Plant Breeding WILEY

Photoperiod trait: Insight in molecular mechanism for growth and maturity adaptation of soybean (*Glycine max*) to different latitudes

Sanjay Gupta[1] | Giriraj Kumawat[1] | Nisha Agrawal[1] | Rachana Tripathi[1] | Vangala Rajesh[1] | Vennampally Nataraj[1] | Shivakumar Maranna[1] | Gyanesh K. Satpute[1] | Subhash Chandra[1] | Milind B. Ratnaparkhe[1] | Manoj K. Srivastava[1] | Nita Khandekar[1] | Meeta Jain[2]

[1]ICAR- Indian Institute of Soybean Research, Indore, Madhya Pradesh, India

[2]Devi Ahilya Vishwavidyalaya, Indore, Madhya Pradesh, India

Correspondence
Sanjay Gupta, Principal Scientist, ICAR-Indian Institute of Soybean Research, Indore, Madhya Pradesh, India.
Email: sanitaishu@gmail.com

Communicated by: Ram Singh

Abstract

Soybeans cover a vast geographical region of 53°N to 40°S latitudes, but individual genotypes have a very narrow latitudinal adaptation of ∼200 km due to photoperiodic limitations. Fourteen soybean maturity groups (MG0000-X) of Northern America have genotypes adapted to very long (MG0000) to short (X) day length conditions. Photoperiod not only affects flowering but other agronomic traits also. Several maturity genes have been mapped, and 12 genes related to the photoperiodic network (*E1, E2, E3, E4, J, FT2a, FT5a, Tof5, Tof11, Tof12, Tof16* and *Tof18*) have been functionally characterized. The role of the paralogues of functionally characterized genes (*E1Ls, COs, PRRs, FULs, SOCs* and *FTs*) is being recently elucidated. Allelic diversity at photoperiodic loci confers latitude specific adaptation. Molecular models (common allelic combination present in an MG) have been developed for different MG using *E* genes but require refining by the addition of other functionally characterized genes to fully explain the flowering and maturity, especially in MG V to X. Three interacting modules *PHYA-E1, GI-CO* and miRNA-dependent have been developed to elucidate the flowering mechanism in soybean.

KEYWORDS
flowering, latitudes, maturity, phenology, photoperiod, soybean

1 | INTRODUCTION

Optimum time for transition from vegetative to reproductive phase to produce progenies in conductive environmental conditions is crucial for survival of plants species. In response to environmental cues, photoperiodism and vernalization are major reactions in plants responsible for this switch. Induction of flowering in response to prolonged photoperiod and low temperatures (vernalization) ensures development of seed in the environment suitable for their survival (Dennis & Peacock, 2009). Garner and Allard (1920) for the first time

described that many plants flowers in response to changes in day length. They demonstrated that some plant species promote flowering when day length falls below a critical day length (short-day plants), whereas other plants accelerate flowering in response to day lengths longer than a critical day length (long-day plants). While obligate photosensitive, they do not flower till they are exposed to inductive day length, the quantitative photosensitive delay flowering. Day length is greatly affected by latitudes and seasons (Figure 1). While the day length remains constant at equator, it increases with latitudes. Although photoperiodism is a survival mechanism, yet it becomes an
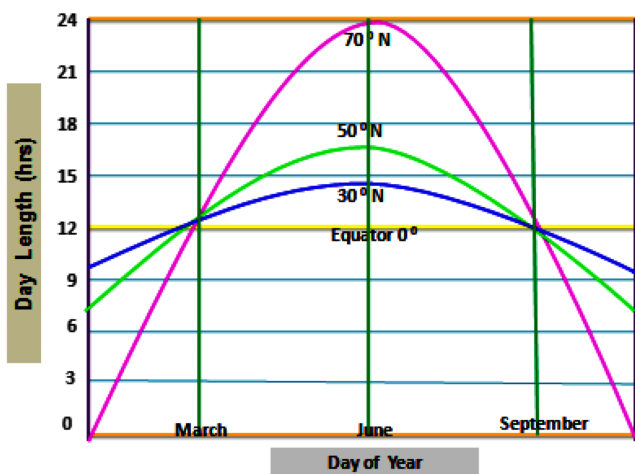
FIGURE 1 Association of day length (hours) with the day length at latitudes [Color figure can be viewed at wileyonlinelibrary.com]

abiotic stress when plant species are introduced in new geographical area or season. For example, when genotype of a short day species from higher latitude area is introduced in short day conditions of lower latitudes, they would flower too early with little biomass and economic yield. Similarly, introduction of genotypes from lower latitude areas in higher latitudes would result in delayed flowering accompanied with excessive vegetative biomass and probable death of plants due to extreme frost conditions later in the season. Soybean is a quantitative photosensitive short day crop. Flowering in soybeans is induced after 5–7 days of exposure to the day length which is shorter than their critical day length (CDL) (Destro et al., 2001; Garner & Allard, 1920; Noggle & Fritz, 1983; Watanabe et al., 2012; Whigham & Minor, 1978). A soybean genotype flowering in 12 h/days in inductive day length conditions may take up to 16 h/days to flower under non-inductive conditions or may not flower at all (Cober & Curtis, 2003). Soybean has originated from its wild ancestor *Glycine soja* in longer photoperiodic and temperate climatic regime of China (Hymowitz, 1970). The crop has adapted from 53°N to 40°S latitudes (Fang et al., 2021). The day length variation in these latitudes varies from 12 h (equator) to 15–16 h (40–50°) during soybean growing seasons. Although soybean as a crop has adapted to such a large latitudinal zone, its individual genotypes adapt to a very narrow latitudinal band of 200 km (Scott & Aldrich, 1983). When genotypes adapted to northern region are grown in southern regions, they flower sooner with less vegetative growth and have lower yield. Conversely, genotypes of higher latitudes when grown in northern regions often flower late in the growing season and do not mature before a killing frost (Lin et al., 2021). Therefore, to solve this contradiction between early maturity and high yield in southern regions, and facilitate designing and breeding of high yielding cultivars, understanding of genetic and molecular mechanism regulating photoperiodic flowering and maturity is imperative (Luo et al., 2022).

Maturity and photoperiodic genes has been the most studied subject in soybean. This article reviews the identification of photoperiodic nature of the crop, inheritance of photosensitivity and identification of loci governing the traits. Moreover, the review focuses on the identification of molecular markers and assigning genes to the photoperiodic loci, genes characterization, correlating multi-allelic combinations of photoperiodic genes with geographical distribution of the crop, molecular pathways and utilizing this trait in breeding programmes.

2 | EFFECT OF PHOTOPERIOD ON SOYBEAN PHENOLOGY

Garner and Allard (1920) were the first to demonstrate the effect of day length on soybean (*Glycine max* [L.] Merr.) flowering. Four soybean varieties, namely, 'Mandarin' (early), 'Peking' (medium), 'Tokyo' (medium) and 'Biloxi' (late), were planted at frequent intervals throughout the growing season and also grown under partially controlled conditions in Washington, DC. In early planting, these cultivars required about 25, 55, 65 and 95 days, respectively, for attaining the flowering stage. These durations were reduced to 25–35 days under artificially shortened day length in mid-summer in field and in naturally shortened days of winters in warm greenhouse. They also conducted an experiment in which these varieties were successively planted at 4–6 days duration from 16 May to 18 August. It was found that the vegetative period shortened due to reduced day length in all the varieties except Mandarin and plant heights were always greater in early sowings. In all, except the very early variety Mandarin, the effects of temperature and length of day on late spring and early summer plantings were additive, both the rising temperature and the decreasing day length favoured earlier flowering with advance of the season. In mid-summer, the average temperature seems to be near the optimum, and only the length of the day acts as a major limiting factor. After mid-summer, when the average temperature begins to fall, effect of day length and temperature on flowering becomes contrast, the former tends to hasten flowering and the latter delays it. In case of Mandarin, neither day length nor temperature was an important limiting factor in mid-summer, while in spring and early fall, temperature was the only primary factor. They concluded that the differences in behaviour of soybean varieties with respect to time of flowering are due primarily to length of day while the relatively low temperatures of late spring and early fall exercise a retarding influence on the flowering stage in both the very early and the very late plantings of all varieties.

Role of darkness in photoperiodic induction and genotypic differences for light duration for flowering were established in a number of studies (Borthwick & Parker, 1939; Hamner, 1940). Very long photoperiods (16–18 h) could also induce flowering if a dark period of 16 h is given in each cycle after photoperiods (Hamner, 1940). During 1950s and 1960s, a number of evidences suggested that floral induction is mediated by an endogenous rhythm with periods of approximately 24 h (Bunning, 1958, 1959, 1960a, 1960b; Bunsow, 1960; Hamner, 1940, 1958, 1960). Nanda and Hamner (1958) and Blaney and Hamner (1957) showed the rhythmical response of photoperiod

on floral bud initiation in soybean. They found that among the seven photoinductive cycles of 8 h of photoperiod followed by the dark period the maximum floral induction response was in 24, 48 and 72 h cycles and the least in 36 and 60 h cycles. Based on their results, they concluded that flowering response is influenced to a marked degree by some endogenous rhythm of 24 h duration and cooler temperatures affect this rhythm. It became evident that photoperiodic perception occurs primarily in leaves (Cajlachjan, 1936) and the most effective leaf on the plant for photoperiodic stimulation is the one that has most recently attained its full size (Borthwick & Parker, 1940). They demonstrated that grafting of stems, splice grafting of petioles, splice grafting of stems and bud from flowering varieties initiated and maintained flowering in non-flowering varieties (Heinze et al., 1942).

All of the phenological stages are affected by photoperiod in soybean (Guthrie, 1972). Seed size is reduced in Harosoy due to longer photoperiod, but another variety 'Acme' was insensitive (Guthrie, 1972). Shorter (11:40 h) and longer (13:20 h) photoperiods produced less pods (Huxley et al., 1976). Patterson et al. (1977) reported that delay of photoinduction in 'Ransom' cultivar resulted in enhanced yield due to more axillary nodes. In determinate cultivars, photoperiod mainly affects pre-flowering phase, while in indeterminate cultivars, it affects duration of flowering and maturity (Hodges & Doraiswamy, 1979). Thomas and Raper (1976, 1978) demonstrated that photoperiod not only affects flowering but pod setting, dry matter partitioning and seed weight also. Short photoperiods given on expansion of the paired primary leaves increased pod setting in the cultivar 'Ransom' (Thomas & Raper, 1976). Morandi et al. (1988) observed the effect of photoperiod on pod lengthening and seed filling duration in addition to flowering. Han et al. (2006) found that post-flowering photoperiod not only regulates reproductive development but also affected vegetative growth. Even when flowers and pods were removed, short-day (SD) treatment promoted leaf senescence. They proposed that the regulation of photoperiod on development of soybean was effective from emergence through maturation, and the post-flowering photoperiod signals were also mediated by phytochromes similar to those before flowering. Cober et al. (1996b) demonstrated that it is not only the photoperiod but the quality of light also affects the soybean flowering. Using different types of lamps for generating 20 h long photoperiodic regime, they showed that decreased Red (R): Far-red (FR) delayed the flowering. Kantolic and Slafer (2007) showed that duration of the R3–R6 period, pod and seed number increases in response to the extension of photoperiod. Zhang et al. (2001) reported that photoperiod length and treatment duration affects soybean floral bud initiation and floral bud development in a quantitative way. The exposure to long photoperiods from R3 to R5 (beginning of seed growth) increased the duration of R3–R6 regardless of the timing of exposure (Kantolic & Slafer, 2007). The stages of development comprised in the R3–R6 phase were delayed by current as well as by previous exposure to long days (LD). A positive relationship was found between seed number and the duration of R3–R6, irrespective of the timing and length of exposure to the long photoperiod.

3 | IDENTIFICATION OF MATURITY LOCI IN SOYBEAN

Photoperiodic genes were initially identified as flowering and maturity loci. In soybean, 12 loci have been reported to control time to flowering and maturity: *E1* and *E2* (Bernard, 1971), *E3* (Buzzell, 1971), *E4* (Buzzell & Voldeng, 1980), *E5* (McBlain & Bernard, 1987), *E6* (Bonato & Vello, 1999), *E7* (Cober & Voldeng, 2001), *E8* (Cober et al., 2010), *E9* (Kong et al., 2014), *E10* (Samanfar et al., 2017), *E11* (Wang et al., 2019) and *J* (Ray et al., 1995). Among these genes, Xia et al. (2012) reported that *E7* is not a separate locus but an allele of *E1*. Recently, *E6* has been identified as an allele of *J* locus (Fang et al., 2021). Photoperiod directly affects *E1*, *E3* and *E4* loci which in turn interact with *E2*, *E9* and *J* for regulating flowering and maturity response. Recently, several *time of flowering* (*Tof*) loci have been reported other than earlier known *E* loci (Dong, Cheng, et al., 2021; Dong, Fang, et al., 2021; Fang et al., 2017; Kou et al., 2022; Lu et al., 2020).

Woodworth (1923) for the first time identified a gene controlling plant height and maturity and reported the dominance of tall and late forms over short and early ones. Owen (1927) and Woodworth (1932) assigned it the name of *E* locus and found its linkage with the pubescence colour on linkage group I. A number of studies on *E1* locus described its effect and sources for dominant and recessive alleles (Hanson, 1961; Haque, 1964; Johnson et al., 1960; Johnson & Bernard, 1962; Matsuura, 1933; Morse & Cartter, 1937; Van Schaik & Probst, 1958; Weiss, 1949; Woodworth & Williams, 1938). Weiss (1970) reported its linkage with pubescence colour and chlorophyll deficiency on linkage group I. Bernard (1971) identified two independent gene pairs (*E1* and *E2*) which affected time of flowering and maturity when brought in a common genetic background (Clark) by backcrossing. Distinguish *e1E2* and *E1e2* were transferred to Clark from T175 and T245, respectively. Both of these genes had codominance, and flowering and maturity in isolines Clark (*E1E2*) and Clark (*E1e2*) were delayed by 23 and 18 days and nine and one day, respectively. Flowering and maturity was hastened by seven and 14 days in Clark (*e1e2*), respectively. Wilcox and Schapaugh (1978) also reported 14 days of early maturity in Clark-*e2*.

Buzzell (1971) studied the inheritance of flowering time under long-day conditions in the greenhouse using natural day length extended to 20 h with cool-white fluorescent light and identified a single major gene with two alleles (E3/e3) to control the flowering response in a cross between sensitive (Harosoy 63) and insensitive (Blackhawk) parents. The dominant allele conferred fluorescent-sensitive delayed flowering response and later maturity in field condition. The recessive allele conferred an insensitive response and resulted in earlier maturity which was confirmed by Bernard and Weiss (1973) under field conditions. Kilen and Hartwig (1971) also found the segregation of one gene in F$_2$s developed from fluorescent sensitive and insensitive parents, and Bernard and Weiss (1973) suggested that this was probably the same gene that Buzzell (1971) had reported. Buzzell (1971) and Bernard (1971) confirmed this suggestion and also demonstrated that *E2* and *E3* are different loci. In 1980, Buzzell and Voldeng, using a similar experimental design as the *E3* study,

screened more varieties under 20 h incandescent light exposures, and discovered another locus, *E4*, while *e4* is observed in fluorescent insensitive varieties, and *e3e4* is found in incandescent insensitive varieties (Voldeng & Saindon, 1991).

In the classical work, Cober et al. (1996b) correlated photoperiodic response and maturity alleles (*E1*, *E3*, *E4*) using different light qualities created by using red (R) and far red (FR) lamps in Harasoy isogenic lines. They showed that decreased R:FR had maximum photoperiodic response resulting in later flowering. *E1* allele required an R:FR approximating that of natural daylight for response to long days, and it was the most sensitive locus among three loci. Since the sensing of the R:FR ratio is the function of phytochrome protein in light-grown plants and *E1*, *E3* and *E4* responded differentially to changes in light qualities, they presumed that these loci are either part of phytochrome family of genes or have some close relation with them. Indeed, *E3* and *E4* genes were later found to encode *Phytochrome A* (Gm*PhyA3* and Gm*PhyA2*) and discussed later in the review.

McBlain and Bernard (1987) identified a new early maturity recessive allele while transferring dense pubescence trait (Pd1) to Harosoy from PI 80837. The new locus was designated as *E5*, and the genetic effect of *E5* on time to flowering and maturity was similar to that of *E2*. However, in a study by Dissanayaka et al. (2016), utilizing Harasoy and Clark isolines and also in original population in which *E5* was identified, no QTL related to this locus was found, and they suggested that the earlier reported effect is probably due to interaction of alleles at *E2* loci and no separate locus exists for *E5*.

J locus was identified by Ray et al. (1995) while studying the delayed flowering under short day conditions (long juvenility) in four near-isogenic pairs (NIPs). NIPs were developed using conventional juvenile and long juvenile parents (PI 159925) and were differed only at juvenility loci. A single recessive allele (*j*) from PI 159925 conferred this trait. Similarly, a single recessive locus controlling long juvenile trait was concluded by Villarroel and Kilen (2009); Tisselli (1981), Carpentieri-Pipolo et al. (2014), Yue et al. (2017), Lu et al. (2017) and Gupta et al. (2021). Bonato and Vello (1999) and Destro (1991) studied the inheritance of long juvenility in the two natural mutants (Paranagoiana and SS-1) of the cultivar 'Parana' and concluded that mutation occurred at the same locus and designated this locus as *E6*. In contrast to *E1*, *E2*, *E3* and *E4*, where dominant alleles conferred delayed flowering and maturity, the dominant alleles at *E6* and *J* loci hasten these responses. However recently it was confirmed that *e6* is an allele of *J* locus (Fang et al., 2021).

Cober et al. (2010) consistently detected a new maturity locus in F_2, F_3 and F_4 generations of the cross of Maple Presto with its early maturing backcross derived line. They transferred this gene to Harosoy background and the isolines were nine and six days earlier in Maple Presto and Harosoy background, respectively. This gene was named as *E8*, and it added a new MG of 000 to the existing MG 00 to MG X. Although the role of this locus in photoperiodic regulation has not been revealed till now but its ability to reduce days to maturity

and to extend MG classification to MG 000, make it a candidate for the same.

Liu et al. (2007) developed RILs between determinate and early maturing TK780 (*Glycine max*), and indeterminate and late flowering and maturing *G. soja* accession Hidaka 4 and identified two QTLs for maturity on LG C2 and LG J. Kong et al. (2014) fine mapped the QTL on LG J and reported the *E9* locus with earliness being conferred by dominant allele.

Wang et al. (2019) consistently detected a QTL on chromosome 07 in a RIL population derived from a cross between Minsoy and Archer and named this locus as *E11*. Same as the *J* and *E9*, NILs for *E11* were significantly earlier in flowering and maturity than *e11* NILs.

In addition to these loci identified through classical breeding, comparative genomics of soybean with Arabidopsis flowering genes has shown the role of other genes like *FT2a*, *FT5a*, *GmmiR156b*, *PRR*, *FUL* in regulation of photoperiod regulated flowering (Jung et al., 2012; Kim et al., 2012; Lu et al., 2020; Sun et al., 2021; Watanabe et al., 2012). These genes and their role in photoperiodic flowering and maturity are described in gene characterization section.

4 | ASSOCIATING CLASSICAL PHOTOPERIODIC LOCI WITH CHROMOSOMES

Since 1990, many of the reports described the construction and integration of molecular (mostly) and classical linkage maps (Cober et al., 1996a; Keim et al., 1990; Lark et al., 1993; Mansur et al., 1996; Palmer & Hedges, 1993; Rafalski & Tingey, 1993; Shoemaker & Specht, 1995). In a major breakthrough, Cregan et al. (1999) for the first time mapped 606 SSR markers in three populations and developed a consensus set of 20 linkage groups (LG). In another classical work, Yamanaka et al. (2000, 2001) used a F_2 population from the cross of Misuzudaizu and Moshidou Gong 503, in which for the first time they identified QTLs for flowering time using a RFLP (from expressed sequence tags) and SSR linkage map of 190 F_2 plants. These studies identified four flowering QTLs *FT1*, *FT2*, *FT3* and *FT4*. All of the 4 QTLs contributed to 88% of the total phenotypic variance for flowering. Since *E1* and T (4 cM) were linked in classical linkage maps and placed on LG C2, where *FT1* also mapped, *E1* was inferred to correspond to *FT1*. Cregan et al. (1999) positioned *E2* maturity locus on LG O which was positioned on LG 15 + 25 in Yamanaka's linkage map. Cregan et al. (1999) and Yamanaka et al. (2001) could putatively show that *E2* corresponds to *FT2*. Cober et al. (1996a) reported that *E3* is mapped at a distance of 27.52 ± 3.23 cM from the growth habit locus *Dt1*. While Yamanaka et al. (2001) map the nearest marker for *FT3*, Satt373 was mapped at a distance of 37.4 cM from *Dt1* which suggested that *FT3* putatively corresponds to *E3*. Abe et al. (2003) hybridized 'Ohyachi 2' (*e3e3e4e4*), and the ILD-sensitive line, 'Harosoy-e3' (*e3e3E4E4*) and reported the segregation for *E4* with its linkage to Enp

TABLE 1 Details of photoperiodic genes with tagging markers

Gene ID	Orthologue	Cross combination	Location	Nearest marker	Gene function	References
E1 (Glyma06g23040)	B3 DNA binding protein and putative bipartite nuclear localization signal	Misuzudaizu × Moshidou Gong 503 (early)	Gm06; linkage group C2	Satt365, Satt557	Flowering and maturity	Bernard (1971); Watanabe et al. (2004); Xia et al. (2012)
E2 GmGla,(Glyma10 g36600)	GIGANTEA (GmGla)	Misuzudaizu (early) × Moshidou Gong 503	Gm10; linkage group O	138GA26	Flowering.	Bernard (1971); Watanabe et al. (2004); Watanabe et al. (2011)
E3 (Glyma19g41210)	Phytochrome A3(GmPhyA3)	Misuzudaizu × Moshidou Gong 503 (early)	Gm19; linkage group L	Satt229	Flowering	Buzzell (1971); Watanabe et al. (2009)
E4 (Glyma10g28170)	Phytochrome A2(GmPhyA2)	TK780 (TK) × Hidaka 4 (H4)	Gm20; linkage group I	Satt354	Flowering	Buzzell and Voldeng (1980); Liu et al. (2008)
E5		Harosoy × L64-4830	Gm10; linkage group O		Maturity	McBlain and Bernard (1987)
E6/J (Glyma04g050200.1/ Glyma04g05280)	ELF3	Paranagoiana × SS-1, Paranagoiana × (Harosoy) PGO (Paranagoiana × OT94-47)	Gm04; linkage group C1	Sat_337 and Satt396	Long juvenile	Cairo et al. (2002, 2009); Lu et al. (2017)
E7	-	-	Gm06; linkage group C2	Satt319	Maturity	Cober and Voldeng (2001); Molnar et al. (2003)
E8	GmCRY1a	-	Gm04; linkage group C1	Sat_404 and Satt136.	Maturity	Cober et al. (2010); Watanabe et al. (2012)
E9 (Glyma16 g26660)	GmFT2a	JS 93–05 × AGS 25	Gm16; linkage group J	Satt215 and Satt431, BARCSOYSSR_16_1015 and BARCSOYSSR_16_1017	Long juvenile	Kong et al. (2014),
E10(Glyma08g47810)	Flowering locus T (GmFT4)	OT98-17 (Maple Presto isoline) and OTO2-18 (Harosoyisoline)	Gm08; linkage group A2	Satt429, Satt538 and Satt378	Maturity	Samanfar et al. (2017)
E11 (Glyma07g48500)		Minsoy (PI27890) × Archer (PI54687)	Gm07;linkage group M	ID7079 and ID7088	Flowering	Wang et al. (2019)
Tof5	FRUITFULL (FUL)	-	Gm05; linkage group A1	GWAS	Flowering	Dong, Cheng, et al. (2021)
Tof11 & Tof12 (Glyma.U034500 & Glyma.12G073900)	PSUDO-RESPONSE REGULATOR (PRR)	Zigongdongdou × Heihe27	Gm11 & Gm12; linkage group B1 & H	GWAS	Flowering and maturity	Lu et al. (2017, 2020); Wang et al. (2020)
Tof16	LATE ELONGATED HYPOCOTYL (LHY)	-	Gm16; linkage group J	GWAS	Flowering	Dong, Fang, et al. (2021)
Tof18	SOC1	-	Gm18	GWAS	Flowering and stem node number	Kou et al. (2022)

(endopeptidase isozyme) located on LG 4. SSR markers Satt239 and Satt496 were identified as linked markers to *E4* (Abe et al., 2003). Molnar et al. (2003) used the isogenic lines for maturity in the genetic background of Harasoy, Maple Arrow and Maple Ambre and confirmed the location of *E1* and *E3* loci on C2 and L linkage groups and located *E4* and *E7* to LG I and C2, respectively.

A long juvenile (LJ) accession PI159925, which showed delayed flowering in short day condition was used to map LJ locus *J* between the SSR markers Sat_337 and Satt396 on chromosome 04 (Cairo et al., 2009; Lu et al., 2017). Yue et al. (2017) used a RIL population developed from the cross Zhonghuang 24 (Conventional juvenile) x Huaxia 3 (LJ) for mapping the LJ trait and identified a QTL on chromosome 04 (LG C1) to which *J* locus was previously mapped. A new locus for delayed flowering *E6*, was mapped near *J* locus (Lu et al., 2017), which was later confirmed as an allele of *J* (Fang et al., 2021; Nissan et al., 2021). Against *E6* and *J*, which have been identified by involving LJ and conventional juvenile parents, another flowering locus *E9* was mapped to LG J between Satt215 and Satt431, through QTL analysis of early flowering trait (Kong et al., 2014). Cober et al. (2010) mapped *E8* between Sat_404 and Satt136 on chromosome C1, and Samanfar et al. (2017) mapped *E10* on LG A2 near SSR markers Satt429, Satt538 and Satt378. Wang et al. (2019) mapped *E11* on chromosome 7 in a RIL population derived from a cross between Minsoy and Archer. Through fine mapping they delimited the QTL region to 40.1 kb between BARCSOYSSR_16_1015 and BARCSOYSSR_16_1017 markers (Tables 1 and 2).

5 | CHARACTERIZATION OF GENES INVOLVED IN PHOTOPERIODIC REGULATORY PATHWAY

5.1 | *E1*, *E1La* and *E1Lb* genes

The major flowering locus *E1* (*FT1*) was located on LG C2 (Yamanaka et al., 2000, 2001, and Yamanaka et al. (2005) fine mapped this locus using novel strategy of residual heterozygous lines (RHL) developed using Misuzudaizu and Moshidou Gong 503 as parents. Through fine mapping, *FT1* was narrowed down between satt365 and GM169 separated with recombination distance of 1.5 cM. Using positional cloning in population derived from crossing two *E1* NILs, Harosoy-*E1* (*E1e2E3E4e5*) and Harosoy-*e1* (*e1e2E3E4e5*), Xia et al. (2012) delimited the *E1* locus to 17.4 Kb region and identified *E1* as an intron free gene. The *E1* encodes a putative transcription factor which contains a putative bipartite nuclear localization signal and a region distantly related to B3 domain. They demonstrated that *E1* expression was significantly suppressed under short-day conditions and showed a bimodal diurnal pattern under long-day conditions, suggesting its response to photoperiod and its dominant effect induced by long-day length. Xia et al. (2021) demonstrated that the main effect of *E1* is to delay flowering under long day condition through negative regulation of *GmFT2a* and *GmFT5a*, two homologues of *FLOWERING LOCUS T* that promote flowering in Arabidopsis (discussed below). *E1*genes have four allelic forms, out of these two are, that is, *e1-nl* (lack 130 kbp region harbouring the entire gene) and *e1-fs* (single base

TABLE 2 Photoperiodic genes with gene ID, exons and amino acid encode

Gene name	Gene ID	Sequence (in bp)	Number of exons	Amino acid encode
E1	Glyma06 g23040	.525/447 bp	1 Start-20007207 End-20007654	149 aa
E2	Glyma10 g36600	22.5/21,357 bp	14 Start-44716808 End-44738165	1178 aa
E3	Glyma19g41210	10.1/8,957 bp	4 Start-47511095 End-47520052	1131 aa
E4	Glyma10g28170	5.5/4,655 bp	4 Start-36963843 End-36968498	1131 aa
E6	Glyma04g05280	4,383 bp	4 Start-4026874 End-4031257	715 aa
E9	Glyma16 g26660	4,964 bp	4 Start-31109999 End-31114963	177 aa
E10	Glyma08g47810	1,720 bp	4 Start-46606934 End-46608654	176 aa

deletion that cause a frameshift mutation that generates a premature stop codon). The conventional dominant allele *E1* differs from recessive allele *e1* (now designated as *e1-as*) which has single amino acid substitution in the putative nuclear localization signal that suppresses the nuclear localization of the protein. Two paralogs of *E1*, *E1La* and *E1Lb*, are present in soybean (Xia et al., 2012; Xu et al., 2015). The expression patterns of these two genes are also similar to that of *E1* under both long and short day conditions. Like *E1*, both genes function as inhibitors of flowering (Xu et al., 2015). Zhu et al. (2019) identified a novel non-functional allele of *E1-Lb* in the Far-Eastern Russian soybean cultivar 'Zeika' (ZE) and supported the findings of Xu et al. (2015). A missense mutation in the *E1La* gene which led to the change of lysine to glutamate at position 82 (e1la:k82E) in 15 *G. soja* and two *G. max* accessions (Dietz et al., 2021). They also identified S34R missense mutation in the *E1Lb* gene of two *G. soja* accessions and *e1lb*:Del variant in 'Williams 82' fast neutron mutant lines. It was demonstrated that in the background of *e1-as*, the lines fixed for *e1la*:K82E and *e1lb*:Del had 4–5 days of early flowering as compared to the reference alleles *e1-as* and *E1L*a. *e1la*:K82E and *e1lb*:Del alleles had the maturity hastening effect of 24 and nine days, respectively.

5.2 | *E2* gene

Watanabe et al. (2011) used RIL population derived from two varieties, Misuzudaizu (Mi) and Moshidou Gong 503 (Mo) and identified RIL 6–8 which was heterozygous at *FT2* locus. From this RHL, they identified two NIL: 6–8-*FT2* and -*ft2* and found that flowering time difference between these two NILs was highly significant. Using these NILs, they could restrict *FT2* to 94 Kbp regions on Gm10, where nine annotated genes (*Glyma10g36580–36,670*) were predicted. One of these genes, *Glyma10g36600*, with a high level of similarity with the *GI* (*Gigantea*) gene, was considered a strong candidate for the *FT2* locus, since the loss of function of *GI* is known to cause drastic changes in the flowering phenotype of other plant species (Fowler et al., 1999; Hecht et al., 2007). They could isolate two *GI* genes (*GmGIa* & *GmGIb*) from the RNA sample extracted from leaves of NILs 6–8-*FT2*. *GmGI* genes isolated from the Mo late-flowering allele (*GmGIa-Mo* and *GmGIb-Mo*) were found to encode proteins consisting of 1,170 and 1,168 amino acids, respectively. The coding sequence of *GmGIa* was extended to a 20-kbp genomic region and contained 14 exons. Compared to *GmGIa-Mo*, the Misuzudaizu early-flowering allele, *GmGIa-Mi*, showed four single nucleotide polymorphisms (SNPs) in its coding sequence. One of these SNPs, detected in 10th exon, introduced a premature stop codon mutation that led to a truncated 521 amino acid GI protein in the *GmGIa-Mi* allele. This stop codon mutation was considered a candidate for a functional nucleotide polymorphism in *GmGIa*. They showed that *e2/e2* genotype caused early flowering by inducing the expression of the soybean florigen gene homologue, *GmFT2a*, while the effect of the *E2* allele on flowering under different environments was stable.

5.3 | *E3* gene

Watanabe et al. (2009) used RHL strategy to identify *E3* gene in the same population that was used for identifying *FT1*, *FT2* and *FT3* QTLs (Yamanaka et al., 2000, 2001). The plants from RIL heterogeneous for this region, designated as RHL1-146, generated NILs1-146-*FT3* and -*ft3* from their progeny. By fine mapping, they could identify a physical region carrying *FT3* locus which contained 11 genes. Based on the suggestion of Yamanaka et al. (2001) that maturity locus *E3* is identical to *FT3*, and Cober et al. (1996b) that *E3* gene shows a larger effect under fluorescent light and has some relation with photoreceptor, one of the gene highly similar to that encoding phytochrome A was considered to be the gene responsible for the *FT3* locus. Using RACE, full length sequence of *Phytochrome A* gene was obtained and named as *GmPhyA3*. *GmPhyA3* obtained from Misuzudaizu (*FT3*) was found to encode a protein composed of 1130 amino acids. A BLAST search found that *GmPhyA3-Mi* displayed normal features of phytochrome A, including a chromophore-attached domain, two PAS domains, and a histidine kinase domain as conserved domains. However, *GmPhyA3* obtained from Moshidou (*ft3*) carried a large insertion in the fourth intron and one single nucleotide polymorphism (SNP) for a non-synonymous amino acid substitution in the third exon. Three dysfunctional alleles of *E3*, *e3-ns*, *e3-fs* and *e3-tr* were reported by Xu et al. (2013). In which allele with deletion mutation in *E3-tr* that lacks the three regions of the gene including exon 4, *E3-fs* is a frame-shift mutation that introduces a stop codon in exon 1, and *e3-ns* is a nonsense mutation in which a single nucleotide substitution in exon 3 creates a stop codon in place of a codon encoding glutamine.

5.4 | *E4* gene

Gene underlying *E4* was identified as *GmPhyA2*, a homologue of *phytochrome A* (Liu et al., 2008). At the recessive *E4* locus, insertion of a Ty1/copia-like retrotransposon in the exon 1 of the *GmphyA2* gene resulted in dysfunction of this gene (Liu et al., 2008). Tsubokura et al. (2013) identified four (*e4-kam*, *e4-oto*, *e4-tsu* and *e4-kes*) recessive alleles of *E4*. Both, *E4* and *E3*, have homeologs in the soybean genome, which are named as *GmPhyA2* and *GmPhyA3*, respectively.

5.5 | *E10* gene

Using genetic stocks and protein–protein interaction (PPI) analysis approach, Samanfar et al. (2017) characterized gene underlying *E10*. Candidate gene prediction and PPI identified that *FT4*, also known as *FTL8*, has the most interacting partners known to be involved in flowering and maturity. By PPI interaction, sequence analysis, SNP analysis and 2D-mRNA structure analysis, *FT4* was proposed as most probable candidate for *E10* (Samanfar et al., 2017).

5.6 | *FT2a* (*E9*) and *FT5a* genes

Flowering locus T (*FT*) gene family synthesizes a flowering compound 'Florigen' in leaf tissues which is transported to the shoot apex for floral initiation. A number of studies have reported that the overexpression of *FT* orthologs induces very early flowering in dicots and monocots (Hayama et al., 2007; Hsu et al., 2006; Kojima et al., 2002; Lifschitz et al., 2006; Yan et al., 2006), and florigen has been shown as essential for flowering with conserved functions among unrelated species. Based on the sequence similarity with Arabidopsis *FT* genes, Kong et al. (2010) identified 10 *FT* homologues arranged in five pairs (*FT1a* and *FT1b*, *FT2a* and *FT2b*, *FT3a* and *FT3b*, *FT5a* and *FT5b*, and *FT4* and *FT6*) in different homologous chromosomal regions in soybean. *GmFT2a* and *GmFT5a* showed diurnal expression in short day but not in long day condition. These genes were highly up and down regulated under short- and long-day conditions, respectively, by the two *PHYA* genes (*E3* and *E4*). The double-mutant soybean line (*e3/e4*) expressed *GmFT2a* and *GmFT*5a at high level under LD and flowered slightly earlier under LD than the wild type (*E3/E4*) grown under SD. Pot transfer experiments, involving the transfer of 10 short day grown plants to long day conditions, demonstrated no noticeable expression of *FT2a* but only a gradual reduction in expression of *FT5a* which remained conserved at a low level. The differential expression pattern of *FT2a* and *FT5a* suggests for a strict photoperiodic control of *FT2a*, but the involvement of some other mechanism also for *FT5a*. *FT2a* has been found to induce and maintain flowering in a model variety ('Zigongdongdou') for studying flowering reversion (Sun et al., 2011). Differential expression pattern of these two genes contribute to the adaptation of soybean to a wide range of photoperiodic environments. CRISPR/cas9 mutation work (Cai et al., 2018, 2019) supports the photoperiodic regulation by *FT2a* as the mutants flowered late under natural conditions (summer). Among other *FT* genes, *FT1a* inhibits flowering (Liu et al., 2018); *GmFT3a*, *GmFT4* and *GmFT6* do not have any relations with flowering, and *FT1b*, *FT2b*, *FT3b* (Su et al., 2022) and *FT5b* have some haplotypes associated with flowering and maturity (Jiang et al., 2019). Su et al. (2022) reported that there were no significant differences observed in flowering time among wild-type, *FT3b* overexpressors and mutant *ft3b* in long or short day conditions. However, the flowering genes *GmFUL1* (*a*, *b*), *GmAP1d* and *GmLFY1* were down-regulated in *ft3b* plants and the floral inducers genes *GmFT5a* and *GmFT5b* were highly expressed. It concluded that the redundant role of *FT3b* in flowering regulated that may be compensated by other *FT* homologues in soybean.

5.7 | *Tof5* gene

FRUITFULL (*FUL*) genes act downstream in flowering pathway genes and are known to have major roles in reproductive transition, floral meristem identity and floral organ identity (Jia et al., 2015). Four homologues of *FUL* were identified in soybean and expression analysis revealed that GmFULa was expressed in the floral meristem, floral organs and their primordia; trifoliate leaves; and the inflorescence

meristem, with the expression induced by SD and inhibited by LD (Jia et al., 2015). In contrast, Yue, Sun, et al. (2021) found one haplotype of the soybean homologue *GmFULa* (*GmFULa-H02*) dominant in cultivated soybeans and transgenic overexpression of *GmFULa* enhanced vegetative growth with more biomass accumulation but without affecting the plant height or changing the flowering and maturity. However, the expression studies revealed that *GmFULc* on chromosome 05 was induced by short days (SD) and promote flowering by inducing *FT*, *SOC1* and *LFY* (Sun et al., 2021). A *Time of Flowering 5* (*Tof5*) was also identified by genome wide association analysis of flowering time in higher latitudes on chromosome 05 (Dong, Cheng, et al., 2021). Candidate gene analysis identified that *Tof5* encodes a homologue of *FUL*. Flowering gene *E1* suppress *FUL* transcription by binding to its promoter, whereas *FUL* physically associates with *FT2a* and *FT5a* to upregulate their expression resulting in promotion of flowering under long days. Four haplotypes were identified for *Tof5*, of which *Tof5*[H1], a gain of function mutation, was under strong artificial selection and contributed to domestication of soybean in high latitudes (Dong, Cheng, et al., 2021).

5.8 | *Tof11*&*Tof12* genes

Fang et al. (2017) and Lu et al. (2020) identified two QTLs through genome wide association studies (GWAS) on chromosome 11 and 12 in panels of 809 and 424 accessions. In addition to GWAS studies bi-parental studies of Li et al. (2019), Lu et al. (2015, 2020) also identified two loci in these regions. These loci have been referred as *Tof11* and *Tof12* loci. In addition, *Glyma.12G073900* was the likely candidate gene underlying *qFT12-2* in a population of 308 RILs derived from a cross late flowering Zigongdongdou (ZGDD) and an early flowering Heihe27 (HH27) (Wang et al., 2020). Lu et al. (2020) refined the genomic locations of *Tof11* and *Tof12* in F_6 heterozygous inbred populations and reported them to putatively encode PSUDO-RESPONSE REGULATOR (PRR) proteins. Both of these genes encoded the full length proteins in H3 but not in Harasoy, and these results correlated with the late flowering and maturity to dominant allele of H3. Their results indicated that *PRR3a* and *PRR3b* are the genes responsible for *Tof11* and *Tof12* loci, and these genes are functionally independent. Lu et al. (2017, 2020) reported that *Tof11* and *Tof12* were detected only in sub-populations carrying functional *E1* allele and not in *E1*[nl] which implied the action of these genes through *E1*. The overexpression of *Tof11* and *Tof12* resulted in increased *E1* expression and reduced *FT2a* and *FT5a* expression. Expression studies of *E3/E4* NILs have demonstrated that these genes are partly under the control of two photoreceptors (Lu et al., 2020). In *Arabidopsis*, PRR proteins associate with the CCT binding motif CACGTG in promoter of two key circadian clock genes, *LATE HYPOCOTYL* (*LHY*) and *CIRCADIAN CLOCK ASSOCIATED 1* (*CCA1*) to reduce their expression (Nakamichi et al., 2012). Soybean genome has four *LHY/CCA1* homologues (*LHY1a*, *LHY1b*, *LHY2a* and LHY2b) which all have CCT promoter motifs and show lower transcript level in *Tof11* and *Tof12* line (Lu et al., 2020). The physical association of *Tof11* and *Tof12* with the

promoters of *LHY* genes was demonstrated through chromatin immune-precipitation-PCR assays and electrophoretic mobility shift assays. The functional significance of this association was demonstrated in a CRISPR-Cas9 quadruple knock down mutant (*lhy1a*, *lhy1b*, *lhy2a*, *lhy2b*) in Harasoy background. This mutant significantly delayed the flowering, relieved the transcriptional suppression of *E1* and reduced the expression of *FT2a* and *FT5a*. LHY was found to influence the expression by binding with AATATC motif in *E1* promoter. All of these experiments elucidated a new model for regulation of flowering in which *E3* and *E4* promote *Tof11* and *Tof12* expression whose proteins associate with the promoter of *LHY* genes and suppress their expression. The role of LHY proteins is to bind to the promoter of *E1* to suppress its transcription and in turn relieve the transcriptional suppression of two key soybean *FT* homologues. Lu et al. (2020) also proposed the key role of *Tof11* and *Tof12* in domestication of soybean. They hypothesized that *tof12* got incorporated first in domesticated soybean and reduced the flowering and maturity period and later *tof11* was selected in the background of *tof12* for development of very early maturing soybeans.

5.9 | *Tof16* gene

Tof16 was identified by genome wide association analysis of flowering time under natural SD conditions in accessions of lower latitudes (Dong, Fang, et al., 2021). Fine mapping and candidate gene analysis identified that *Tof16* is encoding a *LATE ELONGATED HYPOCOTYL* (*LHY*) gene. *Tof16* (*LHY1a*) directly binds to *E1* promoter and suppresses its expression, thereby relieving *FT2a* and *FT5a*. The soybean genome contains four *LHY/CCA1* homologues (*LHY1a*, *LHY1b*, *LHY2a*, and *LHY2b*) (Lu et al., 2020). Loss-of-function mutations of *LHY1a* in the Harosoy background showed significantly later flowering and maturity and improved overall grain yield relative to Harosoy (Dong, Fang, et al., 2021). Multiple mutant analyses showed that mutant combination *lhy1a/1b/2b* showed best plant architecture and higher yield under natural SD conditions. Four loss of function alleles were identified for *Tof16*, which were independently originated and selected in two important soybean growing areas of the tropics (Brazil and India).

5.10 | *Tof18* gene

A new flowering locus, *Tof18* was identified by resequencing and genome wide association analysis of flowering time under natural LD conditions in 349 soybean accessions (Kou et al., 2022). Candidate gene analysis of *Tof18* identified a *SOC1* homologue with conditions early flowering and lesser stem node number in LD as well as SD conditions. Of the two *SOC1* homologues present in soybean, *SOC1a* at *Tof18*, had shown stronger effect on time of flowering and stem node number compared to *SOC1b* (Kou et al., 2022). Double mutants of *SOC1a* and *SOC1b* showed stronger functional effect than either of the single mutants. Haplotype analysis revealed that *Tof18*[G] allele of

haplotype H2 have high frequency in genotypes of high latitude regions whereas *Tof18*[A] allele have higher frequency in genotypes of lower latitudes suggesting the role of *Tof18* in latitudinal adaptation of cultivated soybean. *SOC1a* and *SOC1b* bind directly to promoters of *FT2a* and *FT5a* and upregulates their expression in leaves and promotes flowering. *SOC1s* also regulates expression of several flowering associated genes in shoot apex and leaves (Kou et al., 2022). *SOC1a* and *SOC1b* physically interact with *Dt2* and the *SOC1s-Dt2* complex represses *Dt1* expression by binding to its promoter and thereby fine tune stem node number.

6 | MOLECULAR MATURITY MODELS

Considering the allelic variability of only nine characterized photoperiodic and maturity genes and their paralogs (*E1*, *E2*, *E3*, *E4*, *J*, *E9*, *FT5a*, *E1La* and *E1Lb*), there would be 211 diverse genotypic combinations for latitude specific maturity. Identification of suitable combination for specific niches for maximizing yield potential (molecular model) would help breeders develop highly adapted varieties in less time. A number of studies have reported the screening of varieties and germplasm of different maturity groups for *E1*, *E2*, *E3* and *E4* genes, and it was found that within the same MG a number of *E* gene combinations were present (Abugalieva et al., 2016; Jiang et al., 2014; Kurasch et al., 2017; Langewisch et al., 2014; Langewisch et al., 2017; Lu et al., 2015; Miladinović et al., 2018; Tsubokura et al., 2013, 2014; Valliyodan et al., 2016; Zhai et al., 2014). For example, Langewisch et al. (2017) predicted different frequencies of *E* gene combinations in 17,762 accessions using SoySNP50K (Figure 2). They conceptualized the idea of 'molecular maturity group' for the most common *E* genotype present in the MG. Based on their study they could provide the molecular model for MG 0-V as *e1-ase2 e3* for MG 0; *e1-as e2 e3*, *e1-as e2 E3* for MG 1; *e1-as e2 E3*, *e1-as E2e3* for MG II; *e1-as E2 E3* for MG III & IV and *E1 E2 E3* for MG V. Kurasch et al. (2017) evaluated 75 European cultivars from five early maturity groups (000 – II) at 22 locations in 10 countries across Europe and reported several haplotypes for the allelic variants at the *E1*, *E2*, *E3*, *E4* genes with each *E* haplotype comprising cultivars from different MGs. Screening of soybean genotypes and local varieties collected from high latitude cold region of Russia, northern part of Northeast China and the far-eastern region of Russia with reference to maturity group reference soybeans of MGs MG000, MG00, and MG0 identified varieties which matured even earlier than MG 000 and a new maturity group MG 0000 was proposed (Jia et al., 2014). Few studies have been conducted in soybeans of lower latitudes. Dos Santos et al. (2016) resequenced 28 Brazilian cultivars adapted to lower latitudes (5–8°S) and found six with dominant *E1*, *E2*, *E3* and *E4* alleles, nine with *e3* allele, two with *e1-as* allele and none with *e4* allele. So the molecular model, that is, the most popular genotypic group for whole India is *E1E2E3E4*. However, this molecular model is insufficient to describe the maturity differences in different zones of India. The discovery of new maturity loci *Tof5*, *Tof11*, *Tof12*, *Tof16*,
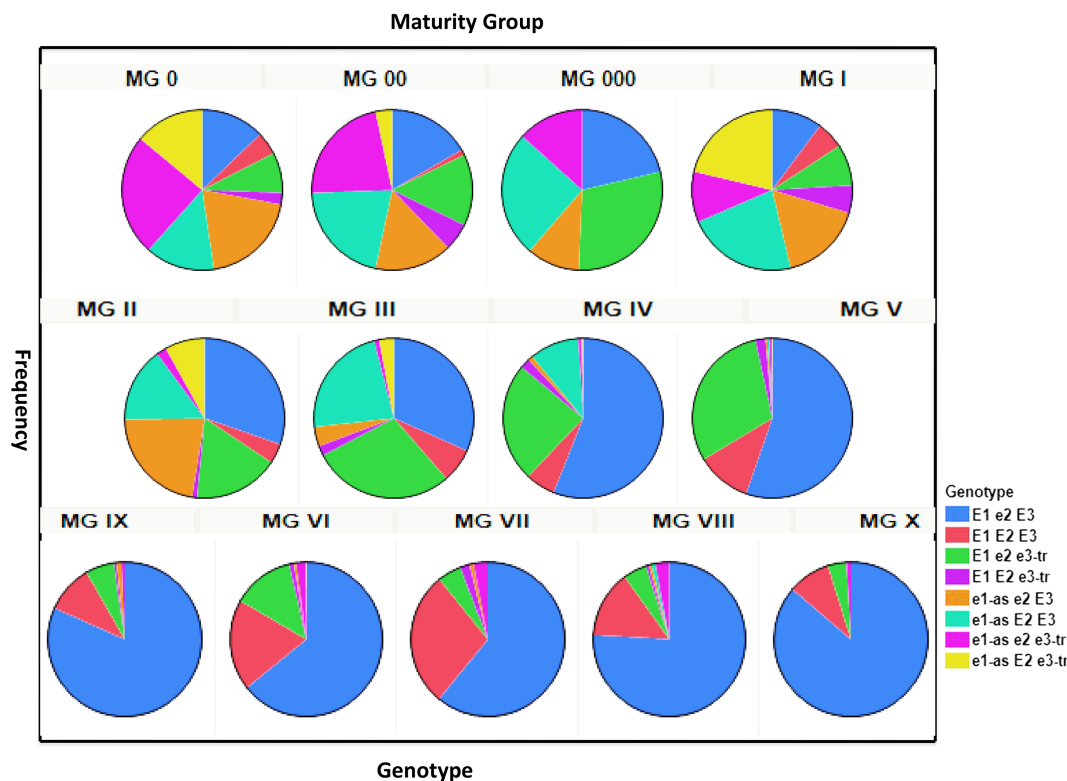
Maturity Group

FIGURE 2 Frequency of early maturity alleles across different maturity groups (Langewisch et al., 2017) [Color figure can be viewed at wileyonlinelibrary.com]

Tof18, E1La and *E1Lb* will be helpful in elucidating molecular models for different maturity groups and latitudinal adaptation.

7 | PHOTOPERIODIC GENE INTERACTION MODULES IN LONG DAYS AND SHORT DAYS

Regulation of flowering and maturity is mediated by three interacting modules *PHYA-E1*, *GI-CO* and *miRNA*-dependent modules (Cao et al., 2017) and a fourth model connecting the *PHYA-E1*, *GI-CO* models has recently been described (Lu et al., 2020). In these pathways *PHYA-E1* module plays a central role, as *E3* and *E4* are major sensors of photoperiod and *E1* is central hub integrating light and circadian clock signals of flowering regulation pathway (Lin et al., 2021). A putative model for photoperiod regulation of flowering in soybean is given in (Figure 3a,b). Light signals in leaves are perceived by multiple photoreceptors which include *E3*, *E4* and *GmCRY1a* (Liu et al., 2008; Watanabe et al., 2009; Zhang et al., 2008). Light induced by phytochrome A proteins GmPhyA2 and GmPhyA3 upregulates *E1* and *E1L* expression, which in turn suppress the expression of *GmFT2a* and *GmFT5a* (Cao, Li, Lu, et al., 2015; Kong et al., 2010; Xia et al., 2012). This *E1* mediated repression of *GmFT2a* and *GmFT5a* in turn delayed reproductive phase transition. The repressive effects of *E1* on two *FT* genes and resulting delay in flowering may be also partially supported by the induction of the inhibitory *FT* genes, *GmFT1a* and *GmFT4* (Zhai et al., 2014; Liu et al., 2018). The *E1* and *E1L* genes show a diurnal expression pattern, with peaks in the early morning and late

afternoon under LDs, but their expression is abolished under SDs and in the *e3/e3 e4/e4* genotypes (Xia et al., 2012; Xu et al., 2015; Zhai et al., 2014). Co-silencing of *E1* and *E1La/b* in an extremely late maturing genotype (MG VIII) resulted in super early flowering phenotype (MG 000) which can be grown at higher latitudes (Liu et al., 2022). Expression of flowering promoter *GmFT2a/GmFT5a* was significantly higher while expression of flowering inhibitor *GmFT4* was low in these transgenic lines.

In Arabidopsis, *CONSTANS* (*CO*) is a key integrator in the induction of *FT* gene expression (Suárez-López et al., 2001), where light signalling pathways and the circadian clock pathway co-ordinate the control of CO activity to induce *FT* (Song et al., 2013). Comparative expression analyses for NILs for *E1–E4* under LDs reveal that *E2* (*GmGI*) expression is up-regulated by *E3* and *E4*, but down-regulated by *E1* (Cao, Li, Lu, et al., 2015). In soybean genome, 26 *CONSTANS-like* (*COL*) genes were predicted, of which two pairs of homeologous genes, *GmCOL1a/1b* and *GmCOL2a/2b*, have high sequence similarity to Arabidopsis *CO* (Wu et al., 2014). Khan et al. (2022) studied natural variation in 21 *CO* family genes (*GmCOLs*) from soybean in 128 varieties covering 14 known maturity groups (MG 0000-MG X from earliest to latest maturity), which revealed mutation in 15 genes. Eight *CO* genes (*GmCOL1/3/4/8/13/15/16/19*) were associated with early flowering and maturity. The expression of *GmCOL1a* and *GmCOL1b* is induced by darkness, inhibited by light, and peaks at dawn, whereas *GmCOL2a* and *GmCOL2b* are expressed at much lower levels and peak both at dawn and in the late afternoon or at dusk (Cao, Li, Lu, et al., 2015; Fan et al., 2014). The overexpression of *GmCOL1a* delays

FIGURE 3 (a) Model for interaction between photoperiodic genes in long days; (b) model for interaction between photoperiodic genes in short day [Color figure can be viewed at wileyonlinelibrary.com]
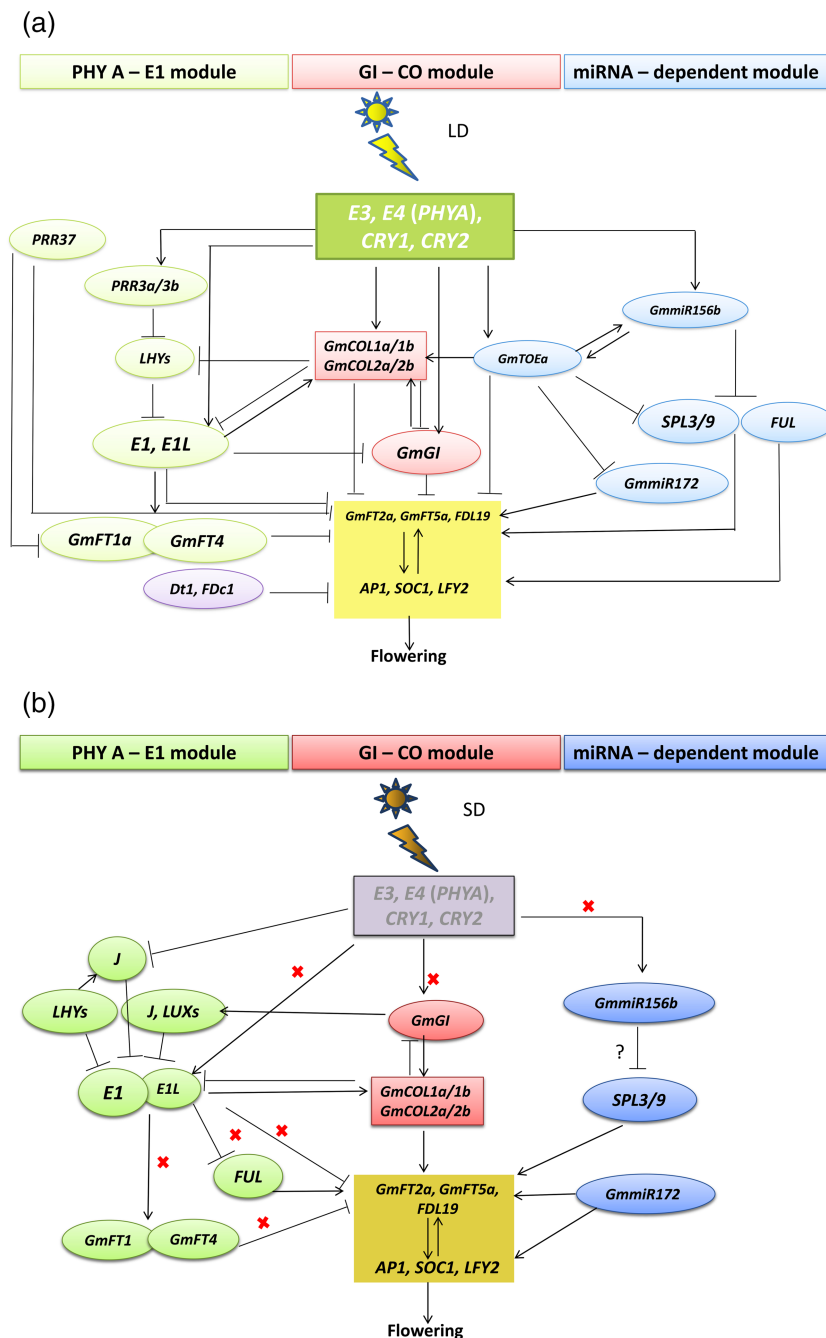
flowering by down-regulating the expression of *GmFT2a* and *GmFT5a* under LD conditions, but upregulates both under SD conditions and induce flowering (Cao, Li, Lu, et al., 2015). *E1*- overexpressing plants showed higher expression of *GmCOL1a* than in the wild type, suggesting that *E1* and *GmCOL1a* influence each other's expression and may function as part of a negative feedback loop (Cao, Li, Lu, et al., 2015). Under short day conditions at lower latitudes *J (GmELF3)* and *E9 (GmFT2a)* genes play an important role. The *J* gene encodes an *ELF3* ortholog that binds to *E1* promoter and represses its expression under SD. *E1* repression is released from this inhibition in cultivars with loss-of-function *j* alleles, allowing *E1* to repress *FT* genes and delay flowering and maturation, resulting in higher yield and biomass (Lu

et al., 2017). The *E3* and *E4* suppress expression of *J* under SD (Lu et al., 2017), indicating that the action of *PHYA* genes is not restricted to LD conditions.

Several circadian clock homologues have been identified and linked to flowering in soybean, including *GmGIa, GmELF3, GmPRR3a, GmPRR3b,* and *GmLHY* orthologs (Li et al., 2019; Lu et al., 2017, 2020; Watanabe et al., 2011). A new module correlating *PHYA-E1, GI-CO* pathways has recently been elucidated (Lu et al., 2020). In this module, circadian clock gene *LHYs* is down regulated by *Tof11* and *Tof12* genes. *LHY* interacts with the promoter of *E1* suppressing its expression and promotes flowering through relieving of *FT2a* and *FT5a* (Dong, Fang, et al., 2021; Li et al., 2020). *LHY/CCA1* has been

shown to induce expression of *ELF3* (*J*) by binding directly to its promoter region (Li et al., 2020). *LUX1* and *LUX2*, the two homologues of *LUX* in soybean, physically interact with *J* to form evening complex to repress *E1* expression and relieving *FT2a* and *FT5a*, leading to early flowering under short days (Bu et al., 2021). There is also interaction among *Dt1*, *FT5a*, a bZIP transcription factor *FDc1* and *APATELLA 1* (*AP*) to regulate reproductive phase transition (Yue, Li, et al., 2021). *FDc1-Dt1* complex binds to *AP1*promoter and represses its expression. To promote *AP1* expression, *FT5a* competes with *Dt1* for binding with *FDc1.AP1* in turn, binds to *Dt1* promoter and suppresses its expression thereby maintaining a regulatory pathway, which balances flowering and growth habit.

Role of *miRNA156* in regulation of transition from the juvenile to the adult phase of shoot development has been shown in *Arabidopsis thaliana* (Guo et al., 2017). Cao, Li, Wang, et al. (2015) overexpressed *miR156b* in soybean and observed delayed flowering under long day conditions but not in short days. The overexpression of *GmmiR156b* down-regulates *GmmiR172*, but up-regulates *GmTOE4a*, a soybean orthologue of *TARGET OF EAT1* (*TOE1*), and regulation of both, *GmmiR156b*and *GmTOE4a*, is mediated by *E1-E4* (Cao, Li, Wang, et al., 2015). Zhao et al. (2015) showed that *GmTOE4a* overexpression up-regulates expression of *GmmiR156b* in both the leaves and shoot apices, but down-regulates expression of *GmmiR172* and *GmSPL* genes in shoot apices.

Recently, Li et al. (2022) reported that a *calcium-dependent protein kinase* (*GmCDPK38*) coordinates flowering time regulation and insect resistance, first time revealing a relationship between flowering time and insect resistance. Late flowering haplotype (Hap2) containing soybeans were more resistant to the common cutworm (*Spodopteralitura fabricius*) than those of Hap3. Moreover, it was observed that Hap2 was abundant in soybeans of low latitudes with a higher frequency in cultivars than in wild soybeans, while Hap3 was widely selected at high latitude soybeans (Li et al., 2022). This report hints at a new dimension to gene interaction modules for flowering time as well as biotic stress resistance pathway genes.

8 | IMPLICATIONS OF IDENTIFIED MOLECULAR PATHWAYS ON SOYBEAN BREEDING IN INDIA

In India and South East Asia the soybean cultivation is monsoon dependent and short-duration varieties (70–85 days) are required to escape terminal drought. In higher latitudes recessive photoperiodic alleles (*e1/e2/e3/e4*) confer photo insensitivity for adaptation in higher latitude but information is lacking for allelic maturity model for lower latitude countries. Tripathi et al. (2021) found that out of 101 Indian soybean varieties, 86 were photosensitive and had dominant alleles at 'E loci'. Four insensitive genotypic classes *e1-as/E2/E3/E4*, *E1/e2/e3/E4*, *E1/e2/E3/E4* and *E1/E2/e3/E4* were observed in 1, 1, 2 and 15 varieties, respectively. Similar to the presence of recessive *e3* allele in most of the Indian photo insensitive cultivars Brazilian lower latitude cultivars also have the same allele in maximum number

of cultivars (dos Santos et al., 2016). Correlating the allelic status of cultivars with their breeder seed production in India for 35 years could infer an adaptive role of photo insensitivity to short rain fed growing conditions. The weighted mean contribution of the photosensitive class (*E1E2E3E4*; 380 Q/year) was far less than that of photo insensitive class (648 Q/year). This study established that although photo insensitivity is essential for perpetuation of crop in higher latitudes, it has helped soybean to adapt to rain fed, short growing and sub-tropical conditions of lower latitudes by conferring earliness. Photo insensitive cultivars introduced in Australia had reduced seed yield due to precocious flowering and poor vegetative growth (James & Lawn, 2011). James and Lawn (2011) introduced long juvenility traits in soybean varieties ('Charleston', 'Sprite 87') and breeding lines (HC78-676BC and HC87-603) of higher latitude (>38°N) and could identify tall, semi-determinate high yielding lines with up to 7.0 tons of yield surpassing the yield potential (2 tons) of local cultivar. Based on current understanding of the molecular pathways, *FT2a*, *J*, *LHYs* and *SOCs* are prime targets for genome editing and haplotype based breeding for the development of high yielding cultivars in lower latitudes.

9 | CONCLUDING REMARKS AND PERSPECTIVES

The advancement in understanding of photoperiod mediated latitudinal adaptation in soybean has come a long way through agronomic, genetic, physiological and molecular research. Using advanced tools of genomics research, we have now better understanding of major loci and their allelic variation which mediate the latitudinal adaptation of the soybean crop. Recent studies have identified molecular basis of these loci, their interaction with each other and integration of different molecular pathways leading to elucidation of mechanism of latitudinal adaptation. Comparative and functional genomics studies identified function and effect of various flowering gene homologues. Although the mechanism of photoperiod flowering is more clear under long days as compared to short days, still several gaps are there to understand interaction among different protein coding and miRNA genes under different photoperiod conditions. Also members of flowering associated genes families act through feedback mechanism and varying dosage, making it difficult to ascertain their exact role. The present molecular maturity models based on *E1*, *E2*, *E3* and *E4* genes are insufficient to describe photoperiodic variation in genotypes of lower latitudes and other genes like *E9*,*E10*,*J*, *Tof5*, *Tof11*, *Tof12*, *Tof16*, *Tof18*, *E1La* and *E1Lb* need to be incorporated in maturity models. Current understanding of the allelic effect of *E9*, *J*, *Tof16* and *Tof18* and their combinations will be helpful in designing and breeding of high yielding cultivars for lower latitudes.

CONFLICT OF INTEREST
The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be constructed as a potential conflict of interest.

AUTHOR CONTRIBUTIONS

DATA AVAILABILITY STATEMENT

ORCID

Sanjay Gupta https://orcid.org/0000-0001-5146-6087

Shivakumar Maranna https://orcid.org/0000-0002-3461-4225

REFERENCES

Abe, J., Xu, D., Miyano, A., Komatsu, K., Kanazawa, A., & Shimamoto, Y. (2003). Photoperiod-insensitive Japanese soybean landraces differ at two maturity loci. *Crop Science*, *43*(4), 1300–1304. https://doi.org/10.2135/cropsci2003.1300

Abugalieva, S., Didorenko, S., Anuarbek, S., Volkova, L., Gerasimova, Y., Sidorik, I., & Turuspekov, Y. (2016). Assessment of soybean flowering and seed maturation time in different latitude regions of Kazakhstan. *PLoS ONE*, *11*, e0166894. https://doi.org/10.1371/journal.pone.0166894

Bernard, R., & Weiss, M. (1973). Qualitative genetics. In *Soybeans: Improvement, production, and uses* (1st ed., pp. 117–154). American Society of Agronomy.

Bernard, R. L. (1971). Two major genes for time of flowering and in soybeans. *Crop Science*, *11*, 242–244. https://doi.org/10.2135/cropsci.0011183X001100020022x

Blaney, L. T., & Hamner, K. C. (1957). Interrelations among effects of temperature, photoperiod and dark period on floral initiation of Biloxi soybean. *Botanical Gazette*, *119*, 10–24. https://doi.org/10.1086/335955

Bonato, E. R., & Vello, N. A. (1999). *E6* a dominant gene conditioning early flowering and maturity in soybeans. *Genetics and Molecular Biology*, *22*, 229–232. https://doi.org/10.1590/S1415-47571999000200016

Borthwick, H. A., & Parker, M. W. (1939). Photoperiodic responses of several varieties of soybeans. *Botanical Gazette*, *101*, 341–365. https://doi.org/10.1086/334874

Borthwick, H. A., & Parker, M. W. (1940). Floral initiation in Biloxi soybeans as influenced by age and position of leaf receiving photoperiodic treatment. *Botanical Gazette*, *101*, 806–817. https://doi.org/10.1086/334916

Bu, T., Lu, S., Wang, K., Dong, L., Li, S., Xie, Q., Xu, X., Cheng, Q., Chen, L., Fang, C., Li, H., Liu, B., Weller, J. L., & Kong, F. (2021). A critical role of the soybean evening complex in the control of photoperiod sensitivity and adaptation. *Proceedings of the National Academy of Sciences of the United States of America*, *118*(8), e2010241118. https://doi.org/10.1073/pnas.2010241118

Bunning, E. (1958). *Die physiologische Uhr*. Springer-Verlag. 10.1007/978-3-662-21804-4

Bunning, E. (1959). In R. B. Withrow (Ed.), *Physiological mechanism and biological importance of the endogenous diurnal periodicity in plants and animals. Photoperiodism and related phenomena in plants and animals* (pp. 507–535). American Association for the advancement of Science.

Bunning, E. (1960a). Circadian rhythms and the time measurement in photoperiodism. *Cold Spring Harbor Symposia on Quantitative Biology*, *25*, 249–256. https://doi.org/10.1101/SQB.1960.025.01.026

Bunning, E. (1960b). Opening address: Biological clocks. *Cold Spring Harbor Symposia on Quantitative Biology*, *25*, 1–9. https://doi.org/10.1101/SQB.1960.025.01.003

Bunsow, R. C. (1960). The circadian rhythm of photoperiodic responsiveness in Kalanchoe. *Cold Spring Harbor Symposia on Quantitative Biology*, *25*, 257–260. https://doi.org/10.1101/SQB.1960.025.01.027

Buzzell, R. I. (1971). Inheritance of a soybean flowering response to fluorescent day length conditions. *Canadian Journal of Genetics and Cytology*, *13*, 703–707. https://doi.org/10.1139/g71-100

Buzzell, R. I., & Voldeng, H. D. (1980). Inheritance of insensitivity to long day length. *Soybean Genetics Newsletter*, *7*, 26–29. https://lib.dr.iastate.edu/soybeangenetics/vol7/iss1/13

Cai, Y., Chen, L., Liu, X., Guo, Y., Sun, S., Wu, C., Jiang, B., Han, T., & Hou, W. (2018). CRISPR/Cas9-mediated targeted mutagenesis of GmFT2a delays flowering time in soybean. *Plant Biotechnology Journal*, *16*, 176–185. https://doi.org/10.1111/pbi.12758

Cai, Y., Wang, L., Chen, L., Wu, T., Liu, L., Sun, S., Wu, C., Yao, W., Jiang, B., Yuan, S., Han, T., & Hou, W. (2019). Mutagenesis of GmFT2a and GmFT5a mediated by CRISPR/Cas9 contributes for expanding the regional adaptability of soybean. *Plant Biotechnology Journal*, *18*, 298–309. https://doi.org/10.1111/pbi.13199

Cairo, C. A., Cambursano, M. V., & Morand, E. N. (2009). Molecular mapping of the juvenile locus in soybean. In: Proceedings of the World Soybean Research Conference VIII, Beijing, China. 10–15 Aug. 2009. Crop Sci. Soc. China, Beijing. 141.

Cairo, C. A., Stein, J., Delgado, L., Bortolotti, S., Guelman, S. A., Ortiz, J. P., & Morandi, E. N. (2002). Tagging the juvenile locus in soybean [*Glycine max* (L.) Merr.] with molecular markers. *Euphytica*, *124*, 387–395. https://doi.org/10.1023/A:1015767623038

Cajlachjan, M. H. (1936). On the mechanism of photoperiodic reaction. *Comptes rendus (Doklady) de l'Académie des sciences de l'URSS*, *1*, 89–93. illus

Cao, D., Li, Y., Lu, S., Wang, J., Nan, H., Li, X., Shi, D., Fang, C., Zhai, H., Yuan, X., Anai, T., Xia, Z., Liu, B., & Kong, F. (2015). GmCOL1a and GmCOL1b function as flowering repressors in soybean under long-day conditions. *Plant & Cell Physiology*, *56*, 2409–2422. https://doi.org/10.1093/pcp/pcv152

Cao, D., Li, Y., Wang, J., Nan, H., Wang, Y., Lu, S., Jiang, Q., Li, X., Shi, D., Fang, C., Yuan, X., Zhao, X., Li, X., Liu, B., & Kong, F. (2015). GmmiR156b overexpression delays flowering time in soybean. *Plant Molecular Biology*, *89*, 353–363. https://doi.org/10.1007/s11103-015-0371-5

Cao, D., Takeshima, R., Zhao, C., Liu, B., Jun, A., & Kong, F. (2017). Molecular mechanisms of flowering under long days and stem growth habit in soybean. *Journal of Experimental Botany*, *68*(8), 1873–1884. https://doi.org/10.1093/jxb/erw394

Carpentieri-Pipolo, V., de Almeida, A. L., de Souza Kiihl, R. A., & Stefani Pagliosa, E. (2014). Inheritance of late flowering in natural variants of soybean cultivars under short-day conditions. *Pesquisa Agropecuária Brasileira*, *49*, 796–803. https://doi.org/10.1590/S0100-204X2014001000006

Cober, E. R., & Curtis, D. F. (2003). Both promoters and inhibitors affected flowering time in grafted soybean flowering time Isolines. *Crop Physiology and Metabolism*, *43*(3), 886–891. https://doi.org/10.2135/cropsci2003.8860

Cober, E. R., Molnar, S. J., Charette, M., & Voldeng, H. D. (2010). A new locus for early maturity in soybean. *Crop Science*, *50*, 524–527. https://doi.org/10.2135/cropsci2009.04.0174

Cober, E. R., Tanner, J. W., & Voldeng, H. D. (1996a). Genetic control of photoperiod response in early-maturing, near-isogenic soybean lines. *Crop Science*, *36*, 601–605. https://doi.org/10.2135/cropsci1996.0011183X003600030013x

Cober, E. R., Tanner, J. W., & Voldeng, H. D. (1996b). Soybean photoperiod-sensitivity loci respond differentially to light quality. *Crop Science*, *36*, 606–610. https://doi.org/10.2135/cropsci1996.0011183X003600030014x

Cober, E. R., & Voldeng, H. D. (2001). A new soybean and photoperiod-sensitivity locus linked to E1 and T. *Crop Science*, *41*, 698–701. https://doi.org/10.2135/cropsci2001.413698x

Cregan, P. B., Jarvik, T., & Bush, A. L. (1999). An integrated genetic linkage map of the soybean genome. *Crop Science*, *39*, 1464–1490. https://doi.org/10.2135/cropsci1999.3951464x

Dennis, E. S., & Peacock, W. J. (2009). Vernalization in cereals. *Journal of Biology*, *8*(6), 57.1-57.4. https://doi.org/10.1186/jbiol156

Destro, D. (1991). Capacidade de Combinação de Genótipos de Soja (Gyicine max. (L.) Merrill) Apropriados para o Consumo Humano. M.S. Thesis. Escola Superior de Agricultura "Luis de Queiroz". USP. Piracicaba

Destro, D., Carpentieri-Pípolo, V., Kiihl, R. A. S., & Almeida, L. A. (2001). Photoperiodism and genetic control of the long juvenile period in soybean: A review. *Crop Breeding and Applied Biotechnology*, *1*, 72–92. https://doi.org/10.13082/1984-7033.v01n01a10

Dietz, N., Combs-Giroir, R., Cooper, G., Stacey, M., Miranda, C., & Bilyeu, K. (2021). Geographic distribution of the E1 family of genes and their effects on reproductive timing in soybean. *BMC Plant Biology*, *21*, 441. https://doi.org/10.1186/s12870-021-03197-x

Dissanayaka, A., Rodriguez, T. O., Di, S., Yan, F., Githiri, S. M., Rodas, F. R., Abe, J., & Takahashi, R. (2016). Quantitative trait locus mapping of soybean maturity gene E5. *Breeding Science*, *66*, 407–415. https://doi.org/10.1270/jsbbs.15160

Dong, L., Cheng, Q., Fang, C., Kong, L., Yang, H., Hou, Z., Li, Y., Nan, H., Zhang, Y., Chen, Q., Zhang, C., Kou, K., Su, T., Wang, L., Li, S., Li, H., Lin, X., Tang, Y., Zhao, X., ... Kong, F. (2021). Parallel selection of distinctTof5 alleles drove the adaptation of cultivated and wild soybean to high latitudes. *Molecular Plant*, *14*, 1–14. https://doi.org/10.1016/j.molp.2021.10.004

Dong, L., Fang, C., Cheng, Q., Su, T., Kou, K., Kong, L., Zhang, C., Li, H., Hou, Z., Zhang, Y., Chen, L., Yue, L., Wang, L., Wang, K., Li, Y., Gan, Z., Yuan, X., Weller, J. L., Lu, S., ... Liu, B. (2021). Genetic basis and adaptation trajectory of soybean from its temperate origin to tropics. *Nature Communications*, *12*(1), 5445. https://doi.org/10.1038/s41467-021-25800-3

dos Santos, J. V. M., Valliyodan, B., Joshi, T., Khan, S. M., Liu, Y., Wang, J., Vuong, T. D., de Oliveira, M. F., Marcelino-Guimarães, F. C., & Xu, D. (2016). Evaluation of genetic variation among Brazilian soybean cultivars through genome resequencing. *BMC Genomics*, *17*, 1–16. https://doi.org/10.1186/s12864-016-3046-y

Fan, C., Hu, R., Zhang, X., Wang, X., Zhang, W., Zhang, Q., Ma, J., & Fu, Y. F. (2014). Conserved CO–FT regulons contribute to the photoperiod flowering control in soybean. *BMC Plant Biology*, *14*, 9. https://doi.org/10.1186/1471-2229-14-9

Fang, C., Liu, J., Zhang, T., Su, T., Li, S., Cheng, Q., Kong, L., Li, X., Bu, T., Li, H., Dong, L., Lu, S., Kong, F., & Liu, B. (2021). A recent retrotransposon insertion of J caused E6 locus facilitating soybean adaptation into low latitude. *Journal of Integrative Plant Biology*, *63*, 995–1003. https://doi.org/10.1111/jipb.13034

Fang, C., Ma, Y., Wu, S., Liu, Z., Wang, Z., Yang, R., Hu, G., Zhou, Z., Yu, H., Zhang, M., & Pan, Y. (2017). Genome-wide association studies dissect the genetic networks underlying agronomical traits in soybean. *Genome Biology*, *18*, 161. https://doi.org/10.1186/s13059-017-1289-9

Fowler, S., Lee, K., Onouchi, H., Samach, A., Richardson, K., Coupland, G., & Putterill, J. (1999). GIGANTEA: A circadian clock-controlled gene that regulates photoperiodic flowering in Arabidopsis and encodes a protein with several possible membrane-spanning domains. *The EMBO Journal*, *18*, 4679–4688. https://doi.org/10.1093/emboj/18.17.4679

Garner, W. W., & Allard, H. A. (1920). Effect of the relative length of day and nightand other factors of the environment on growth and reproduction in plants. *Journal of Agricultural Research*, *18*, 553–603. https://doi.org/10.1175/1520-0493(1920)482.0.CO;2

Guo, C., Xu, Y., Shi, M., Lai, Y., Wu, X., Wang, H., Zhu, Z., Poethig, R. S., & Wu, G. (2017). Repression of miR156 by miR159 regulates the timing of the juvenile-to-adult transition in Arabidopsis. *The Plant Cell*, *29*(6), 1293–1304. https://doi.org/10.1105/tpc.16.00975

Gupta, S., Kumawat, G., Yadav, S., Tripathi, R., Agrawal, N., Maranna, S., Satpute, G. K., Channappa, G., Arya, M., Husain, S. M., Bhatia, V. S., Devi, N., Varghese, P., Mahatre, S. P., Singh, K., Shrivastav, A. N., Pandey, S., & Mohan, Y. (2021). Identification and characterization of a novel long juvenile resource AGS 25. *Genetic Resources and Crop Evolution*, *68*, 1149–1163. https://doi.org/10.1007/s10722-020-01055-7

Guthrie, M. L. (1972). Soybean response to photoperiodic extension under field conditions. Unpublished M.S. thesis. Library, Iowa State University, Ames, Iowa.

Hamner, K. C. (1940). Interrelation of light and darkness in photoperiodic induction. *Botanical Gazette*, *101*, 12–27.

Hamner, K. C. (1958). The mechanism of photoperiodism in plants. Photobiology. Proc.19th. Annual Biology Colloquium, Oregon State College.

Hamner, K. C. (1960). Photoperiodism and circadian rhythms. *Cold Spring HarborSymp. Quant. Biol.*, *25*, 269–277. https://doi.org/10.1101/SQB.1960.025.01.029

Han, T., Wu, C., Tong, Z., Mentreddy, R. S., Tan, K., & Gai, J. (2006). Post flowering photoperiod regulates vegetative growth and reproductive development of soybean. *Environmental and Experimental Botany*, *55*, 120–129. https://doi.org/10.1016/j.envexpbot.2004.10.006

Hanson, W. D. (1961). *Heritability, statistical genetics and plant breeding. National Academy of Science* (pp. 125–140). National Research Council.

Haque, M. F. (1964). Linkage between resistance to Phytophthora root rot and plant seed characteristics in soybean. *Indian Journal of Genetics and Plant Breeding*, *24*(2), 99–105.

Hayama, R., Agashe, B., Luley, E., King, R., & Coupland, G. (2007). A circadian rhythm set by dusk determines the expression of *FT* homologs and the short-day photoperiodic flowering response in *Pharbitis*. *Plant Cell*, *19*, 2988–3000.

Hecht, V., Knowles, C. L., Schoor, J. K. V., Liew, L. C., Jones, S. E., Lambert, M. J., & Weller, J. L. (2007). Pea LATE BLOOMER1 is a GIGANTEA ortholog with roles in photoperiodic flowering, deetiolation, and transcriptional regulation of circadian clock gene homologs. *Plant Physiology*, *144*, 648–661. https://doi.org/10.1104/pp.107.096818

Heinze, P. H., Parker, M. W., & Borthwick, H. A. (1942). Floral initiation in Biloxi soybean as influenced by grafting. *Botanical Gazette*, *103*, 518–530. https://doi.org/10.1086/335066

Hodges, T. & Doraiswamy, P. C. (1979). Crop phenological. Literature review for com, soybean, wheat, barley, sorghum, cotton, and sunflower. NASA Technical Report no. JSC-16088.

Hsu, C. Y., Liu, Y., Luthe, D. S., & Yuceer, C. (2006). Poplar *FT2* shortens the juvenile phase and promotes seasonal flowering. *The Plant Cell*, *18*, 1846–1861. https://doi.org/10.1105/tpc.106.041038

Huxley, P. A., Summerfield, R. J., & Huges, A. P. (1976). Growth and development of soybean CV. TK5 as affected by tropical daylengths, day-/night temperatures and nitrogen nutrition. *The Annals of Applied Biology*, *82*, 117–133. https://doi.org/10.1111/j.1744-7348.1976.tb01679.x

Hymowitz, T. (1970). On the domestication of the soybean. *Economic Botany*, *24*, 408–421. https://doi.org/10.1007/BF02860745

James, A. T., & Lawn, R. J. (2011). Application of physiological understanding in soybean improvement. II. Broadening phenological adaptation across regions and sowing dates. *Crop & Pasture Science*, *62*, 12–24. https://doi.org/10.1071/CP10290

Jia, H., Jiang, B., Wu, C., Lu, W., Hou, W., Sun, S., Yan, H., & Han, T. (2014). Maturity group classification and maturity locus genotyping of early-maturing soybean varieties from high-latitude cold regions. *PLoS ONE*, *9*, e94139. https://doi.org/10.1371/journal.pone.0094139

Jia, Z., Jiang, B., Gao, X., Yue, Y., Fei, Z., Sun, H., Wu, C., Sun, S., Hou, W., & Han, T. (2015). GmFULa, a FRUITFULL homolog, functions in the flowering and maturation of soybean. *Plant Cell Reports*, *34*(1), 121–132. https://doi.org/10.1007/s00299-014-1693-5

Jiang, B., Nan, H., Gao, Y., Tang, L., Yue, Y., Lu, S., Ma, L., Cao, D., Sun, S., Wang, J., Wu, C., Yuan, X., Hou, W., Kong, F., Han, T., & Liu, B. (2014).

Allelic combinations of soybean maturity loci E1, E2, E3 and E4 result in diversity of maturity and adaptation to different latitudes. *PLoS ONE, 9*(8), e106042. https://doi.org/10.1371/journal.pone.0106042

Jiang, B., Zhang, S., Song, W., Khan, M. A. A., Sun, S., Zhang, C., Wu, T., Wu, C., & Han, T. (2019). Natural variations of FT family genes in soybean varieties covering a wide range of maturity groups. *BMC Genomics, 20*, 230. https://doi.org/10.1186/s12864-019-5577-5

Johnson, H. W., & Bernard, R. L. (1962). Soybean genetics and breeding. *Advances in Agronomy, 14*, 149–221. https://doi.org/10.1016/S0065-2113(08)60438-1

Johnson, H. W., Borthwick, H. A., & Leffei, R. C. (1960). Effects of photoperiod and time of planting on rates of development of the soybean in various stages of the life cycle. *Botanical Gazette, 122*, 77–95. https://doi.org/10.1086/336090

Jung, C. H., Wong, C. E., & Singh, M. B. (2012). Comparative genomic analysis of soybean flowering genes. *PLoS ONE, 7*, e38250. https://doi.org/10.1371/journal.pone.0038250

Kantolic, A. G., & Slafer, G. A. (2007). Development and seed number in indeterminate soybean as affected by timing and duration of exposure to long photoperiods after flowering. *Annals of Botany, 99*(5), 925–933. https://doi.org/10.1093/aob/mcm033

Keim, P., Diers, B. W., Olson, T. C., & Shoemaker, R. C. (1990). RFLP Mapping in soybean: Association between marker loci and variation in quantitative traits. *Genetics, 126*, 735–742. https://doi.org/10.1093/genetics/126.3.735

Khan, M. A. A., Zhang, S., Emon, R. M., Chen, F., Song, W., Wu, T., Yuan, S., Wu, C., Hou, W., Sun, S., & Fu, Y. (2022). CONSTANS polymorphism modulates flowering time and maturity in soybean. *Frontiers in Plant Science, 13*, 817544. https://doi.org/10.3389/fpls.2022.817544

Kilen, T. C., & Hartwig, E. E. (1971). Inheritance of a light-quality sensitive character in soybeans. *Crop Science, 11*, 559–561. https://doi.org/10.2135/cropsci1971.0011183X001100040030x

Kim, M. Y., Shin, J. H., Kang, Y. J., Shim, S. R., & Lee, S. H. (2012). Divergence of flowering genes in soybean. *Journal of Biosciences, 37*, 857–870. https://doi.org/10.1007/s12038-012-9252-0

Kojima, S., Takahashi, Y., Kobayashi, Y., Monna, L., Sasaki, T., Araki, T., & Yano, M. (2002). *Hd3a*, A rice ortholog of the *Arabidopsis FT* gene, promotes transition to flowering downstream of *Hd1* under short-day conditions. *Plant & Cell Physiology, 43*, 1096–1105. https://doi.org/10.1093/pcp/pcf156

Kong, F., Liu, B., Xia, Z., Sato, S., Kim, B. M., Watanabe, S., Yamada, T., Tabata, S., Kanazawa, A., Harada, K., & Abe, J. (2010). Two coordinately regulated homologs of *FLOWERING LOCUS T* are involved in the control of photoperiodic flowering in soybean. *Plant Physiology, 154*, 1220–1231. https://doi.org/10.1104/pp.110.160796

Kong, F., Nan, H., Cao, D., Li, Y., Wu, F., Wang, J., Lu, S., Yuan, X., Cober, E. R., Abe, J., & Liu, B. (2014). A new dominant gene E9 conditions early flowering and maturity in soybean. *Crop Science, 54*, 2529–2535. https://doi.org/10.2135/cropsci2014.03.0228

Kou, K., Yang, H., Li, H., Fang, C., Chen, L., Yue, L., Nan, H., Kong, L., Li, X., Wang, F., Wang, J., Du, H., Yang, Z., Bi, Y., Lai, Y., Dong, L., Cheng, Q., Su, T., Wang, L., … Kong, F. (2022). A functionally divergent SOC1 homolog improves soybean yield and latitudinal adaptation. *Current Biology, 32*(8), 1728–1742. https://doi.org/10.1016/j.cub.2022.02.046

Kurasch, A. K., Hahn, V., Leiser, W. L., Vollmann, J., Schori, A., Bétrix, C. A., Mayr, B., Winkler, J., Mechtler, K., Aper, J., Sudaric, A., Pejic, I., Sarcevic, H., Jeanson, P., Balko, C., Signor, M., Miceli, F., Strijk, P., Rietman, H., … Würschum, T. (2017). Identification of mega-environments in Europe and effect of allelic variation at maturity E loci on adaptation of European soybean. *Plant, Cell & Environment, 40*, 765–778. https://doi.org/10.1111/pce.12896

Langewisch, T., Lenis, J., Jiang, G. L., Wang, D., Pantalone, V., & Bilyeu, K. (2017). The development and use of a molecular model for soybean maturity groups. *BMC Plant Biology, 17*, 91. https://doi.org/10.1186/s12870-017-1040-4

Langewisch, T., Zhang, H., Vincent, R., Joshi, T., Xu, D., & Bilyeu, K. (2014). Major soybean maturity gene haplotypes revealed by SNPViz analysis of 72 sequenced soybean genomes. *PLoS ONE, 9*(4), e94150. https://doi.org/10.1371/journal.pone.0094150

Lark, K. G., Weisemann, J. M., Matthews, B. F., Palmer, R., Chase, K., & Macalma, T. (1993). A genetic map of soybean (Glycine max L.) using a intraspecific cross of two cultivars: 'Minsoy' and 'noir 1'. *Theoretical and Applied Genetics, 86*, 901–906. https://doi.org/10.1007/BF00211039

Li, C., Li, Y., Li, Y., Lu, H., Hong, H., Tian, Y., Li, H., Zhao, T., Zhou, X., Liu, J., Zhou, X., Jackson, S. A., Liu, B., & Qiu, L. J. (2020). A domestication-associated gene GmPRR3b regulates circadian clock and flowering time in soybean. *Molecular Plant, 13*, 745–759. https://doi.org/10.1016/j.molp.2020.01.014

Li, M. W., Liu, W., Lam, H. M., & Gendron, J. M. (2019). Characterization of two growth period QTLs reveals modification of PRR3 genes during soybean domestication. *Plant & Cell Physiology, 60*, 407–420. https://doi.org/10.1093/pcp/pcy215

Li, X., Hu, D., Cai, L., Wang, H., Liu, X., Du, H., Yang, Z., Zhang, H., Hu, Z., Huang, F., Kan, G., Kong, F., Liu, B., Yu, D., & Wang, H. (2022). CALCIUM-DEPENDENT PROTEIN KINASE38 regulates flowering time and common cutworm resistance in soybean. *Plant Physiology*. https://doi.org/10.1093/plphys/kiac260 Epub ahead of print. PMID: 35640995

Lifschitz, E., Eviatar, T., Rozman, A., Shalit, A., Goldshmidt, A., Amsellem, Z., Alvarez, J. P., & Eshed, Y. (2006). The tomato *FT* ortholog triggers systemic signals that regulate growth and flowering and substitute for diverse environmental stimuli. *Proceedings of the National Academy of Sciences of the United States of America, 103*, 6398–6403. https://doi.org/10.1073/pnas.0601620103

Lin, X., Baohui, L., Weller, J. L., Abe, J., & Kong, F. (2021). Molecular mechanisms for the photoperiodic regulation of flowering in soybean. *Journal of Integrative Plant Biology, 63*(6), 981–994. https://doi.org/10.1111/jipb.13021

Liu, B., Fujita, T., Yan, Z. H., Sakamoto, S., Xu, D., & Abe, J. (2007). QTL mapping of domestication-related traits in soybean (Glycine max). *Annals of Botany, 100*(5), 1027–1038. https://doi.org/10.1093/aob/mcm149

Liu, B., Kanazawa, A., Matsumura, H., Takahashi, R., Harada, K., & Abe, J. (2008). Genetic redundancy in soybean photoresponses associated with duplication of the phytochromeA gene. *Genetics, 180*(2), 995–1007. https://doi.org/10.1534/genetics.108.092742

Liu, L.-F., Gao, L., Zhang, L.-X., Cai, Y.-P., Song, W.-W., Chen, L., Yuan, S., Wu, T.-T., Jiang, B.-J., Sun, S., Wu, C.-X., Hou, W.-S., & Han, T.-F. (2022). Co-silencing E1 and its homologs in an extremely late-maturing soybean cultivar confers super-early maturity and adaptation to high-latitude short-season regions. *Journal of Integrative Agriculture, 21*, 326–335. https://doi.org/10.1016/S2095-3119(20)63391-3

Liu, W., Jiang, B., Ma, L., Zhang, S., Zhai, H., Xu, X., Hou, W., Xia, Z., Wu, C., Sun, S., Wu, T., Chen, L., & Han, T. (2018). Functional diversification of flowering locus T homologs in soybean: GmFT1a and GmFT2a/5a have opposite roles in controlling flowering and maturation. *The New Phytologist, 217*(3), 1335–1345. https://doi.org/10.1111/nph.14884

Lu, S., Dong, L., Fang, C., Liu, S., Kong, L., Cheng, Q., Chen, L., Su, T., Nan, H., Zhang, D., & Zhang, L. (2020). Stepwise selection on homeologous PRR genes controlling flowering and maturity during soybean domestication. *Nature Genetics, 52*, 428–436. https://doi.org/10.1038/s41588-020-0604-7

Lu, S., Li, Y., Wang, J., Srinives, P., Nan, H., Cao, D., Wang, Y., Li, J., Li, X., Fang, C., & Shi, X. (2015). QTL mapping for flowering time in different latitude in soybean. *Euphytica, 206*(3), 725–736. https://doi.org/10.1007/s10681-015-1501-5

Lu, S., Zhao, X., Hu, Y., Liu, S., Nan, H., Li, X., Fang, C., Cao, D., Shi, X., Kong, L., Su, T., Zhang, F., Li, S., Wang, Z., Yuan, X., Cober, E. R., Weller, J. L., Liu, B., Hou, X., … Kong, F. (2017). Natural variation at the soybean J locus improves adaptation to the tropics and enhance yield. *Nature Genetics*, 49, 773–779. https://doi.org/10.1038/ng.3819

Luo, X., Yin, M., & He, Y. (2022). Molecular genetic understanding ofPhotoperiodic regulation ofFlowering time in Arabidopsis and soybean. *International Journal of Molecular Sciences*, 23, 466. https://doi.org/10.3390/ijms23010466

Mansur, L. M., Orf, J. H., Chase, K., Jarvik, T., Cregan, P. B., & Lark, K. G. (1996). Genetic mapping of agronomic traits using recombinant inbred lines of soybean. *Crop Science*, 36, 1327–1336. https://doi.org/10.2135/cropsci1996.0011183X003600050042x

Matsuura, H. (1933). *Glycine soja. Pp. 100-110. A bibliographical monograph plant genetics* (2nd ed.). Hokkaido Imperial University.

McBlain, B. A., & Bernard, R. L. (1987). A new gene affecting the time of flowering and maturity in soybean. *The Journal of Heredity*, 78, 160–162. https://doi.org/10.1093/oxfordjournals.jhered.a110349

Miladinović, J., Ćeran, M., Đorđević, V., Balešević-Tubić, S., Petrović, K., Đukić, V., & Miladinović, D. (2018). Allelic variation and distribution of the major maturity genes in different soybean collections. *Frontiers in Plant Science*, 9, 1286. https://doi.org/10.3389/fpls.2018.01286

Molnar, S. J., Rai, S., Charette, M., & Cober, E. R. (2003). Simple sequence repeat (SSR) markers linked to E1, E3, E4, and E7 maturity genes in soybean. *Genome*, 46, 1024–1036. https://doi.org/10.1139/g03-079

Morandi, E. N., Casano, L. M., & Reggiardo, L. M. (1988). Post-flowering photoperiodic effect on reproductive efficiency and seed growth in soybean. *Field Crops Research*, 18(4), 227–241. https://doi.org/10.1016/0378-4290(88)90017-2

Morse, W. J. & Cartter, J. L. (1937). Yearbook Agr. U.S. Dept. Agr. (pp. 1154–1189).

Nakamichi, N., Kiba, T., Kamioka, M., Suzuki, T., Yamashino, T., Higashiyama, T., Sakakibara, H., & Mizuno, T. (2012). Transcriptional repressor PRR5 directly regulates clock-output pathways. *Proceedings of the National Academy of Sciences of the United States of America*, 109(42), 17123–17128. https://doi.org/10.1073/pnas.1205156109

Nanda, K. K., & Hamner, K. C. (1958). Studies on the nature of the endogenous rhythm affecting photoperiodic response of Biloxi soybean. *Botanical Gazette*, 120, 14–25. https://doi.org/10.1086/335992

Nissan, N., Cober, E. R., Sadowski, M., Charette, M., Golshani, A., & Samanfar, B. (2021). Identifying new variation at the J locus, previously identified as e6, in long juvenile 'Paranagoiana' soybean. *Theoretical and Applied Genetics*, 134, 1007–1014. https://doi.org/10.1007/s00122-020-03746-2

Noggle, G. R., & Fritz, G. T. (1983). *Introductory plant Plivsiology* (p. 627). prentice hall Inc.

Owen, F. V. (1927). Inheritance studies in soybeans. II. Glabrousness, color of pubescence, time of maturity, and linkage relations. *Genetics*, 12, 519–529. https://doi.org/10.1093/genetics/12.6.519

Palmer, R. G., & Hedges, B. R. (1993). Linkage map of soybean [Glycine max (L.) Merr.]. In S. J. O'Brien (Ed.), *Genetic maps* (pp. 6.139–6.148). Cold Spring Harbor Laboratory Publisher.

Patterson, D. T., Peet, M. M., & Bunce, J. A. (1977). Effect of photoperiod and size at flowering on vegetative growth and seed yield in soybeans. *Agronomy Journal*, 69, 631–635. https://doi.org/10.2134/agronj1977.00021962006900040028x

Rafalski, J. A., & Tingey, S. V. (1993). RFLP map of soybean (Glycinemax) 2N = 40. In S. J. O'Brien (Ed.), *Genetic maps* (pp. 149–156). Cold Spring Har-bor Laboratory.

Ray, J. D., Hinson, K., Mankono, J. E. B., & Malo, M. F. (1995). Genetic control of a long-juvenile trait in soybean. *Crop Science*, 35, 1001–1006. https://doi.org/10.2135/cropsci1995.0011183X003500040012x

Samanfar, B., Molnar, S. J., Charette, M., Schoenrock, A., Dehne, F., Golshani, A., Belzile, F., & Cober, E. R. (2017). Mapping and identification of a potential candidate gene for a novel maturity locus, E10, in

soybean. *Theoretical and Applied Genetics*, 130, 377–390. https://doi.org/10.1007/s00122-016-2819-7

Scott, W. O., & Aldrich, S. R. (1983). *Modern soybean production*. S & A Publications Inc.

Shoemaker, R. C., & Specht, J. E. (1995). Integration of the soybeanmolecular and classical genetic linkage groups. *Crop Science*, 35, 436–446. https://doi.org/10.2135/cropsci1995.0011183X003500020027x

Song, Y. H., Ito, S., & Imaizumi, T. (2013). Flowering time regulation: Photoperiod- and temperature-sensing in leave. *Trends in Plant Science*, 18, 575–583. https://doi.org/10.1016/j.tplants.2013.05.003

Su, Q., Chen, L., Cai, Y., Chen, Y., Yuan, S., Li, M., Zhang, J., Sun, S., Han, T., & Hou, W. (2022). Functional redundancy of FLOWERING LOCUS T 3b in soybean flowering time regulation. *International Journal of Molecular Sciences*, 23, 2497. https://doi.org/10.3390/ijms23052497

Suárez-López, P., Wheatley, K., Robson, F., Onouchi, H., Valverde, F., & Coupland, G. (2001). CONSTANS mediates between the circadian clock and the control of flowering in Arabidopsis. *Nature*, 410, 1116–1120. https://doi.org/10.1038/35074138

Sun, H., Jia, Z., Cao, D., Jiang, B., Wu, C., Hou, W., Liu, Y., Fei, Z., Zhao, D., & Han, T. (2011). GmFT2a, a soybean homolog of FLOWERING LOCUS T, is involved in flowering transition and maintenance. *PLoS ONE*, 6(12), e29238. https://doi.org/10.1371/journal.pone.0029238

Sun, J., Wang, M., Zhao, C., Liu, T., Liu, Z., Fan, Y., Xue, Y., Li, W., Zhang, X., & Zhao, L. (2021). GmFULc is induced by short days in soybean and may accelerate flowering in transgenic Arabidopsis thaliana. *International Journal of Molecular Sciences*, 22(19), 10333. https://doi.org/10.3390/ijms221910333

Thomas, J. F., & Raper, C. D. Jr. (1976). Photoperiodic control of seed filling for soybeans. *Crop Science*, 16, 667–672. https://doi.org/10.2135/cropsci1976.0011183X001600050017x

Thomas, J. F., & Raper, C. D. Jr. (1978). Photoperiodic Alteration of Dry Matter Partitioning and Seed Yield in Soybean. *Crop Science*, 18, 654–656.

Tisselli, O. Jr., (1981). Inheritance study of the long-juvenile characteristic in soybeans under long and short-day conditions. Ph.D. Diss. Mississippi State University, Miss. State, MS. 77. 10.1590/S1415-47572002000400016

Tripathi, R., Agrawal, N., Kumawat, G., Gupta, S., Kuchlan, M., Maranna, S., Nataraj, V., Kuchlan, P., Satpute, G. K., Ratnaparkhe, M. B., Rajesh, V., Chandra, S., Bhatia, V. S., & Chand, S. (2021). Novel role of photoinsensitive alleles in adaptation of soybean [Glycine max (L.) Merr.] to rainfed short growing seasons of lower latitudes. *Genetic Resources and Crop Evolution*, 68, 2455–2467. https://doi.org/10.1007/s10722-021-01142-3

Tsubokura, Y., Matsumura, H., Xu, M., Liu, B., Nakashima, H., Anai, T., Kong, F., Yuan, X., Kanamori, H., Katayose, Y., Takahashi, R., Harada, K., & Abe, J. (2013). Genetic variation in soybean at the maturity locus E4 is involved in adaptation to long days at high latitudes. *Agronomy*, 3, 117–134. https://doi.org/10.3390/agronomy3010117

Tsubokura, Y., Watanabe, S., Xia, Z., Kanamori, H., Yamagata, H., Kaga, A., Katayose, Y., Abe, J., Ishimoto, M., & Harada, K. (2014). Natural variation in the genes responsible for maturity loci E1, E2, E3 and E4 in soybean. *Annals of Botany*, 113, 429–441. https://doi.org/10.1093/aob/mct269

Valliyodan, B., Qiu, D., Patil, G., Zeng, P., Huang, J., Dai, L., Chen, C., Li, Y., Joshi, T., Song, L., & Vuong, T. D. (2016). Landscape of genomic diversity and trait discovery in soybean. *Scientific Reports*, 6, 23598. https://doi.org/10.1038/srep23598

van Schaik, P. H., & Probst, A. H. (1958). Effects of some environ-mental factors on flower production and reproductive efficiency in soybean. *Agronomy Journal*, 50, 192–197. https://doi.org/10.2134/agronj1958.00021962005000040007x

Villarroel, D. A., & Kilen, T. C. (2009). Effect of a long-juvenile trait upon lowering in soybeans grown in short and long photoperiods. *Crop Science*, *35*, 1001–1006.

Voldeng, H. D., & Saindon, G. (1991). Registration of seven long-daylength insensitive soybean genetic stocks. *Crop Science*, *31*, 1399-1400. https://doi.org/10.2135/cropsci1991.0011183X003100050095x

Wang, F., Nan, H., Chen, L., Fang, C., Zhang, H., Su, T., Li, S., Cheng, Q., Dong, L., Liu, B., Kong, F., & Lu, S. (2019). A new dominant locus, E11, controls early flowering time and maturity in soybean. *Molecular Breeding*, *39*, 70. https://doi.org/10.1007/s11032-019-0978-3

Wang, L., Sun, S., Wu, T., Liu, L., Sun, X., Cai, Y., Li, J., Jia, H., Yuan, S., Chen, L., Jiang, B., Wu, C., Hou, W., & Han, T. (2020). Natural variation and CRISPR/Cas9-mediated mutation in GmPRR37 affect photoperiodic flowering and contribute to regional adaptation of soybean. *Plant Biotechnology Journal*, *18*, 1869–1881. https://doi.org/10.1111/pbi.13346

Watanabe, S., Harada, K., & Abe, J. (2012). Genetic and molecular basis of photoperiod responses of flowering in soybean. *Breeding Science*, *61*, 531–543. https://doi.org/10.1270/jsbbs.61.531

Watanabe, S., Hideshima, R., Xia, Z., Tsubokura, Y., Sato, S., Nakamoto, Y., Yamanaka, N., Takahashi, R., Ishimoto, M., Anai, T., & Tabata, S. (2009). Map-based cloning of the gene associated with the soybean maturity locus E3. *Genetics*, *182*, 1251–1262. https://doi.org/10.1534/genetics.108.098772

Watanabe, S., Tajuddin, T., Yamanaka, N., Hayashi, M., & Harada, K. (2004). Analysis of QTLs for reproductive development and seed quality traits in soybean using recombinant inbred lines. *Breeding Science*, *54*, 399–407.

Watanabe, S., Xia, Z. J., Hideshima, R., Tsubokura, Y., Sato, S., Yamanaka, N., Takahashi, R., Anai, T., Tabata, S., Kitamura, K., & Harada, K. (2011). A map-based cloning strategy employing a residual heterozygous line reveals that the *GIGANTEA* gene is involved in soybean maturity and flowering. *Genetics*, *188*, 395–U260. https://doi.org/10.1534/genetics.110.125062

Weiss, M. G. (1949). Soybeans. In A. G. Norman (Ed.), *Advances inagronomy* (2nd ed., Vol. 1, pp. 77–157). Academic Press.

Weiss, M. G. (1970). Genetic linkage in soybeans: Linkage group I. *Crop Science*, *10*, 69–72. https://doi.org/10.2135/cropsci1970.0011183X001000010027x

Whigham, D. K., & Minor, H. C. (1978). Agronomic characteristics and environmental stress. In A. G. Norman (Ed.), *Soybean physiology, agronomy, and utilization* (pp. 77–112). Academic Press. 10.1016/B978-0-12-521160-4.50009-8

Wilcox, J. R., & Schapaugh, W. T. Jr. (1978). Competition between two soybean Isolines in hill plots. *Crop Science*, *18*(2), 346–348. https://doi.org/10.2135/cropsci1978.0011183X001800020041x

Woodworth, C. M. (1923). Inheritance of growth habit, pod color, and flower color in soybeans. *Journal of the American Society of Agronomy*, *15*, 481–495. https://doi.org/10.2134/agronj1923.00021962001500120002x

Woodworth, C. M. (1932). Genetics and breeding in the improvement of the soybean. *Bulletin (University of Illinois (Urbana-Champaign campus). Agricultural Experiment Station)*, *384*, 297–404.

Woodworth, C. M., & Williams, L. F. (1938). Recent studies on the genetics of the soybean. *Journal of the American Society of Agronomy*, *30*, 125–129. https://doi.org/10.2134/agronj1938.00021962003000020006x

Wu, F., Price, B. W., Haider, W., Seufferheld, G., Nelson, R., & Hanzawa, Y. (2014). Functional and evolutionary characterization of the CONSTANS gene family in short-day photoperiodic flowering in soybean. *PLoS ONE*, *9*, e85754. https://doi.org/10.1371/journal.pone.0085754

Xia, Z., Zhai, H., Wu, H., Xu, K., Watanabe, S., & Harada, K. (2021). The synchronized efforts to decipher the molecular basis for soybean maturity loci E1, E2, and E3 that regulate flowering and maturity. *Frontiers in Plant Science*, *12*, 632754. https://doi.org/10.3389/fpls.2021.632754

Xia, Z. J., Watanabe, S., Yamada, T., Tsubokura, Y., Nakashima, H., Zhai, H., Anai, T., Sato, S., Yamazaki, T., Lü, S., & Wu, H. (2012). Positional cloning and characterization reveal the molecular basis for soybean maturity locus E1 that regulates photoperiodic flowering. *Proceedings of the National Academy of Sciences of the United States of America*, *109*, E2155–E2164. https://doi.org/10.1073/pnas.1117982109

Xu, M., Xu, Z., Liu, B., Kong, F., Tsubokura, Y., Watanabe, S., Xia, Z., Harada, K., Kanazawa, A., Yamada, T., & Abe, J. (2013). Genetic variation in four maturity genes affects. *BMC Plant Biology*, *13*, 91. https://doi.org/10.1186/1471-2229-13-91

Xu, M., Yamagishi, N., Zhao, C., Takeshima, R., Kasai, M., Watanabe, S., Kanazawa, A., Yoshikawa, N., Liu, B., Yamada, T., & Abe, J. (2015). The soybean-specific maturity gene E1 family of floral repressors controls night-break responses through down-regulation of FLOWERING LOCUS T orthologs. *Plant Physiology*, *168*, 1735–1746. https://doi.org/10.1104/pp.15.00763

Yamanaka, N., Nagamura, Y., Tsubokura, Y., Yamamoto, K., Takahashi, R., Kouchi, H., Yano, M., Sasaki, T., & Harada, K. (2000). Quantitative trait locus analysis of floweringtime in soy-bean usinga RFLP linkage map. *Breeding Science*, *50*, 109–115. https://doi.org/10.1270/jsbbs.50.109

Yamanaka, N., Ninomiya, S., Hoshi, M., Tsubokura, Y., Yano, M., Nagamura, Y., Sasaki, T., & Harada, K. (2001). An informative linkage map of soybean reveals QTLs for flowering time, leaf morphology and region of segregation distortion. *DNA Research*, *8*, 61–72. https://doi.org/10.1093/dnares/8.2.61

Yamanaka, N., Watanabe, S., Toda, K., Hayashi, M., Fuchigami, H., Takahashi, R., & Harada, K. (2005). Fine mapping of the *FT1* locus for soybean flowering time using a residual heterozygous line derived from a recombinant inbred line. *Theoretical and Applied Genetics*, *110*, 634–639. https://doi.org/10.1007/s00122-004-1886-3

Yan, L., Fu, D., Li, C., Blechl, A., Tranquilli, G., Bonafede, M., Sanchez, A., Valarik, M., Yasuda, S., & Dubcovsky, J. (2006). The wheat and barley vernalization gene *VRN3* is an orthologue of *FT*. *Proc Natl Acad Sci USA*, *103*, 19581–19586. https://doi.org/10.1073/pnas.0607142103

Yue, L., Li, X., Fang, C., Chen, L., Yang, H., Yang, J., Chen, Z., Nan, H., Chen, L., Zhang, Y., Li, H., Hou, X., Dong, Z., Weller, J. L., Abe, J., Liu, B., & Kong, F. (2021). FT5a interferes with the Dt1-AP1 feedback loop to control flowering time and shoot determinacy in soybean. *Journal of Integrative Plant Biology*, *63*, 1004–1020. https://doi.org/10.1111/jipb.13070

Yue, Y., Liu, N., Jiang, B., Li, M., Wang, H., Jiang, Z., Pan, H., Xia, Q., Ma, Q., Han, T., & Nian, H. (2017). A single nucleotide deletion in J encoding GmELF3 confers long juvenility and is associated with adaption of tropic soybean. *Molecular Plant*, *10*, 656–658. https://doi.org/10.1016/j.molp.2016.12.004

Yue, Y., Sun, S., Li, J., Yu, H., Wu, H., Sun, B., Li, T., Han, T., & Jiang, B. (2021). GmFULa improves soybean yield by enhancing carbon assimilation without altering flowering time of maturity. *Plant Cell Reports*, *40*, 1875–1888. https://doi.org/10.1007/s00299-021-02752-y

Zhai, H., Lu, S., Wang, Y., Chen, X., Ren, H., Yang, J., Cheng, W., Zong, C., Gu, H., Qiu, H., & Wu, H. (2014). Allelic variations at four major maturity E genes and transcriptional abundance of the E1 gene are associated with flowering time and maturity of soybean cultivars. *PLoS ONE*, *9*(5), e97636. https://doi.org/10.1371/journal.pone.0097636

Zhang, L., Wang, R., & Hesketh, J. D. (2001). Effects of photoperiod on growth and development of soybean floral bud in different maturity. *Agronomy Journal*, *93*, 944–948. https://doi.org/10.2134/agronj2001.934944x

Zhang, Q., Li, H., Li, R., Hu, R., Fan, C., Chen, F., Wang, Z., Liu, X., Fu, Y., & Lin, C. (2008). Association of the circadian rhythmic expression of GmCRY1a with a latitudinal cline in photoperiodic flowering of soybean. *Proceedings of the National Academy of Sciences of the*

United States of America, *105*(52), 21028–21033. https://doi.org/10.1073/pnas.0810585105

Zhao, X., Cao, D., Huang, Z., Wang, J., Lu, S., Xu, Y., Liu, B., Kong, F., & Yuan, X. (2015). Dual functions of GmTOE4a in the regulation of photoperiod-mediated flowering and plant morphology in soybean. *Plant Molecular Biology*, *88*, 343–355. https://doi.org/10.1007/s11103-015-0322-1

Zhu, J., Takeshima, R., Harigai, K., Xu, M., Kong, F., Liu, B., Kanazawa, A., Yamada, T., & Abe, J. (2019). Loss of function of the E1-like-b Gene Associates with early flowering under long-day conditions in soybean. *Frontiers in Plant Science*, *9*, 1867. https://doi.org/10.3389/fpls.2018.01867