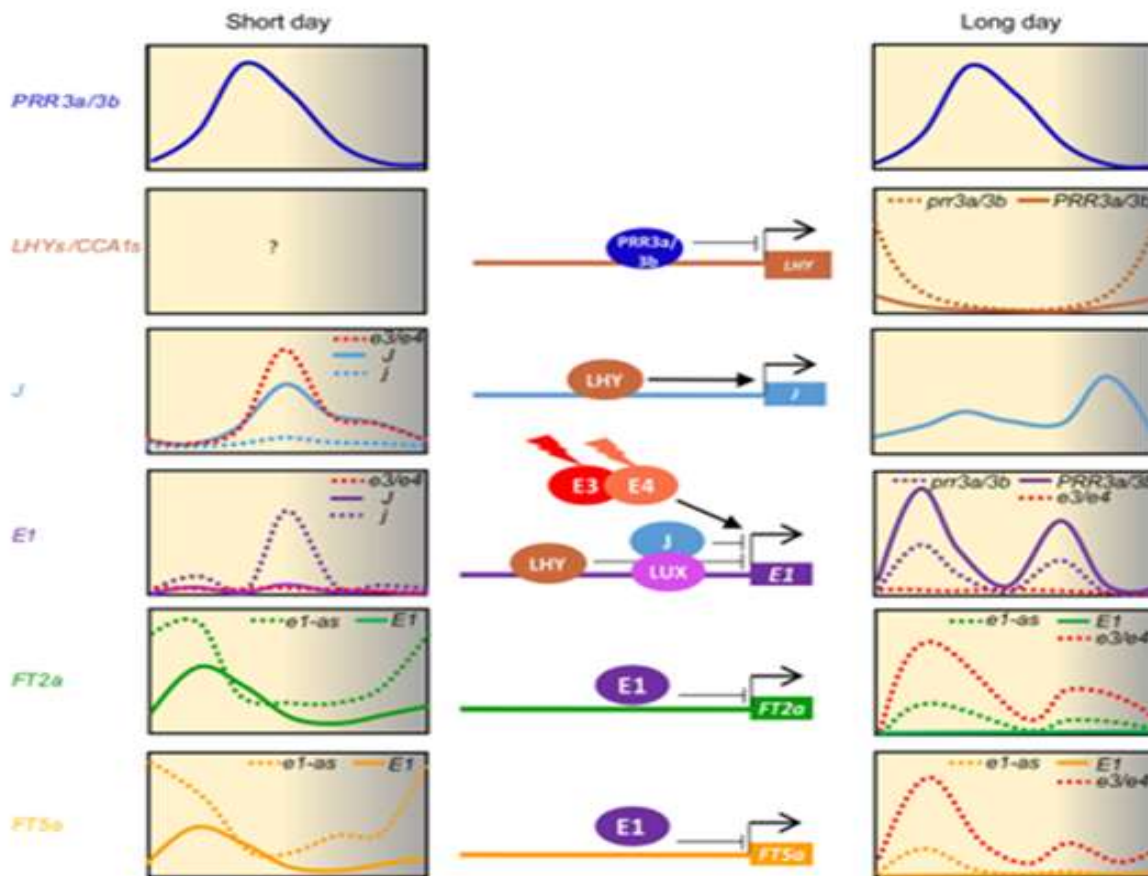


**Figure 11. Photoperiodic and circadian flowering regulatory mechanisms in soybean E2, E3 and E4 mediate flowering responses under high ratios of R and FR light, respectively.**

### 2.7.2. Photoperiodic regulation of flowering in soybean

Under LD, E3 and E4 induce the expression of E1 and E1Lb (figure 11). PRR3a (Gp11/Tof11) and PRR3b (qFT12-1/Gp12/Tof12) inhibit GmLHYs/GmCCA1s expression by binding to their promoters. GmLHYs/GmCCA1s bind to the E1 promoter to suppress its expression (Zhai et al., 2015). E1 inhibits the expression of flowering-inducing factors GmFT2a and GmFT5a and promotes the expression of flowering-inhibitory factors GmFT1a and GmFT4. As a result,

flowering is delayed under LD. Under SD, the functions of E3 and E4 are greatly weakened, and the induction of E1 also decreases. At the same time, J, whose expression is partially controlled by E3 and E4, inhibits the expression of E1. As a result, the expression level of E1 is very low in SD (figure 12) (Zhai et al., 2015; Romera et al., 2020; Lin et al., 2021). The inhibition of GmFT2a and GmFT5a by E1 is weakened, and the induction of GmFT1a and GmFT4 is weakened. Therefore, flowering is strongly promoted under this condition and other circadian clock genes such as PRR3a/b are also transcriptionally affected by the phytochromes E3 and E4 (Zhai et al., 2015; Romera et al., 2020; Lin et al., 2021).



**Figure 12. Photoperiodic regulation of FT in soybean PRR3a and PRR3b transcript abundance peaks in the middle of the day in both LD and SD.**

PRR3a and PRR3b bind to the promoters of GmLHYs/ GmCCA1s to repress their expression. The daily oscillation of GmLHYs/GmCCA1s transcript levels is opposite that of PRR3a and PRR3b under LD. GmLHYs/GmCCA1s bind to the promoter of E1 to inhibit its expression, and they also bind to the promoter of J to induce its expression. E3 and E4 induce E1 transcription, with peaks in the early morning and dusk in LD. Under SD, J (a component of the evening complex) binds to a LUX binding element in the E1 promoter to repress its expression. J transcript levels oscillate throughout the day with a peak at dusk in SD, but its function in LD remains unexplored. E1 protein levels during the day are still unclear, but E1 inhibits the peak expression of GmFT2a and GmFT5a in LD, likely by binding directly to their promoters. E1 has a weak effect in a dominant J background under SD (Greenham et al., 2015; Lin et al., 2021).

### 3. CONCLUSION AND PERSPECTIVES

This review provides insight into regulatory mechanisms for phytochrome-mediated light signaling pathway; and the roles of phytochromes and their downstream signaling components, molecular mechanisms light-perceiving photoreceptors and other positive and negative regulators of light signaling as well as interactions between these components during plant growth and development. Genetic and molecular evidence for the basis of light signaling mechanisms are discussed as well as the importance of light signaling in plant development. And also this review then aims to update knowledge on hormonal control of flowering, and integrate it into the entire flowering homeotic gene network.

Correct timing of the floral transition is crucial to ensure reproductive success. The timing of flowering is determined by endogenous genetic components as well as various environmental factors, such as day length, temperature, and stress. The genetic elements and molecular mechanisms that rule this process have been examined in the long-day-flowering plant *Arabidopsis thaliana* and short-day flowering rice (*Oryza sativa*) that specify the pattern, morphology and structure of flowers and their component organs. Research has advanced from the cloning of the first floral-homeotic genes towards understanding the combinatorial control of floral-organ identity at the molecular and biochemical levels.

Recent molecular genetic studies have begun to reveal the transcriptional regulatory cascades that control early patterning events during flower formation,

the dynamics of the gene-regulatory interactions, and the complex combinatorial mechanisms that create a distinct final floral architecture and form have been discussed. The floral transition is thus regulated by an intricate network of multiple genetically defined pathways have been identified that control flowering that perceive and respond to a variety of endogenous and environmental stimuli. The vernalization pathway refers to the acceleration of flowering on exposure to a long period of cold. The photoperiod pathway refers to regulation of flowering in response to day length and quality of light perceived. The gibberellin pathway refers to the requirement of gibberellic acid for normal flowering patterns. The autonomous pathway refers to endogenous (molecular) regulators that are independent of the photoperiod and vernalization pathways. Most recently, an endogenous pathway that adds plant age to the control of flowering time. The molecular mechanisms of these pathways have been studied extensively in *Arabidopsis thaliana* and several other flowering plants.

The gene regulatory network in the photomorphogenic control of photomorphogenesis and the control of flowering in model plants is reviewed. This review highlights:-

- Molecular mechanisms of the control of the flowering in plant and the process in controlling seedlings from germination to flowering.
- The gene network (homeotic MADS box genes) in the photoperiodic control of flowering.
- The hormonal control of flowering, and the roles of the florigen (FT) activation complex and DELLA protein.
- Epigenetic control of flowering

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