



# Molecular breeding for improvement of photothermal adaptability in soybean

Tingting Wu · Sijia Lu · Yupeng Cai · Xin Xu · Lixin Zhang · Fulu Chen ·  
Bingjun Jiang · Honglei Zhang · Shi Sun · Hong Zhai · Lin Zhao ·  
Zhengjun Xia · Wensheng Hou · Fanjiang Kong · Tianfu Han 

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**Abstract** Soybean (*Glycine max* (L.) Merr.) is a typical short-day and temperate crop that is sensitive to photoperiod and temperature. Responses of soybean to photothermal conditions determine plant growth and development, which affect its architecture, yield formation, and capacity for geographic adaptation. Flowering time, maturity, and other traits associated with photothermal adaptability are controlled by multiple major-effect and minor-effect genes and genotype-by-environment interactions. Genetic studies

have identified at least 11 loci (*E1-E4*, *E6-E11*, and *J*) that participate in photoperiodic regulation of flowering time and maturity in soybean. Molecular cloning and characterization of major-effect flowering genes have clarified the photoperiod-dependent flowering pathway, in which the photoreceptor gene *phytochrome A*, circadian evening complex (EC) components, central flowering repressor *E1*, and *FLOWERING LOCUS T* family genes play key roles in regulation of flowering time, maturity, and adaptability to photothermal conditions. Here, we provide an overview of recent progress in genetic and molecular analysis of traits associated with photothermal adaptability, summarizing advances in molecular breeding practices and tools for improving these traits. Furthermore, we discuss methods for breeding

Tingting Wu, Sijia Lu, and Yupeng Cai contributed equally to this work.

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T. Wu · Y. Cai · X. Xu · L. Zhang · F. Chen · B. Jiang ·  
H. Zhang · S. Sun · W. Hou (✉) · T. Han (✉)  
MARA Key Laboratory of Soybean Biology (Beijing),  
Institute of Crop Sciences, Chinese Academy  
of Agricultural Sciences, Beijing 100081, China  
e-mail: houwensheng@caas.cn

T. Han  
e-mail: hantianfu@caas.cn

S. Lu · F. Kong (✉)  
Guangdong Key Laboratory of Plant Adaptation  
and Molecular Design, Guangzhou Key Laboratory  
of Crop Gene Editing, Innovative Center of Molecular  
Genetics and Evolution, School of Life Sciences,  
Guangzhou University, Guangzhou 510006, China  
e-mail: kongfj@gzhu.edu.cn

H. Zhai · Z. Xia  
Key Laboratory of Soybean Molecular Design Breeding,  
Northeast Institute of Geography and Agroecology,  
Chinese Academy of Sciences, Harbin 150081, China

L. Zhao  
Key Laboratory of Soybean Biology of Ministry  
of Education of China, Northeast Agricultural University,  
Harbin 150030, China

soybean varieties with better adaptability to specific ecological regions, with emphasis on a novel strategy, the Potalaization model, which allows breeding of widely adapted soybean varieties through the use of multiple molecular tools in existing elite widely adapted varieties.

**Keywords** Soybean · Photoperiod · Temperature · Adaptability · Molecular breeding

## Introduction

Soybean (*Glycine max* (L.) Merr.) was domesticated from the wild annual progenitor *Glycine soja* in the temperate regions of China; its distributing area was then expanded northward to high-latitude cold zones and southward to low-latitude tropical regions (Broich and Palmer 1981; Hymowitz and Newell 1981). Currently, soybean is grown over a wide range of latitudes worldwide, from over 53°N to 35°S (Zhang et al. 2020b). Soybean is a typical short-day plant (SDP) and is thus intrinsically sensitive to photothermal conditions, particularly to photoperiod. Responses to photothermal conditions determine soybean capacity for growth, development, yield formation, and geographic adaptation (Setiyono et al. 2007; Cober and Morrison 2010; Wu et al. 2015a; Lin et al. 2021). Among the variable traits that allow soybean to adapt to different regions, flowering time and maturity are the most important. Previous studies have indicated that natural variations in genes associated with flowering time and maturity and specific combinations of alleles for such genes were strong contributors to the northward and southward soybean expansions (Wang et al. 2020a; Lin et al. 2021; Dong et al. 2022, 2023). In recent years, genetic, genomic, and molecular biological methods have been applied to identify quantitative trait loci (QTL) and key genes in the soybean photoperiod-dependent and temperature-dependent flowering pathways. Discoveries of specific alleles in relevant genes have made molecular breeding a powerful tool for improvement of soybean photothermal adaptation. In this review, we summarize recent progress in basic research that has yielded mechanistic insights into soybean responses to photoperiod and temperature. We also discuss recent advances in molecular breeding practices and introduce strategies for integrating conventional and molecular breeding

methods. Together, gene discovery and novel breeding methods offer efficient methods of optimizing photothermal adaptability in this economically and nutritionally valuable species.

## Photothermal responses in soybean

### Photoperiod responses

The phenomenon of plant photoperiodism was first identified in soybean and tobacco (Garner and Allard 1920). Many key traits in soybean such as flowering time, maturity, plant architecture (including internode length, branch number, and node number), seed quality, and grain yield are photoperiod-sensitive (Garner and Allard 1920; Han et al. 1996, 1997; Zhang et al. 2020b). The photoperiodic responses occur in the whole life cycle of soybean plants from emergence to maturity (Han and Wang 1995; Xu et al. 2021). When photoperiod-sensitive soybean varieties are transferred from inductive short-day (SD) to non-inductive long-day (LD) conditions, they revert to vegetative growth in a process termed “reversion of flowering” (Han et al. 1998; Washburn and Thomas 2000; Wu et al. 2006). This indicates that SD is essential for induction and maintenance of reproductive development in soybean (Sun et al. 2011). In some early-maturing soybean varieties, SD treatment prior to flowering does not alter flowering time, but significantly promotes maturity and other post-flowering developmental stages, even if plants are then moved to LD conditions. This demonstrates a type of memory-like “after effect” of photoperiod induction (Han and Wang 1995; Han et al. 2006c).

### Thermal responses

Soybean is a temperate legume that generally thrives in warm ambient temperatures. The ideal mean daily temperatures for soybean emergence, flowering, and maturity are 15–22 °C, 20–25 °C, and 15–22 °C, respectively (Liu et al. 2008b). Within a suitable temperature range, increases in ambient temperature promote soybean growth and development by accelerating emergence, flowering time, and maturity; in contrast, decreased temperatures suppress or delay those processes (No et al. 2021). For example, when soybean is grown below 10 °C, seedlings can take as

long as 26 days to emerge; the seedling emergence rate is decreased by 50%; and plant growth is halted (Pan et al. 1983). However, exposure to temperatures above 35 °C causes heat stress responses, which accelerate senescence and decrease yield (Onat et al. 2017). A recent study demonstrated temperature-dependent differences in soybean flowering time; under SD conditions, 30 °C (ordinary high temperature) accelerated flowering, whereas 35 °C (harsh high temperature) delayed flowering (Tang et al. 2022). Expansion of soybean into areas with higher or lower temperatures would therefore require genetic manipulation to allow normal plant development.

### Photothermal interactions

Plants coordinate growth and development in response to light and temperature signals by an elaborate network (Li et al. 2022c). Photoreceptors, including red/far-red light receptors phytochromes (Phys), blue/(UV-A) light receptors cytochromes (Crys), ZTL family genes, and UV-B light receptor, participate in temperature response (Miyazaki et al. 2015; Legris et al. 2016; Ma et al. 2016; Fujii et al. 2017; Hayes et al. 2017). Endogenous circadian rhythms and phytohormones also participate in temperature response (Zheng et al. 2016; Luo and Shi 2019; Sanchez et al. 2020; Li et al. 2022c). Experiments with soybean have demonstrated clear interactions between photoperiod and temperature on soybean growth and development under the photothermal treatments of artificially control photoperiod (short daylength (SD) 12 h (h); long daylength (LD) 16 h) and serial planting season (spring planting (SP) and summer planting (SU)) and the field condition of spring planting and summer planting (Mao et al. 2017). Photoperiod dictates developmental stage progression, with SD promoting reproductive development and LD maintaining vegetative growth, whereas temperature affects the developmental rate (Han 2007; Mao et al. 2017). Usually, high-temperature (HT) conditions accelerate reproductive development under an inductive SD photoperiod, but enhance vegetative growth under a non-inductive LD photoperiod. In contrast, low-temperature (LT) conditions reduce the promotional effects of SD and the inhibitory effects of LD on reproductive growth (Han 2007). However, when temperatures are perceived as heat stress, they therefore delay flowering (Tang et al. 2022). In the field, photoperiod and temperature do not change synchronously; soybean adaptation to a specific

ecological environment is thus dependent on adjustment to local combinations of photoperiodic and thermal conditions (Mao et al. 2017).

## Molecular bases of photothermal adaptability in soybean

### QTL mining

#### *QTL for photoperiod responses*

Flowering time and maturity are quantitative traits controlled by multiple genes, including several major-effect and minor-effect genes (Malk and Singh 1991). At least 11 classical genetic flowering and maturity loci have been identified and characterized, namely, *E1-E4*, *E6-E11*, and *J*, which are all involved in photoperiod-associated regulation of soybean growth (Bernard 1971; Buzzell 1971; Ray et al. 1995; Bonato and Vello 1999; Cober and Voldeng 2001; Cober et al. 2010; Kong et al. 2014; Samanfar et al. 2017; Wang et al. 2019). A majority of these loci have been cloned and the molecular identity has been characterized (Liu et al. 2008a; Watanabe et al. 2009; Watanabe et al. 2011; Xia et al. 2012; Lu et al. 2017; Samanfar et al. 2017; Yue et al. 2017). Other loci associated with flowering time and maturity, such as *Time of flowering 4 (Tof4)/E1-Like a (E1La)* (Xu et al. 2015; Dong et al. 2023; Tang et al. 2022), *GmFULa* (Jia et al. 2014), *Tof5/FRUITFULL (GmFUL2a)* (Dong et al. 2022), *qDTF-J1* (Takeshima et al. 2016), *Gp1/qFT12-1/Tof12/GmPRR37/GmPRR3b* (Li et al. 2019; Lu et al. 2020; Wang et al. 2020a), *Tof11/Gp11/GmPRR3a* (Li et al. 2020; Lu et al. 2020), *Tof16/LATE ELONGATED HYPOCOTYL (GmLHY1a)* (Dong et al. 2021), and *Tof18/SUPPRESSOR OF OVEREXPRESSION OF CONSTANS 1 (GmSOC1a)* (Na et al. 2013; Kou et al. 2022), have also been identified (Table 1). In previous studies, joint segregation analyses using F<sub>1</sub>, F<sub>2</sub>, and F<sub>2,3</sub> populations have shown that many of these QTL are associated with four growth period traits: total growth duration (TGD), vegetative period (VP), reproductive period (RP), and the RP to VP ratio (R/V). Two major-effect QTL for RP identified in natural conditions or photoperiod-controlled conditions, each contain two potential causative genes; *qRP-c-1* contains *E8* and *GmCRY1a*, whereas *qRP-l-1*

**Table 1** Major genes in regulating photothermal flowering in soybean

Gene name	Locus	Effect	Associated pathway	Reference
<i>E1</i>	<i>Glyma.06G207800</i>	Inhibitory	Photoperiodic and thermal pathways	Xia et al. 2012; Tang et al. 2022
<i>E1La (Tof4)</i>	<i>Glyma.04G156400</i>	Inhibitory	Photoperiodic and thermal pathways	Xu et al. 2015; Tang et al. 2022
<i>E1Lb</i>	<i>Glyma.04G143300</i>	Inhibitory	Photoperiodic and thermal pathways	Xu et al. 2015; Tang et al. 2022
<i>E2</i>	<i>Glyma.10G221500</i>	Inhibitory	Photoperiodic and thermal pathways	Watanabe et al. 2011; Wang et al. 2022
<i>E3</i>	<i>Glyma.19G224200</i>	Inhibitory	Photoperiodic and thermal pathways	Watanabe et al. 2009; Tang et al. 2022
<i>E4</i>	<i>Glyma.20G090000</i>	Inhibitory	Photoperiodic pathway	Liu et al. 2008a, b; Tang et al. 2022
<i>GmELF3</i>	<i>Glyma.04G050200</i>	Promotive	Photoperiodic pathway	Lu et al. 2017; Yue et al. 2017
<i>GmFT1a</i>	<i>Glyma.18G298900</i>	Inhibitory	Photoperiodic pathway	Liu et al. 2018
<i>GmFT1b</i>	<i>Glyma.18G299000</i>	Inhibitory	Photoperiodic pathway	Guo et al. 2015
<i>GmFT2a</i>	<i>Glyma.16G150700</i>	Promotive	Photoperiodic and thermal pathways	Kong et al. 2010; Sun et al. 2011; Tang et al. 2022
<i>GmFT2b</i>	<i>Glyma.16G151000</i>	Promotive	Photoperiodic pathway	Chen et al. 2020b
<i>GmFT3a</i>	<i>Glyma.16G044200</i>	Promotive	Photoperiodic pathway	Yuan et al. 2022
<i>GmFT5a</i>	<i>Glyma.16G044100</i>	Promotive	Photoperiodic and thermal pathways	Kong et al. 2010; Fan et al. 2014; Tang et al. 2022
<i>GmFT5b</i>	<i>Glyma.19G108200</i>	Promotive	Photoperiodic pathway	Fan et al. 2014
<i>GmFT4</i>	<i>Glyma.08G363100</i>	Inhibitory	Photoperiodic pathway	Zhai et al. 2014
<i>GmLHY1b</i>	<i>Glyma.07G048500</i>	Promotive	Photoperiodic pathway	Lu et al. 2017
<i>GmLHY2a</i>	<i>Glyma.19G260900</i>	Promotive	Photoperiodic pathway	Lu et al. 2017
<i>GmLHY2b</i>	<i>Glyma.03G261800</i>	Promotive	Photoperiodic pathway	Lu et al. 2017
<i>GmLUX1</i>	<i>Glyma.12G060200</i>	Promotive	Photoperiodic pathway	Bu et al. 2021
<i>GmLUX2</i>	<i>Glyma.11G136600</i>	Promotive	Photoperiodic pathway	Bu et al. 2021; Fang et al. 2021a, b, c
<i>GmLHY1a (Tof16)</i>	<i>Glyma.16G017400</i>	Promotive	Photoperiodic pathway	Lu et al. 2017; Dong et al. 2021
<i>GmPRR3a (Tof11)</i>	<i>Glyma.U034500</i>	Inhibitory	Photoperiodic pathway	Li et al. 2020; Lu et al. 2020
<i>GmPRR3b/GmPRR37/GmPRR7a(Tof12)</i>	<i>Glyma.12G073900</i>	Inhibitory	Photoperiodic pathway	Li et al. 2020; Lu et al. 2020; Wang et al. 2020a
<i>GmFULa</i>	<i>Glyma.06G22650</i>	Promotive	Photoperiodic pathway	Jia et al. 2014
<i>GmFUL2a (Tof5)/GmFULc</i>	<i>Glyma.05G018800</i>	Promotive	Photoperiodic pathway	Sun et al. 2021; Dong et al. 2022
<i>GmSOC1a (Tof18)</i>	<i>Glyma.18G224500</i>	Promotive	Photoperiodic pathway	Na et al. 2013; Kou et al. 2022
<i>GmSOC1b/GmSOC1-like</i>	<i>Glyma.09G40230.1</i>	Promotive	Photoperiodic pathway	Na et al. 2013; Kou et al. 2022
<i>QNE1</i>	<i>Glyma.06G23400</i>	Promotive	Photoperiodic pathway	Xia et al. 2022
<i>GmFLC-like</i>	<i>Glyma.05G148700</i>	Inhibitory	Thermal pathway	Lyu et al. 2020
<i>GmPIF4b</i>	<i>Glyma.14G032200</i>	Promotive	Thermal pathway	Arya et al. 2018
<i>GmRAV</i>	<i>Glyma.10G204400</i>	Inhibitory	Photoperiodic pathway	Wang et al. 2021
<i>GmGBP</i>	<i>Glyma.01G008600</i>	Promotive	Photoperiodic pathway	Zhao et al. 2018
<i>GmEID1</i>	<i>Glyma.03G214300</i>	Promotive	Photoperiodic pathway	Qin et al. 2023
<i>GmTFLc</i>	<i>Glyma.11G209500</i>	Inhibitory	Photoperiodic pathway	Wang et al. 2023
<i>GmTFLd</i>	<i>Glyma.10G071400</i>	Inhibitory	Photoperiodic pathway	Wang et al. 2023

contains the maturity-related genes *E3* and *GmPhyA3* (Cheng et al. 2011; Wang et al. 2015a).

Since the release of the soybean reference genome, reference- and sequence-based mapping methods, including linkage analyses and association mapping, have been favored for soybean quantitative genetic studies (Lu et al. 2017, 2020; Yue et al. 2017; Li et al. 2020; Wang et al. 2020b; Dong et al. 2021). QTL mapping in two  $F_2$  populations revealed a major QTL on chromosome 4 that is associated with the long-juvenile (LJ) trait, which causes delayed flowering in the tropical region, e.g., Guangzhou, China (23.17° N, 113.36° E) with the average daylength from 10.8 to 13.5 h in the growing season. Other studies used map-based cloning of heterozygous inbred progenies that segregated at the *J* locus, or near isogenic lines (NILs) for both the *E1* and *J* loci under artificial short-day conditions in the field (12-h light/12-h dark) at the Experimental Station of the Northeast Institute of Geography and Agroecology, Chinese Academy of Sciences, Harbin (45.75°N, 126.63° E); these studies confirmed that the *J* locus is the causative gene for LJ trait (Lu et al. 2017; Yue et al. 2017). Natural populations have also been used in genome-wide association studies (GWAS) to identify flowering and maturity loci (Kim et al. 2020; Yang et al. 2022). Most of the major QTL identified to date correspond to known loci such as *E1-E4* (Kim et al. 2020). In total, over 104 QTL related to flowering time and 174 related to maturity have been described (<http://soybase.org/>).

#### *QTL for thermal responses*

Expansion of the soybean growth range to the north revealed that soybean pubescence color is associated with chilling tolerance; the latter trait reduces grain yield. Under chilling conditions, NILs with the *To7B* allele have tawny pubescence (T) and higher chilling tolerance than NILs with the *To7G* allele, which show gray pubescence (t). The same study revealed several maturity loci that affect chilling tolerance (*E1*, *E2*, *E3*, *E4*, and *E7*), as quantified by pigmentation and cracking of the seed coat (Takahashi et al. 2005). In addition, other loci, including *T*, *PI*, *APX1*, and *Dt1*, were also reported to be related to chilling tolerance (Funatsuki and Ohnishi 2009). A QTL for cold tolerance at the flowering stage was recently identified on chromosome 11 with all plants grown at 25 °C/20 °C (10-h day/14-h night) in a climate chamber for 30 days and then half

under the condition of 15 °C/10 °C, 12-h day/12-h night and the other half under the condition of 25 °C/20 °C, 12-h day/12-h night for 3 weeks (Jähne et al. 2019). Zhang et al. (2020a) also detected a QTL associated with flowering time on chromosome 19 under the combinations of daylengths of 14 h, 16 h, and 18 h at a constant air temperature of 25 °C and a daylength of 16 h at constant temperatures of 18 °C, 25 °C, and 32 °C; further mapping narrowed the interval to a 214-kb region that contains 11 annotated genes. The candidate gene *CONSTANS-LIKE 2b* (*GmCOL2b*) was determined to be most likely responsible for the flowering time trait; gene expression analysis showed that its expression levels are modulated by temperature (Zhang et al. 2020a).

#### *QTL for comprehensive photothermal adaptability*

Comprehensive photothermal responses are defined as traits that are responsive to both photoperiod and temperature. The majority of QTL associated with comprehensive photothermal responses overlap with major QTL for flowering time (Wang et al. 2015a; Mao et al. 2017; Sun et al. 2019; Zhang et al. 2020a). For example, two QTL associated with flowering time that are located on chromosomes 16 and 19 have been detected in experiments conducted under multiple photothermal conditions (e.g., long daylength and spring planting of pot experiment, summer planting in field experiment in 2015), indicating that they play important roles in photothermal adaptability. QTL on chromosome 6 (spring sowing season with natural daylength in pot experiment) and chromosome 11 (summer planting in the field experiment of 2014 in Beijing) have been identified to be associated with flowering time in specific environments (Mao et al. 2017). Mao et al. (2017) showed that the effects of several soybean flowering time QTL are dependent upon photothermal conditions; there are more loci associated with flowering time under LD than under SD conditions. Variety-specific variations in soybean flowering time are primarily a result of epistatic-by-environment or additive-by-environment interactions.

#### Gene isolation and functional analyses

##### *Genes involved in photoperiod responses*

*E3* and *E4* are homologs of the *Arabidopsis* photoreceptor gene *phytochrome A* (Liu et al. 2008a;

Watanabe et al. 2009). They sense photoperiod signals and transmit those signals to downstream genes, including the legume-specific gene *E1*, which plays a key role in flowering regulation (Xia et al. 2012; Xu et al. 2015). *FLOWERING LOCUS T (FT)* genes act downstream of *E1* and encode proteins that are involved in the synthesis of florigens, which are transported from the leaves to the shoots or lateral apical meristems to regulate flowering (Kong et al. 2010; Sun et al. 2011). Soybean thus controls photoperiodic flowering through the basic *E3/E4-E1-GmFT* regulatory module (Lin et al. 2022), in contrast to the conserved *CO-FT* module used by other plants (Shim et al. 2017).

The expansion of soybean from its origin (the Huang-Huai-Hai River Valley of China) to a wider region could be through two ways: one was from the domestication center to higher latitudes with LD and the other was to lower latitudes with SD (Stacey 2008; Sedivy et al. 2017). *E6* and *J* are the major loci that regulate flowering time under SD conditions (i.e., low-latitude regions). The candidate genes for both loci are homologs of the *Arabidopsis* gene *EARLY FLOWERING 3 (ELF3)* (Yue et al. 2017; Lu et al. 2017; Fang et al. 2021a); *ELF3* interacts with *LUX ARRATHMO (LUX)* to form the evening complex (EC), which binds the *E1* promoter to repress *E1* expression (Bu et al. 2021). Soybean has two *LUX* homeologs, *LUX1* and *LUX2* (Bu et al. 2021; Fang et al. 2021b); the protein products of these genes can interact with each other and function as a homodimer (*LUX1-LUX1* or *LUX2-LUX2*) or as a heterodimer (*LUX1-LUX2*). Mutation of either *LUX* gene has no influence on flowering time because they are functionally redundant. However, double *LUX* mutants are insensitive to photoperiod which demonstrates that EC is a critical center for photoperiodic flowering pathway in soybean (Bu et al. 2021). The *EID1* gene (*EMPFINDLICHER IM DUNNKELROTEN LICHT 1*) links light receptor phytochrome A (*E3/E4*) with EC and interacts with *J* to promote flowering (Qin et al. 2023).

Under SD conditions, *GmLHY1a* also binds the *E1* promoter to influence flowering time (Dong et al. 2021). Genetic analysis revealed that *Tof16/GmLHY1a* and *J* are genetically dependent on *E1*, but control flowering time independently of one another. Further studies have shown that a combination of mutant

alleles in *Tof16*, *J*, and *E1* is the major genetic basis of soybean adaptation to the tropics. Similarly, combinations of *E3*, *E4*, and *E1* genotypes play key roles in soybean adaptation to high latitudes (Xu et al. 2013; Jia et al. 2014; Jiang et al. 2014). EC and *LHY* function between *E3/E4* and *E1*, and variations in EC and *LHY* influence soybean adaptability to low latitudes. Recently, *SOC1* genes (*GmSOC1a* and *GmSOC1b*) and *QNE1*, a QTL near *E1*, were found to activate *GmFT2a* and *GmFT5a*, promoting flowering in soybean (Xia et al. 2022; Kou et al. 2022) (Table 1). Additional two QTL under SD conditions corresponding to *LJ16.1/GmFT2a* and *LJ16.2/GmFT5a* were also identified and characterized (Li et al. 2021). Natural variation and artificial selection of each gene of *GmFT2a* and *GmFT5a* improved soybean adaptation into low latitude. Interestingly, genetic compensation response occurred when single *ft2a* or *ft5a* loose functions with very few flowering delay (4–6 days), but double mutant showed much later flowering (20–30 days) under the short-day condition (Cai et al. 2020b; Li et al. 2021). Therefore, in addition to *J/E6* and *Tof16*, combination and introgression of natural variation of *GmFT2a* and *GmFT5a* is another option to develop cultivars to adapt to low latitude (Supplementary Fig. 1).

Previous research demonstrated that *Tof11/GmPRR3a* and *Tof12/GmPRR37/GmPRR3b*, homologs of the *Arabidopsis* gene *PRR3*, act downstream of *E3* and *E4* (Li et al. 2020; Lu et al. 2020; Wang et al. 2020b). These soybean PRRs directly bind the *LHY* promoter, and *LHY* in turn directly binds the *E1* promoter. Mutations in *Tof11* and *Tof12*, which were selected in stepwise pattern during domestication and diversification, have contributed to high-latitude adaptation (Li et al. 2020; Lu et al. 2020; Wang et al. 2020b). Lin et al. (2022) found that *E3* and *E4* regulate *E1* at both the transcriptional and post-transcriptional levels. On the one side, *E3* and *E4* interact with and mediate the degradation of *LUX* proteins, eliminating *E1* inhibition. These results indicate that EC is the core element controlling flowering pathways under both LD and SD conditions, consistent with findings in rice (Andrade et al. 2022; Pearce 2022) and maize (Zhao et al. 2023). On the other side, *E3* and *E4* can also associate with and stabilize *E1* and *E1* homologs. *E1* directly represses *Tof5/GmFUL2a/GmMDE05*, a homolog of *AtFUL* to mediate the *GmFT2a* and *GmFT5a* expression (Dong et al. 2022; Zhai et al. 2022). Recent research found that *E1* also directly binds *GmMDE* promoters and represses

their expression by increasing levels of tri-methylation on histone H3 lysine 27 (H3K27me3). GmMDE and GmFT2a/GmFT5a form a positive regulatory feedback loop that promotes flowering. Another *AtFUL* homolog (*GmFULa*) also regulates soybean flowering time and maturity and is induced under SD and inhibited under LD conditions (Jia et al. 2015); GmFULc/GmFUL2a suppresses *TPL* transcriptional activity and induces *FT*, *SOC1*, and *LFY* expression to promote flowering and is induced by SD conditions (Sun et al. 2021). In addition, *GmSOC1-like* and *GmGBP1* also promote flowering (Na et al. 2013; Zhao et al. 2018). Under the LD condition, *TFL1c* and *TFL1d* (*TERMINAL FLOWER 1*) repress the expressions of the four *API* homologs and act as flowering inhibitors (Wang et al. 2023).

*FT* homologs in soybean act downstream of *E1* and serve as integrators in the photoperiodic flowering pathway. *FT* family members have diverse functions in regulating soybean reproductive development (Kong et al. 2010; Sun et al. 2011; Zhai et al. 2014; Fan et al. 2014; Guo et al. 2015; Wang et al. 2015b; Liu et al. 2018; Chen et al. 2020b; Yuan et al. 2022; Su et al. 2022). The “Teeter-board” model of flowering time regulation demonstrated that expression levels of floral inhibitors (e.g., *GmFT1a*, possibly *GmFT4*) and floral activators (e.g., *GmFT2a* and *GmFT5a*) determine the direction of soybean development (Liu et al. 2018). *GmFT* genes are involved in incorporating symbiotic signals into the flowering induction pathway (Yun et al. 2023). Elicited by fixed nitrogen, symbiotic *miR172c* and local *miR172c* induce *GmFT2a/5a* by inhibiting *TARGET OF EAT1-like 4a* (*GmTOE4a*) and facilitate the growth and reproduce of legumes under the low-nitrogen conditions (Yun et al. 2023).

#### *Genes involved in thermal responses*

Researches on mechanism of thermal response in plants are extensively studied (Li et al. 2022c; Jung et al. 2023). Plants can sense the temperature change via  $\text{Ca}^{2+}$  and reactive oxygen species (ROS) signaling which triggers the expression of key transcription factors (Tsegaw et al. 2023). Phytochrome interactive factor 4 (PIF4) acts as the core hub in regulating thermomorphogenesis in plants (Liu et al. 2022). Photoreceptor phyB also acts as a thermosensor for temperature perception and response (Legris et al. 2016). The SUPPRESSOR OF PHYA-105 s (SPAs) promote

thermomorphogenesis by regulating the phyB-PIF4 module (Lee et al. 2020). EARLY FLOWERING3 (ELF3), the main component of EC, is also involved in the thermoresponsive growth in *Arabidopsis* and interacts physically with PIF4 and controls the activity of PIF4 to mediate thermomorphogenesis (Box et al. 2015). In response to cold, plant histidine kinases, such as *Arabidopsis* HISTIDINE KINASE 2 (AHK2), AHK3, and ETHYLENE RESPONSE 1 (ETR1), are upregulated after cold treatment and primarily sense the temperature change (Jeon and Kim 2013). H2A.Z is a histone variant which can change chromatin occupancy in response to changing temperature (Kumar and Wigge 2010).

The crosstalk between light and temperature signals coordinately regulates plant growth and development (Liu et al. 2022). In soybean, photoperiod exerts a significant influence on soybean thermal response (Wu et al. 2015a, b). It is difficult to separate thermal response from photoperiodic response, and photothermal effects on soybean flowering and growth have a complex mechanism which increases the difficulty for studies on soybean thermal response (Wang et al. 2015a, b, c; Tang et al. 2022). Few studies were reported about the effect of temperature on soybean flowering (Du et al. 2022). For instance, soybean flowering time is varied under different levels of high temperatures with the SD condition, which is not necessarily true with the LD condition (Tang et al. 2022). Here, we review few reports of the molecular mechanisms underlying thermal effects on soybean flowering. Although soybean is not a cold-requiring species, the vernalization pathway gene *GmFLC-like* reportedly functions in late flowering triggered by low temperatures through *GmFT2a* repression (Lyu et al. 2020). Phytochrome interacting factors (PIFs) are pivotal integrators of light and temperature signals and have important roles as central phytochrome that regulate flowering (Lee et al. 2020). *GmPIF4b* is expressed under the high temperature of 35 °C and short day (8-h light/16-h dark), and exogenous expression of this gene in *Arabidopsis* causes an early flowering phenotype (Arya et al. 2018). High temperature also induces *GmFT2a*, *GmFT5a*, and *GmCOL* and inhibits *E1* and *E2* expression (No et al. 2021). In soybean, tobacco, and *Arabidopsis*, overexpression of *GmGBP1*, a GAMYB-BINDING

PROTEIN (GBP1) homolog, induces flowering and enhances thermal tolerance (Zhang et al. 2013; Zhao et al. 2018). Recently, Tang et al. (2022) found that soybean flowering was accelerated at 30 °C comparing to 25 °C under SD conditions, but delayed at 35 °C. Further investigation showed that soybean utilizes different flowering mechanisms depending on the temperature; at 35 °C, *phyA-E1* is the key flowering pathway, whereas *GmFT2a* and *GmFT5a* are up-regulated at 30 °C, promoting flowering through an *E1*-independent pathway (Supplementary Fig. 1).

#### Evolution and domestication of photothermal adaptability traits in soybean

Soybean landraces flower earlier than the wild *G. soja* plants from which they were domesticated (Lu et al. 2020). However, there is an ongoing debate regarding whether flowering time is a domestication-related trait. In recent years, molecular evidence has shown that early flowering/maturity may be the core soybean domestication trait (Li et al. 2020; Lu et al. 2020; Wang et al. 2020a). Lu et al. (2020) found that *tof12-1*, an early-flowering allele of *Tof12/GmPRR37/GmPRR3b*, was selected during domestication. Selection of *tof12-1* also broadly coincided with selection for other domestication-related genes, such as *Hs1-1* for seed hardness, *G* for dormancy, and *Shat1-5* for shattering (Gong 2020). In wild soybean, *Tof4/E1La*, an *E1* homolog, represses flowering by directly regulating levels of *GmFT2a*, *GmFT5a*, and *Tof5/GmFUL2a* under LD conditions. Weak alleles of *Tof4*, which enhance wild soybean adaptability to high latitude, have been subject to natural selection (Dong et al. 2023). In contrast, *Tof5* haplotypes have undergone different types of selection; the *Tof5<sup>H1</sup>* allele was artificially selected after early domestication of cultivated soybean, whereas *Tof5<sup>H2</sup>* was under natural selection in wild soybean (Dong et al. 2022). After the process of domestication, landraces and varieties were planted in broader geographic areas and brought to new regions. To allow optimal growth in these new environments (namely, LD and LT at high latitudes and SD and HT at low latitudes), alleles for photoperiod and temperature insensitivity were selected.

#### Molecular breeding tools and practices to improve photothermal adaptation in soybean

##### Marker-assisted selection (MAS)

MAS is used to select elite genotypes with desired target traits by employing function-linked molecular markers. For molecular breeding, the frequently used molecular markers are the high-density single nucleotide polymorphisms (SNPs) and insertion/deletion mutations (InDels) (Li et al. 2022a). Kompetitive Allele-Specific PCR (KASP) genotyping utilizes competitive allele-specific PCR integrated with a fluorescence-based reporting system to detect SNPs and InDels (He et al. 2014). Allelic variations in *E1-E4* were identified using soybean accessions from a variety of maturity groups (MGs) throughout China (Jiang et al. 2014; Li et al. 2017; Liu et al. 2020), Europe (Kurasch et al. 2017), and North America (Wolfgang and An 2017). An efficient MAS method using KASP and *E1-E4* molecular markers integrated with off-site generation advancement can yield at least four generations of soybean per year. Adaptability of the progeny to specific regions was assessed with *E* genotyping; for example, progeny with *e1-fs*, *e2-ns*, *e3-tr/e3-ns/e3-fs*, or *e4-kes/e4-SORE-1* genotypes was considered to be well-adapted to grow in high-latitude regions (Fang et al. 2021c). Polymorphic sites in *J*, *GmPRR3a*, *GmPRR3b*, and *FT* genes (*GmFT1b*, *GmFT2a*, *GmFT2b*, *GmFT5a*, and *GmFT5b*), and *CO* genes (*GmCOL2*, *GmCOL5*, *GmCOL9*, *GmCOL13*, *GmCOL15*, *GmCOL16*, *GmCOL25*, and *GmCOL28*) have been used as molecular markers for genetic improvement of photothermal adaptation (Yue et al. 2017; Lu et al. 2017, 2020; Jiang et al. 2019; Wang et al. 2020a; Li et al. 2020; Khan et al. 2022). Microarray technology is another method for rapid and accurate genotyping and selection (Rasheed et al. 2017). The high-throughput functional array ZDX1 contains 90.92% of known genes and sites associated with breeding traits. One notable study genotyped 817 soybean accessions, including parental lines and their progeny from practical breeding, at the maturity-related loci *E1*, *E3*, and *E4*. This allowed identification of genotypes associated with precocity and late maturity, facilitating early evaluation of parents and selection of desirable progeny in the early stages (Sun et al.



2022). Using MAS through KASP or microarray technology efficiently speeds up the improvement of photothermal adaptability.

### Genomic selection (GS)

GS, also called genomic prediction, is a method used to predict genomic estimated breeding values (GEBVs) of unphenotyped materials using genome-wide genetic markers (Meuwissen et al. 2001). Because it involves analysis of the combined effects of numerous markers, GS is considered a promising tool for increasing genetic gains and improving breeding efficiencies for quantitative traits governed by multiple loci. The performance and accuracy of GS are determined by the training population size, marker density, and predictive model used (Ravelombola et al. 2020). Xavier et al. (2016) optimized a GS model for the trait of full maturity time (R8) in soybean. In this case, the optimal training population size was 1000–2000 individuals, and the best-performing model was a combination of reproducing kernel Hilbert space (RKHS) and Bayesian B (BB). Importantly, the number of markers had little effect on prediction accuracy. Azodi et al. (2019) assessed GS results for 18 traits in six species (including maturity time in soybean) using 12 algorithms, broadly classified into two types: six linear algorithms (ridge regression best linear unbiased predictor (rrBLUP), Bayesian A (BA), BB, Bayesian least absolute shrinkage and selection operator (LASSO) (BL), Bayesian-ridge regression (BRR), and support vector regression (SVR) with a linear kernel (SVRLin)) and six non-linear algorithms (SVR with polynomial kernel (SVRpoly), SVR with radial basis function kernel (SVRrbf), random forest (RF), gradient tree boosting (GTB), artificial neural network (ANN), and convolutional neural network (CNN)). The results indicated that no single model performed best in all scenarios, but a combination of results generated with different algorithms (i.e., ensemble GS) stably outperformed all other methods. The field of soybean GS is relatively new, and future studies are expected to optimize algorithms and other relevant parameters (Li et al. 2022a). Genomic-assisted breeding for soybean photothermal adaptation will require predictions of photothermal traits (e.g., flowering time and maturity) across multiple environments. Artificial intelligence (AI)-based methods,

such as machine learning, provide solutions for integrating genotypes and environmental factors to allow accurate phenotype prediction during ongoing selection (Yan and Wang 2022).

### Genetic modifications

Many studies have assessed regulation of the soybean growth period in lines with key genes knocked out, silenced, or overexpressed. For instance, overexpression of one *FT* homolog (*GmFT2a*, *GmFT2b*, *GmFT3a*, or *GmFT5a*) can significantly promote flowering time and maturity under LD or SD conditions (Sun et al. 2011; Nan et al. 2014; Chen et al. 2020b; Cai et al. 2020b; Yuan et al. 2022). Overexpression of a transcription factor such as *GmPIF4b*, *Glyma.06G204300*, or *FDC1* can significantly promote soybean flowering (Arya et al. 2021; Yue et al. 2021; Xia et al. 2022). Transgenic plants overexpressing *GmAGL1* or *GmNMHC5* exhibit early flowering and maturity (Zeng et al. 2018; Wang et al. 2020b). *GmAPIa* overexpression causes early flowering but reduced soybean plant height (Chen et al. 2020c). In an extremely late-maturing soybean variety (“Zigongdongdou”), co-silencing *E1* and its homologs *E1La* and *E1Lb* confers super-early flowering and maturity (Liu et al. 2022). Overexpression of *GmMDE06* can promote flowering and post-flowering termination of stem growth (Zhai et al. 2022). In contrast, overexpression of *GmFT1a* can significantly delay soybean flowering and maturity (Liu et al. 2018). Overexpression of *GmCOL1a* can delay flowering under LD and natural conditions (Cao et al. 2015a) and enhance salt and drought tolerance by promoting *GmP5CS* expression (Xu et al. 2023). Silencing *GmCOL1* and *GmCOL2* via RNA interference (RNAi) causes early flowering (Wu et al. 2019). *GmTOE4a* overexpression results in late flowering under LD and SD conditions; it also affects plant architecture by increasing stem thickness and reducing plant height, internode length, and leaf size (Zhao et al. 2015). *GmmiR156b* or *GmPRR37/GmPRR3b* overexpression can delay soybean flowering time under LD and natural conditions (Cao et al. 2015b; Wang et al. 2020a). Overexpression of *GmUBC9*, which encodes a ubiquitin-conjugating enzyme, delays flowering time (Chen et al. 2020a). *GmRAV*-overexpressing transgenic lines exhibit later flowering and maturity, whereas *GmRAV* inhibition causes earlier flowering time and

maturity; *GmRAV* expression limits plant height (Lu et al. 2014; Wang et al. 2021; Xue et al. 2022). These results demonstrate the broad applicability of transgenic technologies in functional genetic studies and their potential for generating novel germplasm with high photothermal adaptability.

### Genome editing

The clustered regularly interspaced short palindromic repeats (CRISPR)/CRISPR-associated protein 9 (Cas9) method of genome editing provides new mechanisms for improvement of soybean regional adaptability. For instance, *ft2a*, *ft2b*, and *ft5a* mutants have been generated with CRISPR/Cas9; the *ft2a* mutants exhibit late flowering under both LD and SD conditions, whereas *ft2b* and *ft5a* mutants show late flowering only under LD conditions. *ft2a ft5a* double mutants flower ~31.3 d later under SD conditions and produce more pods and seeds per plant than wild-type plants; these mutants therefore show great potential for increasing soybean yield in tropical regions (Cai et al. 2018a, 2020b; Chen et al. 2020b; Li et al. 2021). Early flowering soybean germplasm has also been generated by knocking out *E1* using CRISPR/Cas9 (Han et al. 2019). In soybean varieties carrying the dominant *E1* allele, knocking out *E1* decreases photoperiod sensitivity and branch number and alters stem growth habits (Wan et al. 2022). Crossing *e1 e1la e1lb* triple mutants with *phyA2 phyA3* double mutants generated 16 allelic combinations with varied flowering times (Lin et al. 2022). Loss of *GmNMHC5* function, which has been accomplished with genome editing tool CRISPR/Cas9, leads to late flowering and maturity (Wang et al. 2020b). *Gmap1* quadruple mutants generated by CRISPR/Cas9 exhibit delayed flowering and increased node number, internode length, and plant height (Chen et al. 2020c). Importantly, genome editing has also been used to coordinate flowering time regulation and common cutworm resistance in soybean (Li et al. 2022b).

In plants, adjustment of the circadian clock can enhance environmental adaptations. *CCA1* and *LHY* are MYB transcription factors that are expressed in the early morning and repress evening-phased clock genes such as *TOC1/PRR1*, *PRR5*, and *LUX*. Sequential expression of genes in the *PRR* family negatively regulates *CCA1* and *LHY* expression throughout the day, forming negative feedback loops (Alabadí et al. 2001; Hazen et al. 2005;

Kamioka et al. 2016). Pulses of light or cold temperature induce phase shifts of the circadian rhythm in soybean. The *Gmlcl* (*LHY* and *CCA1 Like*) quadruple mutants generated by CRISPR/Cas9 exhibit an extremely short-period circadian rhythm and a late-flowering phenotype (Wang et al. 2020c). *Gmprrr37* mutants generated by CRISPR/Cas9 have a significant early-flowering phenotype under LD conditions (Wang et al. 2020a). The *Gmlhy* quadruple mutants generated by CRISPR/Cas9 show delayed flowering under LD conditions (Lu et al. 2020). The soybean *lux1 lux2* double mutants generated by CRISPR/Cas9 show extremely late flowering and a significantly extended flowering phase (Bu et al. 2021). CRISPR/Cas9 has also been applied to improve soybean regional adaptability through deletion of large genomic fragments and targeted base editing. For instance, targeted deletions of DNA fragments of *GmFT2a* and *GmFT5a* were achieved in soybean using a dual-sgRNA/Cas9 design. The “transgene-free” homozygous *ft2a* mutants with a 1618 bp deletion exhibited late-flowering phenotype (Cai et al. 2018b). This research can benefit future research on improving agriculture via chromosome engineering in soybean. In addition, targeted single base substitutions were successfully introduced to *GmFT2a* and *GmFT4* in soybean and generated *ft2a* mutants showing slightly late flowering phenotype (Cai et al. 2020a). These results indicated that base editing technology holds great potential for future customized genetic improvement. Overall, CRISPR/Cas9 has proven to be a powerful and promising tool for expanding the regional adaptability of elite soybean varieties.

### Breeding of soybean varieties adapted to specific ecological regions

Photothermal conditions in Chinese soybean production regions

The soybean production region in China has great variability in photothermal conditions and farming systems (Pu and Pan 1982; Song et al. 2016, 2023). Chinese soybean cultivation areas can be divided into three major regions based on the effective cumulative temperature, photoperiod, and farming system of each: the Northern Spring-Planting Region, the Huang-Huai-Hai Summer-Planting Region, and the Southern Multiple-Cropping Region (Pu and Pan 1982). The dynamic changes in

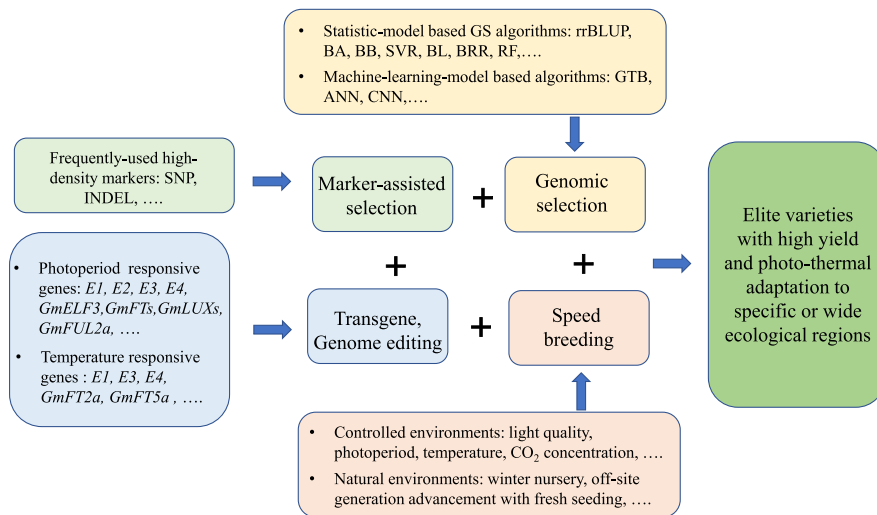
daylength and temperature during the growth period vary between regions. The maturity group (MG) system was used to classify soybean varieties based on their photothermal response. Soybean has been grouped into 14 MGs, and varieties of each MG are particularly suited to grow in a specific ecological region (Song et al. 2019).

The Northern Spring-Planting Region is the largest of the three soybean production regions. The daylength and temperature in this region show great variation throughout the soybean growth period; daylength is getting longer after soybean is planted in April or May and reaches its peak in late June and gradually becomes short again toward the late growth stages in September. Temperatures follow a similar pattern, but changes in temperature lag behind those in daylength (Pu and Pan 1982; Jia et al. 2014). Soybean varieties in this single-cropping region range from MG 0000 to MG IV. Photothermally insensitive varieties are favored in the north part of this region because photothermally sensitive varieties fail to reach flowering and maturity in the high latitude areas (Jia et al. 2014; Liu et al. 2020). In the Huang-Huai-Hai Summer-Planting Region, soybean is planted after the wheat in the summer (from early to mid-June) and harvested in late September or early October in a double-cropping system. Daylengths range from long to short and temperatures range from high to low during the growth period. Varieties cultivated in this region are moderately photothermally sensitive and MG categories of the varieties grown in this region are MG III to MG V (Zhang et al. 2020a, b; Liu et al. 2020). The Southern Multiple-Cropping Region has abundant rainfall, high temperatures, and long frost-free periods. In this region, soybeans are planted in multiple-cropping systems in the spring, summer, autumn, and even winter. The daylength is relatively short compared to the other major regions. For soybeans planted in the spring, the daylength changes from short to long over the growth period, and the temperature changes from low to high. For those planted in the summer, the daylength ranges from long to short and the temperature ranges from high to low. For those planted in the autumn, the daylength exclusively decreases and the temperature varies from high to low. Soybean varieties grown in this region span a large variation in MG, from MG I to MG IX (Li et al. 2017; Liu et al. 2020).

## Breeding of soybean varieties adapted to specific regions and farming systems

In the Northern Spring-Planting Region, several recessive mutations in *E* genes (primarily in *E1*, *E2*, *E3*, and *E4*) have been discovered above 47°N (Liu et al. 2020). Early or super-early flowering phenotypes can be induced by overexpression of the flowering-promotion genes *GmFT2a*, *GmFT5a*, or *GmFT2b*, or by silencing or mutation of flowering-inhibition genes such as *E1*, *E1La*, *E1Lb*, *E2*, *E3*, *E4*, *GmPRR3a*, *GmPRR3b*, *GmFT1a*, or *GmFT4*; such alterations would allow plants to adapt to the LD conditions and low temperatures of high and super-high latitudes (Zhai et al. 2014; Liu et al. 2018; Cai et al. 2020b; Chen et al. 2020b; Li et al. 2020; Lu et al. 2020; Wang et al. 2020a; Liu et al. 2022). In the Huang-Huai-Hai Summer-Planting Region, the most dominant *E* genotype is *E1/e2-ns/E3/E4* (Liu et al. 2020; Zhang et al. 2020b). *E*-gene molecular markers could be used to assist in selection for varieties with similar genotypes to be grown in this area. Varieties adapted to this area could also be generated through transfer of a flowering-promotion gene into a late-flowering variety or with CRISPR/Cas9-mediated targeted mutagenesis of a flowering-inhibition gene.

In the Southern Multiple-Cropping Region, which has SD conditions and high temperature, import of the LJ trait would allow soybean growth range expansion. Mutants for the J-LUX complex or *Tof16/GmLHY1a* (Lu et al. 2017; Yue et al. 2017; Bu et al. 2021; Dong et al. 2021; Fang et al. 2021b), either generated artificially or discovered in natural variations, would be ideal for growth in tropical regions. *Gmft2a Gmft5a* double mutants generated with CRISPR/Cas9 could be manipulated to optimize adaptability to tropical regions (Cai et al. 2020b; Li et al. 2021). *E* genes also play important roles in soybean adaptation to low latitudes; dominant wild-type *E* alleles have been discovered in these regions, with the *E1/e2-ns/E3/E4* genotype primarily occurring in spring-planting soybean and the *E1/E2/E3/E4* genotype primarily found in summer and autumn-planting varieties (Liu et al. 2020). In addition to tropical areas, high-altitude regions at low latitudes, such as the eastern Qinhai-Tibetan Plateau in southwestern China, have the potential for soybean production if suitable genotypes can be identified or generated. Varieties from the middle or mid-northern region of



**Fig. 1** Schematic diagram of molecular breeding tools for the improvement of photothermal adaptation in soybean. SNP single nucleotide polymorphism, InDel insertion/deletion mutation, rrBLUP ridge regression best linear unbiased predictor, BA Bayesian A, BB Bayesian B, SVR support vector regres-

sion, BL Bayesian least absolute shrinkage and selection operator (LASSO), BRR Bayesian-ridge regression, RF random forest, GTB gradient tree boosting, ANN artificial neural network, CNN convolutional neural network

Northeast China, or spring-planting varieties from the Yangtze River Valley, could be mutated in the J-LUX complex and *Tof16/GmLHY1a* locus to improve photothermal adaptability to such high-altitude, low-latitude regions.

Soybean was originated in central China and disseminated worldwide (Wang et al. 2016a, b; Zhang et al. 2020b). Domestic cultivars and foreign cultivars with similar maturity groups can be exchanged; therefore, the molecular tools for soybean breeding used in Chinese soybean production regions shed lights on global soybean production regions (Liu et al. 2017). For instance, the molecular breeding strategies for varieties in the Northern Spring-Planting Region can be introduced to the cultivars in the Far east of Russia, Sweden, Canada, and North USA regions, whereas that for the Huang-Huai-Hai Summer-Planting Region and spring-planting ecotype in the Southern Multiple-Cropping Region can be introduced to the Mid- and South-USA, and that for summer- and autumn-planting ecotype in the Southern Multiple-Cropping Region is similar as that in the Latin America, Africa, and Southeast Asia (Han et al. 2006a, 2006b; Liu et al. 2017).

Strategies for breeding widely adapted soybean varieties

Over the past century, widely adapted varieties, which have good agronomic traits and high yield performance, have been selected from practical farming varieties as exceptional accessions (Wu et al. 2015b, 2017; Wang et al. 2016a, b). New widely adapted varieties are characterized by shortened pre-flowering and prolonged post-flowering phases; overall, they have nearly unchanged or only slightly shortened maturity times compared with older widely adapted varieties (Wu et al. 2015a; Wang et al. 2016a, b). Genomic studies have shown that newer widely adapted varieties contain more desirable loci from elite parents, of which are also widely adapted varieties (Qi et al. 2021). Using these unique resources, a breeding strategy called “Potalization” has been developed, in which soybean improvement is based on these elite varieties. Comprehensive phenotyping and whole-genome resequencing or functional-loci KASP genotyping allows researchers to fully characterize the advantages and disadvantages of each widely adapted variety. Modern technologies, such as

transgenics or genome-editing, can be used as part of this strategy to precisely modify target sites based on the suboptimal qualities of any given variety to effectively obtain desirable traits. Recurrent selection and MAS can also be employed; use of the male-sterile gene *GmMSI* allows generation of widely adapted male-sterile soybean varieties for pyramiding elite target genes via recurrent selection (Jiang et al. 2021). Thus, the Potalaization model allows researchers to take advantage of elite genotypes with high genetic diversity, then make genetic gains by utilizing conventional and molecular breeding methods in selected genotypes. This model provides an effective avenue for advanced soybean breeding, enabling finely tuned changes to promote adaptation to diverse and dynamic conditions (Fig. 1).

## Perspective

Expanding the soybean planting area is an effective solution to meet the increasing consumer demand for soybean products, but this strategy requires improvement of soybean adaptability to a range of latitudes. Growth in higher latitudes necessitates production of more super-early varieties with LD and LT insensitivity or tolerance. For regions with multiple cropping systems, diverse varieties with different maturity are needed. It is therefore urgent to identify genes that shorten the growth period without impacting yield. Another method of enlarging the soybean planting area would be to expand into high-altitude regions at low latitudes, e.g., the eastern Qinhai-Tibetan Plateau in southwestern China. Further studies of the molecular mechanisms on photothermal adaptability enabling soybean adaptation to extreme photothermal environments are thus of great importance.

The continued development of high-throughput genomic and molecular technologies mean that a wide range of high-efficiency, low-cost options are available for breeding to improve photothermal traits, including transgenics, genome editing, MAS and GS. Rather than a single breeding practice, the use of ensemble tools, such as the Potalaization model, could facilitate the development of widely adapted varieties capable of withstanding future environmental changes. In the future, with the knowledge of inherited mechanism and regulatory network of photothermal adaptability and the

high-efficiency modern breeding tools as described above would provide insights into the molecular design of desired photothermal adaptability.

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