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Floral-promoting *GmFT* homologs trigger photoperiodic after-effects: An important mechanism for early-maturing soybean varieties to regulate reproductive development and adapt to high latitudes

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Abstract

Soybean (*Glycine max*) is a typical short-day plant, but has been widely cultivated in high-latitude long-day (LD) regions because of the development of early-maturing genotypes which are photoperiod-insensitive. However, some early-maturing varieties exhibit significant responses to maturity under different daylengths but not for flowering, depicting an evident photoperiodic after-effect, a poorly understood mechanism. In this study, we investigated the postflowering responses of 11 early-maturing soybean varieties to various preflowering photoperiodic treatments. We confirmed that preflowering SD conditions greatly promoted maturity and other postflowering developmental stages. Soybean homologs of *FLOWERING LOCUS T* (*FT*), including *GmFT2a*, *GmFT3a*, *GmFT3b* and *GmFT5a*, were highly accumulated in leaves under preflowering SD treatment. More importantly, they maintained a high expression level after flowering even under LD conditions. *E1* RNAi and *GmFT2a* overexpression lines showed extremely early maturity regardless of preflowering SD and LD treatments due to constitutively high levels of floral-promoting *GmFT* homolog expression throughout their life cycle. Collectively, our data indicate that high and stable expression of floral-promoting *GmFT* homologs play key roles in the maintenance of photoperiodic induction to promote postflowering reproductive development, which confers early-maturing varieties with appropriate vegetative growth and shortened reproductive growth periods for adaptation to high latitudes.

KEYWORDS
flowering time, maintenance, maturity, photoperiod sensitivity

Junya Wang and Xin Xu contributed equally to this study.

1 | INTRODUCTION

Soybean (*Glycine max* (L.) Merr.) has evolved to adapt to a broad range of climates in regions from 53°N to 35°S latitude across the world (Hyten et al., 2006; Zhang et al., 2020), although it is a typical short-day plant (SDP). Since photoperiod is determined by latitude, soybean varieties with divergent photoperiod sensitivity are utilised in different regions (Zhang et al., 2020). A total of 14 Maturity Groups (MG) from MG 0000 to MG X are characterised to describe photoperiod sensitivity (Alliprandini et al., 2009; Jia et al., 2014; Song et al., 2019; Wu et al., 2013; Zhang et al., 2007). Nowadays, high-latitude regions with long-day (LD) environments are some of the major soybean production areas (Sinegovskii et al., 2018; Wilcox, 2004; Xu et al., 2021). In the northern part of northeast China, the early-maturing varieties belong to MG 0000–MG 0 (Jia et al., 2014; Liu, Song, et al., 2020). Indeed, these early-maturing soybean varieties present a similar flowering time when grown under SD and LD photoperiods, while displaying a diverse maturation (Han et al., 1995, 2006).

The molecular basis of high-latitude adaptation in early-maturing varieties has been systematically investigated. Mutations in multiple *E* genes, mostly recessive at the *E1*, *E2*, *E3* and *E4* loci, were first discovered to contribute to the adaption of early-maturing varieties in northern regions (Liu et al., 2008; Watanabe et al., 2009, 2011; Xia et al., 2012). Additionally, the floral-promoting genes *GmFT2a* (Kong et al., 2010; Li et al., 2021; Sun et al., 2011), *GmFT5a* (Cai et al., 2020; Li et al., 2021; Yue et al., 2021), *GmFT5b* (Su et al., 2024), *GmFT2b* (Chen et al., 2020), *GmFUL2a* (Dong, Cheng, et al., 2022) and *GmSOC1a* (Kou et al., 2022) and the floral-inhibiting genes *GmPRR3b* (Li et al., 2020; Lu et al., 2020; Wang et al., 2020) and *E1La* (Dong, Li, et al., 2022) were found to regulate the maturation of soybean. According to the 'Teer-board' model, breeders can create early-maturing soybean varieties by modifying the expression levels of floral inhibitors and floral promoters bilaterally (Liu et al., 2018).

Florigen is a graft-transmissible signal produced in the leaves that induces floral initiation at the shoot apex (Andrés & Coupland, 2012). FT (FLOWERING LOCUS T) protein is likely at least a part of the florigen signalling pathway that promotes floral development (Corbesier et al., 2007). GmFT2a and GmFT5a, the floral-promoting FT homologs in soybean, have been demonstrated as the mobile factors that move from leaves to roots (Wang et al., 2021). In soybean, *FT* homologs serve various roles in flowering: *GmFT2a*, *GmFT2b*, *GmFT3a*, *GmFT3b* and *GmFT5a* promote flowering and maturity, while *GmFT1a* and *GmFT4* repress these processes (Cai et al., 2020; Kong et al., 2010; Lee et al., 2021; Liu et al., 2018; Nan et al., 2014; Su et al., 2022; Sun et al., 2011; Yuan et al., 2022).

In 1920, Garner and Allard performed preflowering (from emergence to flowering) SD treatments to early-maturing soybean plants and found that this treatment produced a weak promotion of flowering, but a more significant promotion of postflowering (from flowering to maturity) development (Garner & Allard, 1920). This phenomenon is referred to as a photoperiodic after-effect (PAE) (Garner, 1937). Subsequently, the PAE was observed in wild and cultivated soybean (Han & Gai, 1999; Han & Wang, 1995a; Han et al., 1995, 2006; Liu et al., 1983; Xu & Lu, 1988; Xu et al., 1990), and also in several other plants such as *Tithonia speciosa* (Stoughton & Hole, 1937) and chrysanthemum (Greulach, 1942). However, the molecular mechanism of the PAE remains poorly understood.

In the present study, we investigated the after-effect of preflowering photoperiodic treatments on the postflowering development and agronomic traits of soybean. We revealed the important function of floral-promoting *GmFT* homologs in the photoperiod after-effect through gene expression analysis and functional analysis of *E1* RNAi plants and *GmFT* overexpression lines. Collectively, we conclude that the PAE is caused by the maintenance of high expression levels of floral-promoting *GmFT* homologs. This phenomenon also indicates that maturity exhibits a stronger photoperiod sensitivity than flowering, which ensures appropriate vegetative growth and shortened reproductive period of the early-maturing soybean varieties to adapt to high latitudes with changing photoperiods from LD to SD in the growing season.

2 | MATERIALS AND METHODS

2.1 | Plant materials

Eleven representative varieties from MG 00 and MG 0 (Supporting Information S1: Table S1), the photoperiod-insensitive and early-maturing variety Heihe27 (HH27) (MG 0) and Dongnong36 (DN36) (MG 000), the photoperiod-sensitive and late-maturing variety Zigongdongdou (ZGDD) (MG XIII), *E1* RNAi transgenic lines at generation T_5 (in the ZGDD background) (Liu, Gao, et al., 2020), and the *35 S:GmFT2a* overexpression (OE) line at generation T_{11} (*35 S:GmFT2a* OE; in the ZGDD background) (Sun et al., 2011) were used in this study.

2.2 | Photoperiodic treatments and growth conditions

Two groups of photoperiodic treatments were conducted in this study, this includes SD → LD and LD → LD. For the SD → LD group, a preflowering (from emergence to flowering) SD photoperiod (12 h light/12 h dark) was applied, and then a postflowering (from flowering to maturity) LD photoperiod (18 h light/6 h dark) was applied. For the LD → LD group, preflowering and postflowering LD photoperiods (18 h light/6 h dark) were applied.

To analyse the after-effect of the preflowering photoperiodic treatments on the postflowering development of early-maturing varieties, the five MG 00 and six MG 0 varieties (Supporting Information S1: Table S1) were grown outdoors in Beijing, China (39°58′N, 116°19′E) from May to September in 2020 and 2021. Varieties planted in 2020 were used to investigate the phenotypes

and agronomic traits, and varieties planted in 2021 were used for crude protein and oil quantification. Soybean plants were exposed to preflowering SD or LD and then postflowering LD treatments. The SD treatments consisted of 12 h light/12 h dark where sunshine was applied from 7:00 to 19:00 and dark treatment was conducted from 19:00 to 7:00 the following day. LD treatments consisted of 18 h light/6 h dark where sunshine was applied from 7:00 to 19:00 and 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ fluorescent light was extended from 19:00 to 1:00 the following day; dark treatment was conducted from 1:00 to 7:00 the following day.

For gene expression and function analysis, HH27, DN36, ZGDD, *E1* RNAi plants and *35 S:GmFT2a* OE plants were grown in growth chambers at 26°C under photoperiod conditions which preflowering SD or LD and postflowering LD treatments were conducted.

2.3 | Transcriptome analysis and gene function annotation

The unifoliolate leaves of HH27 treated with preflowering SD or LD and postflowering LD were sampled at 4 h after day light at R1 (beginning bloom) and R3 (beginning pod) stages. Each sample was collected from three individual plants. Three biological replicates were analysed. Total mRNA from leaves was extracted using RNA Easy Fast Plant Tissue kits (Tiangen) and used for cDNA library building and sequencing. cDNA was sequenced with the HiSeq. A total of 4000 platform (Illumina) following the manufacturer's protocols. Clean reads were obtained by removing reads with adapters, reads containing ploy-N ($N > 10\%$) and low-quality reads (reads with Q < 5 bases for >50% in the raw data). The clean data were mapped to the soybean genome Wm82.a4.v1. Gene expression levels were determined using the fragments per kilobase of transcript per million reads (FPKM) to compare among the different samples.

2.4 | Gene expression analysis

The unifoliolate leaves of HH27 plants treated with preflowering SD or LD and postflowering LD were sampled at 4 h after dawn at the V1 (unifoliolate fully developed), V2 (first trifoliolate fully developed), V3 (second trifoliolate fully developed), R1, R3 and R5 (beginning seed). The unifoliolate leaves of *E1* RNAi plants and *35 S:GmFT2a* OE plants treated with preflowering SD or LD and postflowering LD were sampled at 4 h after dawn at R5. Each sample was collected from three individual plants. Total mRNA from leaves was isolated using RNA Easy Fast Plant Tissue kits (Tiangen) and cDNA was synthesised using FastKing RT kits (Tiangen). The transcript levels of the floral-promoting genes (*GmFT2a*, *GmFT3a*, *GmFT3b*, *GmFT5a* and *GmFT6*), and floral-inhibiting genes (*GmFT1a*, *GmFT4* and *E1*) were detected using KAPA SYBR DNA Polymerase (KAPA Biosystems) on a QuantStudio 7 Flex system (Applied Biosystems). The qPCR data were analysed using the $2^{-\Delta\Delta C_t}$ method with *GmActin* as an internal reference gene (Jian et al., 2008). Primers used for qPCR are listed in Supporting Information S2: Table S2.

2.5 | Phenotyping and statistical analysis

Soybean developmental stages of emergence (VE), V1, V2, V3, R1 (one open flower at any node on the main stem), R3 (a 0.5-cm long pod on one of the four uppermost nodes on the main stem), R5 (a 3-mm long seed in pod in one of the four uppermost nodes on the main stem), beginning maturity (R7, one pod on the main stem has reached mature pod colour) and full maturity (R8, 95% of pods have reached mature pod colour) were recorded according to the description of Fehr and Caviness (1977). We recorded the VE, V1, V2, V3, R1, R3, R5 and R7 of eleven early-maturing soybean varieties treated with preflowering SD or LD and postflowering LD photoperiods (Supporting Information Table S3). A total of seven ~ twenty plants were recorded for each variety. Once these plants reached the R8, we documented their plant height, node number, branch number and seed number per plant (Supporting Information Table S4).

The photoperiod response sensitivity (PRS) was calculated using Equation (1) indicated below, and the PAE was calculated according to Equation (2) (Fei et al., 2009). The data were analysed using Excel and R packages, and are presented as the mean ± standard deviation. Student's *t* tests were used to assess the significance of the observed differences ($n = 15$ plants for each variety).

$$PRS(\%) = \frac{DTF_{LD} - DTF}{DTF_{LD}} \times 100\%. \quad (1)$$

$$PAE(\%) = \frac{DTM_{LD+LD} - DTM_{+LD}}{D_{LD(R1-R7)}} \times 100\%. \quad (2)$$

DTF_{SD}: days to flowering (R1) from emergence under SD condition. DTF_{LD}: days to flowering from emergence under LD conditions. DTM_{SD+LD}: days to maturity (R7) from flowering under preflowering SD and postflowering LD. DTM_{LD+LD}: days to maturity from flowering under pre- and postflowering LD conditions.

2.6 | Crude fat and crude protein analysis

We measured the crude fat and crude protein content of seeds of eleven early-maturing soybean varieties treated with preflowering SD or LD and postflowering LD photoperiods (Supporting Information Table S5) using an multi purpose analyzer Type Fourier Transform Near Infrared Grain Analyzer (Bruker) following the manufacturer's protocols described in a previous study (Song et al., 2016). Three biological replicates were measured for each sample (Supporting Information Table S5).

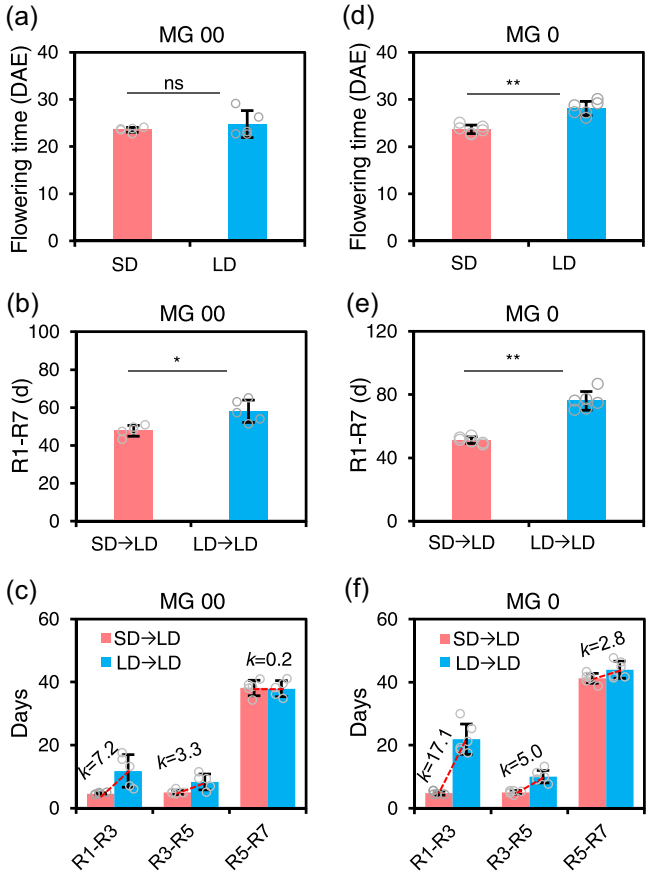

FIGURE 1 Effects of preflowering photoperiodic treatments on flowering and maturity of early-maturing soybean varieties. (a and d) The flowering time of early-maturing varieties in MG 00 (a) and MG 0 (d). (b and e) Days from R1 to R7 of the early-maturing varieties MG 00 (b) and MG 0 (e). (c and f) The period of different developmental stages at R1–R7 of early-maturing varieties in MG 00 (c) and MG 0 (f). The arrows indicate that varieties were grown under preflowering SD (12 h light/12 h dark) or LD (18 h light/6 h dark) and postflowering LD (18 h light/6 h dark) conditions outdoors in Beijing, China, in 2020. Data are means ± standard deviation (n = 5 MG 00 varieties and 6 MG 0 varieties). Statistical significance was determined by applying a Student's t test (*p < 0.05; **p < 0.01). DAE, d after emergence; k, slope value; LD, long day; MG, maturity groups; ns, not significant; R1, beginning bloom; R3, beginning pod; R5, beginning seed; R7, beginning maturity; SD, short day. [Color figure can be viewed at wileyonlinelibrary.com]

3 | RESULTS

3.1 | The postflowering responses of early-maturing soybean varieties to preflowering photoperiodic treatments

Five and six early-maturing varieties in the MG 00 and MG 0 groups, respectively, were selected to identify the PAE (Supporting Information S1: Table S1). These plants were treated with preflowering SD or LD and postflowering LD. The results showed that the flowering time (VE–R1) and maturity (R1–R7) of varieties in MG 00 exhibited no significant difference (p > 0.05) between preflowering SD and LD treatments (Figure 1a), while maturation occurred 10.3 days earlier (p < 0.05) in plants treated with preflowering SD compared to plants treated with preflowering LD (Figure 1b). The PAE sensitivity was 16.9% ± 11.2%. For the early-maturing varieties in MG 0, the flowering time and maturity occurred 4.4 and 24.9 days earlier (p < 0.01), respectively, in plants treated with preflowering SD compared to plants treated with preflowering LD conditions (Figure 1d,e). The PRS was 15.6% ± 4.7%, while the PAE sensitivity was 32.4% ± 7.1%, suggesting that preflowering SD treatment has a greater tendency to promote maturity than does flowering time. Thus, the early-maturing varieties in MG 00 and MG 0 demonstrate a significant PAE from preflowering treatments.

To examine the growth stage which the PAE mainly affected during reproductive growth, we examined the R1, R3, R5 and R7 of MG 00 and MG 0 varieties. We found that R1 to R3 was the most significantly accelerated period in MG 00 and MG 0 varieties (k = 7.2 and k = 17.1) following preflowering SD compared to plants treated with preflowering LD, followed by R3 to R5 (k = 3.3 and k = 5.0) and R5 to R7 (k = 0.2 and k = 2.8) (Figure 1c,f). This indicates that the PAE was more impactful at the early stage of reproductive growth than in later stages.

3.2 | Effects of preflowering photoperiodic treatments on the agronomic traits of early-maturing soybean varieties

To analyse the influence of the PAE on important agronomic traits, five MG 00 and six MG 0 varieties were grown under preflowering SD or LD and postflowering LD conditions. We monitored the plant height, node number, branch number and seed number per plant at R8, and found that plant height was significantly lower (p < 0.01) in MG 00 and MG 0 plants treated with preflowering SD (24.1 ± 6.4 and 18.4 ± 2.8 cm, respectively) than plants treated with preflowering LD (32.5 ± 8.2 and 27.9 ± 4.2 cm, respectively) (Figure 2a). The node number also displayed a significant decrease of 3.5 and 4.7 (p < 0.01) in MG 00 and MG 0 plants treated with preflowering SD than plants treated with preflowering LD, respectively (Figure 2b). However, we observed no significant difference (p > 0.05) in branch number and seed number between MG 00 and MG 0 plants treated with preflowering SD or LD (Figure 2c,d). Thus, the PAE reduced plant height and node number in early-maturing soybean plants.

We also verified whether the PAE influences protein and oil content in soybean seeds in MG 00 and MG 0 varieties. We found that the protein and oil content of MG 00 varieties showed no significant difference (p > 0.05) between preflowering SD and LD treatments (Figure 2e,f). However, in MG 0 varieties, there was a significant (p < 0.01) decrease in seed protein content and an increase in seed oil content in plants treated with preflowering SD compared to LD-treated plants (Figure 2e,f). This suggests that preflowering treatments impact agronomic traits of soybean.

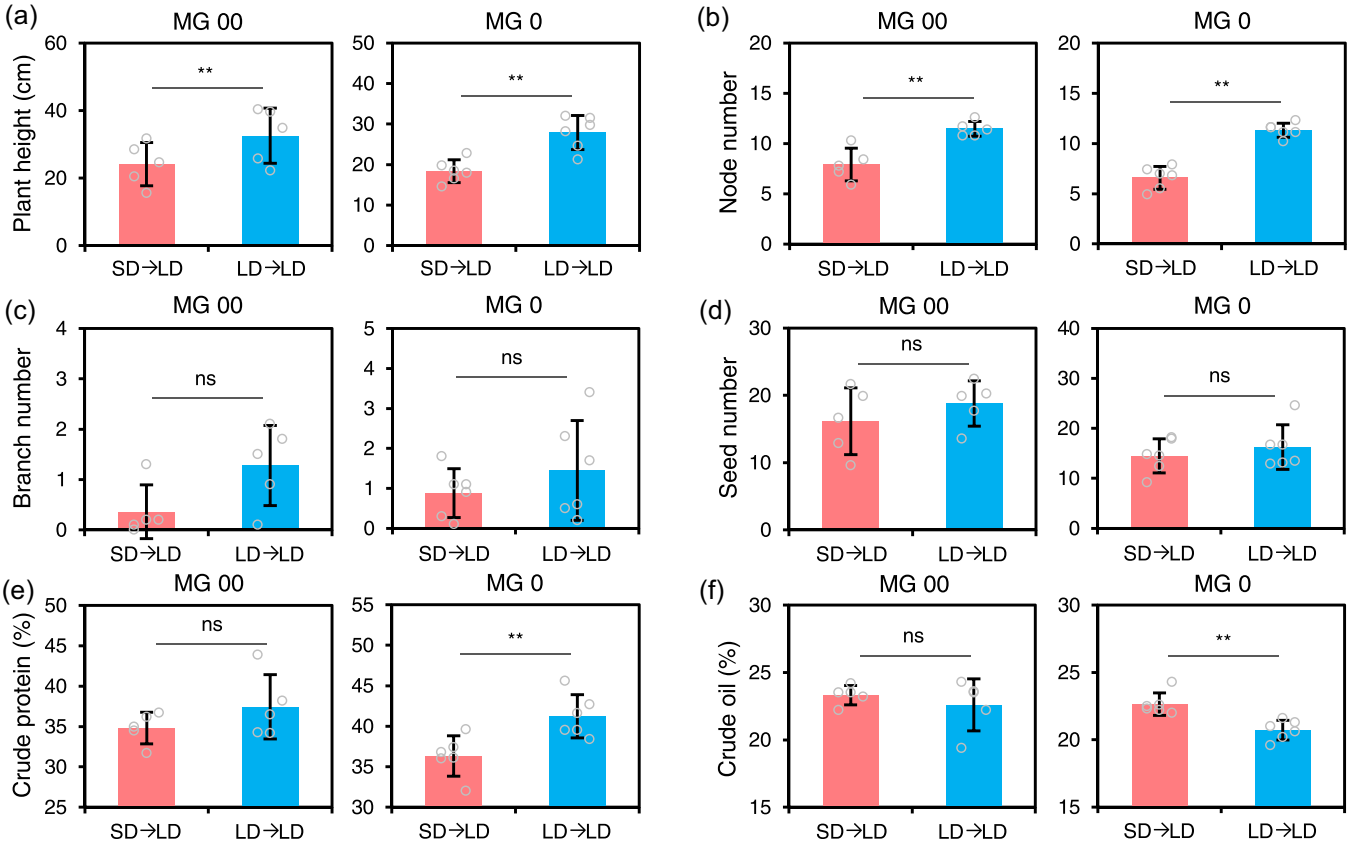

FIGURE 2 Effects of preflowering photoperiodic treatments on the agronomic traits of early-maturing soybean varieties. (a–f): The plant height (a), node number (b), branch number (c), seed number (d), protein content (e) and oil content (f) of early-maturing varieties in MG 00 and MG 0. The arrows indicate that varieties that were grown under preflowering SD (12 h light/12 h dark) or LD (18 h light/6 h dark) and postflowering LD (18 h light/6 h dark) conditions outdoors in Beijing in 2020 (a–d) and 2021 (e and f), respectively. Data are means ± standard deviation (n = 5 MG 00 varieties and 6 MG 0 varieties). Statistical significance was determined by applying a Student's t test (**p < 0.01). LD, long day; MG, maturity groups; ns, not significant; SD, short day. [Color figure can be viewed at wileyonlinelibrary.com]

3.3 | Transcriptome profiling and expression analysis of flowering-time genes in soybean plants responsive to preflowering photoperiodic treatments

To identify the flowering-time related genes influenced by preflowering SD treatments, we identified differentially expressed genes (DEGs) by performing transcriptomic sequencing of the early-maturing variety Heihe27 (MG 0) at R1 and R3 under preflowering SD or LD and postflowering LD conditions. A total of 8608 and 7650 DEGs were found to be up-regulated and down-regulated, respectively, in plants treated with SD compared to LD at R1 (Figure S1), and 10 615 and 10 282 DEGs showed differential expression at R3 (Figure S2). A majority of DEGs were classified under the molecular function category at R1 (Figure S3), whereas most DEGs belonged to the cell component category at R3 (Figure S4). There were 10 308 DEGs that exhibited differential expression patterns in both R1 and R3 (Figure S5). Further analysis revealed that among these common DEGs, 25 DEGs shew homology to flowering-time related genes through screening their functional annotations (Figure 3).

The first set of DEGs included *FT* (*GmFT2a*, *GmFT3a*, *GmFT3b*, *GmFT5a* and *GmFT6*), *CONSTANS-LIKE* (*Glyma.16G067000*), *RELATIVE OF EARLY FLOWERING* (*Glyma.04G191900*, *Glyma.06G174000*, *Glyma.04G192000* and *Glyma.06G173800*), *EARLY FLOWERING MYB* (*Glyma.17G178500* and *Glyma.06G213400*), *EARLY FLOWERING IN SDS* (*Glyma.06G117700* and *Glyma.04G245400*), *EARLY FLOWERING 8* (*Glyma.15G176400*) and *FLOWERING TIME CONTROL PROTEIN FPA* (*Glyma.13G075300*) homologs that were significantly up-regulated (p < 0.05) at R1 and R3 in Heihe27 plants treated with preflowering SD compared to those treated with preflowering LD (Figure 3). In contrast, another set of genes like *CRYPTOCHROME* (*GmCRY1a* and *GmCRY1b*), *GIGANTEA* (*E2* and *GmGI3*), *PHYTOCHROME-INTERACTING FACTOR 3* (*Glyma.19G222000*), *FLOWERING LOCUS K* (*Glyma.03G160000*), *EARLY FLOWERING* (*Glyma.08G361700* and *Glyma.17G231600*), *CONSTANS-LIKE* (*Glyma.02G152900*) homologs were significantly down-regulated (p < 0.05) at R1 compared to R3 (Figure 3).

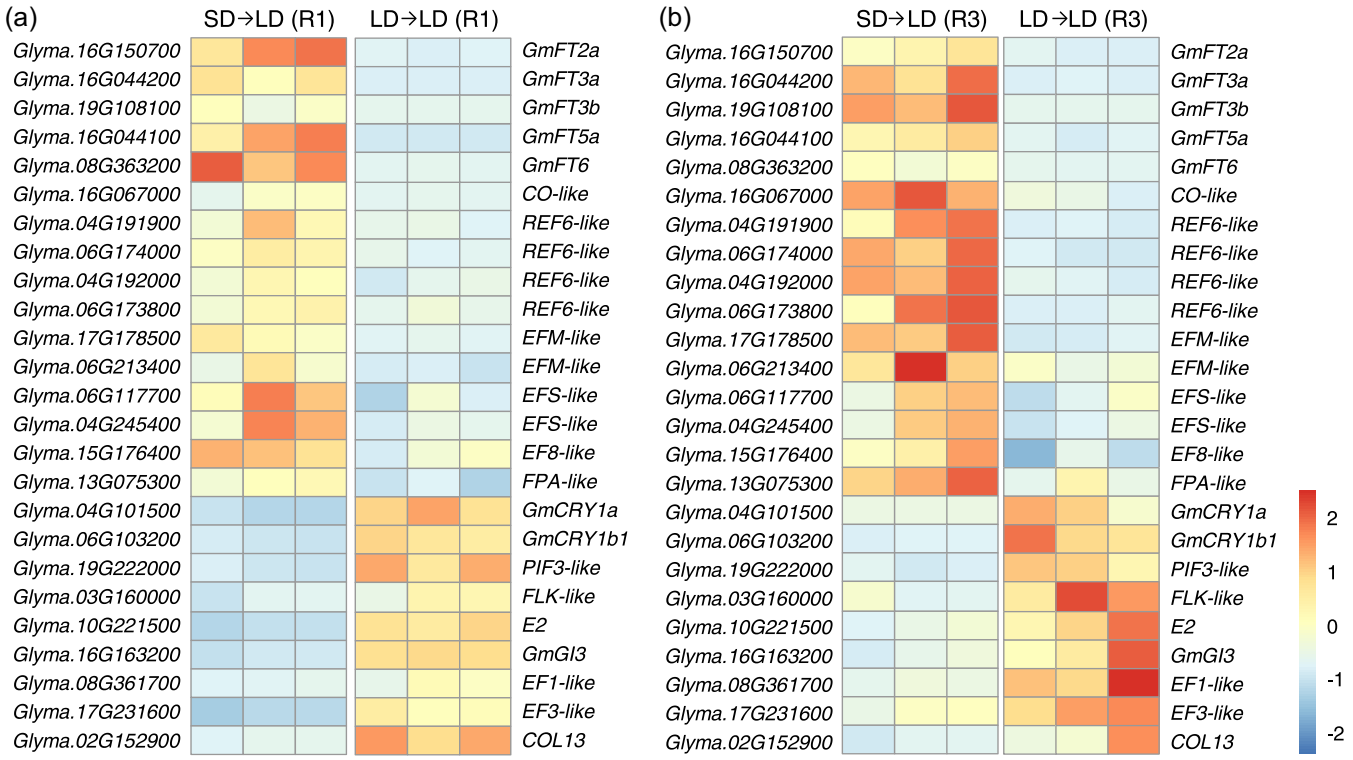

FIGURE 3 Differential expression of flowering-time related genes in an early-maturing soybean variety under different preflowering photoperiodic treatments. (a and b) The differential expression of genes related to flowering time at R1 (a) and R3 (b). The arrows indicate that the early-maturing soybean variety Heihe27 (MG 0) was grown under preflowering SD (12 h light/12 h dark) or LD (18 h light/6 h dark) and postflowering LD (18 h light/6 h dark) conditions in growth chambers at 26°C. The unifoliolate leaves were sampled at 4 h after day light at R1 and R3. Each sample was collected from three individual plants. Three biological replicates were analysed. LD, long day; MG, maturity groups; R1, beginning bloom; R3, beginning pod; SD, short day. [Color figure can be viewed at wileyonlinelibrary.com]

FT is regarded as the integrator of signals in the flowering pathway of plants (Andrés & Coupland, 2012). In soybean, *FT* homologs are divided into two types including floral promoters (e.g., *GmFT2a*, *GmFT2b*, *GmFT3a*, *GmFT3b*, *GmFT5a* and *GmFT5b*) and floral inhibitors (e.g., *GmFT1a* and *GmFT4*) (Cai et al., 2020; Kong et al., 2010; Liu et al., 2018; Nan et al., 2014; Su et al., 2022, 2024; Sun et al., 2011; Yuan et al., 2022). To confirm the expression pattern of *GmFT* homologs during reproductive growth, we performed qPCR targeting *GmFT2a*, *GmFT3a*, *GmFT3b*, *GmFT5a* and *GmFT6* at vegetative growth stages (V1, V2 and V3) and reproductive growth stages (R1, R3 and R5). Our results revealed that all five of the above genes were significantly up-regulated ($p < 0.01$) at V1, V2 and V3 in plants treated with preflowering SD compared to plants treated with preflowering LD (Figure 4a–e). Additionally, these *GmFT* homologs also maintained a higher ($p < 0.01$) expression level at R1, R3 and R5 in plants treated with preflowering SD than in plants treated with preflowering LD (Figure 4a–e). Furthermore, *GmFT2a* and *GmFT5a* were down-regulated from R1 to R5 (Figure 4a,d), *GmFT3a* and *GmFT6* were up-regulated from R1 to R3 and down-regulated from R3 to R5 (Figures 3e and 4b), and *GmFT3b* was consistently up-regulated from R1 to R5 stage (Figure 4c). Additionally, we observed similar expression patterns in another early-maturing variety DN36 except the *GmFT6* which displayed a down-regulated expression in plants treated with preflowering SD than in plants treated with preflowering LD (Figure S6). These results indicate that the floral-promoting *GmFT* homologs (*GmFT2a*, *GmFT3a*, *GmFT3b* and *GmFT5a*) were significantly up-regulated in early-maturing soybean treated with preflowering SD and continuously maintain a higher expression level at the postflowering stage.

Subsequently, we analysed the expression level of the floral-inhibiting genes of *GmFT1a* and *GmFT4*, and *E1* (the specific transcriptional factor in legume that acts as the upstream gene of *FT* homologs) (Xia et al., 2012). We found that they exhibited the opposite expression pattern compared to floral-promoting *GmFT* homologs (Figure 4f–h). *GmFT1a*, *GmFT4* and *E1* were greatly down-regulated ($p < 0.01$) during the V1, V2 and V3 vegetative stages and maintained lower ($p < 0.01$) expression levels during the R1, R3 and R5 in plants treated with preflowering SD compared to those treated with preflowering LD (Figure 4f–h). These results suggested that the synergy of the low expression of floral-inhibiting homologs and high expression of floral-promoting homologs caused by preflowering SD treatment likely promotes postflowering development.

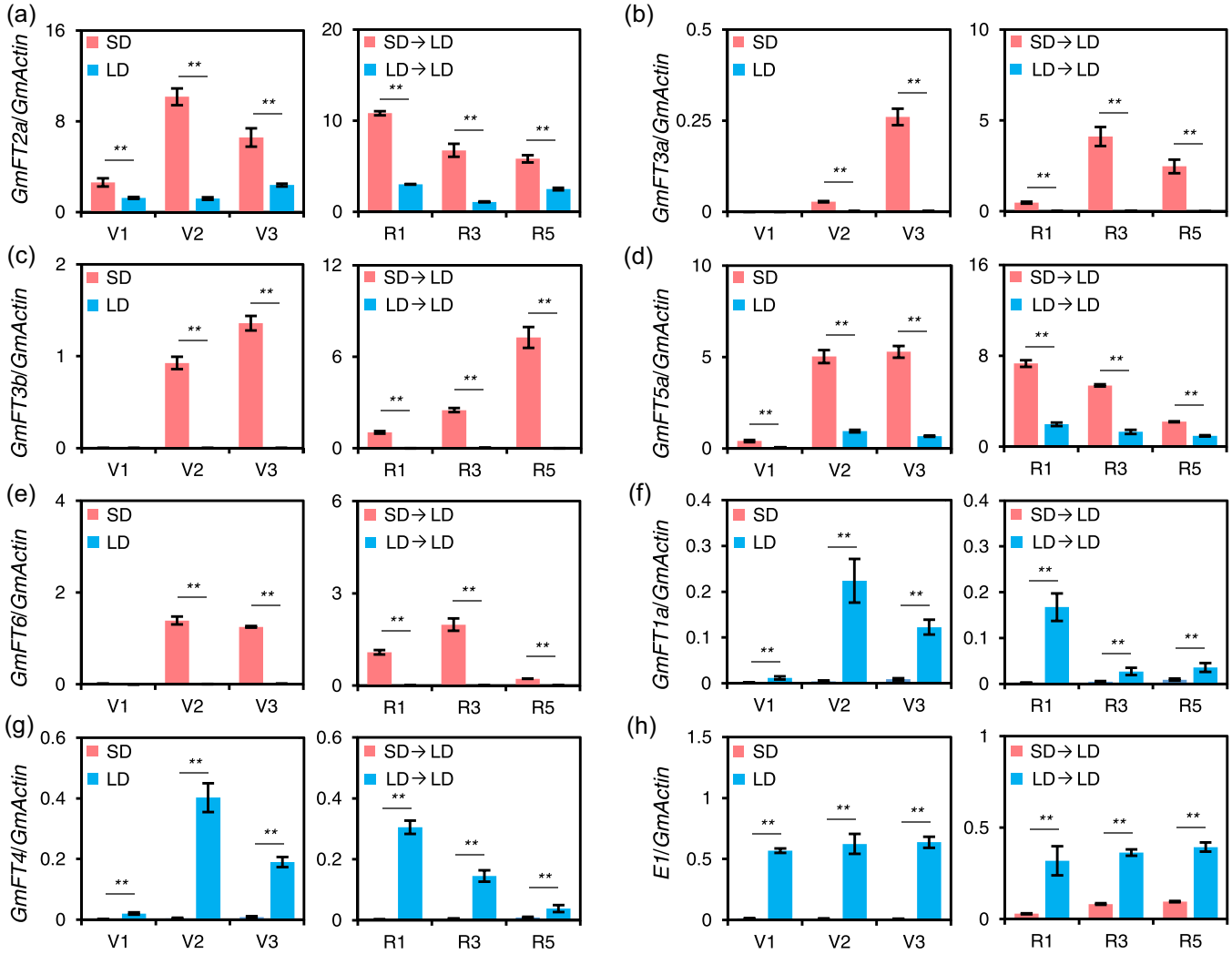

FIGURE 4 The expression pattern of *GmFT* homologs and *E1* under preflowering photoperiodic treatments. (a–e) The expression levels of *GmFT2a* (a), *GmFT3a* (b), *GmFT3b* (c), *GmFT5a* (d), *GmFT6* (e), *GmFT1a* (f), *GmFT4* (g) and *E1* (h). The arrows indicate that the early-maturing soybean variety Heihe27 (MG 0) was grown under preflowering SD (12 h light/12 h dark) or LD (18 h light/6 h dark) and postflowering LD (18 h light/6 h dark) conditions in growth chambers at 26°C. Unifoliolate leaves were sampled at 4 h after day light at V1, V2, V3, R1, R3 and R5. Data are represented as mean ± standard deviation ($n = 3$ for each sample). Statistical significance was determined by applying a Student's *t* test (**$p < 0.01$). LD, long day; MG, maturity groups; R1, beginning bloom; R3, beginning pod; R5, beginning seed; SD, short day; V1, unifoliolate fully developed; V2, first trifoliolate fully developed; V3, second trifoliolate fully developed. [Color figure can be viewed at wileyonlinelibrary.com]

3.4 | The PAE of early-maturing soybean lines overexpressing floral-promoting *GmFT* homologs

E1 has a high expression level in LD and a low expression level in SD and regulates the flowering and maturity of soybean by inhibiting the expression of floral-promoting *GmFT* (Chen et al., 2020; Nan et al., 2014; Su et al., 2022; Xia et al., 2012). We grew *E1* RNAi (in ZGDD background) and wild-type ZGDD plants under preflowering SD or LD and postflowering LD conditions. The results indicated that the flowering time and maturity of *E1* RNAi plants displayed no significant difference ($p > 0.05$) between preflowering SD and LD (Figure 5a,b). In *E1* RNAi plants, *E1* was dramatically down-regulated ($p < 0.01$) and the floral-promoting *GmFT2a*, *GmFT3a*, *GmFT3b* and *GmFT5a* were all highly up-regulated ($p < 0.01$) compared to wild-type ZGDD plants (Figure 5c–g). Importantly, *GmFT2a*, *GmFT3a*, *GmFT3b* and *GmFT5a* exhibited a higher expression level both in preflowering SD and LD when *E1* was suppressed (Figure 5d–g).

To test whether the floral-promoting *GmFT* homologs are required for the PAE in soybean, *35 S:GmFT2a* overexpression plants (*35 S:GmFT2a* OE, in ZGDD background) and wild-type ZGDD plants were treated with preflowering SD or LD and postflowering LD. The flowering time of *35 S:GmFT2a* OE plants was 12.1 ± 1.5 and 11.7 ± 0.6 d after emergence under SD and LD conditions, which were significantly earlier than the MG 00 and MG 0 varieties (Figures 1a,d and 6a). Moreover, the flowering time and maturity of *35 S:GmFT2a* OE plants displayed no significant difference ($p > 0.05$) between preflowering SD and LD treatments (Figure 6a,b). Next, we analysed the expression level of *GmFT2a* in *35 S:GmFT2a* OE and wild-type ZGDD plants and found

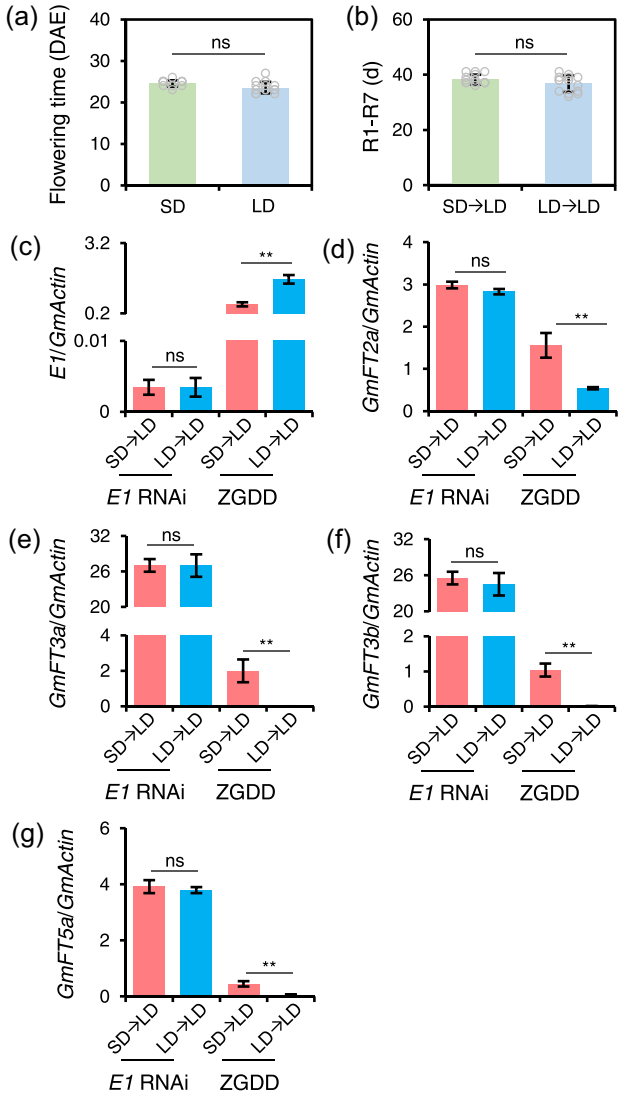

FIGURE 5 The photoperiodic after-effects on flowering and maturity of *E1* RNAi plants. (a and b) The flowering time (a) and days from R1 to R7 (b) of *E1* RNAi plants (in Zigongdongdou background). Data are represented as mean ± standard deviation ($n = 14$ for each sample). (c–h) The expression pattern of *E1* (c), *GmFT2a* (d), *GmFT3a* (e), *GmFT3b* (f) and *GmFT5a* (g). Data are represented as mean ± standard deviation ($n = 3$ for each sample). The arrows indicate that plants were grown under preflowering SD (12 h light/12 h dark) or LD (18 h light/6 h dark) and postflowering LD (18 h light/6 h dark) conditions in growth chambers at 26°C. The unifoliolate leaves were sampled at 4 h after day light at R5 (beginning seed). Statistical significance was determined by applying a Student's *t* test (**$p < 0.01$). DAE, d after emergence; LD, long day; ns, not significant; SD, short day. [Color figure can be viewed at wileyonlinelibrary.com]

that *35 S:GmFT2a* OE plants showed a high expression level of *GmFT2a* even under LD → LD conditions (Figure 6c). Additionally, *GmFT2a* displayed constitutively high expression levels no matter the preflowering SD and LD treatment (no significant difference; $p > 0.05$) (Figure 6c). Thus, the high expression of the floral-promoting *GmFT2a* regulates the PAE of early-maturing varieties.

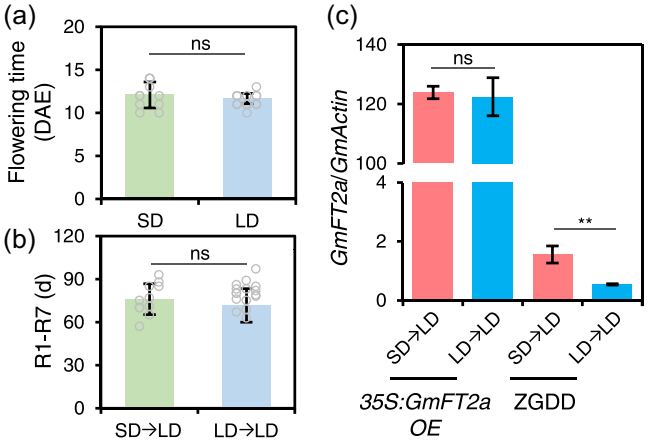

FIGURE 6 The photoperiodic after-effects on flowering and maturity of the overexpression line of floral-promoting *GmFT2a*. (a and b) The flowering time (a) and days from R1 to R7 (b) of *35 S:GmFT2a* overexpression plants (*35 S:GmFT2a* OE, in Zigongdongdou [ZGDD] background). Data are represented as mean ± standard deviation ($n = 11$ plants in SD or SD → LD, and 16 plants in LD or LD → LD photoperiods). (c) The expression pattern of *GmFT2a* in *35 S:GmFT2a* OE and wild-type ZGDD plants. Data are represented as mean ± standard deviation ($n = 3$ for each sample). The arrows indicate that plants were grown under preflowering SD (12 h light/12 h dark) or LD (18 h light/6 h dark) and postflowering LD (18 h light/6 h dark) conditions in growth chambers at 26°C. The unifoliolate leaves were sampled at 4 h after day light at R5 (beginning seed). Statistical significance was determined by applying a Student's *t* test (**$p < 0.01$). DAE, d after emergence; LD, long day; ns, not significant; OE, overexpression; SD, short day. [Color figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

4.1 | The characteristics of photoperiodic after-effect (PAE) in early-maturing soybean varieties

Soybean is an SDP in which flowering is promoted by SD conditions and suppressed by LD conditions (Garner & Allard, 1920; Wu et al., 2006). The PAE was discovered in parallel with the photoperiodic response in soybean (Garner & Allard, 1920). Indeed, the PAE is a continuation of the photoperiodic response in soybean plants after flowering. Thus, preflowering SD-induced factors are also required for postflowering developments. This phenomenon is consistent with the previous notion that the photoperiodic response exists in the whole life cycle from emergence to maturity in soybean (Han et al., 1995, 2006; Wu et al., 2006; Xu et al., 2021). Early-maturing varieties display no difference in the flowering time under SD and LD conditions but greatly accelerated the postflowering maturation process after SD preflowering exposure compared to LD. Hence, the maturation of early-maturing soybean varieties is sensitive to photoperiods and is impacted during reproductive growth, but not during vegetative growth. In other words, the maturity of early-maturing varieties is more sensitive to photoperiod than flowering time. According to this, we propose that early-

maturing varieties adapt to high latitudes mainly by adjusting the length of their reproductive maturation period.

Besides the developmental status, the PAE also influences the formation of important agronomic traits including plant height, node number, pod number, seed number, biomass and so on (Han et al., 1995; Liu et al., 1983; Xu et al., 1990). Additionally, quality-related traits, like protein and oil content, oleic acid and linoleic acid proportions in oil, are also influenced by preflowering photoperiodic treatments (Han et al., 1995). Protein content is negatively correlated with the PAE, revealing that the preflowering SD treatment is unbeneficial to seed protein accumulation for early-maturing varieties with low levels of protein content that are prevalently found in high latitudes (Han et al., 1995, 1997; Song et al., 2016).

4.2 | Floral-promoting *GmFT* homologs play key roles in the PAE

The photoperiodic response of soybean is controlled by multiple genes, including the photoreceptor phytochrome A (*E3* and *E4*) (Liu et al., 2008; Watanabe et al., 2009), circadian evening complex components (*J* and *LUX*) (Bu et al., 2021; Lu et al., 2017; Yue et al., 2017), central flowering repressor (*E1*) (Xia et al., 2012) and downstream integrators (floral-promoting *GmFT2a* and *GmFT5a*, and floral-inhibiting *GmFT1a*) (Liu et al., 2018; Nan et al., 2014; Sun et al., 2011). In the present study, we demonstrated that these integrators, mainly the floral-promoting *GmFT* homologs of *GmFT2a*, *GmFT3a*, *GmFT3b* and *GmFT5a*, are greatly up-regulated in the early-maturing varieties treated with preflowering SD and continuously maintain a high expression level postflowering even under LD conditions. It was proposed that *E1-FT* module may play a central role in the PAE and two factors may contribute to maintaine high expression levels of the floral-promoting *GmFT* homologs after photoperiod conversion. First, *E1*, the upstream inhibiting gene of floral-promoting *GmFT* homologs, showed low expression level under preflowering SD treatment compared to preflowering LD treatment. Second, the total or partial dysfunction of E1 resulting from mutations in early-maturing soybean varieties decrease the inhibition to the expression of flowering-promoting *GmFTs*. These observations revealed that PAE on postflowering development are caused by the same mechanism as the photoperiodic response before flowering, and further indicate that the PAE is another presentation of the complete photoperiodic response in the whole life cycle of soybean (Han & Wang, 1995b).

FT is a part of the florigen signal that promotes floral development (Corbesier et al., 2007; Tamaki et al., 2007). In soybean, the floral-promoting GmFT homologs GmFT2a and GmFT5a have been demonstrated as the mobile factors that move from leaves to roots (Wang et al., 2021). In our study, we characterised the effect of floral-promoting *GmFT* homologs on both vegetative and reproductive development, especially how *GmFT* responds to preflowering SD on the postflowering development in early-maturing soybean varieties. It is noticeable that the floral-promoting *GmFT* homologs are significantly induced upon preflowering SD treatment and maintained high expression levels throughout flowering under LD conditions, resulting in a shortened reproductive period and earlier maturation. Additionally, we have observed that the upstream photoperiodic-related genes *CRY*, *PIF*, *GI* and *CO*, and the temperature-responsive and epigenetic modification-related genes *REF* and *EFM* homologs showed significant decrease and increase under preflowering SD treatments, respectively. Future studies will focus on these genes to elucidate the regulatory mechanisms underlying PAE in early-maturing varieties and geographic adaptation of soybean to high-latitude regions.

4.3 | The PAE facilitates the adaptation of early soybean varieties to high latitudes

Suitable photoperiod sensitivity facilitates the optimal utilisation of environmental cues for crop cultivation. In high-latitude regions located above 47.5° N in China, early-maturing (MG 0 or earlier) soybean varieties are mainly planted in the early to middle of May and harvested at the middle to end of September (Jia et al., 2014; Pu & Pan, 1982). In these areas, with limited frost-free seasons, achieving a high yield and ensuring a suitable growth period is a major challenge for soybean. If the vegetative growth period is too short, the vegetative organs are under-developed and ultimately result in low yields as they are unable to adequately fuel the reproductive sink tissues. In contrast, if the reproductive growth period is too long, maturity may not be achieved before the onset of frost. In light of our findings that the super-early maturing soybean varieties are more responsive to photoperiods in the reproductive stage than in the vegetative stage, we propose a strategy of soybean adaptation to the high latitude regions as follows: preflowering photoperiod insensitivity enables a longer vegetative growth period, thus facilitating the sufficient growth of vegetative organs. Meanwhile, the floral promoting *GmFT* homologs can be induced and their products like florigen accumulate after emergence, thereby serving as a means of remembering floral induction cues to accelerate postflowering reproductive development and maturation to support rapid and robust fruit development to avoid the coming frost. We observed that the varieties in low latitudes also employ a longer vegetative growth phase (the well-known long-juvenile trait) to accumulate enough biomass for reproductive tissue support (Lu et al., 2017; Yue et al., 2017), indicating that prolonged vegetative growth is a common adaptation and yield formation strategy for soybean plants to maximise yields when adapting to different environments.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All raw data for RNA sequencing have been submitted to NCBI as BioProject PRJNA1027571.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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