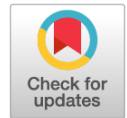


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Review Article



Genetic mechanisms underlying the expansion of soybean *Glycine max* (L.) Merr. cultivation to the north

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Soybean [*Glycine max* (L.) Merr.] is produced in 93 countries of the world on 120.5 million hectares. The production area of the crop is located between 56°N. (Russian Federation) and 35–37°S (Argentina). In the gene pool of the crop, there is a wide variety of genotypes of different maturity groups, which every has a relatively narrow latitudinal adaptability, which depends on heat and moisture supply and the duration of photoperiod. An urgent problem of our time is the creation of early matured varieties which allow to expand soybean cultivation to the north. In soybean 12 major loci (*E1–E11* and *J*) have been identified, which control the flowering initiation and the response to the photoperiod. The time of maturation, photothermal response and, ultimately, the adaptation of the crop to different latitudes also depend on various allelic combinations and the interaction of these loci. All these loci have been mapped, and for some of them genes have been identified, their allelic diversity has been characterized and the mechanisms of their functioning and interaction have been described. But the molecular-genetic nature of the early maturity of soybean has not yet been revealed in detail. This review presents the current understanding of the structure and nature of the interaction of molecular genetic determinants of early maturity of soybean, which regulate the timing of its flowering and maturation at different photoperiods and their influence on other plant traits, including the type of growth and productivity. As a result, an idea of the optimal genotype for northern latitudes was proposed, with a combination of alleles providing the earliest flowering and maturation in relatively northern regions with a long day.

Keywords: soybean; *Glycine max*; early maturity; loci; photoperiod; allelic combinations; northern latitudes.

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Обзорная статья

Молекулярно-генетические механизмы, лежащие в основе продвижения ареала возделывания сои к северу

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Сою [*Glycine max* (L.) Merr.] производят в 93 странах мира на 120,5 млн га. Возделывание этой культуры осуществляют между 56° с. ш. (Российская Федерация) и 35–37° ю. ш. (Аргентина). В генофонде сои большое разнообразие генотипов разных групп спелости, каждой из которых необходимы определенные тепло- и влагообеспеченность, а также продолжительность светового дня. Площадь выращивания конкретных сортов, как правило, ограничена узким широтным интервалом. Актуальная проблема современности — создание скороспелых сортов, позволяющих расширять производственные посевы к северу. К настоящему времени у сои определено 12 главных локусов (*E1–E11* и *J*), контролирующих сроки цветения и реакцию на фотопериод. От аллельных комбинаций и взаимодействия этих локусов зависят сроки созревания и, в конечном счете, адаптация культуры к разным широтам. Эти локусы картированы, и для части из них идентифицированы гены, охарактеризовано их аллельное разнообразие, описаны механизмы их функционирования и взаимодействия. В данном обзоре изложены современные представления о структуре и характере взаимодействия молекулярно-генетических детерминант скороспелости сои, регулирующих сроки ее цветения и созревания при разном фотопериоде и их влияние на другие признаки, включая характер роста и продуктивность. В итоге сформировано представление об оптимальном для северных широт генотипе, с сочетанием аллелей, обеспечивающих самое раннее цветение и созревание в сравнительно северных областях с длинным световым днем.

Ключевые слова: соя; *Glycine max*; скороспелость; локусы; фотопериод; аллельные комбинации; северные широты.

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BACKGROUND

Soybean [*Glycine max* (L.) Merr.] are grown in a wide range of geographic latitudes in both hemispheres of the globe, spanning more than 120.5 million hectares in 93 countries [1]. The modern boundaries of soybean range are 56° north in the Russian Federation and 35–37° south in Argentina. Soybean was first domesticated in North-east China, in the southern part of its temperate climate zone [2]. From there, soybean cultivation spread to the north and south, with the species developing adaptations to different agro-climatic parameters

The main limiting factors affecting soybean production at different latitudes are temperature, moisture supply, and daylight hours [3–5]. Expansion of soybean to the north, termed northing, is the result of creation of early – matured varieties. Northing poses a significant challenge because soybean is a short-day plant with a strong photoperiodic sensitivity (PS). Longer daylight exposures can cause delayed onset of flowering, especially in the most photoperiod-sensitive varieties. These plants remain at the vegetative stage, resulting in enhanced growth of the vegetative mass. In contrast, some varieties have a weak or almost absent PS [6].

The reverse of northing is the expansion of soybean into tropical latitudes, where most varieties have drastically reduced prebloom period, growth, and seed production. The introduction of the long juvenile (LJ) period trait into varieties in the late 1970s played a key role in the expansion of soybean in these regions [7, 8].

Therefore, when searching for soybean varieties for expansion to higher latitudes, it is necessary to identify the genetic determinants of photoperiod sensitivity / insensitivity. This work aimed to review the genetic mechanisms that determine soybean early maturation, which can guide the expansion of soybean cultivation to the north.

Diversity of the soybean gene pool coding for maturing terms and photoperiod sensitivity.

There are two main classification systems used to classify soybean varieties. The International Descriptor of the Council for Mutual Economic Assistance [9] and the United States classification. The former is used by N.I. Vavilov All-Russian Institute of Plant Genetic Resources (Russia). According to this scheme, soybean varieties take from 80 to 150 or more days from germination to maturation [9].

The US classification scheme recognizes 13 groups of soybeans varieties according to time to maturity, which corresponds to the latitudinal production of different varieties. Initially, only seven maturity groups (MGI–VII) were recognized based on the existing gene pool. Three more groups were added (MG0, MG00, MG000) as soon as early matured varieties were created for northing

in the US and Canada. For cultivation toward over southern latitudes, the three maturity groups were introduced (MGVIII–X). In the US collection, MG000 included 147 accessions, 536 accessions in MG00, 1176 in MG0, 1745 in MGI, 2071 in MGII, 1985 in MGIII, 4108 in MGIV, 2721 in MGVI, 1551 in MGVI, 944 in MGVII, 913 in MGVIII, none in MGIX, and in MGX [10]. Identification of accessions that mature earlier than MG000 in North China and the Amur region of Russia led to the proposal of another early maturity rank, MG0000. It was proposed to call them as varieties of high-latitude cold regions [11].

It should be noted that it is not easy to reconcile the American and Russian classifications because specific varieties have a limited latitudinal range that depends on the photoperiod and the sum of active temperatures in a particular latitude. Furthermore, the northern limits of soybean cultivation in the US, China, and the Russian Federation are different. The soybean belt in the US ranges from latitudes 27–49° N, with its northern boundary located just at the latitude of Volgograd.

There is a great variation in the soybean gene pool for day length sensitivity. The International Descriptor distinguishes five groups of PS, from very high to very low [9]. The VIR soybean collection includes 7,000 accessions of cultivated soybean, with 2,500 accessions in the Krasnodar Territory characterized as early- matured (maturing for a period of up to 110 days). Of these, more than 2,000 accessions from 43 countries of the world were tested in a field experiment in the Leningrad province. Only 400 accessions (from 33 countries) were able to form viable seeds under these conditions, indicating their weak PS and low heat requirements [6].

The PS coefficient is calculated as the ratio of the duration of the period from germination to flowering on a natural long day (LD) and the duration of the same transition on a short-day (SD). In a photoperiodic experiment performed in the Leningrad region, the PS coefficient varied from 1.0 to 2.4 (LD length can reach up to 18 h 46 min, while SDs last for 12h.). Of the 94 accessions studied, 35 had the lowest PS (1.0 to 1.15). These include the Svetlaya variety, which was created in the Ryazan region, and the experimental accessions PEP 17 and PEP 18, which were created in the Leningrad region as a result of repeated selections [12].

Genes that determine soybean early – maturity

To date, researchers have identified 12 loci that control the time of flowering and maturation in soybean: *E1–E11* and *J*. *E1*, *E2*, and *E3* were first described in the 1970s [13, 14], *E4* and *E5* in the 1980s [15, 16], *E6* and *J* in the 1990s [17, 18]. At the beginning of the 2000s, the *E7* gene was described [19], while the *E8*, *E9*, and *E10* genes were later described from 2010 to 2017 [20–24]. *E11* was reported only recently, in 2019 [25]. Their loci on the chromosomes have been mapped [26].

The alleles of *E1–E4*, *E9*, and *E10* genes have been characterized and the molecular mechanisms of their functions have been described [24, 27, 28].

In 2010, the genome of the soybean (*G. max*) American variety Williams 82 was sequenced. It is contained in 20 chromosomes ($2n = 40$). The soybean genome size is 1115 Mb [29], with 85% of the base pairs annotated. About 78% of the genes are located in the distal regions of the chromosomes, which represents less than half of the entire genome but is responsible for almost all genetic recombination.

Sequencing revealed that soybean are paleopolyploid. The genome of the hypothetical soybean ancestor underwent two genome-wide duplications 59 and 13 million years ago, causing almost 75% of the genes to have several copies in the genome. Homologous blocks containing an average of 75 genes (8 to 1377) are noted in two or three chromosomes, with most genes having a homologous copy. Besides duplication, the soybean genome underwent diversification, gene loss, and numerous chromosomal rearrangements, resulting in a present genome organized as in diploid organisms [30]. Wild soybean (*G. soja* Sieb. et Zucc.) is paleopolyploid, with its genome differing from cultivated soybean by no more than 0.31% [31]. These duplication and diversification events in the genome are thought to have paved the way for the emergence of flexible and diverse phenotypes related to flowering onset under various environmental conditions.

In addition to annotated genes, numerous quantitative trait loci (QTLs) that control the timing of flowering and maturing have been identified. In the 1990s, the relationship of certain QTLs with the temporal regulation of soybean maturity was established [32, 33], with some of these QTLs possessing pleiotropic effects on flowering, maturing, and morphological traits [34]. These efforts were continued in the first decade of the 21st century, which revealed the QTLs that were critical in determining the timing of flowering and maturing [35] and other pleiotropic effects by QTLs binding to chromosome sites was shown, as well as dependence of different traits (time of maturation, seed pigmentation, cleistogamous pollination in buds) from the same QTLs [36–42]. Other studies have shown the ability to compare genes of PS and QTLs determining the flowering and maturing time [43–45]. It has been shown that different QTLs can perform similar control of flowering time in varieties of different origin [46–49]. The main QTL that determines the delay of flowering in wild soybean has the same effect in cultivated varieties (in interspecific cross-breeding) [50]. The corresponding QTLs for the gene extending the juvenile stage were also identified [51].

The set of genes that control flowering time is evolutionarily conserved. Using the model plants *Arabidopsis* and *Oryza*, great progress has been made in understanding the mechanisms that control flowering in response to

seasonal changes in day length and temperature [52–54]. For *Arabidopsis*, a database has been created that includes more than 300 genes that regulate flowering time [55]. In the soybean genome, 844 genes were identified through their homology to *Arabidopsis* genes and candidate genes were revealed for QTLs that control flowering [26, 56, 57]. Analyses of nucleotide polymorphism were used to develop allele-specific markers for genotyping *E1–E4* [58–62], *E7* [63], *E8* [64], *E9* [22], *E10* [24, 65], and *J* [66, 67] (Fig. 1).

These genes and QTLs have different effects on soybean flowering and play various roles in the photoperiodic response [68, 69]. Their interactions with each other and the environment strongly influence the temp of flowering and maturing, morphology, productivity, and tolerance to stressors. The vegetation period is the total time of plant development and is divided into the vegetative and reproductive stages. The duration of these individual stages varies with temperature and photoperiod [70, 71]. These indicate that adaptation to the place of cultivation involves fine-tuning of the soybean genetic apparatus. To precisely coordinate the soybean agricultural cycle to the duration of plant development specific to a local climate, it is necessary to take advantage of the genetic variability available in the gene pool.

In 2010, an atlas of the soybean transcriptome was created [72], cDNA of 57,352 genes from 14 different soybean tissues were sequenced, revealing tissue-specific differences in the expression levels of various genes. The soybean gene expression atlas is used in comparative studies with plant model organisms, such as *Medicago truncatula* Gaertn., *Lotus japonicus* (Regel) K. Larsen, *Arabidopsis thaliana* (L.) Heynh. [73].

Molecular genetic mechanisms that determine the time of flowering and maturation in soybean

Dominant alleles at the *E1–E4*, *E7*, *E8*, and *E10* loci delay flowering and maturation, while dominant alleles at the *E6*, *E9*, *E11*, and *J* loci, on the contrary, promote early flowering.

***E1* gene.** Among the identified genes, *E1* exhibits the most pronounced effect on the initiation of flowering [28, 68, 74]. It is located on chromosome 6 and encodes a legume-specific transcription factor containing a B3 domain that acts as a repressor of flowering. Six *E1* alleles, *e1-as*, *e1-fs*, *e1-n1*, *e1-re*, and *e1-p* [27, 28], have been identified. Two of these, *e1-n1* and *e1-fs*, are non-functional alleles associated with early flowering under LD conditions [27, 75]. On the other hand, the effects of *e1-re* and *e1-p* alleles on flowering have not been determined [28]. Non-functional *E1* alleles were intensively selected in the northern latitudes of Asia, particularly in northern and northeastern China and northern USA [27, 76].

In a study by Z.Xia et al. [27], accessions with the *e1-as* allele exhibited a flowering period intermediate

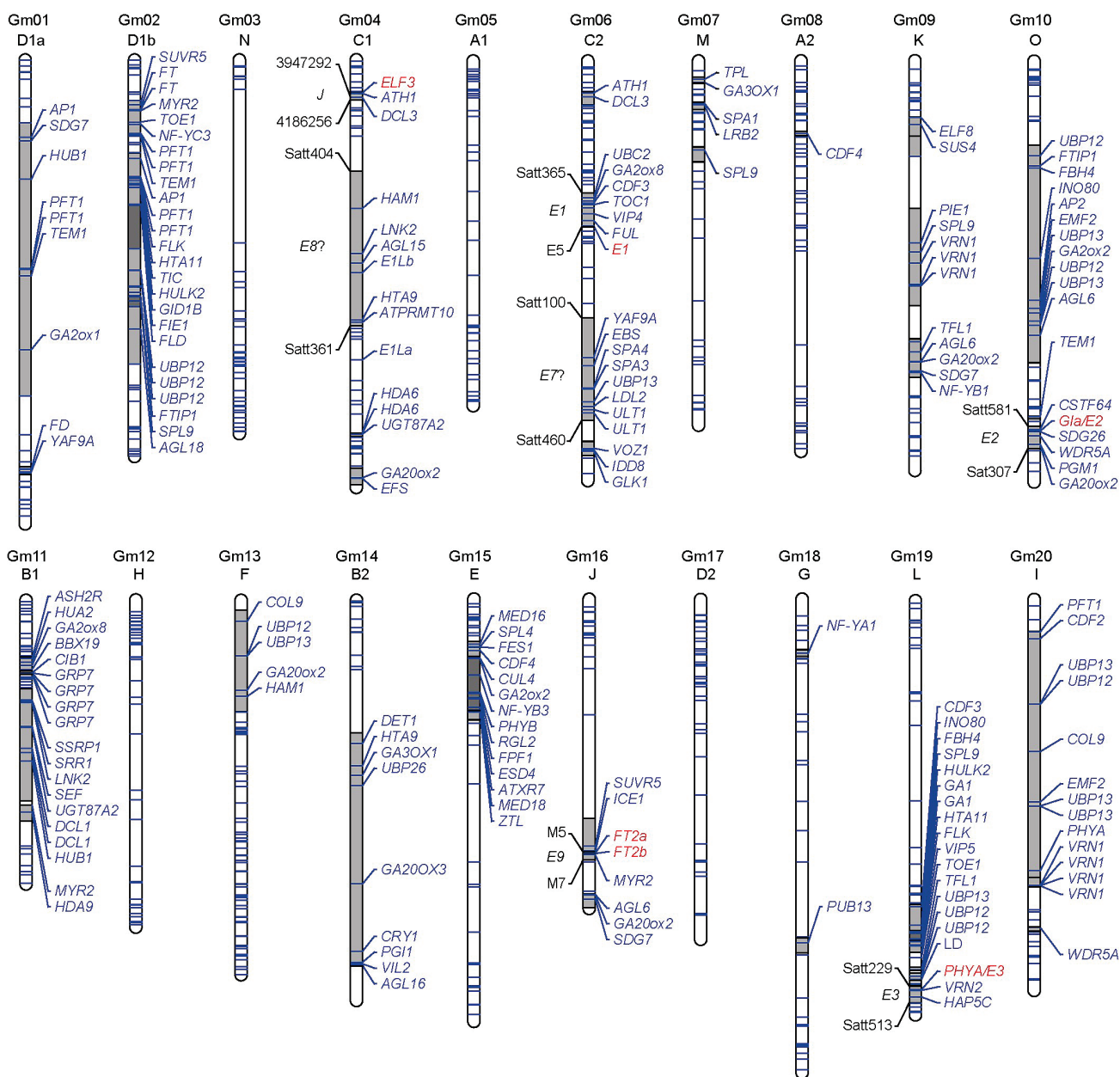


Fig. 1. The distribution of candidate genes that determine the onset of flowering and associated QTLs in the soybean genome. Columns represent soybean chromosomes. Areas containing QTLs are marked in gray, whereas darker areas indicate overlaps between different QTLs. The *E1*, *E2*, *E3*, *E7*, *E8*, *E9*, and *J* loci are on the left side of the chromosomes, with the corresponding molecular markers in black. Question marks next to the loci indicate that the corresponding genes for these QTLs remain unknown. The blue lines on the chromosomes indicate the position of the soybean orthologs of flowering genes in *Arabidopsis*. Orthologs located in the QTL are labeled as *Arabidopsis* gene symbols in blue, and red letters denote the characterized genes corresponding to the QTL (according to Zhang et al., 2017 [26]).

between the active *E1* and the inactive *e1* alleles. Thus, *e1-as* was determined as partially preserved *E1* allele function. The partially functional *e1-as* allele has consistently been detected in early- and mid- matured cultivars (MG000–MGIV), including cultivars adapted to northern latitudes [77].

In the soybean genome, two *E1* homologs were revealed (*E1-La* and *E1-Lb*). These are located in the centromeric region of chromosome 4, a region homologous to chromosome 6. The *E1-L* genes inhibit flowering by downregulating *FT* (*Flowering locus T*) gene.

The *E1-L* genes expression exert weaker effects than *E1* [78]. The non-functional *e1-lb* allele carries a single nucleotide deletion in the coding region and determines insensitivity to photoperiod independently of the *E1* gene. This allele is present among varieties of the Russian Far East that are weakly sensitive to photoperiod [79].

The expression of *E1*, *E1La*, and *E1Lb* are activated under LD conditions and strongly inactivated under SD. SD-induced down regulation of these genes depends on the duration of the dark phase. This interruption leads to gene reactivation and, as a result, late flowering [27, 78, 80].

In *Arabidopsis* and *Oryza*, *E1* homologs have not been identified [27]. Meanwhile, the *E1* homolog in *M. truncatula* (*MtEL1*) was shown to inhibit flowering but another homolog in *Phaseolus vulgaris* L. (*PvE1L*) does not affect blooming [81].

E2 gene. *E2* is the second most important gene for regulating the PS of flowering. It is one of three soybean orthologs of the *Arabidopsis* *GIGANTEA* gene (*GmGla*, *GmGlb*, and *GmGlc*) [60]. *GmGla* (*E2*) is involved in the regulation of the circadian rhythm and flowering processes, causing late flowering during LD [60, 82].

The recessive allele *e2-ns* has a nonsense mutation, resulting in a premature stop codon. In varieties with the *e2e2* genotype, a response to light exposure was noted. This can be interpreted as a compensatory function of the other orthologs or the non-involvement of *E2* in the light-sensitive control of photoperiodism [78]. In population genetic studies done in China, three *E2* haplotypes (non-functional *H1* and functional *H2* and *H3*) were identified in both *G. max* (*GmGla*) breeding varieties and *G. soja* (*GsGla*) wild soybean accessions. The *H1* haplotype bears a stop codon in exon 10 and is the most common haplotype in China [82]. This haplotype showed the greatest effect in early flowering and may have contributed to the spread of the domesticated soybean.

E3 and E4 genes. The *E3* and *E4* genes encode the phytochrome A isoforms *GmPhyA3* and *GmPhyA2*. These control flowering at high and low red light to far red (R/FR) ratios, respectively. High R/FR ratios occur under direct sunlight, while low R/FR ratios occur at dusk, sunset, and sunrise or under a shade. A high R/FR value under LD conditions increases the effects of *E3* alleles, while a low R/FR activates *E4* [19, 58, 59, 83]. Non-functional alleles of the *E3* and *E4* loci emerged recently and independently in different East Asian soybean cultivars [61, 84].

The dominant alleles *E3* and *E4* activate the expression of *E1* and cause late flowering under both SD and LD conditions. The recessive alleles *e3* and *e4* control insensitivity to LD and lead to an increase in the expression of *FT* genes, which contributes to flowering under LD [58, 59, 78].

GmPHYA4, *E3* homolog, and *GmPHYA1*, *E4* homolog, are genes in the phytochrome A (*PHYA*) family that have been identified in the soybean [26, 58, 59, 85]. Their functions are not completely understood. Inactive *GmphyA1* alleles have been shown to control photoperiod insensitivity under LD conditions [58, 86].

E5 locus. The *E5* locus slows down flowering and maturation during LD [16]. Based on QTL analysis, *E5* shares a similar location as *E2*. When mapping the *E5* locus, the F_2 population did not split in an expected manner, casting doubt on the existence of the *E5* gene and supporting the argument that it is merely *E2* [87].

E6 and J loci. The *E6* and *J* loci are mapped on chromosome 4 and are closely linked [66, 67, 88]. The dominant *E6E6* genotype codes early flowering and maturation. The mechanisms of *E6* function are poorly understood and a candidate gene has not yet been identified. The *E6* locus downregulates *E1* expression, affecting the active *E1* allele more than the *e1-as* allele. In turn, the *E6* activity depends on the active *E1* allele (that is, the dominant *E1* allele has an epistatic effect on *E6*). In plants with the *e1-ts/e1-fs* genotype, the *E6*-mediated control over flowering is lost [22, 88].

The *J* locus is an ortholog of the *Arabidopsis* *Early Flowering 3* (*ELF3*) gene [66, 89]. *ELF3* is a highly conserved plant nuclear protein that is crucial in maintaining circadian rhythms and controlling flowering time in several species, including *Arabidopsis* and various crops. In LD plants, such as *Arabidopsis*, the *ELF3* gene delays flowering by indirectly downregulating the key flowering activator *FT* and its main targets [90]. In comparison, *ELF3* induces flowering in SD plants by decreasing the expression of key *FT* repressors (primarily *E1* in soybean).

The active *J* allele controls early flowering of soybean. The inactive allele *j* is responsible for the LJ trait, which is characterized by late flowering and high productivity under SD conditions. *J* has six non-functional alleles, *j1–6*, and two weak alleles, *j7–8*. The *ELF3* protein binds to the *E1* gene promoter and represses *E1* transcription. This weakens the repression of two important *FT* genes (*GmFT2a*, *GmFT5a*) and promotes early flowering under SD conditions. When the *J* allele is attenuated, *E1* expression becomes unrepressed, resulting in *FT* downregulation and a prolonged vegetative phase. *J* functions in the signalling cascade downstream of *E3* and *E4*. In turn, phytochrome proteins *PHYA* (*E3*, *E4*) downregulate *J* expression in SD [66].

E7 locus. *E7* is a late flowering and maturation locus. However, it has the weakest effect on delayed flowering. It was identified under LD condition, with the *E7E7* plants characterized by late flowering. *E7* has been mapped to chromosome 6, 6.2 cM away from the *E1* locus [19, 26]. Markers for the *E7* locus are *Satt100*, *Satt319*, and *Satt460* [63]. This region contains eight homologs of flowering genes, including two homologs of *SPA1*, a key regulator of the *PHYA* signal transduction pathway. These two homologs, *Glyma06G241900* and *Glyma06G242100*, are presumed to be candidates for the *E7* gene [26].

E8 locus. The *e8* locus contributes to the inhibition of flowering. Varieties with the *E8E8* genotype exhibit late maturation, while varieties with inactive *e8e8* alleles are characterized by early – maturation. *E8* is mapped to the pericentromeric region of chromosome 4 [26, 65]. This region contains six flowering genes, including the homolog of the *E1* gene (*E1Lb*). These genes are suitable candidates for *E8*. This region also contains the QTL

responsible for the duration of the reproductive period (QTL 3–4, QTL 2–2), whose phenotypic expression can be influenced by *E8* [20, 78].

E8 may also be associated with the expression of the *qRP-c-1* locus, located in a small region of 1.8 cM in the C1 linkage group between the markers *Sat_404* and *Satt136*. The closest marker to both loci is *Sat_085* [20, 38], which, in turn, is closely associated with the *GmCRY1a* gene [91, 92]. *GmCRY1a* controls the production of cryptochromes, which presumably mediate light-regulated plant development and growth and is involved in the regulation of soybean flowering onset [93]. Therefore, *qRP-c-1* is most probably associated with *GmCRY1a* and plays an important role in soybean development during the reproductive period [45].

***E9* gene.** *E9* causes early flowering and maturation. It was mapped to chromosome 16 and identified as an ortholog of the Arabidopsis *FT* (*GmFT2a*) gene. In Arabidopsis, *FT* is a key flowering activator. Soybean has twelve *FT* homologs [94, 95]. Six of these genes have been experimentally shown to activate flowering in the *ft*-mutant of Arabidopsis. Their expression profiles vary by tissue and growth stage, indicating their functional specialization during soybean flowering.

Two of these homologs, *FT2a* and *FT5a*, were studied for their role in photoperiod changes. *GmFT5a* promotes early flowering in LD, while *GmFT2a* promotes early flowering in SD [94–96]. Different levels of *FT2a* and *FT5a* co-expression directly regulate the natural variation in soybean flowering time [96]. A total of 17 polymorphic sites were revealed in *GmFT2a* (10 SNPs, 2 insertions, 5 SSRs). In early-matured varieties, three alleles were identified (*FT2a-TO*, *FT2a-HA*, *FT2a-HY*). The *FT2a-TO* allele has a 10-bp deletion in the 5'-UTR promoter region, and SNP do not affect expression levels. In the first intron, an insertion of the SORE-1 retrotransposon weakens gene expression and delays flowering [22]. CRISPR-induced mutants of *GmFT2a* show delayed flowering under both LD and SD conditions [97]. Thirteen *GmFT5a* haplotypes and seven *GmFT2a* haplotypes were identified, of which *GmFT5a-Hap2/GmFT2a-Hap2* plants exhibited the earliest flowering [96]. Nevertheless, flowering induction by FT proteins can start regardless of the amount of *GmFT2a* and *GmFT5a* transcripts.

The *GmFT2a* and *GmFT5a* photoperiod responses occur via distinct mechanisms. *GmFT2a* expression is strictly regulated by photoperiodic changes and is activated immediately in SD. In contrast, *GmFT5a* expression changes in response to the photoperiod are gradual. *GmFT5a* expression is initially retained at a low level, even under conditions of LD and is activated only later during development [21, 94].

Products of *GmFT2a* and *GmFT5a* have florigen-like functions, i.e., they accelerate the onset of flowering. The *GmFT2a* and *GmFT5a* proteins interact with the bZIP

GmFDL19 transcription factor, which can bind to the ACGT cis-element of the *GmAP1* promoter. Furthermore, the FT/FD complex triggers the transformation of the vegetative meristem into the floral meristem by activating the expression of the flower formation gene homologs *APETALA1* (*GmAP1*) and *LEAFY* (*GmLFY*) and *GmSOC1*. The soybean homolog *GmAP1* is expressed in the flower, especially in the sepals and petals. *GmFDL19* may function as a key component in the photoperiod-regulated flowering pathway controlled by *GmFT2a* and *GmFT5a*. Expression of *FT2a* and *FT5a* is regulated by the *E1* locus (PHYA-mediated photoperiod-dependent regulation, E1-PHYA pathway) and its homologs (*E1La*, *E1Lb*), which, in turn, are controlled by the *E3* and *E4* loci [23, 27, 78, 94].

Under LD conditions, *E2* inhibits *FT2a* expression, probably through the GI-Co pathway, resulting in late flowering. Soybean has 26 *Co*-like genes (*CONSTANS*), of which four (*GmCOL1a*, *GmCOL1b*, *GmCOL2a*, *GmCOL2b*) have the greatest sequence similarity with Arabidopsis *Co*-genes [23]. *GmCOL1a* and *GmCOL1b* are key activators of flowering in SD, while they increase the expression of *GmFT5a* in the morning hours and are repressors in LD [98]. The mechanisms of GI-Co module function in the regulation of *FT* genes are poorly understood. *E2* was shown to have no influence on the expression of *GmFT5a*. Thus, *GmFT2a* and *GmFT5a* show both similarities and differences in their regulatory pathways [96, 98].

The *GmFT1a* gene is expressed in leaves and is activated under LD conditions to inhibit flowering and maturation [50]. It supports vegetative growth in soybean, an effect that is diametrically opposed to that of *GmFT2a* and *GmFT5a*.

The *GmFT2b* gene has a high homology with *GmFT2a*. Its overexpression promotes flowering under LD conditions, while the inactive allele inhibits flowering only under LD conditions. For *GmFT2b*, 4 haplotypes (Hap1–4) were identified, with Hap3 showing the earliest flowering. *GmFT2b* activates *GmFT2a* and *GmFT5a* under conditions of LD [99].

Recently, a clear role of *GmFT2b-ox* in accelerating the onset of flowering in soybeans was demonstrated under LD conditions [99]. It has been posited that this stimulating effect occurs by upregulating the flowering activating genes *GmFT2a/2b*.

***E10* locus.** The *E10* locus was mapped to chromosome 8. A candidate gene, *FT4*, was revealed in the *E10* locus [24]. *FT4* is expressed in parallel with *E1* but functions downstream of *E1* as a repressor of soybean flowering [100]. It is activated by LD, resulting in late flowering, while it is blocked under SD conditions, resulting in early flowering.

Several SNPs in the *FT4* gene were identified between the recessive and dominant alleles in introns, 5'-UTR (GM08:44608620), 3'-UTR (GM08:46607056), and exon 4.

The exon 4 SNP (*E10*: ACT, *e10*: ATT) results in the replacement of threonine by isoleucine. This amino acid substitution is located very close to the outer loop encoded by exon 4 and affects protein function. This substitution in the *FT* and *TFL1* genes (flowering end gene) has been observed in all flowering plant species [101]. This substitution in the inactive *e10* allele induces early flowering. However, the *e10e10* genotype was rarely detected in 300 Canadian early matured soybean accessions and the mechanisms contributing to their flowering have not been identified [24].

***E11* locus.** The *E11* locus induces early flowering and maturation under LD conditions. It plays an important role in the regulation of flowering, independent of *E1*. It was mapped to chromosome 7. Possible candidate genes were identified as *Glyma07g48500*, *Glyma07g049000*, and *Glyma07g049200*, homologs of *LHY* (*LATEELONGATEDHYPOCOTYL*), *CURT1B* (*CURVATURETHYLAKOID1B*), and *MTP3* (*METALTOLERANCEPROTEIN3*) of Arabidopsis, respectively [25].

Identification of QTLs that affect the timing of flowering onset

There are several pieces of evidence that document the role of QTLs in regulating soybean flowering onset [38, 40, 102]. There is a possibility that some of the detected QTLs and known *E1* [41, 102], *E3* [42, 43], *E4* [42], *E7* [44], *E11* [25], and *LJ* [51] genes are identical. Soybean QTL data are stored in the SoyBase database [103].

The QTL *qDTF-J* was detected on chromosome 16, near the *GmFT5a* locus, and contains *ef* (early flowering), a rare allele that occurs in both cultivated and wild soybean populations. It activates the expression of *GmFT5a* under conditions of LD, regardless of the allelic state of the *E1* locus. It contributes to the adaptation of soybean to northern latitudes. Presumably, the *GmFT5a* gene may be a candidate for *qDTF-J* [104].

The *GmPRR37* gene (qFT12-2) on chromosome 12, a homolog of the Arabidopsis *APRR7* gene, is involved in the regulation of flowering time. In LD, the *GmPRR37* gene downregulates *GmFT2a* and *GmFT5a* and activates *GmFT1a*, leading to a delay in flowering. However, it does not affect the expression of the *J* (*GmELF3*), *E2* (*GmGla*), *GmCOL1a*, and *GmCOL1b* genes in LD. CRISPR/cas9-induced knockout of this gene resulted in early flowering during LD. During SD, there were no phenotypic differences in flowering time observed between active and inactive alleles. Furthermore, *GmFT2a*, *GmFT5a*, *GmFT1a*, *J* (*GmELF3*), *E2* (*GmGla*), *GmCOL1a*, and *GmCOL1b* gene expression are unaffected in SD. Among Chinese varieties, accessions with recessive alleles that carry a non-sense mutation in the CCT domain are characterized by early flowering [105].

Key genes and QTLs that control flowering time often have pleiotropic effects on other agriculturally important

traits, such as plant height and productivity [37, 39, 65], degree of self-pollination [42], pigmentation, and cold stress-induced seed coat cracking [41, 106]. A recent study identified new loci that act in a non-pleiotropic manner, namely *R1-1* on chromosome 9, which controls flowering, and *R8-1* and *R8-2* on chromosomes 13 and 18, respectively, which control maturation. However, *R1-1* also overlapped with QTLs controlling other agronomic traits. The pleiotropy of flowering and maturing may be genetically separate; however, artificial selection during soybean cultivation may have favoured pleiotropic loci such as *E*, which control both flowering and maturation processes [107].

In total, 228 QTLs controlling PS have been registered in soybean [25, 51, 88, 103]. The genetic system that determines the flowering time involves complex QTL-gene networks that include a number of biological processes that are directly or indirectly related to flowering time [108].

Promising genotypes for soybean northing

Graphical models have been proposed to describe the transition from vegetative to reproductive development in soybean [99, 109]. In these models, the *E1* locus acts as a photoperiod-dependent modulator that can upregulate the expression of flowering inhibitor genes (*GmFT1a* and *GmFT4*) and downregulate the expression of flowering activator genes (*GmFT2a* and *GmFT5a*). Figure 2 presents our own modification of these models.

In soybean, genetic control of flowering time has been used in classical breeding programs for many years and is important for the effective creation of varieties that can thrive in higher latitudes, mainly in Northeast China, Northern Russia, and North America [11, 65, 110].

Soybean cultivars adapted to northern latitudes are known to be weakly sensitive to the photoperiod, which is determined by various combinations of mutant alleles at the *E1*, *E2*, *E3*, and *E4* loci [11, 28, 62, 111].

Active alleles in the *E1*–*E4* loci were consistently observed in mid- and late- matured accessions. Recessive alleles *e1*–*e4* were more common in early – matured varieties developed for the northern parts of cultivation areas [77, 88, 112]. Photoperiod sensitivity decreases as the number of recessive alleles is increased. When comparing different genotypes, *E1/E2/E3/E4* showed maximal PS, *e1-as/E2/E3/E4*, *e1-as/e2/E3/E4*, and *e1-as/e2/e3/E4* genotypes exhibit decreased PS. In the *E1/e2/E3/E4*, *e1-as/E2/E3/E4*, and *E1/E2/E3/E4* genotypes, the non-functional *e1* allele reduces the PS more significantly than the non-functional *e2* allele, indicating a more profound role of *E1* in controlling flowering time [112].

Three allelic combinations have been identified, which determine the decrease in PS, namely *e2/e3/e4*, *e1/e3*, or *e1/e2/e4*, *e1-as/e2/e3/E4*. Among low-sensitivity genotypes, the variant with two inactive alleles *e3* and *e4*,

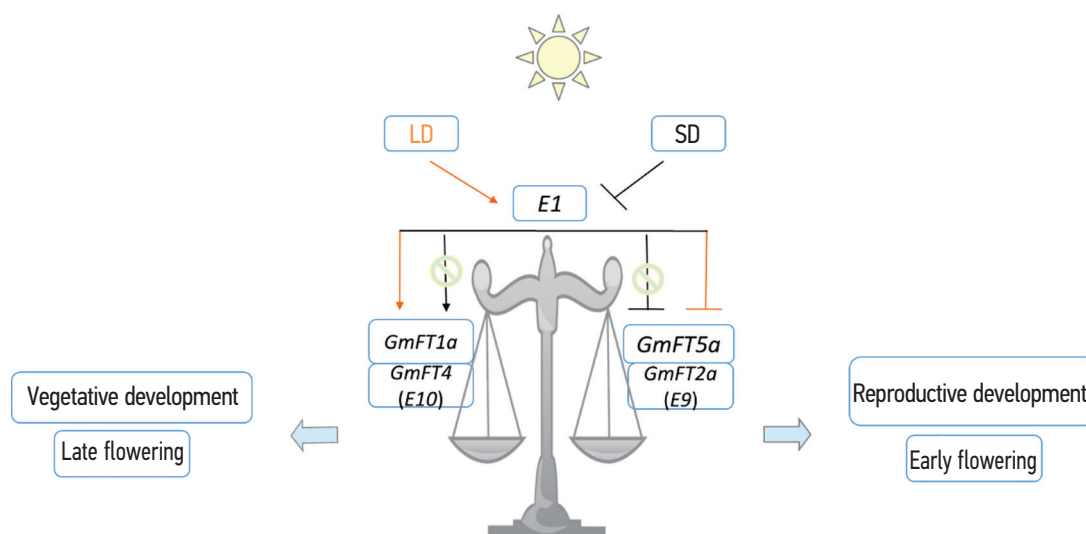


Fig. 2. Regulation of the transition from vegetative phase to reproductive phase in soybean during long days (LD) and short days (SD). Arrows: stimulation of gene expression. Gray T-shaped arrow: inhibition of gene expression. Crossed-out black arrow: absence of gene stimulation. Crossed-T-shaped line: absence of gene inhibition. Black T-shaped line: no effect of SD. Broad arrows: over all influence of genes on plant development

was the most common; i.e., the dysfunction of phytochrome PHYA proteins is probably the most crucial mechanism of photoperiod insensitivity in soybean. Non-functional alleles of *E1* play a similar role in attenuating or deactivating the photoperiodic responses regulated by the *E3* and *E4* alleles.

Among the analysed accessions insensitive to the pre-bloom photoperiod, inactive alleles were generally observed in the *E3* or *E4* loci (*e3* and *e4*). If one of these alleles was active (*E3/E4*), then the inactive allele *e1-fs/e1-nl* or hypomorphic allele *e1-as* was always revealed in the *E1* locus. In the case of the active *E1* allele, it was in combination with inactive *e3* and *e4*. For the *e1-as/e2/e3/E4* allele combination, photoperiod insensitivity is determined by unknown genes [62]. Thus, the photoperiod-insensitive Japanese variety Sakamotowase has the same genotype as the isogenic line of the variety Harosoy, NIL-*e3, e1e1e2e2e3e3E4E4* [113]. However, unlike Sakamotowase, NIL-*e3* does not form buds under LD conditions since the non-functional *e1* allele in the presence of the functional *E4* allele cannot induce photoperiod insensitivity [86]. Based on the differences between Sakamotowase and NIL-*e3*, it was suggested that there is another locus that functions independently or jointly with the *e1* allele to promote the flowering of soybean with the *e1e1e2e2e3e3E4E4* genotype under LD conditions [44, 62, 114].

In several studies, early-matured accessions have the same duration of vegetation period but differed in the duration of their reproductive periods [11, 62]. It was suggested that post-flowering photoperiodic responses play the most important role in the maturing of soybean seeds under LD conditions and that the duration of the reproductive stage is rather independent of the time of flowering [11, 115, 116].

Photoperiod responses during the flowering and maturation stages are controlled by the phytochrome-coding (PHY) *E3* and *E4* loci, whereas the *E1* and *E2* loci have a significant effect on the pre-flowering phase. The *E3* and *E4* genes also activate the expression of the *Dt1* gene (in the dominant state, which determines the indeterminate type of growth) at the stage after the onset of flowering. This leads to an increase in the time of pod formation, the number of nodes and pods per shoot, and the formation of a longer main shoot [62]. Thus, the *E3* and *E4* loci are of great importance for increasing soybean productivity.

Varieties with the same *E1–E4* genotypes differed in flowering time and maturing rate. This suggests either the contribution of other *E* loci to these differences or may be due to the influence of environmental factors, such as temperature [117]. In varieties grown in relatively northern latitudes, *E3* and *E4* have opposite effects on the rate of maturation, probably due to low average temperatures. The active *E3* allele activates maturation but slows down the onset of flowering, *e3* promotes flowering. *E4* slows down maturing, but both *E4/e4* alleles in the heterozygote do not affect flowering [11]. Among photoperiod-insensitive lines, the temperature has been suggested to play an important role in the regulation of *GmFT2a* expression. The expression of *GmFT2a* in the photoperiod-insensitive Heihe 27 cultivar was significantly higher at high temperatures and under LD conditions. For cultivars sensitive to the photoperiod, on the contrary, high temperature suppressed *GmFT2a* expression [118].

Thus, we can conclude that the genotypes with the largest number of inactive alleles (*e1, e2, e3, e4, e7, e9*) provide the earliest flowering and maturation in relatively

northern areas with LD. Combinations of *e9(FT2a-TO)/e1-nl/e2/e3/e4* alleles can be considered the best genotype for soybean selection under LD conditions [28, 77, 88, 119]. The replacement of functional *E3E3* and *E4E4* alleles with non-functional ones, which can be achieved by marker-based selection and site-directed mutagenesis, can be a promising approach for the northing of soybean varieties with the most common genotypes *e1e1e2e2E3E3E4E4*, *e1e1E2E2e3e3E4E4*, and *e1e1E2E2E3E3E4E4* [120].

CONCLUSION

Over the past decade, significant progress has been made in elucidating the molecular-genetic mechanisms underlying the photoperiod-dependent regulation of flowering and maturation in soybean. From the Williams 82 variety genome sequence, the critical genes and QTLs associated with flowering and maturation times were identified. However, the precise mechanisms of gene-QTL networks have not been fully elucidated. Experiments are currently being performed around the world to determine the PS of soybean genotypes grown in various photoperiodic and temperature regimes at different latitudes, as well as in simulations of different day lengths. A specific gene pool has been identified, which is characterized by a reduced PS, early flowering, and maturation.

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A hypothetical genotype optimal for northern latitudes was proposed, namely *e9(FT2a-TO)/e1-nl/e2/e3/e4*.

Future studies to better understand the regulatory mechanisms controlling PS and flowering time in soybean are warranted. Further characterization of identified soybean genes and search for novel loci are needed. Findings from these studies can help optimize highly adapted and productive varieties for different local conditions and can help expand the soybean gene pool to promote its cultivation in northern regions.

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