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Photoperiodism dynamics during the domestication and improvement of soybean

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Soybean (*Glycine max*) is a facultative short-day plant with a sensitive photoperiod perception and reaction system, which allows it to adjust its physiological state and gene regulatory networks to seasonal and diurnal changes in environmental conditions. In the past few decades, soybean cultivation has spread from East Asia to areas throughout the world. Biologists and breeders must now confront the challenge of understanding the molecular mechanism of soybean photoperiodism and improving agronomic traits to enable this important crop to adapt to geographical and environmental changes. In this review, we summarize the genetic regulatory network underlying photoperiodic responses in soybean. Genomic and genetic studies have revealed that the circadian clock, in conjunction with the light perception pathways, regulates photoperiodic flowering. Here, we provide an annotated list of 844 candidate flowering genes in soybean, with their putative biological functions. Many photoperiod-related genes have been intensively selected during domestication and crop improvement. Finally, we describe recent progress in engineering photoperiod-responsive genes for improving agronomic traits to enhance geographic adaptation in soybean, as well as future prospects for research on soybean photoperiodic responses.

photoperiodism, soybean, circadian clock, flowering

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INTRODUCTION

Soybean (*Glycine max*), a short-day plant, initiates flowering when the day length declines below a certain threshold. Many photoperiod-responsive alleles have undergone intensive selection and improvement during domestication due to their functional importance in geographic adaptability (Zhou et al., 2015). Soybean was domesticated from wild soybean (*Glycine soja*) in East Asia approximately 3,000–9,000 years ago (Hyten et al., 2006), but the detailed origin and history of soybean cultivation remains under debate. A recent study based on archaeological evidence indicated that soybean cultivation and selection occurred around 6,000–7,000 BCE (Before the Common Era) in China, 3,000–5,000 BCE in Japan and 1,000–1,500 BCE in Korea (Lee et al., 2011). Now, soybean cultivation has spread throughout the world. According to the Global Soybean Production report by the United States Department of Agriculture (USDA), global soybean production reached 313 million tons in 2016 (http://www.globalsoybeanproduction.com/). Approximately 94% of the soybean crop

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is produced by the United States (34.1%), Brazil (30.8%), Argentina (18.1%), China (3.8%), Paraguay (2.9%), India (2.3%), and Canada (2.0%), as shown in Figure 1A.

With the increase in soybean farming over the past several decades, the soybean industry now must confront many challenges. For example, breeding "ideal tropical soybean" cultivars with traits including late flowering and tolerance to drought or flooding stress (Kamal and Komatsu, 2016; Nachappa et al., 2016) and strong resistance to various diseases including leaf rust and red leaf blotch (Miranda et al., 2013) has been a main objective of breeders and scientists in North/South America and West Africa.

Another major challenge for soybean agriculture is the adaption of soybean to various photoperiodic environments at different latitudes. Soybean prefers to grow in middle- or high-latitude regions with warm, humid conditions and soybeans are now cultivated between the latitudes of ~35°S and ~54°N (Figure 1A). The highest yields of soybean per unit area are obtained in Turkey and Italy, with average nationwide soybean yields reaching 4.9 tons per hectare, which is much higher than the average worldwide yield of 2.6 tons per hectare (data obtained from the Statistics Division of Food and Agriculture Organization of the United Nations, http://faostat3.fao.org/browse/Q/QC/E). By contrast, photoperiodic incompatibility in low-latitude areas such as Brazil, Paraguay, India, and Ghana seriously hampers soybean yields (Figure 1A) (Brown et al., 2005; Morton et al., 2006). Hence, there is an urgent need for plant researchers to identify alleles controlling important photoperiodic traits and to dissect their underlying molecular mechanisms, in order to enable breeders to produce elite soybean cultivars that are geographically adapted. In this review, we summarize the regulatory mechanisms of photoperiodism in plants and the progress on the studies of photoperiodic responses in soybean. Furthermore, we provide an annotated list of 844 soybean orthologs of *Arabidopsis* flowering genes and this information should help researchers identify the genes corresponding to known quantitative trait loci (QTLs) for flowering.

PHOTOPERIODISM AND REGULATORY MECHANISMS

Plant photoperiodism was originally defined as the response of the vegetative-to-reproductive phase transition to the length of light and dark periods (Figure 1B–D) (Garner and Allard, 1920; Hamner and Bonner, 1938). Flowering plants can be classified as long-day plants, short-day plants, and neutral-day plants according to their photoperiodic flowering behavior. However, increasing evidence demonstrates that

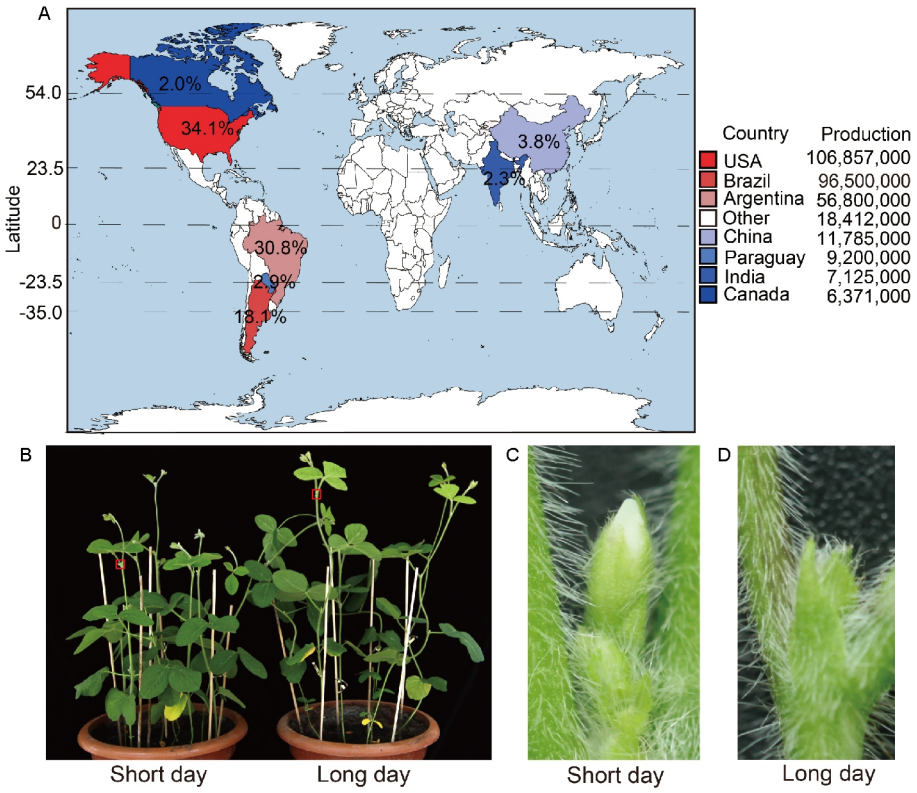

Figure 1 Worldwide soybean production and photoperiodic flowering phenotypes. A, Distribution and production of soybean by country. B, Images of photoperiodic flowering phenotypes in soybean cultivar Williams 82 which was grown for 5 weeks under long-day or short-day conditions. The red box indicates the flower bud under short day conditions or the leaf bud under long day conditions. Also, enlarged images of the flower buds and leaf buds are shown in C and D, respectively.

photoperiodism affects many other factors such as shoot, stem and root development, phytohormone signaling responses, nutritional metabolism, leaf movement, leaf senescence, photosynthate partitioning, pod setting, seed filling, and stress responses (Borniger and Nelson, 2017; Covington and Harmer, 2007; Greenham and McClung, 2015; Han et al., 2006; James et al., 2008; Lu et al., 2005; Nico et al., 2016; Nusinow et al., 2011; Song et al., 2015; Voss et al., 2015).

Since the discovery of photoperiodic phenomena, numerous studies have explored the underlying mechanisms. In 1964, Colin Pittendrigh and Dorothea Minis, who were inspired by Erwin Bünning's earlier study (Bünning, 1936; Pittendrigh and Minis, 1964), proposed the "external coincidence model", which has now been widely accepted by plant biologists. This model describes how the active forms of receptors, sensors, and the protein degradation machinery induced by light or other external photoperiodic signals interact with the oscillation of an intrinsic circadian clock that controls genes, proteins, and/or substrates (Pittendrigh and Minis, 1964). The rhythmically activated downstream factors then trigger photoperiodic responses, such as the vegetative-to-reproductive phase transition. This review does not cover every detail in the field; we encourage interested readers to refer to other review articles for a more comprehensive understanding of the "external coincidence model" (Greenham and McClung, 2015; Song et al., 2015; Yamashino, 2013).

THE CIRCADIAN CLOCK REGULATORY NETWORK

The circadian clock functions as a timekeeper that synchronies internal biological processes with the rhythms of environmental changes (Imaizumi, 2010). The intrinsic circadian clock system that controls genes and proteins is indispensable for photoperiodic responses. Genetic evidence, primarily in the model plant *Arabidopsis thaliana*, has identified the main components controlling the circadian clock system. The regulatory network is controlled by several core transcription factors, including CIRCADIAN CLOCK ASSOCIATED 1 (CCA1), LATE ELONGATED HYPOCOTYL (LHY), PSEUDO-RESPONSE REGULATOR 9 (PRR9), PRR7, PRR5, TIMING OF CAB1 (TOC1/PRR1), and the EVENING COMPLEX (EC) comprising EARLY FLOWERING 3 (ELF3), ELF4, and LUX ARRHYTHMO (LUX). These core oscillators and EC components have been evolutionarily conserved in plants, and the regulatory mechanism has been extensively reviewed (Hernando et al., 2017; Johansson and Staiger, 2015; McClung and Gutiérrez, 2010; McWatters and Devlin, 2011; Nakamichi, 2011; Yamashino, 2013). In brief, the intrinsic regulatory network of the circadian clock is composed of several feedback loops of time-phase-specific genes (Figure 2). *CCA1* and *LHY* encode MYB-like transcription factors and their expression peaks at dawn. CCA1 and LHY repress the expression of *PPR5*, *TOC1*, *LUX*, and *ELF4* through physical interactions with specific *cis*-elements in the promoter regions of these genes (Lau et al., 2011). Interestingly, CCA1 and LHY can also bind to the promoters of *PRR9* and *PRR7*, but they activate *PRR9* and *PRR7* transcription (Farré et al., 2005). This is supported by the finding that the *cca1 lhy* double mutant shows reduced *PRR9* and *PPR7* transcript levels. *PRR9*, *PPR7*, *PPR5*, and *TOC1* are expressed with gradually delayed peaks from morning up to the early evening, which leads to the suppression of *CCA1* and *LHY1* during the day (Nakamichi et al., 2010). Notably, *TOC1* is mainly expressed in the early evening and directly represses *CCA1*, *LHY*, *PRR9*, *PRR7*, *LUX*, and *ELF4* expression by binding to their promoters (Gendron et al., 2012; Huang et al., 2012; Pokhilko et al., 2012). The EC components ELF3, ELF4, and LUX exhibit peak gene expression in the evening and repress *PRR9*, *PRR7*, and *LUX* expression (Dixon et al., 2011; Helfer et al., 2011). In turn, *ELF3*, *ELF4*, and *LUX* are suppressed by CCA1 and LHY (Hsu et al., 2013).

In addition to the core oscillators, the circadian clock network is also modulated by other feedback loops. The F-Box protein ZEITLUPE (ZTL), which is stabilized by GIGANTEA (GI), can interact with and degrade PRR5 and TOC1 (Fujiwara et al., 2008). CCA1 hiking expedition (CHE), a TCP family transcription factor, represses *CCA1* expression (Pruneda-Paz et al., 2009). Recent studies have uncovered several transcriptional activators that also regulate the plant circadian network. The morning clock factors REVEILLE 4 (RVE4), RVE6, and RVE8, members of the MYB-like transcription factor family, positively regulate the transcription of evening clock genes including *PRR5*, *TOC1*, *ELF4*, and *LUX* (Hsu et al., 2013). Moreover, night light-inducible and clock-regulated 1 (LNK1) and LNK2 promote *PRR5, TOC1*, and *ELF4* expression (Rugnone et al., 2013).

To translate the *Arabidopsis* research to soybean, we searched for the orthologs of genes encoding core oscillators and EC components in *Arabidopsis* based on the soybean genome annotation Wm82.a2.v1 from Phytozome V12.0 (Goodstein et al., 2012; Schmutz et al., 2010). Using MEGA6 with the Neighbor-Joining method (Tamura et al., 2013), we uncovered the phylogenetic relationships of these proteins (Figure 2). Soybean, a paleopolyploid species, possesses numerous duplicated genes (Du et al., 2012; Schmutz et al., 2010); indeed, the soybean genome encodes four orthologs of *CCA1*/*LHY*, which were previously named *LHY* and CCA1-like (*LCL*) (Liu et al., 2009), five orthologs of *PRR5/9*, four orthologs of *PRR7*, four orthologs of *TOC1*, two orthologs of *ELF3*, three orthologs of *ELF4* and two orthologs of *LUX*. These results indicate that soybean has a more complex circadian regulatory network than that of

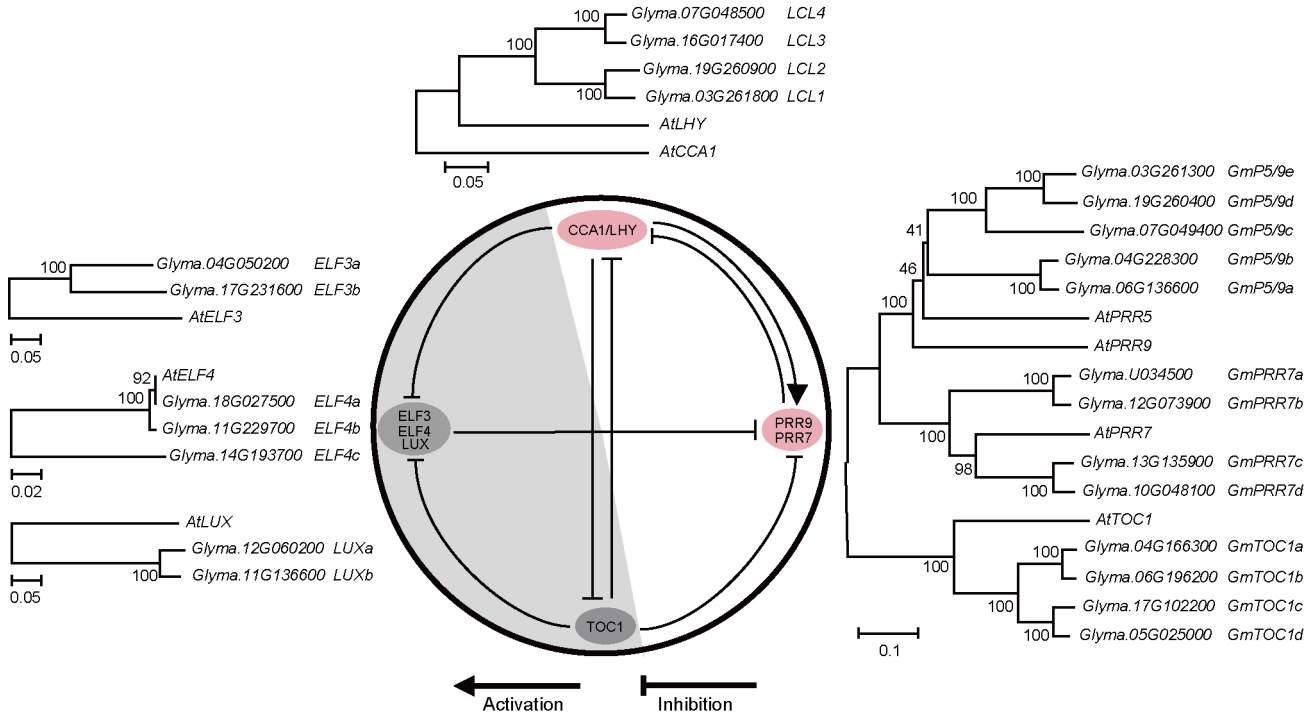

Figure 2 (Color online) The core circadian genes in soybean. The white half of the circle represents day and the gray half represents night. The phylogenetic trees were generated by MEGA6 with the Neighbor-Joining method, using the amino acid sequences of core circadian oscillation genes from soybean and *Arabidopsis*. The sequences of core oscillators and evening complex components in *Arabidopsis* were obtained from The *Arabidopsis* Information Resource (TAIR, http://www.arabidopsis.org/), and the sequences of their soybean homologs were acquired from Phytozome v11 (https://phytozome.jgi.doe.gov/pz/portal.html).

Arabidopsis, although the expression specificity, functional redundancy, and evolutionary diversification of these duplicated genes remain to be investigated.

Plants can adjust and synchronize the internal rhythms of their circadian clock with diurnal signals, such as the light/dark period or periodic temperature variations, through multiple input pathways via a process called entrainment. The light/dark period is the most frequently studied entraining cue. Plants use different light receptors to sense and distinguish the dynamics of the light environment. Phytochromes sense red and reversible far-red light, whereas cryptochromes sense blue light (Casal, 2013; Liu et al., 2010a). Phytochromes and cryptochromes can affect circadian entrainment, thus altering the expression of circadian clock genes (Hu et al., 2013; Somers et al., 1998; Strasser et al., 2010). The soybean genome contains eight phytochrome and seven cryptochrome genes (Table S1 in Supporting Information). The *GmPhyA* loci regulate photoperiodic flowering (Liu et al., 2008; Watanabe et al., 2009). We previously characterized *GmCRY1a* and *GmCRY2a* in soybean (Meng et al., 2013; Zhang et al., 2008). We found that the rhythmic patterns of GmCRY1a protein levels correspond to the flowering times of soybean varieties cultivated at different latitudes in China, which implies that GmCRY1a helps regulate photoperiodic flowering (Zhang et al., 2008). GmCRY2a regulates leaf senescence through its blue-light-dependent interaction with cryptochrome interacting basic helix-loop-helix 1 (GmCIB1) (Meng et al., 2013).

THE PHOTOPERIODIC FLOWERING REGULATORY NETWORK

The "external coincidence model" includes two main elements: (i) light signals entrain the oscillation of circadian clock genes; (ii) the components, such as receptors, sensors, or protein degradation machinery, are only activated by the light. Then the coincidence of the peak expression of circadian genes and the presence of the activated components triggers photoperiodic responses, such as flowering. In *Arabidopsis*, the cooperation of these two elements restricts the abundance of the key regulator, CONSTANS (CO) protein, to high levels only in the afternoon under long-day conditions, when CO increases the abundance of *FLOWERING LOCUS T* (*FT*) mRNA (Putterill et al., 1995; Suárez-López et al., 2001). FT protein is subsequently transported to the meristem to initiate the transition to flowering (Corbesier et al., 2007).

Transcriptional and post-translational regulation plays essential roles in the control of CO protein levels (Shim and Imaizumi, 2015; Song et al., 2015). Cycling DOF factor (CDF) family proteins repress the transcription of *CO* in the morning by binding to the CTTT motif enriched in its promoter (Fornara et al., 2009; Imaizumi et al., 2005). The expression of *CDF* is upregulated by CCA1 and LHY in the morning (Nakamichi et al., 2007; Schaffer et al., 1998; Wang

and Tobin, 1998) and suppressed by PRRs in the afternoon (Nakamichi et al., 2010; Nakamichi et al., 2012). CDF proteins are present at high levels only in the morning and are degraded by the 26S proteasome in the afternoon. This degradation process is mediated by a blue-light-dependent complex of GIGANTEA (GI) and flavin-binding, kelch repeat and f box 1 (FKF1) proteins (Fornara et al., 2009). The peaks of *GI* and *FKF1* transcription are under the control of the circadian clock. Under long-day conditions, peak *GI* and *FKF1* expression occurs at approximately zeitgeber time 13 (ZT-13), when the levels of both GI and FKF1 are sufficient to form a blue-light-dependent complex to degrade CDF proteins (Sawa et al., 2007). Without repression of CDFs, *CO* expression begins and peaks at ZT-12 to ZT-16, thus promoting *FT* transcription.

CO is also the target of the ubiquitin-dependent degradation machinery (Jang et al., 2008; Lazaro et al., 2012; Valverde et al., 2004) involving constitutive photomorphogenic 1 (COP1) and suppresser of PHYA-105 1 (SPA1). COP1 and SPA1 form a complex to degrade CO in the absence of light (Laubinger et al., 2006; Saijo et al., 2003). The blue-light-dependent interaction between CRY2 and SPA1 suppresses the activity of the COP1-SPA1 complex, resulting in the accumulation of CO (Liu et al., 2011; Zuo et al., 2011). Under far-red light, PHYA antagonizes the degradation of CO and stabilizes this protein, whereas under red light, PHYB promotes the degradation of CO (Valverde et al., 2004). Recently, high expression of osmotically responsive genes 1 (HOS1) was found to promote CO degradation in response to red light, which is responsible for the restriction of CO levels in the morning. Furthermore, the finding of a physical interaction of HOS1, PHYB, and CO may represent the missing link in the PHYB-mediated flowering pathway (Lazaro et al., 2015; Lazaro et al., 2012). Collectively, transcriptional and post-translational regulation restricts the abundance of CO in the afternoon under long days to promote flowering.

PREDICTING PHOTOPERIODIC FLOWERING GENES BY COMPARATIVE GENOMIC ANALYSIS

In the past few decades, biologists have explored the genes involved in flowering time, and a subset of these genes is evolutionarily conserved. The Flowering Interactive Database catalogs more than 300 genes that regulate flowering time in *Arabidopsis* (Bouché et al., 2016). By performing evolutionary conservation analysis using this collection, we identified 844 homologs of these genes in the soybean genome Wm82.a2.v1 (Table S1 in Supporting Information). The biological functions of several genes on this list have already been reported. For example, the levels of GmCRY1a protein are associated with photoperiodic flowering in various soybean varieties (Zhang et al., 2008). Knock-down lines of *GmRAV2* transcription factor genes show early flowering phenotypes (Lu et al., 2014). Overexpressing *GmSOC1* (suppressor of overexpression of CONSTANS 1) promotes flowering (Hernando et al., 2017), whereas overexpressing the microRNA *GmiR156b* delays flowering (Nakamichi et al., 2010). Expressing *GmFLD* in *Arabidopsis* results in early flowering phenotypes (Lau et al., 2011). Constitutive induction of *GmMADS28* in tobacco leads to early flowering and altered petal identity phenotypes (Farré et al., 2005).

The list of 844 candidate flowering genes in soybean may serve as a rich resource for further exploration of the corresponding genes and regulatory elements of flowering-associated QTLs in soybean (Figure 3). For instance, among the *E* loci controlling soybean flowering time, less is known about the *E7* and *E8* loci. Our data provided some clues about the corresponding genes. *E7* was identified in plants under long-day conditions using a low red to far-red (R:FR) light source. Under 20-hour long-day conditions, *E7E7* lines exhibited delayed flowering (by ~7 days) when the R:FR light ratio was similar to that of natural daylight (1.2 ratio) and by 15 days when subjected to low R:FR (0.7 ratio) light compared with *e7e7* lines. The *E7* locus is located between Satt100 and Satt460 on chromosome 6 (Cober and Voldeng, 2001a). The genomic position of the *E7* locus is from nucleotides 31,490,651 to 44,049,996 on chromosome 6. This region contains eight flowering-gene homologs, including *Glyma.06G241900* and *Glyma.06G242100*, which are homologs of *SPA1*, the key regulator of the *PHYA* signal transduction pathway (Fittinghoff et al., 2006; Saijo et al., 2003). *Arabidopsis* has four genes encoding members of the SPA protein family containing a WD-repeat domain and a kinase-like domain. SPA proteins function redundantly in suppressing photomorphogenesis in the dark; an *Arabidopsis spa* quadruple mutant exhibits strong constitutive photomorphogenesis in the dark. However, among the four *SPAs*, *SPA1* has the strongest regulatory effect on flowering time (Fittinghoff et al., 2006; Laubinger et al., 2006; Liu et al., 2011; Zuo et al., 2011). As *E7* is involved in photoperiodic flowering under low R:FR conditions, the two SPA homologs in soybean are strong potential candidates corresponding to the *E7* locus. The *E8* locus functions as a flowering suppressor (Cober et al., 2010). *E8* is located in the C1 linkage group between Sat_404 and Satt136 (Cober et al., 2010). *E8* maps between 13,613,810 and 32,617,873 on chromosome 4. There are six flowering candidate genes located in this region including *E1Lb* which is homologous to *E1*.

LOCI CONTROLING PHOTOPERIODIC FLOWERING IN SOYBEAN

Soybean varieties carry numerous natural mutations that have occurred concomitantly with the adaption to various envir-

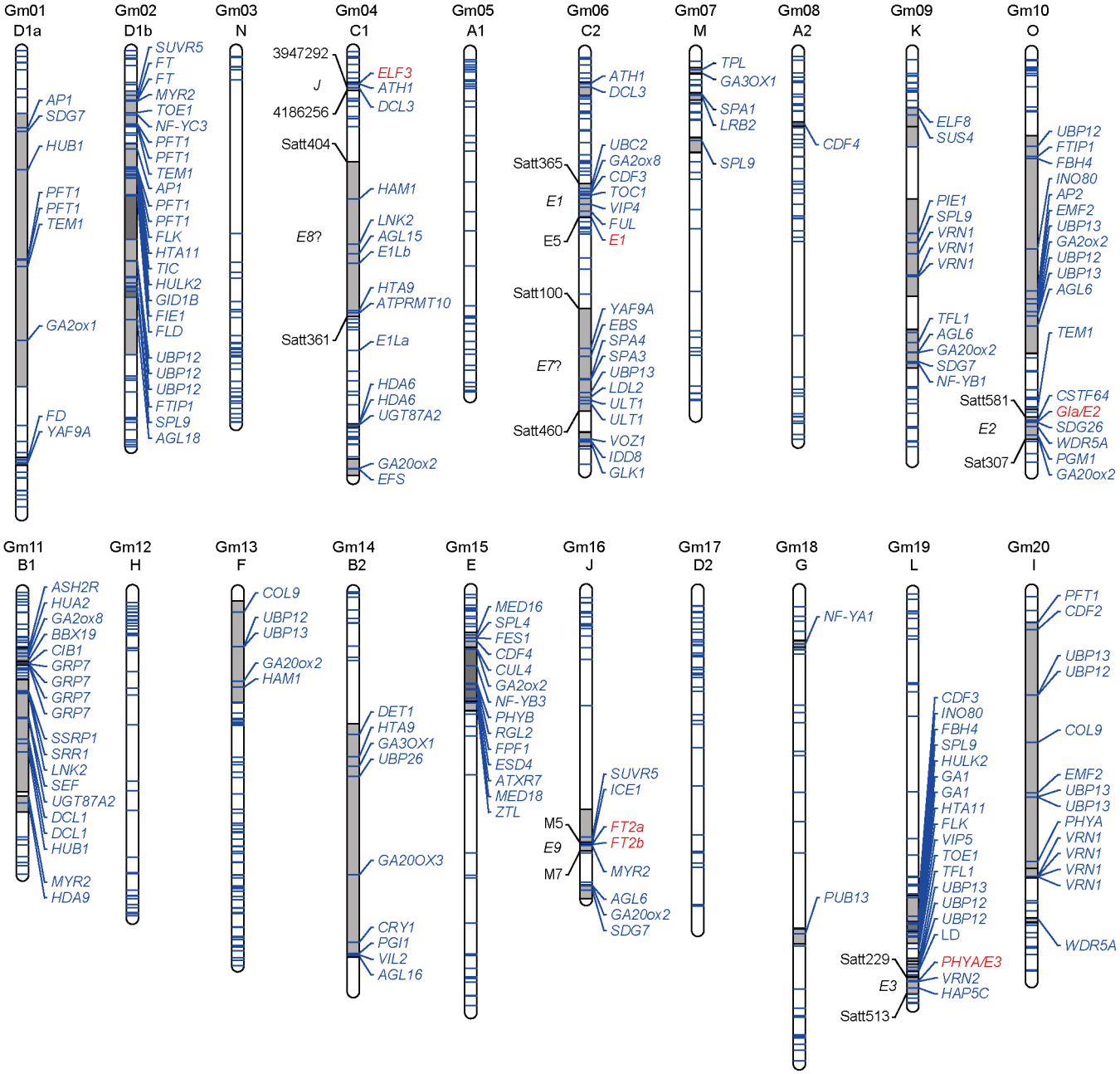

Figure 3 The distribution of candidate flowering genes and the associated flowering QTLs in the soybean genome. The columns represent the different chromosomes in soybean. The gray bars represent the regions containing the QTLs, and the darker bars indicate the overlaps between different QTLs. *E1*, *E2*, *E3*, *E7*, *E8*, *E9* and *J* loci are shown at the left side of respective chromosome and the corresponding molecular marks are present in black. Question marks beside the loci indicate that the corresponding genes of the QTLs remain unknown. The blue lines on chromosomes indicate the positions of soybean orthologs of *Arabidopsis* flowering genes. The orthologs located within QTLs are labeled as *Arabidopsis* gene symbols in blue, and red letters indicate the characterized genes corresponding for the QTL.

onments; these mutations provide rich resources for investigating photoperiodic responses, especially photoperiodic flowering. Ten major loci that were identified through forward genetics studies, designated *E1* to *E9* and *J*, have long been known to control flowering and maturity time in soybean (Bonato and Vello, 1999; Buzzell, 1971; Buzzell and Voldeng, 1980; Cober et al., 2010; Cober and Voldeng, 2001b; Gould et al., 2013; Kilen and Hartwig, 1971; Kong et al., 2014; McBlain and Bernard, 1987; Ray et al., 1995).

It has long been known that the *E1* locus plays a major role in regulating photoperiodic flowering. Xia et al. delimited the *E1* locus to a single gene (*Glyma.06G207800*), which encodes a putative transcription factor containing a B3 domain (Xia et al., 2012). Its dysfunctional forms have been intensively selected in high-latitude regions of Asia and North America (Xia et al., 2012; Zhou et al.,

2015). In the soybean genome, *E1* has two highly similar homologs (*Glyma.04G156400*and *Glyma.04G143300*, designated *E1La* and *E1Lb*, respectively). The three genes are severely repressed under short-day conditions and induced, with rhythmic expression patterns, under long-day conditions (Xia et al., 2012; Xu et al., 2015; Zhai et al., 2015). The darkness phase under short-day conditions (ZT-16 to ZT-17) is required for their repression. Interruption of the darkness phase by light leads to de-repression of these genes and delayed flowering phenotypes (Xu et al., 2015). Plants with early flowering phenotypes carry a mutation in the *E1* promoter that prevents expression of *E1* (Xia et al., 2012). Introducing a functional form of *E1* back into *e1e1* soybeans can partially rescue their early flowering phenotypes (Xia et al., 2012). In addition, knock-down experiments showed that silencing *E1La* and *E1Lb* causes elevated expression of *FT* genes and early flowering (Xu et al., 2015).

The *E2* locus, containing a homolog of *GI* (*GmGIa*, *Glyma.10G221500*), was identified from a segregating population generated from a cross of Misuzudaizu, a Japanese cultivar with early flowering phenotypes, and the Chinese landrace Moshidogong 503 (Watanabe et al., 2011). Misuzudaizu carries the *GmGIa* allele with a truncated opening reading frame, leading to early flowering phenotypes. The phenotypes were reproducibly observed in another line containing a point mutation in *GmGIa*, leading to the production of a dysfunctional protein (Watanabe et al., 2011). A recent population genetics study identified three common haplotypes of *GmGIa*, H1, H2, and H3, in cultivated and wild soybean varieties in China (Wang et al., 2016). H1, which carries a stop codon in exon 10, is distributed throughout China. H2 and H3 encode normal forms of GmGIa. H2 is mainly distributed in the southern region of China, while H3 is preferentially cultivated in the northernmost region of China. Functional compensation experiments in *Arabidopsis* revealed that only overexpression of H1 could rescue the late flowering phenotypes of the *gi* mutant.

In addition to *GmGIa* at the *E2* locus, the soybean genome encodes two other homologs of *GI*, whose biological functions remain to be investigated. In the long-day plant *Arabidopsis*, *GI* is a single-copy gene that promotes flowering under long-day and short-day conditions through degradation of CDFs and activation of *CO* and *FT* (Johansson and Staiger, 2015; Putterill et al., 1995; Sawa et al., 2007; Suárez-López et al., 2001; Wong et al., 2014). In soybean, however, *GmGIa* delays the initiation of flowering only under long-day conditions (de Montaigu et al., 2015). This observation may be ascribed to the functional diversity of the genes downstream of GI, such as *CO*, in soybean. In soybean and other short-day plants, CO-like proteins may activate *FT* homologs under short-day conditions to trigger flowering, whereas under long-day conditions, they may repress the expression of *FT* homologs (Cao et al., 2015; Hayama et al., 2003). These findings suggest that soybean contains a complex gene regulatory network of *GmGIs*, *GmCOs*, *GmFTs*, and their downstream genes, which ensures that soybean plants can precisely fine-tune their photoperiodic flowering process to acclimatize to various environmental conditions.

The *E3* and *E4* loci contain two soybean *PhyA* homologs, *GmPhyA3* and *GmPhyA2*, respectively (Buzzell, 1971; Cober et al., 1996; Kilen and Hartwig, 1971). Plants carrying *GmPhyA3* alleles at the *E3* locus containing an amino acid substitution from glycine to arginine or a 40-bp deletion in the first exon show accelerated flowering phenotypes (Buzzell, 1971; Kilen and Hartwig, 1971; Watanabe et al., 2009). GmPhyA2, encoded by the *E4* locus, also regulates flowering. The presence of a *GmPhyA2* allele harboring a retrotransposon in its first exon leads to early flowering phenotypes (Liu et al., 2008). In addition to flowering initiation, *GmPhyA2* also regulates development in young seedlings. In *GmphyA2*-defective mutant lines, de-etiolation is partially disturbed under far-red light (Cober et al., 1996). *E3* and *E4* function upstream of *E1* and its homologs. In the *e3e3 e4e4* double mutant, *E1* and its homologs have lost their photoperiod-responsive expression patterns under long-day conditions (Xu et al., 2015). In addition to *GmPhyA3* and *GmPhyA2*, the soybean genome contains two more *PhyA* homologs whose functions remain to be characterized.

The *E9* locus, harboring an *FT*-like (*FTL*) gene, *FT2a* (*Glyma.16G150700*), was isolated from recombinant inbred lines generated by crossing the Canadian cultivar TK780 with the Japanese wild soybean line Hidaka (Kong et al., 2014). The insertion of a transposon in the first intron of *FT2a* reduces the expression level of *FT2a*, resulting in delayed flowering phenotypes (Zhao et al., 2016). This allele is mainly present in northern Japanese cultivars, with null alleles in the *E1*, *E3*, and *E4* loci; the reduced expression of *FT2a* helps maintain the vegetative stage to increase yields in these cultivars (Zhao et al., 2016).

As a short-day plant, soybeans flower early and have an extremely low yield in low-latitude area. The introduction of long-juvenile (LJ) trait delays the transition time from vegetative stage to reproductive stage, resulting in remarkable improvement in grain yield at low latitude region, such as Brazil. The long juvenile trait has been known to be controlled by *J* locus for several decades (Ray et al., 1995). Until recently, two groups have independently identified *J* as the orthorlog gene of *Arabidopsis ELF3* (Lu et al., 2017; Yue et al., 2017). Lu et al. further revealed that GmELF3 physically interacts with the *E1* promoter and suppresses its transcription to accelerate flowering under short-day condition (Lu et al., 2017). Loss-of-function *GmELF3* results in the upregulation of *E1* and consequently extents the vegetative phase of soybean. Plenty of natural variations in *GmELF3* gene were identified and those dysfunctional alleles are restricted to the low-latitude accessions, some of which have been utilized to

develop elite soybean cultivars adaption to tropic regions (Lu et al., 2017; Yue et al., 2017).

FTLs belong to the phosphatidylethanolamine binding protein family (PEBP), which function as determinative regulators of the flowering pathway in higher plants (Banfield et al., 1998). In soybean, 23 PEBP genes have been identified (Wang et al., 2015). Phylogenetic analysis classified these genes into three clades: thirteen *FTL* genes, eight *TFL* (terminal flower 1)-*like* genes, and two *MFT* (mother of FT and TFL1)-*like* genes (Wang et al., 2015). Among *FTLs*, *FT5a* can also promote flowering, acting redundantly with *FT2a* (Kong et al., 2010). *FT4* functions downstream of *E1* to suppress flowering under long-day conditions (Wang et al., 2015).

TFL genes also regulate the determinate habit in soybean. *Dt1* and *Dt2* are major loci controlling stem growth habit in soybean. The corresponding gene of the *Dt1* locus, *GmTFL1*, induces the transition from the indeterminate to determinate growth phenotype (Liu et al., 2010b; Tian et al., 2010). The corresponding gene of the *Dt2* locus encodes a MADS-domain factor belonging to the APETALA1/SQUAMOSA subfamily (Ping et al., 2014). Dt2 can associate with GmSOC1 to repress *Dt1* expression in the shoot apical meristem (Liu et al., 2016).

The *E5*, *E6*, *E7* and *E8* loci also regulate flowering (Bonato and Vello, 1999; Cober et al., 2010; Cober and Voldeng, 2001b; McBlain and Bernard, 1987). Existence of *E5* are still under debate. In addition to these *E*-loci, mapping studies have identified some QTLs related to flowering; these QTLs have been recorded in SoyBase (Table S2 in Supporting Information). In addition to controlling flowering time, photoperiod-responsive genes are also involved in regulating post-flowering development, during which pod setting and seed filling are determinative factors in soybean yield. In general, node and pod numbers increase under long-day conditions, whereas seed maturation accelerates under short-day conditions (Han et al., 2006; Jiang et al., 2011; Nico et al., 2016; Nico et al., 2015). The underlying mechanism remains unclear.

CONCLUSIONS AND FUTURE PERSPECTIVES

The complexity of the soybean genome makes it much more difficult to map the genes corresponding to QTLs in this crop, compared with *Arabidopsis*. Due to the extensive efforts of many groups, great progress has been made in identifying the molecular components of the flowering network in *Arabidopsis*, which provides important clues for research on photoperiodic flowering in soybean. The "external coincidence model" has been demonstrated in *Arabidopsis* and might therefore also function in soybean. Consistent with this model, sensors of light signals were found to be encoded by *E3* and *E4* genes, but many components in the soybean photoperiodic response network remain to be identified. For instance, the light-dependent ubiquitin machinery has not been identified in soybean. Reverse-genetics approaches are useful for exploring the functions of the homologs of *Arabidopsis* flowering genes, which would help reveal the mechanism of photoperiodic flowering in soybean.

Genomics studies have shown that more than 30% of genes in the *Arabidopsis* genome show rhythmic expression patterns under short-day and/or long-day conditions, indicating that the circadian pathway can globally regulate many genes in plants (Covington et al., 2008). However, photoperiod-responsive genes and their alternative splicing patterns in the soybean genome have not been systematically identified. Comprehensive identification of photoperiod-responsive genes under short-day and long-day conditions in different soybean cultivars on a genomic scale will provide crucial information to help reveal the underlying networks of photoperiodic responses.

In addition to transcriptional mechanisms, epigenetic regulation, post-transcriptional regulation (such as alternative splicing, noncoding RNAs, and RNA degradation pathways), and post-translational regulation play important roles in regulating photoperiodism (Doherty and Kay, 2012; Floris et al., 2009; Koike et al., 2012; Kojima et al., 2011; Romanowski and Yanovsky, 2015). For examples, *CCA1* produces two mRNA isoforms encoding different proteins with antagonistic functions through alternative splicing (Seo et al., 2012). SNW/Ski-interacting protein (SKIP) can interact with the pre-mRNAs of *PRR7* and *PRR9* and regulate their alternative splicing to modulate circadian pathways (Wang et al., 2012). Intriguingly, the factors controlling alternative splicing and RNA processing are regulated by circadian pathways, such as *LSM* (SM-like) genes, encoding the components of the U6 complex (Perez-Santángelo et al., 2014). In addition to alternative splicing, noncoding RNAs play important regulatory roles in photoperiodic responses (Liu et al., 2015; Shafiq et al., 2016). In soybean, however, the post-transcriptional regulation of photoperiodic responses remains unclear and must be further addressed.

Compliance and ethics *The author(s) declare that they have no conflict of interest.*

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SUPPORTING INFORMATION

Table S1 Soybean flowering candidate genes

Table S2 Flowering QTLs in soybean

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