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Molecular mechanisms for the photoperiodic regulation of flowering in soybean[FA]

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ABSTRACT

Photoperiodic flowering is one of the most important factors affecting regional adaptation and yield in soybean (*Glycine max*). Plant adaptation to long-day conditions at higher latitudes requires early flowering and a reduction or loss of photoperiod sensitivity; adaptation to short-day conditions at lower latitudes involves delayed flowering, which prolongs vegetative growth for maximum yield potential. Due to the influence of numerous major loci and quantitative trait loci (QTLs), soybean has broad adaptability across latitudes. Forward genetic approaches have uncovered the molecular basis for several of these major maturity genes and QTLs. Moreover, the molecular characterization of orthologs of *Arabidopsis thaliana* flowering genes has enriched our understanding of the photoperiodic flowering pathway in soybean. Building on early insights into the importance of the photoreceptor phytochrome A, several circadian clock components have been integrated into the genetic network controlling flowering in soybean: E1, a repressor of *FLOWERING LOCUS T* orthologs, plays a central role in this network. Here, we provide an overview of recent progress in elucidating photoperiodic flowering in soybean, how it contributes to our fundamental understanding of flowering time control, and how this information could be used for molecular design and breeding of high-yielding soybean cultivars.

Keywords: molecular-designed breeding, photoperiodic flowering, soybean

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INTRODUCTION

As outlined in the Perspective (by Editor/s), our understanding of flowering time control in soybean (*Glycine max*) dates back to early experiments in the United States exploring the relationship between time of sowing and flowering. Garner and Allard (1920) recognized the importance of daylength and used a "dark chamber" to manipulate this parameter independently of temperature (Garner and Allard, 1920). This thorough analysis revealed the strong influence of daylength on soybean flowering and maturity and clearly demonstrated that soybean is a short-day (SD) plant. Of particular relevance to this review, they also characterized considerable variation in sensitivity to photoperiod among four different varieties of soybean they examined, and speculated on the relevance of this variation for adaptation.

Soybean is intrinsically sensitive to photoperiod

Photoperiod sensitivity is important for local adaptation and suitable cultivars will make full use of the growing season in the target region. However, this adaptation is generally limited to a narrow range of latitudes, primarily because it is based on specific sensitivity to photoperiod.

Soybean is a major source of vegetable protein and oil worldwide. Soybean was domesticated in a region between 30–45°N in China (Broich and Palmer, 1981; Hymowitz and Newell, 1981; Guo et al., 2010; Li et al., 2010; Han et al., 2016; Wang et al., 2016a) and is currently cultivated worldwide across a wide range of latitudes, from 53°N to 35°S (Zhang et al., 2020a). Reproductive phenology (i.e., the timing of flowering and maturity) is one of the most important considerations for maximizing soybean yields under these various photoperiod and climate conditions. For example, in high-latitude environments where the summer growing season is limited, soybean must flower under LD conditions in early summer and mature before the onset of frost in autumn. These conditions inherently delay flowering and maturity in soybean. The reduced length of the growth cycle has primarily been achieved via the reduction or loss of sensitivity to LD. At the other end of the latitudinal range, in the tropics, warm temperatures and short photoperiods strongly promote rapid flowering and early maturity in photoperiod-sensitive cultivars to such an extent that the vegetative phase is very short and yields are low. Thus, in these environments, a delay in flowering and extension of the reproductive phase are needed to generate and sustain sufficient vegetative growth and thus support higher yields.

The general challenge of regional adaptation is to some extent similar to that faced by other SD crops such as rice (*Oryza sativa*). However, the unique features of soybean as a member of the legume family and its taxonomic distance from rice and other prominent SD crops limit the utility of comparative approaches. Therefore, guiding the molecular design and breeding of new high-yielding soybean cultivars suitable for various growing environments will require a specific, molecular understanding of the photoperiodic regulation of flowering in soybean.

Diverse photoperiod responses confer broad adaptability

One hundred years after Garner and Allard (1920), we now know that the broad ecological adaptability of soybean is due to genetic variation at major gene loci and quantitative trait loci (QTLs) controlling flowering and maturity. Multiple naturally occurring variants at these loci have been targets of human selection and provide soybean with the flexibility needed to adapt to different areas and photoperiod conditions (Table S1). To date, forward genetic approaches have identified the major genetic loci *E1* to *E11* and *J*, and several QTLs, such as *Tof11/Gp11*, *Tof12/Gp1/qFT12-1*, and *qDTF-J*. Dominant alleles at *E1*, *E2*, *E3*, *E4*, *E7*, *E8*, and *E10* confer late flowering, whereas dominant alleles at *E6*, *E9*, *E11*, and *J* confer early flowering (Table 1). In addition to influencing time to flowering and maturation, most maturity genes and QTLs affect various agronomic traits that are dependent on reproductive development, such as grain yield and seed quality (Takahashi and Abe, 1999; Curtis et al., 2000; Yang et al., 2002; Cober and Morrison, 2010). Moreover, reverse-genetic approaches using the soybean genome sequence have uncovered several orthologs of *Arabidopsis* flowering genes (Schmutz et al., 2010; Jung et al., 2012; Li et al., 2013; Fan et al., 2014; Wu et al., 2014; Cao et al., 2015; Marcolino-Gomes et al., 2017; Zhang et al., 2017; Wu et al., 2019). The findings obtained in these studies have paved the way for the identification of the flowering regulatory networks in soybean that enable this crop to adapt to a wide range of photoperiods.

CLASSICAL FLOWERING LOCI AND THEIR MOLECULAR IDENTITIES

E1 and its homeologs

E1 was the first classical soybean maturity locus to be identified and is arguably the most important, with large effects on flowering and maturation and crucial roles in regulating photoperiod sensitivity (Upadhyay et al., 1994; Xu et al., 2015; Han et al., 2019). *E1* encodes a 20.3 kDa B3 domain protein that localizes to the nucleus and is a putative transcription factor that inhibits flowering (Xia et al., 2012a). E1 is distantly related to members of the *Arabidopsis* TEMPRANILLO protein family, which also contain a B3 domain (Castillejo and Pelaz, 2008; Matías-Hernández et al., 2014).

E1 is mainly expressed in leaves and is expressed at very low levels in other tissues (Xia et al., 2012a). *E1* transcript levels peak in the early morning and at dusk under LD but are strongly suppressed under SD and in the photoperiod-insensitive *e3 e4* genotype under LD (Xia et al., 2012a; Xu et al., 2015). *E1* expression is strongly dependent on light, as it requires light at the proper time for induction; the replacement of the light phase with a dark period beginning at 6 h before dusk in LD (18-h light/6-h dark) abolishes the second peak of expression at dusk, as well as the morning peak in the next daily cycle (Xu et al., 2015).

Several hypomorphic and loss-of-function alleles of *E1* have been identified (Cao et al., 2017). The most common allele, the *e1-as* allele (originally designated *e1*), carries a mutation in the nuclear localization signal that impairs its import into the nucleus, thereby conferring earlier flowering (Xia et al., 2012a).

E1 has two homeologs in soybean, *E1La* and *E1Lb* (Xia et al., 2012a; Xu et al., 2015), with expression patterns similar to that of *E1* under both LD and SD. Both genes function as inhibitors of flowering, like *E1*, as revealed by virus-induced gene silencing (Xu et al., 2015). Furthermore, a single-base deletion in the *E1Lb* coding sequence confers earlier flowering under both red (R) light and far-red (FR) light-enriched LD, independently of *E1* (Zhu et al., 2019).

E1 is legume-specific, but the function of its orthologs does not appear to be tightly conserved (Zhang et al., 2016). The overexpression of *E1* in soybean represses the expression of orthologs of the florigen gene *FLOWERING LOCUS T* (*FT*) and inhibits flowering (Xia et al., 2012a; Zhang et al., 2016). Ectopic expression of the E1 ortholog from

Table 1. Genes involved in photoperiodic flowering in soybean

Locus	Gene	Accession number	Function	Reference
E1	*E1*	Glyma.06G207800	Inhibits flowering	Xia et al., 2012a
	E1La	Glyma.04G156400	Inhibits flowering	Xu et al., 2015
	E1Lb	Glyma.04G143300	Inhibits flowering	Watanabe et al., 2011; Xu et al., 2015
E2	*GmGI*	Glyma.10G221500	Inhibits flowering	Watanabe et al., 2011
E3	*GmphyA3*	Glyma.19G224200	Inhibits flowering	Watanabe et al., 2009
E4	*GmphyA2*	Glyma.20G090000	Inhibits flowering	Liu et al., 2008a
	GmphyA1	Glyma.10G141400	Unknown	Liu et al., 2008a
E5	None[a]			Dissanayaka et al., 2016
E6	Unknown		Promotes flowering	Cober, 2011
E7	Unknown		Inhibits flowering	Cober and Voldeng, 2001b
E8	Unknown		Inhibits flowering	Cober et al., 2010
E9	*GmFT2a*	Glyma.16G150700	Promotes flowering	Kong et al., 2010, 2014; Zhao et al., 2016
E10	*GmFT4*	Glyma.08G363100	Inhibits flowering	Zhai et al., 2014; Samanfar et al., 2017
J	*GmELF3*	Glyma.04G050200	Promotes flowering	Lu et al., 2017; Yue et al., 2017
	GmFT5a	Gyma.16G044100	Promotes flowering	Kong et al., 2010; Fan et al., 2014
	GmFT1a	Glyma.18G298900	Inhibits flowering	Guo et al., 2015
	GmFT1b	Glyma.18G299000	Inhibits flowering[b]	Guo et al., 2015
	GmFT2b	Glyma.16G151000	Promotes flowering	Fan et al., 2014
	GmFT2c	Glyma.02G069500	Pseudogene	Wu et al., 2017
	GmFT3a	Glyma.16G044200	Promotes flowering	Fan et al., 2014
	GmFT3b	Glyma.19G108100	Promotes flowering	Fan et al., 2014
	GmFT5b	Glyma.19G108200	Promotes flowering	Fan et al., 2014
	GmFT6	Glyma.08G363200	Inhibits flowering[b]	Wang et al., 2015
E11	Unknown		Promotes flowering	Wang et al., 2019
Tof1111	*PRR3a*	Glyma.U034500	Inhibits flowering	Lu et al., 2017
Tof12	*PRR3b*	Glyma.12G073900	Inhibits flowering	Lu et al., 2017
	LHY1a	Glyma.16G017400	Promotes flowering[c]	Lu et al., 2017
	LHY1b	Glyma.07G048500	Promotes flowering[c]	Lu et al., 2017
	LHY2a	Glyma.19G260900	Promotes flowering[c]	Lu et al., 2017
	LHY2b	Glyma.03G261800	Promotes flowering[c]	Lu et al., 2017

[a]Mapping by Dissanayaka et al. (2016) suggested that "A unique E5 gene may not exist."; [b]Speculation based on existing data; [c]Four LHYs together serve as a flowering inducer based on genetic data; however, only one or fewer than four of these LHYs might function in this process

common bean (*Phaseolus vulgaris*) inhibited flowering in soybean, whereas the *Medicago truncatula* ortholog did not affect flowering (Zhang et al., 2016).

E2 and its homeologs

E2 encodes a soybean ortholog of *Arabidopsis* GIGANTEA (GmGIa), which plays multiple roles in the circadian clock and flowering (Watanabe et al., 2011). The functional E2 allele encodes a full-length protein of 1170 amino acids, whereas the main natural variant, the recessive *e2* allele, encodes a truncated protein of 521 amino acids. The *e2* allele and a loss-of-function mutant from the TILLING population also encoding a truncated protein show early flowering phenotypes (Watanabe et al., 2011). When overexpressed under the control of the *Cauliflower mosaic virus* (CaMV) 35S promoter, *E2* failed to complement the delayed flowering phenotype of the *Arabidopsis gi* mutant, and it delayed the flowering of wild-type (Col-0) *Arabidopsis* plants, whereas the *e2* allele partially rescued the *gi* phenotype but had no effect on the flowering of Col-0 (Wang et al., 2016b). These findings suggest that the functions of E2 differ from those of GI in *Arabidopsis*.

E2 also differs from AtGI in terms of its interaction with the micro RNA miR172. In *Arabidopsis*, GI promotes the transcription of pre-miR172 (Jung et al., 2007). However, the overexpression of *E2* did not lead to the upregulation of pre-miR172a. Instead, it promoted the maturation of miR172a via the increased expression of soybean homologs of *DICER-LIKE 1* and *SERRATE*, encoding key enzymes in the miRNA synthesis pathway (Wang et al., 2016c). Like *E1*, *E2* has two homeologs in the soybean genome, *GmGIb* (*GmGI1*), and *GmGI2* (Watanabe et al., 2011; Li et al., 2013), the former of which has two alternative splicing forms (Li et al., 2013). These three *GI* homeologs encode nuclear proteins (Li et al., 2013). In a yeast two-hybrid assay, the two soybean orthologs of *Arabidopsis* FLAVIN-BINDING, KELCH REPEAT, F-BOX1 (FKF1), GmFKF1 and GmFKF2, bound to GmGI1 (GIb) and GmGI2 and to the CYCLING DOF FACTOR 1 (CDF1)

ortholog GmCDF1, but not to E2 (GI3/GIa) (Li et al., 2013). The findings suggest that E2 might play a unique role in controlling flowering in soybean. In a free-running circadian rhythm experiment involving release from LD or SD into constant light, *GmGI2* showed a persistent rhythmic expression pattern under entraining and constant light conditions, whereas *E2* and *GmGI1* showed irregular rhythms, with the peaks moving forward or backward, suggesting these genes are controlled by distinct regulatory systems (Li et al., 2013).

E3, E4, and their homologs

E3 and *E4* both encode homologs of the *Arabidopsis* photoreceptor phytochrome A (phyA), i.e., GmphyA3 and GmphyA2, respectively (Liu et al., 2008a; Watanabe et al., 2009). *E3* and *E4* play crucial roles in regulating photoperiodic flowering under both natural daylength conditions and artificially induced LD conditions (Cober et al., 1996a). The *E3* and *E4* loci were initially characterized in experiments examining flowering in response to artificial LD, where natural daylength was extended to 20 h using light sources enriched in R or FR (Cober et al., 1996b). The response to R-enriched LD was influenced only by *E3*, whereas *E4* was needed for the response to FR-rich LD, which still occurred in the absence of *E3* (i.e., in the *e3* background). Therefore, the two phyA proteins together confer sensitivity to LD, particularly to FR-enriched LD (Cober et al., 1996b). In natural environments, *E3* has large effects on flowering in a wide range of latitudes, whereas the effect of *E4* is confined to higher latitude regions (Lu et al., 2015). Together, these observations point to a degree of functional redundancy, but also specificity, in signal transduction by light.

The combined activity of E3 and E4 in mediating the flowering response to a wide range of R:FR ratios contrasts with phyA in *Arabidopsis*, which is mainly responsible for flowering responses to FR-rich day extensions (Johnson et al., 1994; Song et al., 2018). There is also evidence that *e3 e4* plants have residual responsiveness to LD, particularly under FR-rich day extensions and in the presence of functional E1 (Cober et al., 1996a, 1996b; Cober and Voldeng, 2001a), pointing to possible contributions from other phytochrome photoreceptors. Both *E4* and *E3* have homeologs in the soybean genome (*GmphyA1* and *GmphyA4*, respectively). The delayed flowering observed in the *E1/e3/e4* genotype under FR-rich LD is most likely attributed to *GmPHYA1* (Cober et al., 1996a; Cober and Morrison, 2010; Watanabe et al., 2012). Interestingly, *GmPHYA1* has lower nucleotide diversity at nonsynonymous sites than *E4*, suggesting it might have a more critical function (Tsubokura et al., 2013), perhaps functioning with *E4* to regulate photomorphogenesis in response to FR (Liu et al., 2008a). *GmphyA4* is a pseudogene in the Williams 82 reference genome, whereas wild soybean accessions contain the functional form of this gene (Li et al., 2014). However, it is not yet known whether this difference influences flowering time. To date, there are no reports on their expression profiles at the gene or protein level, and how they regulate *E1* remains unknown.

E6 and J confer the long-juvenile trait

In contrast to the *E1-E4* loci, *E6* and *J* are primarily involved in promoting flowering under SD. Recessive *e6* or *j* alleles inhibit flowering and prolong both the vegetative and reproductive growth periods, a phenotype known as "long-juvenile," which is an important adaptive trait at low latitudes (Ray et al., 1995; Bonato and Vello, 1999). In a comparison of isolines, the delaying effect of *e6* was only evident under daylengths shorter than 14 h, with maximum effects observed at daylengths of 12 h (Cober, 2011). The *J* gene is a homolog of *Arabidopsis EARLY FLOWERING 3*, as revealed by forward genetics, QTL mapping, map-based cloning, and transgenic complementation (Lu et al., 2017; Yue et al., 2017). Functional analysis of *J* using transgenic and conventional near-isogenic lines revealed a role for this gene in promoting flowering not only under SD but also under daylengths of 14 h (Lu et al., 2017). The molecular basis of *E6* has not yet been determined, although genetic analysis indicated that *E6* is tightly linked to *J* (Li et al., 2017).

E7 and E8

The *E7* and *E8* loci were characterized through genetic analysis of variation in the early-flowering *e1-as/e3/e4* genetic background (Cober and Voldeng, 2001b; Cober et al., 2010). However, their molecular identities are not yet known. Recessive alleles at both loci conferred earlier flowering and maturity under FR-enriched LD or natural daylengths in Ottawa, Canada (45.42°N). *E7* is located on chromosome (Chr) 6 approximately 6 cM from *E1* (Cober and Voldeng, 2001a; Molnar et al., 2003), a position that clearly excludes *E1* itself, the two *E1L* genes (Chr4), and *GmphyA1* (Chr10) as candidates. Recombinant inbred lines (RILs) generated from a cross between Suinong 14 and Enrei, which both have the *E1/e2/e3/E4* genotype, segregated for a major flowering/maturity QTL in the flanking region of *E1–E7* on Chr6, likely corresponding to *E7* (Kong et al., 2018). *E8* is located on Chr4 near the two *E1L* genes (Cober et al., 2010) and was likely detected as a major flowering/maturity QTL in RILs generated from a cross between Dongnong 50 and Williams 82, both with the *e1-as/E2/E3/E4* genotype (Kong et al., 2018), and in other studies (Cheng et al., 2011; Watanabe et al., 2017). Therefore, the allelic effects of the *E7* and *E8* loci may not only be relevant in early flowering genetic backgrounds, but they may also contribute to the control of flowering time and maturity in combination with various maturity genotypes.

E9, E10, and other FT homologs

More recently, several other flowering time loci were shown to encode members of the well-known FT (florigen) protein

family. These FT homologs belong to the phosphatidylethanolamine binding protein (PEBP) family (Wang et al., 2015) and serve as major points of integration in flowering time control (Takeshima et al., 2016; Jiang et al., 2019; Ogiso-Tanaka et al., 2019; Sun et al., 2019). Many *FT* genes are expressed in leaves under flower-inducing conditions. FT proteins are thought to be transported from leaves to shoots or lateral apical meristems through the phloem, where they induce the development of floral meristems (Golembeski and Imaizumi, 2015). Soybean contains 12 *FT*-like genes in six homeologous pairs: *GmFT1a/b*, *GmFT2a/b*, *GmFT2c/d*, *GmFT3a/b*, *GmFT5a/b*, and *GmFT4/6*. Among these, *GmFT2d* is nonfunctional in both cultivated and wild soybeans due to a structural genomic rearrangement (Wu et al., 2017), and *GmFT2c* is a transposon-disrupted pseudogene in the Williams 82 reference genome and in several landraces. Wild soybean accessions carry the functional *GmFT2c* allele, and evidence from interspecific populations indicates that this allele can promote flowering (Li et al., 2014; Wu et al., 2017). Of the ten other *FT* genes, four (*GmFT2b*, *GmFT4*, *GmFT5b*, and *GmFT6*) are expressed at very low levels in trifoliate leaves under inductive SD conditions (Kong et al., 2010).

When ectopically expressed under the control of the CaMV 35S promoter, *GmFT2a/b*, *GmFT3a/b*, and *GmFT5a/b* all promoted flowering in *Arabidopsis* Col-0, suggesting they function as floral inducers (Kong et al., 2010; Thakare et al., 2011; Fan et al., 2014; Guo et al., 2015). Of these six genes, *GmFT2a* and *GmFT5a* appear to be the major functional *FT* family members, as they were strongly induced under SD (Kong et al., 2010), caused early flowering when overexpressed (Sun et al., 2011; Nan et al, 2014; Guo et al., 2015), and delayed flowering when downregulated by RNA interference (RNAi) (Guo et al., 2015). *GmFT2a* and *GmFT5a* have also been detected in genetic analyses of natural variation, with *GmFT2a* identified as the causal gene for the *E9* locus (Kong et al., 2014; Zhao et al., 2016) and *GmFT5a* underlying *qDFT-J*, a QTL for the long-juvenile trait on Chr16 (Takeshima et al., 2016).

Analysis of CRISPR/Cas9-generated loss-of-function mutants suggested these genes play distinct roles in floral induction, with a delay observed primarily under SD for *GmFT2a* mutants and LD for *GmFT5a* mutants (Cai et al., 2018, 2020). These distinct functions might reflect their different interactions with homologs of the *Arabidopsis* bZIP transcription factor FD (Takeshima et al., 2019). Both FT2a and FT5a interact with FD-like 19 (FDL19), which upregulates the expression of soybean *APETALA1* orthologs by binding to their promoters (Nan et al., 2014). In addition, GmFT5a, but not GmFT2a, interacts with FDL6, which inhibits the indeterminacy of the primary inflorescence (i.e. promotes shoot determinacy) by upregulating *APETALA1* and *FRUITFULL* orthologs (Takeshima et al., 2019; Chen et al., 2020).

In contrast to most florigen proteins, GmFT1a and GmFT4 are inhibitors of flowering. Both *GmFT1a* and *GmFT4* are expressed at higher levels under LD vs. SD and are induced rather than repressed by E1 (Zhai et al., 2014; Liu et al., 2018a). Overexpression of *GmFT1a* delayed flowering in soybean (Liu et al., 2018a), and *GmFT4* delayed flowering when ectopically expressed in *Arabidopsis* (Zhai et al., 2014). A mapping study suggested that *GmFT4* may be responsible for *E10* (Samanfar et al., 2017), which delays flowering. *GmFT1b* exhibits a similar expression pattern to *GmFT1a* and *GmFT4* and might also inhibit flowering (Liu et al., 2018a). When ectopically expressed in *Arabidopsis*, *GmFT6* did not affect flowering time (Fan et al., 2014). However, when expressed under the control of the *Arabidopsis TERMINAL FLOWER1* (*TFL1*) promoter, *GmFT6* fully rescued the early flowering phenotype of the *Arabidopsis tfl1-1* mutant, indicating that GmFT6, like TFL1, inhibits flowing (Wang et al., 2015; Wickland and Hanzawa, 2015).

E11

E11 is a recently identified locus on Chr7 that affects flowering time and maturity (Wang et al., 2019). A mapping study revealed that the most likely candidate gene for *E11* (Glyma.07G48500) is one of the four soybean homologs of *Arabidopsis CIRCADIAN CLOCK ASSOCIATED 1* (*CCA1*) and *LATE ELONGATED HYPOCOTYL* (*LHY*) (Wang et al., 2019). Indeed, a quadruple knockout mutant generated by CRISPR-Cas9 showed significantly delayed flowering and modified plant height (Cheng et al., 2019; Lu et al., 2020; Wang et al., 2020b).

The Tof11 and Tof12 loci are PSEUDO-RESPONSE REGULATOR homologs

Two QTLs controlling flowering time and maturity were recently identified by genetic analysis of the progeny of crosses between improved cultivars and landraces or wild soybean or via genome-wide association analysis (GWAS) (Liu et al., 2018b, 2018c; Li et al., 2019b, 2020; Gong, 2020; Lu et al., 2020; Wang et al., 2020a). These QTLs, *Gp11/Tof11* and *qFT12-1/Gp12/Tof12*, are located in homeologous genomic regions on Chr11 and 12 and are orthologs of *Arabidopsis PSEUDO-RESPONSE REGULATOR* (*PRR*) *3*, *GmPRR3a*, and *GmPRR3b* (Li et al., 2019a, 2019b, 2020; Lu et al., 2020). GmPRR3a and GmPRR3b share 41% and 61% amino acid sequence identity with *Arabidopsis* PRR3, respectively, and form a closely related but distinct clade from the *Arabidopsis* PRR7 and monocot PRR37 clades, as revealed by phylogenetic analysis (Li et al., 2019b).

The wild-type GmPRR3a and GmPRR3b proteins contain a pseudo-receiver domain, EAR motif, and CCT domain, whereas those from improved cultivars are mutant proteins that lack the CCT domain due to a single-base deletion and frame-shift (GmPRR3a) or a nonsense mutation (GmPRR3b) (Li et al., 2019b, 2020; Lu et al., 2020). GmPRR3 proteins contain two nuclear localization signals (NLS) (Li et al., 2019b, 2020), one of which is located in the CCT domain. Analysis of GmPRR3b proteins fused to the yellow fluorescent protein (YFP) reporter indicated that a mutant protein

lacking the CCT domain accumulated in the nuclei of *Arabidopsis* protoplasts at lower levels than the wild type (Li et al., 2019b, 2020). This finding confirms the partial loss of function of the major *PRR3b* allele in cultivated soybean, and it suggests that the two NLS play an additive role in the nuclear localization of PRR3 proteins (Li et al., 2020).

Promoter-binding assays using YFP-GmPRR3b fusions in *Arabidopsis* protoplasts demonstrated that both the wild-type and mutant forms of PRR3b directly repress the expression of a reporter gene under the control of the *GmLHY* promoter by binding to promoter regions containing G-box, TBS, and TGTG elements (Li et al., 2020; Lu et al., 2020). In addition, overexpressing *GmPRR3a* and *GmPRR3b* resulted in increased *E1* expression and reduced *GmFT2a* and *GmFT5a* expression (Li et al., 2020; Lu et al., 2020). This positive effect of PRR3 proteins on *E1* expression is indirect and is mediated by their negative effects on the expression of *LHY* genes, which are themselves direct negative regulators of *E1* expression (Lu et al., 2020).

ADAPTATION OF SOYBEAN TO DIFFERENT LATITUDES

Flowering genes involved in the adaptation of soybean to high latitudes

At high latitudes, the suitable growing season for soybean is late summer to early autumn, when photoperiods are long. Therefore, the adaptation of soybean plants to high latitudes requires them to be able to flower and mature early in LD. This has mainly been achieved through the accumulation of alleles that reduce photoperiod sensitivity. Understanding the distribution of such alleles and their degree of fixation provides insight into their importance with respect to location and time. Irrespective of their origins, virtually all improved soybean cultivars carry *tof12*, suggesting that this allele experienced strong artificial selection during domestication and early diversification (Li et al., 2019b, 2020; Lu et al., 2020; Wang et al., 2020a). The mutant alleles *GmPRR3a* (*tof11*) and *GmGIa* (*e2)* are also predominant in cultivars grown in northern China and in photoperiod-insensitive cultivars (Xu et al., 2013; Wang et al., 2016b; Lu et al., 2020). These three alleles may have provided the basis for the initial improvement of soybean production in the soybean domestication center and the early stages of the northward expansion of soybean cultivation.

The maturity loci *E1*, *E3*, and *E4* also play major roles in modifying photoperiod sensitivity and adaptation to high latitudes (Cober et al., 1996a; Abe et al., 2003; Liu and Abe 2010; Xu et al., 2013). With respect to these three loci, the most common genotype in photoperiod-insensitive cultivars is the double recessive *e3 e4* genotype; 70% of the cultivars from East Asia possess this genotype (Xu et al., 2013). The second largest group is genotypes carrying *e1* and either *e3* or *e4* alleles (i.e., *e1 e3 E4* or *e1 E3 e4*). Loss-of-function alleles at *E1* alone reduce but do not eliminate photoperiod insensitivity, which likely reflects the functional redundancy of *E1L* genes (Cober et al., 1996a, 1996b; Xu et al., 2013). This conclusion is supported by the finding that RNAi-mediated suppression of *E1La* and *E1Lb* abolished the residual flowering response of the null *e1-nl* mutant to a night-break (Xu et al., 2015). The third group of insensitive accessions carry a partial loss-of-function allele of *e1* (*e1-as*) together with *e3* and *E4*, but they also carry a loss-of-function allele at *E1Lb* (Zhu et al., 2019) or a hypermorphic allele at *qDTF-J*(Chr16)/*GmFT5a* conferring increased expression of *GmFT5a* (Takeshima et al., 2016). These two alleles presumably counteract the repressive effect of *E4* by modifying the downstream pathway, reducing the residual E1-like activity or directly increasing *FT5a* expression. Therefore, the adaptation of soybean to longer daylengths at high latitude has been conferred through the accumulation of loss-of-function alleles at the *E3* and *E4* (*PHYA*) and *E1*/*E1L* loci. The functions of GmphyA1 and E1La, which are homeologs of E4 and E1/E1Lb, respectively, have not yet been directly examined and remain poorly understood, although this issue could be addressed in the future via CRISPR/Cas9 gene editing.

Flowering genes involved in the adaptation of soybean to low latitudes

Brazil is the world's second-largest soybean producer. Prior to 1960, Brazilian soybean cultivars were imported from the United States, and the cultivation areas were limited to latitudes above 22°S (Neumaier and James, 1993). This limitation was overcome by the introduction of the long juvenile (LJ) trait in the 1970s, allowing soybean production to expand to lower latitude (tropical) areas (Neumaier and James, 1993; Carpentieri-Pípolo et al., 2002). The LJ trait features a prolonged vegetative growth period under SD, allowing sufficient vegetative biomass to be produced to support a larger grain yield (Carpentieri-Pípolo et al., 2002).

Historically, the LJ trait has not received as much attention as early flowering, but a growing number of loci that contribute to it are being defined, including *J* and *E6*, and more recently described QTLs such as *LJ16.1* and *LJ 16.2* (Bonato and Vello, 1999; Li et al., 2017; Lu et al., 2017; Fang et al., 2019). The *J* gene encodes an ELF3 ortholog that represses *E1* expression under SD by binding to its promoter. In cultivars with loss-of-function *j* alleles, *E1* expression is released from this inhibition, allowing E1 to delay flowering and maturation (Lu et al., 2017), resulting in yield increases of 30%–50% (Lu et al., 2017). The expression of *J* is repressed by E3 and E4 under SD (Lu et al., 2017), indicating that the action of *PHYA* genes is not restricted to LD conditions. J binds to a LUX binding element in the *E1* promoter, pointing to the involvement of the circadian clock evening complex (ELF4-ELF3-LUX) (Nusinow et al., 2011) in controlling *E1* expression under SD. This implies that reduced functions of the evening complex components ELF4 and LUX could contribute to the LJ trait, an idea that requires further investigation. However, consistent with this possibility, Lu et al. (2017) detected an allele with a 12-bp insertion in the

C-terminal domain of a *LUX* gene (*GmLUX2*) in 11 of 125 low-latitude accessions carrying a functional *J* allele.

It is also likely that the LJ phenotype can be generated by modifying genes downstream of the evening complex. For example, *J* is dependent on its direct target, *E1* (Lu et al., 2017), indicating that a functional E1 is required for adaptation to lower latitudes. Indeed, a recent study demonstrated that after *J*, *E1* has the next most important effect on time to maturity in tropical environments (Miranda et al., 2020). Finally, *GmFT2a* may also have been a target for delayed flowering, as a non-synonymous amino acid substitution in exon 4 is tightly associated with late flowering (Jiang et al., 2019; Ogiso-Tanaka et al., 2019; Sun et al., 2019).

Different key genes control soybean flowering under LD and SD

Although several signaling pathways that regulate photoperiodic flowering in soybean have been proposed (Watanabe et al., 2012; Xia et al., 2012b; Cao et al., 2017), the primary pathway is a soybean-specific *E1*-mediated regulatory pathway (Figure 1). Under LD, E3 and E4 provide differential sensitivity to R:FR for the induction of *E1* and *E1L* expression, in turn suppressing the expression of *GmFT5a* and *GmFT2a* and delaying flowering (Kong et al., 2010; Thakare et al., 2011; Xia et al., 2012a; Cao et al., 2015; Zhu et al., 2019). The repressive effects of E1 on flowering may also partially involve the induction of the inhibitory *FT* genes *GmFT1a* and *GmFT4* (Zhai et al., 2014; Liu et al., 2018a). E1 and E1Lb contribute to overall E1/E1L activity to repress *GmFT2a* and *GmFT5a* expression, as the loss-of-function of either gene causes early flowering (Zhu et al., 2019). *E1* is also regulated by the circadian clock components GmLHY and GmPRR3 at the transcriptional level. A proposed model for the photoperiodic flowering regulatory pathway in soybean under LD is shown in Figure 1. This proposed pathway involves phyA (E3 E4)/circadian clock-E1/E1L-FT (Figure 1). GmCRY1a might also function under LD, as the levels of this protein at noon are clearly correlated with flowering time (Zhang et al., 2008).

E3 and *E4* are much less important for controlling flowering under SD, as loss-of-function *e3* and *e4* alleles have only minor effects compared to their respective wild-type alleles (Lu et al., 2017). In conventional cultivars, the expression of *E1* is usually suppressed by J (and presumably the evening complex) under SD, whereas the loss-of-function

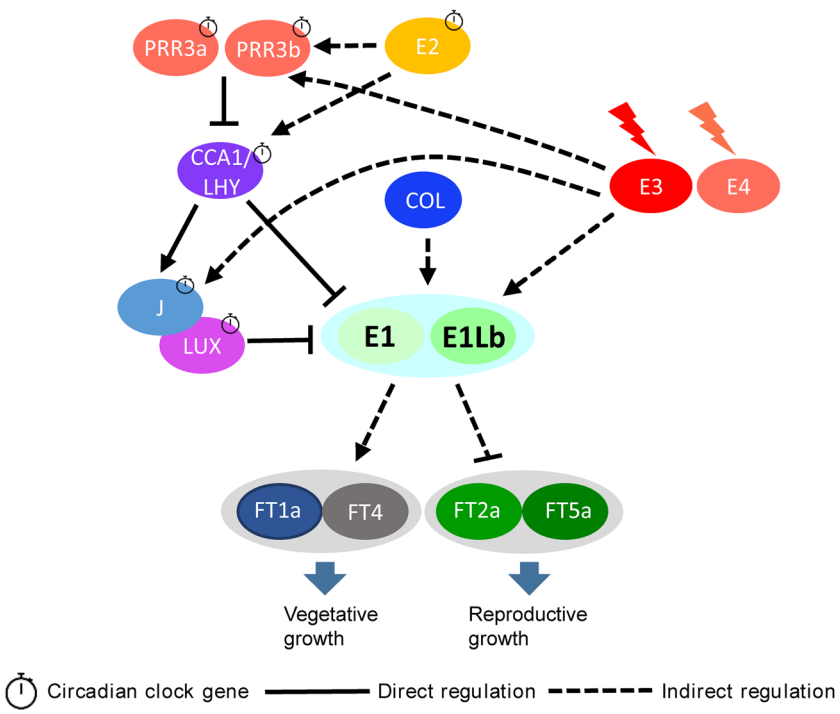

Figure 1. Photoperiodic flowering regulatory mechanisms in soybean

E3 and E4 mediate flowering responses under high ratios of R and FR light, respectively. Under LD, E3 and E4 induce the expression of *E1* and *E1Lb*. 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. 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. 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. Other circadian clock genes such as *PRR3a/b* are also transcriptionally affected by the phytochromes E3 and E4. The solid and dotted lines represent direct and indirectly regulation, respectively. The arrow and T-shape symbols indicate positive and negative regulation, respectively.

j allele results in the upregulated expression of *E1* at dusk under SD, thus leading to late flowering (Lu et al., 2017). How J regulates the two *E1L* genes has not yet been established, but the mechanism may be similar to that of E1. The proposed model of the photoperiodic flowering regulatory pathway in soybean under SD is shown in Figure 1; this pathway involves J (EC)-E1-FT.

CIRCADIAN CLOCK GENES CONTROL FLOWERING TIME IN SOYBEAN

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: 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*). The transcriptional regulatory relationships among these components restrict their expression to specific times of day (Oakenfull and Davis, 2017). A growing number of circadian clock homologs have been linked to flowering in soybean, including *E2* (*GmGIa*), *J* (*GmELF3*), *Gp11/Tof11* (*GmPRR3a*), *qFT12-1/Gp12/Tof12* (*GmPRR3b*), and *GmLHY* orthologs (Watanabe et al., 2011; Lu et al., 2017, 2020; Li et al., 2019b; Lu et al., 2020). Like their orthologs in *Arabidopsis* (Bendix et al., 2015), the expression levels of these genes oscillate throughout the day. Under 16 h/8 h LD cycles, *PRR3a/PRR3b* transcripts reach peak levels at zeitgeber time

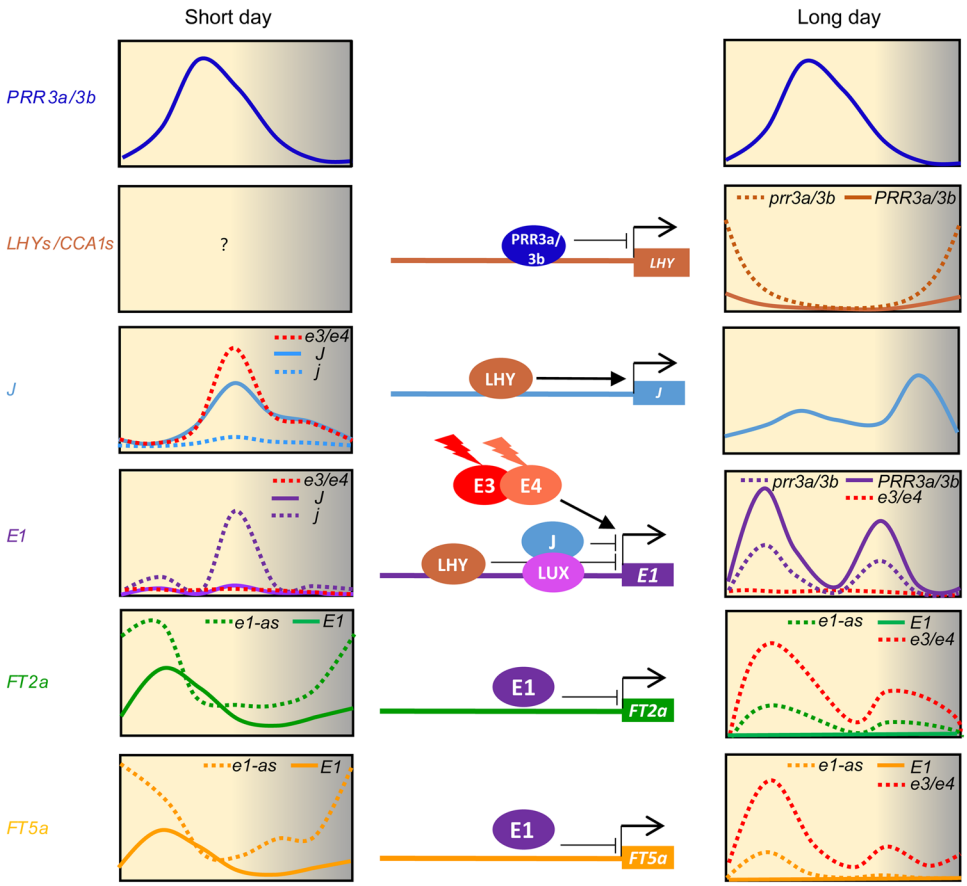

Figure 2. Photoperiodic regulation of *FT* in soybean

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. Consequently, *GmFT2a* and *GmFT5a* are induced, with peak expression early in the morning, thereby promoting flowering. The difference in flowering time between *E1* and *e1-as* near isogenic lines is small. In the *e1-as* background, the expression of *GmFT2a* and *GmFT5a* peaks at dawn. The effects of E3 and E4 on the expression of downstream genes are very small in SDs. The solid lines indicate transcript levels in wild-type plants, and the red dotted lines indicate transcript levels in *e3e4*. Other lines are described in the corresponding boxes in the figure. The arrow and T-shape symbols indicate positive and negative transcriptional regulation, respectively.

(ZT)8 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 2). Overexpressing mutant *GmPRR3b* decreased the mRNA levels of multiple circadian clock genes, suggesting that GmPRR3b affects the expression of other components in the central circadian oscillator machine (Li et al., 2020). LHY/CCA1 orthologs bind directly to the promoter region of *J* to induce its expression (Li et al., 2020). This mechanism appears to be distinct in soybean and *Arabidopsis*, as morning-phased clock components LHY and CCA1 inhibit the transcription of the evening-expressed gene *ELF3* in *Arabidopsis* (Kamioka et al., 2016; Sanchez and Kay, 2016).

Although *E2* is a circadian clock gene, it has not yet been integrated into the circadian clock regulatory pathway. However, RNA-seq analysis revealed that many orthologs of circadian clock and clock-controlled genes are under the control of E2, including *LHY/CCA1*, *TIMING OF CAB EXPRESSION 1* (*TOC1*), and *CYCLING DOF FACTOR* (*CDF*) (Wu et al., 2019), suggesting that E2 is the upstream regulator of these genes. This notion is supported by the finding that the de-repression of *GmFT2a* and *GmFT5a* by the mutant *GmPRR3a* and *GmPRR3b* alleles was mainly confined to lines harboring *e2* (Li et al., 2019b). Since *E2* is an important maturity gene that helps determine reproductive phenology in soybean, it is surprising that it is still not clear how it is integrated into the flowering pathway. As in *Arabidopsis*, circadian clock components in soybean are self-regulated, but they are also regulated by photoreceptors. Specifically, circadian clock genes such as *J* (Lu et al., 2017), *LHY* (Wu et al., 2019), *PRR3a*, *PRR3b* (Lu et al., 2020), and other *PRRs* (Wu et al., 2019) are also under the control of the phytochromes E3 and E4 (Figure 1A). Further research is needed to determine whether these regulatory effects are direct or indirect.

E1 IS A CENTRAL HUB IN THE PHOTOPERIODIC FLOWERING MECHANISM IN SOYBEAN

The molecular nature of the photoperiod response mechanism and its major integrating component(s) has been a central focus of study in several groups of plants. The above discussions establish a clear role for light perception and circadian clock-related genes in the photoperiod response pathway in soybean, which in general is conserved in *Arabidopsis* and other systems. In *Arabidopsis*, the B-box/CCT protein CONSTANS (CO) plays a central role in integrating light and circadian inputs for photoperiod measurement (Shim et al., 2017). In soybean, however, *CO*-like genes have not emerged as major targets for adaptive change. Instead, most of the focus has been placed on the functional importance of the *E1/E1L* genes and their legume-specific nature as potential key integrators of light and circadian inputs.

Substantial genetic and regulatory evidence locates *E1* immediately upstream of *FT* genes as a direct transcriptional regulator but downstream of most other flowering time loci. In soybean, light signals are perceived by multiple photoreceptors (including E3, E4, and GmCRY1a) and integrated into photoperiodic flowering (Liu et al., 2008a; Zhang et al., 2008; Watanabe et al., 2009). The phytochrome A proteins E3 and E4 are activated by light signals under LDs and upregulate *E1* transcription. The functions of circadian clock genes including morning phased genes (*GmPRR3-GmLHY/CCA1*) and conventional evening complex genes (*J* and *GmLUX*) are genetically dependent on *E1*. The effects of these genes on flowering are lost in the null *e1-nl* background (Lu et al., 2017, 2020), suggesting that E1 is a target of these clock genes, a concept consistent with their roles in regulating *E1* expression. E1 may therefore function as a central hub that integrates light and circadian clock signals and transfers these signals to FT orthologs as output (Figures 1, 2), a function similar to that of CO in *Arabidopsis* (Shim et al., 2017) and Hd1/Ghd7 in rice (Song et al., 2015). The light-dependent induction of *E1* (Xu et al., 2015) supports that notion that *E1* plays a pivotal role in setting critical daylengths in individual soybean cultivars, as does Ghd7 in rice (Itoh et al., 2010).

The broad functional similarity of soybean E1 to CO orthologs in *Arabidopsis* and rice suggests that E1 might have been effectively substituted for CO in soybean. This raises the question of whether CO genes contribute to flowering time regulation in soybean, and if so, what is their relationship with E1? The soybean genome contains 26 *COL* genes, including two pairs of homeologs (*COL1a/b* and *COL2a/b*) that are co-orthologs of *Arabidopsis CO* (Wong et al., 2014) and can complement the phenotype of the *Arabidopsis co* mutant, suggesting they have retained CO function (Wu et al., 2014). However, functional analysis in soybean indicated that these homeologs delay flowering in LD, similar to *Hd1* in rice (Cao et al., 2015, Wu et al., 2019). Since no flowering time-related loci co-locate with the four *COL* genes, their functions in photoperiodic flowering have not been extensively explored. Intriguingly, the downregulation of *COL1a/b* by RNAi resulted in the downregulation of *E1* (Wu et al., 2019). Furthermore, *E1* and *E1Lb* were induced by chilling at 18°C in LD, but such induction was not observed in an early-flowering mutant in which a 214 kb segment containing *COL2b* was deleted (Zhang et al., 2020b). These findings suggest that soybean *COL* genes could function as activators of *E1* expression, an interesting hypothesis to be addressed in the future.

Soybean *CO-Like* (*COL*) genes were not included in a list of genes differentially regulated by *E2* and *e2* (Wu et al., 2019), unlike *GI* in *Arabidopsis* and *OsGI* in rice (Hayama et al., 2003; Lee and An, 2015; Kubota et al., 2017). Accumulating evidence indicates that E1 activity in soybean is regulated at the transcriptional level by multiple upstream

factors in the photoperiod response pathway. However, our understanding of these interactions falls short of explaining the precise molecular mechanism by which different photoperiods are distinguished in soybean. It remains possible that E1 is also regulated at the post-translational level or even through direct protein–protein interactions with unknown factors analogous to *Arabidopsis* CO (Suárez-López et al., 2001; Valverde et al., 2004; Jang et al., 2008; Liu et al., 2008b; Lazaro et al., 2012; Song et al., 2012; Rosas et al., 2014) and rice Hd1 (Song et al., 2015). The investigation of these other potential modes of *E1* regulation should therefore be a high priority for future studies.

CONCLUDING REMARKS AND PERSPECTIVES

It is clear that our understanding of photoperiodic flowering in soybean has come a long way since Garner and Allard first described this phenomenon 100 years ago. Over the subsequent decades, careful genetic analyses by many groups have systematically dissected the genetic control of photoperiodic flowering in soybean, and many loci that contribute to broad and more localized variation in soybean flowering time have been characterized. More recent studies have identified the molecular nature of these loci, outlined their various interactions, and revealed how they combine in different ways to help soybean adapt to different latitudes. Studies are increasingly making use of new molecular technologies for reverse genetic analysis of soybean, overcoming the limitations of its most recent genome duplication and allowing for the systematic functional dissection of key gene families and molecular interactions involved in this process.

These advances allow gene functions and pathways in soybean to be compared with those in other species, including *Arabidopsis*, as well as other SD plants such as rice and related LD plants such as pea (*Pisum sativum*). Such comparisons have revealed features that are conserved with other major crop and model species, but also some major features and many details that may be unique to soybean. This comparative approach has the potential to provide further insight into soybean pathways and to accelerate progress by defining potential candidates using forward genetic analysis and GWAS and by guiding reverse genetic analysis towards potential key pathway components.

This continued progress merely serves to define further questions of interest to address in the future. For example, do photoreceptors other than phyA contribute to light sensing for the photoperiod response in soybean, and what signaling components are involved? How is E1 regulated at other levels, and could its activity be the key point of integration for photoperiod measurement? Given the central role of *COL* genes in other systems, what is their importance in soybean, and how do they interact with *E1*? Is the profound effect of circadian evening complex genes achieved merely via altered rhythmic regulation of their targets, or do they play a more direct role? How can the *E2* gene be better integrated into our understanding of flowering time control in soybean? Are key genes in other species (e.g., *CDF* family genes) and potential parallel pathways for flowering time integration (e.g., *SOC1* and *miR172*) also important in the soybean flowering pathway?

Insights from soybean promise to accelerate efforts to understand flowering time adaptation in other legume species. The most direct benefits are likely to be for warm-season SD legume crops such as various *Vigna* and *Phaseolus* species. Comparisons with the LD legumes such as pea and *Medicago truncatula* may also be valuable for understanding the molecular basis and evolution of the differences between SD and LD plants, differences in the regulation of flowering by temperature, and the functional divergence of *FT* genes and other PEBP family members.

Finally, in addition to these mechanistic insights and questions, we are also beginning to gain a clearer picture of the origins, distribution, and molecular evolution of specific soybean flowering time alleles thanks to the power of recent large-scale genome-wide diversity analyses. In the coming years, the combination of these approaches should provide us with a richer and more detailed understanding of the adaptation of wild soybean, as well as its domestication, expansion, and diversification. At the same time, such approaches will facilitate the development of valuable new molecular design strategies to further improve the flowering time adaptation and productivity of soybean, the most important legume crop worldwide.

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AUTHOR CONTRIBUTIONS

X.L. drafted the manuscript. J.A., J.L.W., and B.L. revised the manuscript. F.K. supervised this project and revised the manuscript. All authors read and approved of its content.

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SUPPORTING INFORMATION

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Table S1. Representative natural variations and functions of maturity genes

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