






REVIEW

Special Section: Tribute to Ron Phillips: Crop Genetics, Genomics and Biotechnology

Exploring the multifaceted dynamics of flowering time regulation in field crops: Insight and intervention approaches

Yogesh Dashrath Naik¹  | Rajeev N. Bahuguna² | Pedro Garcia-Caparrós³ |
 Rebecca S. Zwart⁴ | M. S. Sai Reddy⁵  | Reyazul Rouf Mir⁶ | Uday Chand Jha⁷ |
 B. Fakrudin⁸ | Manish K. Pandey⁹  | Dinakar Challabathula¹⁰ |
 Vinay Kumar Sharma¹ | Umesh K. Reddy¹¹ | Chanda Venkata Sameer Kumar¹² |
 Venugopal Mendu¹³ | P. V. Vara Prasad¹⁴ | Somashekhar M. Punnnuri¹⁵ |
 Rajeev K. Varshney¹⁶  | Mahendar Thudi^{4,15} 

¹Department of Agricultural Biotechnology and Molecular Biology, Dr. Rajendra Prasad Central Agricultural University, Pusa, Bihar, India²National Agri-Food Biotechnology Institute, Mohali, Punjab, India³Agronomy Department of Superior School Engineering, University of Almería, Almería, Spain⁴Centre for Crop Health and School of Agriculture and Environmental Science, University of Southern Queensland, Toowoomba, Australia⁵Department of Entomology, Dr. Rajendra Prasad Central Agricultural University, Pusa, Bihar, India⁶Faculty of Agriculture, Sher-e-Kashmir University of Agricultural Sciences and Technology, Sopore, Kashmir, India⁷Indian Council of Agricultural Research, Indian Institute of Pulses Research, Kanpur, Uttar Pradesh, India⁸Department of Biotechnology and Crop Improvement, University of Horticultural Sciences, Bagalkot, Karnataka, India⁹International Crops Research Institute for the Semi-Arid Tropics, Hyderabad, Telangana, India¹⁰Department of Biotechnology, Central University of Tamil Nadu, Thiruvavur, Tamil Nadu, India¹¹Department of Biology, West Virginia State University, Morgantown, West Virginia, USA¹²Department of Genetics and Plant Breeding, Professor Jayashankar Telangana State Agricultural University, Hyderabad, Telangana, India¹³Department of Agronomy, Agribusiness & Environmental Sciences, Texas A&M University, Kingsville, Texas, USA¹⁴Department of Agronomy, Kansas State University, Manhattan, Kansas, USA¹⁵College of Agriculture, Family Sciences and Technology, Fort Valley State University, Fort Valley, Georgia, USA¹⁶WA State Agricultural Biotechnology Centre, Centre for Crop and Food Innovation, Murdoch University, Murdoch, Western Australia, Australia

Correspondence

Mahendar Thudi and Somashekhar M.
 Punnnuri, College of Agriculture, Family
 Sciences and Technology, 1005 State
 University Dr, Fort Valley State University,

Abstract

The flowering time (FTi) plays a critical role in the reproductive success and yield of various crop species by directly impacting both the quality and quantity of grain yield. Achieving optimal FTi is crucial for maximizing reproductive success and ensuring

Abbreviations: AP1, *apetala1*; *CO*, *CONSTANS*; Ehd2, early heading date-2; *FLC*, *FLOWERING LOCUS C*; *FT*, *FLOWERING LOCUS T*; FTi, flowering time; FUL, *fruitful*; G1, *gigantea*; GWAS, genome-wide association studies; Hd, heading date; LFY, *leafy*; NGS, next-generation sequencing; OsG1, *OsGigantea*; PVE, phenotypic variance explained; QTL, quantitative trait loci; QTL-seq, QTL-sequencing; SEP3, *sepallata-3*; *SOCI*, *SUPPRESSOR OF OVEREXPRESSION OF CONSTANS-1*; SPL15, squamosa promoter binding protein-like-15; TAR2, tryptophan aminotransferase related 2; TILLING, targeting induced local lesions in genomes; TOE1, target of eat 1; Vgt1, vegetative to generative transition 1; VRN, vernalization.

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Fort Valley, GA, USA.

Email: mahendar.thudi@usq.edu.au and
punnuris@fvsu.edu

Rajeev K. Varshney, WA State Agricultural
Biotechnology Centre, Centre for Crop and
Food Innovation, Murdoch University,
Murdoch, WA 6150, Australia.

Email: rajeev.varshney@murdoch.edu.au

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overall agricultural productivity. While genetic factors undoubtedly influence FTi, photoperiodism and vernalization are recognized as key contributors to the complex physiological processes governing flowering in plants. Identifying candidate genes and pathways associated with FTi is essential for developing genomic interventions and plant breeding to enhance adaptability to diverse environmental conditions. This review highlights the intricate nature of the regulatory mechanisms of flowering and emphasizes the vital importance of precisely regulating FTi to ensure plant adaptability and reproductive success. Special attention is given to essential genes, pathways, and genomic interventions geared toward promoting early flowering, particularly under challenging environmental conditions such as drought, heat, and cold stress as well as other abiotic stresses that occur during the critical flowering stage of major field crops. Moreover, this review explores the significant progress achieved in omics technologies, offering valuable insights and tools for deciphering and regulating FTi. In summary, this review aims to provide a comprehensive understanding of the mechanisms governing FTi, with a particular focus on their crucial role in bolstering yields under adverse environmental conditions to safeguard food security.

Plain Language Summary

Flowering is crucial in agricultural crops because it produces seeds that grow into new plants or are used for human consumption. The timing of flowering is also important, particularly in the context of climate change. Extreme weather conditions can adversely affect flowering and reduce crop productivity. Early-flowering varieties complete their life cycle prior to the onset of extreme environmental conditions, allowing them to escape the detrimental effects of heat and drought stress. Recent advances in DNA sequencing have led to the identification of key genes directly involved in flowering, such as *FT* (*FLOWERING LOCUS T*), *FLC* (*FLOWERING LOCUS C*), and *VRN* (Vernalization). Additionally, various genomic approaches such as QTL-seq, genome editing, trait mapping, and speed breeding have been used to better understand the complexity of flowering time. This integrated approach provides a promising solution for regulating flowering time and improving crop adaptability to adverse conditions.

1 | INTRODUCTION

Crop production and climate change are intricately linked, with climate change serving as a prominent instigator of both biotic and abiotic stresses that adversely impact crop yields (Abbass et al., 2022). Climate change manifests through elevated carbon dioxide (CO₂) levels, temperature fluctuations, intensified rainfall, and an increased frequency of extreme weather events (Parmesan & Hanley, 2015). The anticipation of more frequent and widespread occurrences of extreme heat, prolonged droughts, and heavy rainfall underscores the urgency to address these challenges. Projections indicate a potential doubling of maize (*Zea mays* L.) yield reduction

due to heat stress during anthesis by 2080, emphasizing the gravity of the situation (Deryng et al., 2014). Severe moisture stress has similarly led to significant yield reductions in maize and soybean (*Glycine max*; H. Nguyen et al., 2023). Grain legume crops like chickpea (*Cicer arietinum*), lentil (*Lens culinaris*), faba bean (*Vicia faba*), and pea (*Pisum sativum*) face heightened vulnerability to terminal heat and drought stresses, necessitating the development of crop varieties resilient to diverse stresses for global food security (V. V. Kumari et al., 2021).

To address these challenges, plant breeders are leveraging the genetic diversity within crops to develop improved varieties with desirable traits. These traits, including canopy

temperature, stay green, leaf chlorophyll, leaf area, stomatal conductance, relative water content, root length and flowering time (FTi), have been identified as crucial features for improving stress tolerance (Fahad et al., 2017). FTi is the duration for a plant to produce fully developed flowers, which emerges as a key trait in mitigating the impacts of terminal heat and drought stresses on crop yield (Shavrukov et al., 2017). The initiation of flowering marks a fundamental transition in the life cycle of annual plants, playing a vital role in their fitness and reproductive success (Rubin et al., 2019). The regulation of FTi is a complex process that integrates multiple internal genetic components and external signals (day length, temperature and adverse environmental conditions) to ensure optimal reproductive success (Amasino, 2010). Epigenetic factors such as histone modifications, DNA methylation, and microRNAs further contribute to this regulatory complexity (Yaish et al., 2011). *Arabidopsis* serves as a model plant for understanding flowering regulation, with vernalization triggering flowering by controlling key genes such as *FLOWERING LOCUS C (FLC)* and *FLOWERING LOCUS T (FT)* (Chavez-Hernández et al., 2022). Legumes, responding to cold for flowering, use their versions of the FTi gene (*FTa*, *FTb*, and *FTc*) (Surkova & Samsonova, 2022), while cereals predominantly rely on vernalization genes (*VRN1*, *VRN2*, and *VRN3*) such as *Vrn-1* and *Ppd-1* in wheat (*Triticum aestivum*; Kennedy & Geuten, 2020; Mizuno et al., 2023).

While the physiological and molecular basis of flowering is not entirely understood, recent advances in next-generation sequencing (NGS) and functional genomics have provided valuable insights into the molecular pathways involved (Chavez-Hernández et al., 2022; D. Ma et al., 2021; Osnato et al., 2022). Whole-genome sequencing aids in identifying single nucleotide polymorphisms, facilitating the identification of genomic regions or candidate genes associated with important traits. Numerous studies have explored the FTi trait in various plant species, including model plants and major crops such as maize, rice (*Oryza sativa* L.), soybean, and chickpea. In the face of climate change, the timing of flowering becomes crucial for many field crops. Initiating flowering early in the growing season can help mitigate the adverse effects of climate change, but careful consideration is needed to avoid limiting seed production (Kehrberger & Holzschuh, 2019). Early maturing legume and oilseed crops offer potential solutions for cultivation in specific areas, utilizing fallow land through short-duration cultivation. Conversely, delaying flowering is essential for crops harvested for plant parts such as tubers or roots, emphasizing the need for precise control over FTi to achieve successful breeding outcomes and expedite genetic enhancement.

This review explores recent advancements in understanding the molecular and physiological basis of flowering in crop plants, focusing on the use of the FTi trait as a tool for

Core Ideas

- Flowering time (FTi) is regulated by intricate molecular processes involving gene expression, hormones, and other internal/external signals.
- FTi is crucial for crops adapting to extreme conditions, affecting seed production and survival.
- Identifying genes and pathways for FTi is vital for genomic interventions and breeding, enhancing adaptability to diverse environments.
- Modern genetic and genomic tools offer sustainable solutions for expediting breeding programs to regulate FTi.

adaptation to abiotic and biotic stresses at terminal growth stages. Key genes, pathways, and genomic interventions promoting early-flowering strategies for enhanced crop productivity are discussed. Additionally, the importance of early maturing varieties and the potential of genomic interventions in improving crop productivity and stress tolerance are highlighted.

2 | IMPACT OF CLIMATE CHANGE ON FLOWERING TIME

In response to dynamic environmental shifts, plants have developed adaptive mechanisms over time. Two crucial elements of climate change, specifically rising temperatures and elevated carbon dioxide (CO₂) levels, can impact plant fitness and various processes related to flowering (Jagadish et al., 2016; Tun et al., 2021) and yield formation (Prasad et al., 2002). Temperature plays a pivotal role in the regulation of FTi, directly influencing both development and vernalization processes. Regions experiencing faster increases in winter temperatures (ranging from 0.4 to 2.4°C) observe a notable reduction in flower numbers and seed production (Jagadish et al., 2016). Intriguingly, plant species with multiple inflorescences are more affected by elevated winter temperatures than those with single inflorescences (Y. Liu et al., 2012). In different species of rice, exposure to higher temperatures (+5°C above ambient) decreased duration from sowing to 50% flowering and decreased pollen production, pollen viability, spikelet fertility, number of filled grains, grain weights, and harvest index (Prasad et al., 2006). Enhanced CO₂ levels are known to stimulate increased accumulation of photosynthate, such as trehalose-6-phosphate (T6P) in plants (Jagadish et al., 2016; Springer & Ward, 2007). Disrupting T6P production also disturbs the activation of the *FT* gene (Wahl et al., 2013). For example, soybean experiments conducted

in controlled chambers with elevated temperature and CO₂ levels demonstrate the induction of early flowering, accompanied by molecular-level changes involving the upregulation of flowering activators and the downregulation of repressors in response to high temperatures (No et al., 2021).

In *Arabidopsis*, drought stress induces early flowering under long daylight but delays flowering under shorter daylight. The photoperiodic gene *GI*, encoding the GIGANTEA protein, plays a crucial role in this process (Riboni et al., 2013). *GI* is present in many plant species, contributing to critical functions such as regulating circadian rhythm, responding to light signals, tolerating cold, signaling hormones, and controlling flowering in a day length-dependent manner (Brandoli et al., 2020). However, it is important to note that while early flowering is a critical adaptation for surviving severe terminal stress, it may adversely impact plant yield under milder chronic stress conditions (Franks, 2011). Another study involving barley (*Hordeum vulgare*) genotypes exposed to nitrogen deficiency, drought, and salinity demonstrated that increased yield is accompanied by pleiotropic effects arising from FTi-associated genes, resulting in a shorter life cycle, an extended grain-filling period, and an increase in grain size in barley (Wiegmann et al., 2019). Salinity significantly delays flowering in *Arabidopsis*, involving several regulatory factors. The flowering delay under salt stress is influenced by DELLA proteins, which act as negative regulators of GA signaling, and by ethylene (Kazan & Lyons, 2015). Additionally, salt stress reduces the expression of *CO* (*CONSTANS*) and *FT*, further contributing to the delayed flowering response (Kazan & Lyons, 2015). Interestingly, high salt stress has been reported to reduce plant biomass while inducing an early-flowering phenotype and smaller flowers in tomato (F. Sun et al., 2024).

3 | PHYSIOLOGICAL BASIS OF FLOWERING TIME

3.1 | Photoperiodic flowering in plants

Field crops can have either a facultative or obligate response to photoperiod, and depending on the crop species, these responses could be accelerated either by short days or long days. A long photoperiod is defined as having at least 16 h of light and not more than 8 h of darkness in a 24-h cycle. On the other hand, a short photoperiod is defined as having no more than 10 h of light and at least 14 h of darkness in a 24-h cycle (Hamner, 1944). Short-day plants will flower earlier, exclusively during short days (long nights), while long-day plants will flower earlier during long days (short nights) (Allard & Garner, 1940) (Figure 1). Plants detect light through specialized structures called photoreceptors, which enable

them to sense a broad range of wavelengths. Phytochromes serve as the primary photoreceptors in plants, detecting red and far-red light and transmitting light signals (Qiu et al., 2023). These photoreceptors in plants are crucial for triggering genome-wide changes in the expression of nuclear and organelle genes, facilitating photomorphogenesis (Griffin & Toledo-Ortiz, 2022). In *Arabidopsis*, the *CO* gene is a central hub for integrating various internal and external signals to induce photoperiodic flowering. In contrast, the *CO* ortholog in rice, *Heading date 1* (*Hd1*), plays a dual role by promoting flowering under short-day conditions and inhibiting it under long-day conditions (C. Sun et al., 2022).

3.2 | Vernalization and flowering time

Temperature plays a crucial role in controlling flowering in many plants, often depending on the plant's developmental stage. Some plants require a prolonged cold period (vernalization) to trigger flowering. They perceive these temperature changes through alterations in cellular processes. For instance, plant cell membranes change their fluidity in response to temperature variations, which can influence various signaling pathways and affect the activity of proteins in the flowering process (Ding & Yang, 2022). Vernalization leads to molecular changes, including epigenetic modifications of the floral repressor gene *FLC* in *Arabidopsis* (P. K. Huang et al., 2024). Before vernalization occurs in *Arabidopsis*, elevated levels of *FLC* prevent the transition to flowering. Notably, this repression is accompanied by increased trimethylation of lysine 27 (*K27me3*) on histone H3, which serves as an epigenetic mark associated with gene silencing. In monocots, such as cereal crops like wheat and barley, *VRN2* serves as a repressor of flowering, and its expression is suppressed by vernalization to induce flowering (Trevaskis et al., 2007; L. Yan et al., 2006). Consequently, the activation of *VRN1* plays an important role in triggering flowering in wheat and barley (Deng et al., 2015; L. Yan et al., 2006). Wild emmer wheat, which served as the progenitor of modern bread wheat, displays substantial variation in the *VRN1* gene (Samineni et al., 2015). Interestingly, utilizing an expedited vernalization technique through an extended photoperiod of 22 h of daylight and 2 h of night time exposure at a temperature of 10°C substantially reduces the generation time for winter wheat and barley, enabling up to five generations per year compared to the standard two generations (Cha et al., 2022). The vernalization process and its epigenetic regulation provide valuable insights for manipulating FTi in crop plants and enhancing agricultural productivity. However, further research in this field is essential to unravel the complexities of vernalization and its molecular mechanisms.

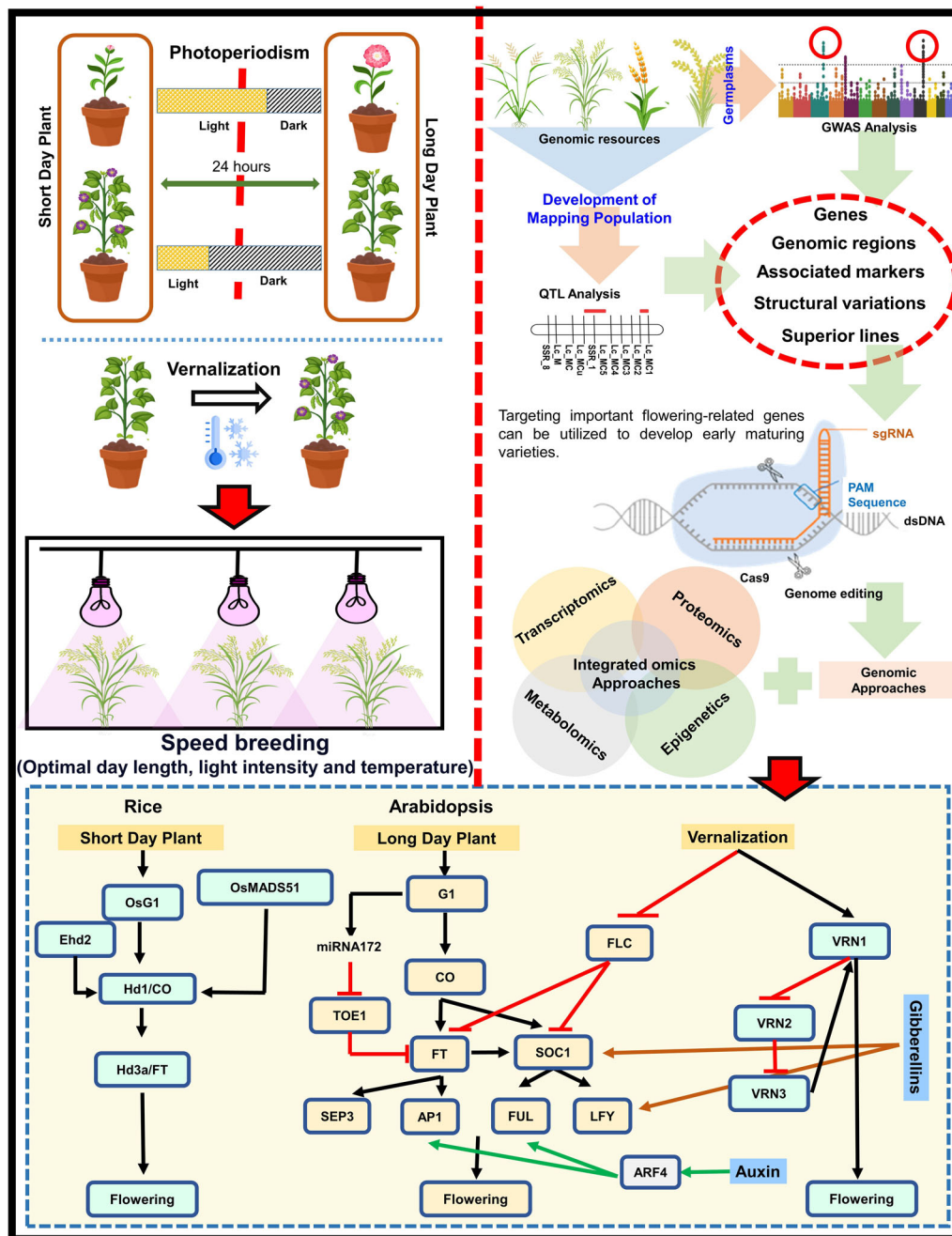


FIGURE 1 Molecular and physiological aspects of flowering. Summary of different environmental cues for flowering response, including photoperiod and vernalization. Understanding these aspects of flowering has led to the development of the speed breeding approach, which minimizes the period required to reach maturity. The figure also illustrates genomic approaches such as QTL mapping, association mapping, and genome editing. It emphasizes the integration of multi-omics approaches for a comprehensive understanding of the molecular basis of flowering. The yellow box below highlights the molecular or genetic control of flowering in short-day plants (rice), long-day plants (*Arabidopsis*), and vernalization. The pathways illustrating how auxin and gibberellin regulate or activate other genes, such as *FUL*, *LFY*, *SOC1*, and *AP1*, are also presented. *AP1*, *APETALA1*; *ARF4*, *AUXIN RESPONSE FACTOR4*; *CO*, *CONSTANS*; *Ehd2*, *Early heading date2*; *FLC*, *FLOWERING LOCUS C*; *FT*, *FLOWERING LOCUS T*; *FUL*, *FRUITFULL*; *G1*, *GIGANTEA*; *Hd*, *Heading date*; *LFY*, *LEAFY*; *OsG1*, *OsGIGANTEA*; *SEP3*, *SEPALLATA 3*; *SOC1*, *SUPPRESSOR OF OVEREXPRESSION OF CONSTANS 1*; *TOE1*, *TARGET OF EAT 1*; *VRN*, *VERNALIZATION*.

3.3 | Plant hormones and flowering time

Plant hormones act as messengers that help plants respond to environmental cues (Campos-Rivero et al., 2017). How-

ever, when it comes to the complex process of flower bud formation, a single plant hormone alone is not enough to exert a strong influence (Domagalska et al., 2010). Interactions among various plant hormones, including auxin, gibberellin,

ethylene, indole-3-acetic acid, cytokinins, and abscisic acid, have been demonstrated to play key roles in triggering flower induction across plant species (Matsoukas, 2014; B. Yan et al., 2019). During plant reproduction, auxin plays a vital role in several aspects. It helps to identify where flowers will form and continues to control the growth and arrangement of flower parts. Additionally, auxin influences later stages of reproduction, determining reproductive success (Krizek, 2011). In rice, increasing the expression of the *OsFPFL4* (FPF1-like protein 4 of rice) gene raises auxin levels while reducing its activity, which lowers auxin levels and influences the FTi (Guo et al., 2020). In wheat (*T. aestivum* L.), the gene *TaIAA15-1A* (Indole-3-Acetic Acid 15-1A) regulates FTi by interacting with the auxin response factor (P. Su et al., 2023). In cultivated strawberry plants, auxin response factor 4 (*FaARF4*) gene is documented to be more active during flowering, and the introgression of this gene in *Arabidopsis* and woodland strawberries (*Fragaria ananassa*) led to early-flowering phenotypes (Dong et al., 2021).

Trehalose 6-phosphate (*T6P*) has been found to stimulate the expression of an auxin biosynthesis gene, tryptophan aminotransferase related 2 (*TAR2*), affecting auxin levels and activating storage processes (Meitzel et al., 2020). During the transition to the flowering stage, increased tissue sucrose levels lead to higher *T6P* levels, which influence FTi. Indeed, lower *T6P* levels have been linked to delayed flowering, while higher *T6P* promotes earlier flowering in plants (Wahl et al., 2013). It has also been reported that GA suppresses the expression of the flowering induction gene *LFY*, while IAA (indole-3-acetic acid) treatment enhances its expression (D. Singh et al., 2023). Hormonal signaling pathways are also involved in the regulation of key flowering genes, such as *FLC*, *CO*, and *FT* (Conti, 2017). For example, GA promotes flowering by activating specific genes such as *SUPPRESSOR OF OVEREXPRESSION OF CONSTANS 1* (*SOC1*), *LEAFY* (*LFY*), and *FT* (Bao et al., 2020; Mutasa-Göttgens & Hedden, 2009). In another study on barley, GA inhibitors, particularly trinexapac-ethyl applied via exogenous spray, showed the greatest potential for delaying flowering (Kupke et al., 2022). Additionally, DELLA proteins and GA homeostasis are essential regulatory elements within the GA pathway (Bao et al., 2020). DELLA proteins are key regulators in the GA signaling pathway, while they control the expression of genes such as *SOC1* and *FT*, which are keys for plant growth and flowering (M. Li, An, et al., 2016). It is also reported that the gibberellin-insensitive mutant causes dwarfing and earlier flowering in *Arabidopsis*, while it delays flowering in maize (Lawit et al., 2010). In *Arabidopsis*, *BRAHMA* (*BRM*) is involved in GA-signaling-mediated flowering through the assembly of the DELLA-BRM-NF-YC module (C. Zhang, Jian, et al., 2023). Florigen is a protein hormone encoded by the *FT* gene, produced in the leaves, and subsequently transported to the shoot apical meristem (Corbesier et al., 2007). It

has a dual role in flowering plants: (i) triggering flowering by promoting the transition to floral development and (ii) growth attenuation in other vegetative meristems (Shalit-Kaneh et al., 2019). All the studies highlight the role of phytohormones in flower development and emphasize their overlapping roles in various developmental processes.

4 | MOLECULAR BASIS OF FLOWERING TIME

4.1 | Genes involved in flowering time were identified in crop plants

The availability of genomic resources and synteny in crops has further advanced the identification of flowering-associated genes. Extensive research in field crops has revealed key insights into the genetic regulation of flowering and identifying various candidate genes (Table 1). Different crop species have unique genetic regulators that control flowering and respond to environmental signals. Many flowering-related genes found in *Arabidopsis* and rice are conserved in legumes (Weller & Ortega, 2015). The *FT* gene belongs to a family found in all angiosperms. *FT* gene is crucial in regulating FTi by integrating environmental signals. They transmit this information from the photoperiod detection site in the leaves to the flower formation site at the shoot apex (N. Lee, Ozaki, et al., 2023). In addition to their role in flowering, *FT* homologs influence various seasonal developmental changes, such as germination, tuber/nodule formation, dormancy onset, and side branching control. This gene family includes *FT* orthologs and paralogs, some of which inhibit flowering (N. Lee, Ozaki, et al., 2023). Another key protein in flowering is the *CO* protein, consisting of an N-terminal B-box domain, a C-terminal *CCT* domain, and a central region rich in glutamine sequences. It is recognized as *AtCO* in *Arabidopsis*, which facilitates flowering in long days and involves stress response (B. Zhang, Feng, et al., 2023). Researchers later identified its rice counterpart, *HDI*, which shares significant amino acid sequence similarities with *AtCO*. Studies have shown that *HDI* functions similarly to *CO* in the flowering pathway, confirming *HDI* as a ortholog of *AtCO* in rice (Nemoto et al., 2016).

4.2 | Transcription factors and their role in flowering time

Transcription factors are essential in regulating early or late flowering in plants. These proteins interact with specific DNA sequences to control gene regulation. The MADS-box transcription factor is a well-known and crucial regulator that plays a central role in floral development. *FLC* gene encodes

TABLE 1 Summary of the important essential genes in major field crops involved in flowering time.

Crop	Gene	Key role	Reference
Maize (<i>Zea mays</i>)	ZEA CENTRORADIALIS 8 (ZCN8)	Functions as a floral activator and is involved in photoperiod sensitivity	Meng et al. (2011)
	ZmCCT	Regulates photoperiod-dependent flowering and also response to abiotic stresses	Hung et al. (2012); Su et al. (2021)
	ZmMADS69	Functions as a flowering activator through the ZmRap2.7-ZCN8 regulatory module	Y. Liang, Liu, et al. (2018)
	ZmCCT9	Enhances maize adaptation to higher latitudes	C. Huang et al. (2017)
Rice (<i>Oryza sativa</i>)	Heading-date 1 (<i>Hd1</i>) and Early heading date 1 (<i>Ehd1</i>)	Involved in regulation of flowering and reduces the number of primary branches in a panicle	Endo-Higashi and Izawa (2011)
	RICE FLOWERING LOCUS T1 (<i>RFT1</i>)	Contributes to flowering time divergence	Ogiso-Tanaka et al. (2013)
	Heading date 3a (<i>Hd3a</i>), Heading date 1 (<i>Hd1</i>), and Early heading date 1 (<i>Ehd1</i>)	Expression of these genes is highly correlated with flowering time	Takahashi et al. (2009)
	Flowering-Related RING Protein 1 (<i>FRRP1</i>)	<i>FRRP1</i> probably regulates flowering time by affecting histone <i>H2B</i> monoubiquitination	Du et al. (2016)
Wheat (<i>Triticum aestivum</i>)	<i>TaFT3</i>	Mutant alleles confer delayed flowering	Halliwell et al. (2016)
	<i>MiR172</i> - <i>APETALA2</i> -like genes	<i>miR172</i> promotes flowering	Debernardi et al. (2022)
	O-linked N-acetylglucosamine transferase (<i>OGT</i>)	Involved in fine regulation of flowering time	Fan et al. (2021)
	EARLY FLOWERING 3	Contributes to the regulation of heading date	Wittern et al. (2023)
Sorghum (<i>Sorghum bicolor</i>)	Pseudoresponse regulator protein 37 (<i>PRR37</i>)	Controls photoperiodic flowering	Murphy et al. (2011)
	Maturity2 (<i>Ma2</i>)	Delayed flowering in long days by selectively enhancing the expression of <i>SbPRR37</i> (<i>Ma1</i>) and <i>SbCO</i>	Casto et al. (2019)
	<i>Ghd7</i> (<i>Ma6</i>)	Increases photoperiod sensitivity and delays flowering by inhibiting expression of the floral activator <i>SbEhd1</i> and genes encoding FT	Murphy et al. (2014)
Barley (<i>Hordeum vulgare</i>)	<i>FLOWERING LOCUS T4</i>	Specifically delayed spikelet initiation and reduced the number of spikelet primordia and grains per spike	Pieper et al. (2021)
	<i>FLOWERING TIME LOCUS T1</i> (<i>FT1</i>) and <i>CONSTANS-LIKE PROTEIN 1</i> (<i>CO1</i>)	Involved in regulating flowering time	Qian et al. (2020)
	VERNALIZATION-H2 (<i>VRN-H2</i>)	Strong repressor of flowering under long days before vernalization	Mulki and von Korff (2016)
	<i>HvCEN</i> , <i>HvELF3</i> , and <i>HvFT1</i> <i>Ppd-H1</i>	Responsible for early flowering The major determinant of photoperiod response	Casas et al. (2021) Cosenza et al. (2024); Maurer et al. (2015)

(Continues)

TABLE 1 (Continued)

Crop	Gene	Key role	Reference
Soybean (<i>Glycine max</i>)	<i>GmMDEs</i>	Regulated flowering time and stem growth habit by affecting the expression levels of other genes	Zhai et al. (2022)
	<i>GmEID1</i>	Modulates light signaling through the evening complex to control flowering time and yield	Qin et al. (2023)
	<i>GmFT3a</i>	Promotes flowering by regulating the expression of downstream flowering-related genes and also affects the expression of other <i>GmFTs</i>	S. Yuan et al. (2022)
Chickpea (<i>Cicer arietinum</i>)	Chickpea Early Flowering 1 (<i>Efl1</i>)	Ortholog of <i>Arabidopsis</i> EARLY FLOWERING 3 (<i>ELF3</i>) that confers early flowering in chickpea	Ridge et al. (2017)
Lentil (<i>Lens culinaris</i>)	<i>LcFTa1</i> , <i>LcFTb1</i> , and <i>LcFTb2</i>	Involved in flowering time in response to light quality.	H. Y. Yuan et al. (2021)
	Early flowering 3 (<i>elf3</i>)	Associated with photoperiod insensitive flowering and fast absolute growth rate	Roy et al. (2023)
	<i>DTF6a</i> and <i>DTF6b</i> (<i>FTa1</i> gene)	Confer early flowering under extremely short photoperiods alone	Rajandran et al. (2022)
<i>Brassica rapa</i>	<i>FLOWERING LOCUS C</i> (<i>BrFLC</i>)	Key gene for vernalization	Takada et al. (2019)
	<i>FT</i> and <i>FLC</i>	Key role in the timing of the initiation of flowering	Scheben et al. (2020)
	<i>PSEUDO RESPONSE REGULATOR 7</i> (<i>PRR7</i>) and <i>FY</i>	Key roles in the circadian clock pathway and upregulated in both leaf and shoot tissues	Jian et al. (2019)
	<i>BnaFTA2</i>	Key role in flowering time regulation	Cai et al. (2021)
Cotton (<i>Gossypium herbaceum</i>)	Early flowering 4 (<i>ELF4</i>)	Participate in the plant biological clock's regulation process, photoperiod, hypocotyl elongation, and flowering time	Tian et al. (2021)
	<i>GhAAI66</i>	Triggers a phase transition to induce early flowering	Qanmber et al. (2019)
	FRUITFULL-like (<i>FUL-like</i>)	Promotes the vegetative-to-reproductive transition and represses inflorescence branching by inducing floral meristem maturation	Jiang et al. (2022)

a MADS-box protein that acts as a repressor of flowering and is essential for the process of vernalization (Sheldon et al., 2000). *FLC* inhibits the expression of two flowering-promoting genes, *FT* and *SOC1* (Deng et al., 2011). Further, it is also reported that *FLC* binds to many other genes and is involved in vegetative development by interacting with the gene *SQUAMOSA PROMOTER BINDING PROTEIN-LIKE 15* (*SPL15*), which delays the transition from juvenile to adult phase (Deng et al., 2011). *HD-ZIP I*-class transcription factor (*GhHB12*) exhibits specific expression in axillary buds in cotton (*Gossypium herbaceum*). Furthermore, in cotton, RNA sequencing analysis revealed that *GhSPL4*, a member

of the *SBP* transcription factor family targeted by *GhmiR156*, was significantly upregulated in early-flowering cultivars (Y. Zhou et al., 2022). Regulatory interaction leads to bushy plant architecture and delayed flowering, specifically under long-day conditions (X. He et al., 2018). In rice, *Hd1 Binding Protein 1* (*HBPI*), two basic helix-loop-helix (*bHLH*) transcription factors, and *POH1* were identified as transcriptional regulators of *Hd1* (Yin et al., 2023). Additionally, B-box transcription factors are pivotal regulators in flowering, photomorphogenesis, shade-avoidance, stress responses, and hormonal pathways (Y. Liu et al., 2020). Recent research has also identified their significance in the flowering of crops

such as tomato (*Solanum lycopersicum*) (Wu et al., 2023; D. Xu et al., 2023). These findings highlight the diverse roles of transcription factors in controlling FTi and their significance in plant adaptation to biotic and abiotic stresses. Additionally, a recent study suggests that the transcription factor *AtERF19* plays a dual role in regulating the number and size of flower organs (P. F. Lee, Zhan, et al., 2023). It achieves this by modulating genes associated with CLV–WUS signaling for flower production and influencing auxin signaling for flower organ size.

Flowering regulation involves *FLD* and *FLC* genes controlled by epigenetic mechanisms such as ubiquitination, acetylation, methylation, and hormone signaling (P. Kumari et al., 2022). In *Arabidopsis* and rice, proteins such as *TRITHORAX* (*TRX*) and *SET DOMAIN GROUP* (*SDG*) control histone methylations. For instance, *SDG2* mainly handles H3K4me3, with a small role played by *ARABIDOPSIS HOMOLOG OF TRITHORAX1* (*AXT1*) and *ATX2*. *SDG8* and *SDG4/26* are responsible for H3K36me3, and *ATXR5/6* focuses on H3K27me1 (see S. Liu et al., 2023). *SDG725*, the initial H3K36-methyltransferase identified in rice, is crucial for depositing H3K36me2/3 on *Hd3a* chromatin, thereby hastening the flowering process (Sui et al., 2013).

4.3 | The regulatory elements associated with flowering time

Gene promoters play a critical role in expressing FTi-related genes by controlling when and where these genes are activated. They serve as regulatory regions upstream of the target genes, providing binding sites for transcription factors and other regulatory molecules. In *Brassica napus*, the discovery of two flower-specific promoters, *FSP046* and *FSP061*, highlights the potential of these promoters for agricultural use due to their tissue specificity and consistent expression in petals (Y. Li, Dong, et al., 2019). Similarly, *AGL24*, a gene in *Arabidopsis*, functions as a positive flowering promoter. Vernalization enhances its expression and activity (Michaels et al., 2003). Differences in DNA methylation within the *ZmCCT10* promoter in maize influenced *ZmCCT10* gene expression, subsequently affecting FTi (Z. Zhou et al., 2023). Salvi et al. (2007) narrowed down the major FTi QTL (vegetative to generative transition 1; *Vgt1*) in maize and identified an ~2-kb noncoding region located 70 kb upstream of an AP2-like transcription factor. Castelletti et al. (2014) identified a miniature transposon (MITE) insertion within this conserved noncoding sequence at *Vgt1*, strongly associated with early flowering across independent analyses. Additionally, it was reported that this region at *Vgt1* was minimally methylated; however, the region near the MITE insertion in the early-flowering maize allele was heavily methylated (Castelletti et al., 2014). A precise understanding of the

structural composition of these noncoding regions and their functional influence on gene expression patterns contributes to our knowledge of FTi control and offers potential targets for crop improvement.

5 | FLOWERING TIME IS A KEY TRAIT IN ADDRESSING ABIOTIC STRESSES

Crops face various challenges and have evolved with different strategies to counteract such constraints on productivity. These strategies involve allocating additional resources to enhance their immune responses and adjusting their reproductive processes to ensure successful reproduction (Lyons et al., 2015). Early-flowering/maturing varieties of crop plants have emerged as a promising strategy to adapt to the impact of abiotic stresses. These varieties exhibit accelerated plant development, allowing the life cycle of the plant to be completed before the onset of adverse environmental conditions, such as terminal drought or terminal heat stress (Mondal et al., 2015; Shavrukov et al., 2017). This adaptive mechanism (stress escape) is widely observed in native plant populations and can be applied to major crops. Additionally, cultivating early maturing legumes into fallow land, particularly in fallow rice land, could provide numerous benefits, such as restoring soil fertility, nitrogen fixation, suppressing weed growth, and utilizing fallow land (Kebede, 2021). Using the concept of early maturation and adopting stress escape mechanisms, plant breeders can enhance resilience and improve agricultural productivity in the face of abiotic stresses, thereby contributing to sustainable farming systems. Early flowering in wheat serves as a survival strategy, even though it can reduce grain yield under long photoperiod conditions, primarily by impacting floral growth and development (Y. Zhang, Guo, et al., 2023). Early flowering may be vital in wheat production under terminal drought, as it reduces the risk of dehydration during the critical flowering and post-anthesis grain filling stages.

In numerous botanical investigations, the intricate interplay between FTi and environmental variables, including complex ecological conditions and abiotic stressors, has been subject to scholarly scrutiny across a spectrum of species. Under conditions of water scarcity, the temporal regulation of FTi undergoes discernible alterations at the molecular level. For instance, K. Song et al. (2017) observed significant alterations in the expression profiles of key genes associated with FTi in response to drought stress in maize. Notably, genes such as *PRR37*, the transcription factor *HY5*, and *CO* were identified as being particularly susceptible to modulation, leading to a hastened onset of anthesis. Similarly, investigations in the model plant *Arabidopsis thaliana* unveiled perturbations in the expression patterns of pivotal flowering-related genes, including *FT*, *SCO1*, and *LEAFY*, consequent to

drought imposition. Such genetic dysregulation was associated with observable floral anomalies, including aberrant anther development and diminished pollen viability (Z. Su et al., 2013). Further elucidating these molecular intricacies, RNA sequencing analyses uncovered noteworthy alterations in the expression levels of flowering-time regulators such as *Hd3a*, *CONZI*, and *ZCN8* in maize, genes conventionally associated with the promotion of flowering under short-day conditions. Notably, under the influence of drought stress, these genes exhibited downregulation, implicating their role in mitigating the floral response under adverse environmental conditions (Kim et al., 2021).

Elevated temperatures exert a pronounced effect on the modulation of FTi under both short-day and long-day conditions in *A. thaliana* (Balasubramanian et al., 2006). This regulatory mechanism involves the upregulation of key MADS-box transcription factors, including *SHORT VEGETATIVE PHASE* (*SVP*), *FLOWERING LOCUS M* (*FLM*), and *FT*. These genes play pivotal roles in the promotion of floral transition, thereby facilitating the acceleration of flowering onset in response to thermal stimuli (Pose et al., 2013). Similarly, in rice, high temperatures elicit an early-flowering response, characterized by the enhanced expression of genes such as *Ghd7*. The transcriptional activation of *Ghd7* serves as a critical molecular determinant in the regulation of FTi under temperature-induced conditions (Luan et al., 2009; V. Song et al., 2012). Furthermore, extending this paradigm, X. Chen et al. (2019) have contributed novel insights into the molecular mechanisms underlying the temperature-mediated regulation of floral development. Specifically, their research highlights the downregulation of HSP70-16, a heat shock protein, at higher temperatures (27°C), which correlates with the manifestation of floral abnormalities characterized by the overlapping tips of two lateral sepals and eventual failure of flower opening. Conversely, empirical evidence from diverse studies consistently underscores the phenomenon of delayed flowering in response to lower temperatures. Noteworthy among these investigations are those delineating the downregulation of key flowering-time regulators such as *FCA* and *FVE* in *A. thaliana* under cooler climatic conditions (Ausin et al., 2004; Y. He et al., 2003). Similarly, investigations by Luan et al. (2009) and V. Song et al. (2012) corroborate these findings, revealing a concomitant decrease in transcript levels of *Ehd1*, *Hd3a*, and *RFT1* in rice plants exposed to reduced temperatures. Moreover, insights from the literature shed light on the intricate regulatory dynamics governing FTi in response to temperature cues. Yoo et al. (2007) illuminate the regulatory influence of *LOVI* on *CO* expression, a pivotal floral promoter, suggesting a mechanism wherein *LOVI* exerts negative modulation over *CO* transcript levels, thereby impacting FTi regulation. Furthermore, the intricate interplay between photoperiod and cold temperature signals in seasonal flowering regulation is elucidated by J. H. Lee and Park (2015), who

delineate an elaborate feedforward-feedback loop involving key regulatory nodes such as *INDUCER OF CBF EXPRESSION 1 (ICE1)*, *FLC*, and *SOC1* in *Arabidopsis*. Collectively, these scholarly endeavors underscore the intricate molecular networks orchestrating the temporal dynamics of flowering in response to temperature fluctuations, thereby enriching our understanding of the adaptive strategies employed by plants to navigate environmental variability.

6 | BIOTIC STRESSES AND THEIR RELATIONSHIP WITH FLOWERING TIME

Biotic factors can exert control over the transition to flowering, with potentially harmful effects on plants. Additionally, different crops exhibit varying photoperiod sensitivities due to adaptation to different growth environments or breeding targets (Gómez-Ariza et al., 2015). Herbivory and pathogen infections can profoundly affect plant development. These effects include early flowering (Elzinga et al., 2007; Lyons et al., 2015) and delayed flowering (Schiestl et al., 2014). Plants use altered flowering timing to escape herbivores (Parachnowitsch & Caruso, 2008). Some plants adjust by increasing flower production during early flowering in response to herbivory, possibly due to the production of defense compounds like glucosinolates (Schiestl et al., 2014).

Mechanical damage or wounding also accelerates flowering (Hanley & Fegan, 2007), suggesting that herbivory-induced effects on flowering may be attributed, at least in part, to wounding. Genetic mechanisms that underlie the crosstalk between stress responses and FTi are crucial. MicroRNAs play a significant role in regulating gene expression in response to both biotic and abiotic stress conditions (Ruiz-Ferrer & Voinnet, 2009), often leading to the reorganization of gene expression associated with flower initiation and development (see Table 2). The interrelationship between biotic stresses and FTi in plants is complex and influenced by various factors, including genetic mechanisms, microRNAs, tolerance levels, and the strategies employed by both plants and stressors to adapt to their environments.

In green gram (*Vigna radiata*) cultivation, insect pests remain a persistent challenge, resulting in yield losses. Notably, it has been observed that early-maturing varieties of green gram experienced decreased pest infestations (Mulwa et al., 2023). In the case of pigeonpea (*Cajanus cajan*), early-flowering genotypes exhibit characteristics such as reduced canopy size, fewer branches, and fewer pods per plant (Saxena et al., 2019). Conversely, late flowering enhances insect pollination in oil crops such as turnip rape (*Brassica campestris*; Toivonen et al., 2019). The intricate relationship between FTi regulation and biotic stressors has received comparatively scant attention in botanical research, with the majority of investigations concentrated within the *Arabidopsis* genus.

TABLE 2 Interrelation of flowering time and biotic stresses.

Sl. No.	Characters	Host	Causal factor/organism	Effects	Reference
A	Resistance and susceptibility of disease/insect pest	<i>Arabidopsis</i>	Early flowering	Increased susceptibility to <i>Verticillium</i> spp.	Veronese et al. (2003)
		<i>Arabidopsis</i>	Late flowering	Resistance to <i>F. oxysporum</i>	Lyons et al. (2015)
		<i>Triticum</i>	Direct impact of Frost on the flowering phase	Increased susceptibility to aphids	Lacoste et al. (2015)
B	Early and delay of flowering	<i>Arabidopsis</i>	<i>Fusarium oxysporum</i>	Alters flowering	Lyons et al. (2015)
		<i>Arabidopsis</i>	<i>Pseudomonas syringae</i>	Alters flowering	Korves and Bergelson (2003)
		<i>Arabidopsis</i>	<i>Myzus persicae</i>	Delays flowering	Züst et al. (2011)
		<i>Brassica rapa</i>	<i>Spodoptera littoralis</i>	Delays flowering	Schiestl et al. (2014)
		<i>Brassica rapa</i>	<i>Pieris brassicae</i>	Increased flower production during the early flowering	Schiestl et al. (2014)
		<i>Arabidopsis</i>	<i>Meloidogyne incognita</i>	Accelerates flowering	Xue et al. (2013)
C	Escape of insect attack	<i>Oenothera biennis</i>	Delaying flowering	Avoid predation by the moth <i>Mompha brevittella</i>	Agrawal et al. (2013)
		<i>Lobelia siphilitica</i>	Late flowering	Decreased herbivory by the weevil, <i>Cleopmptiarus hispidulus</i>	Parachnowitsch and Caruso (2008)
D	Photoperiod effects	<i>Zea mays HmlA</i>	<i>Cochliobolus carbonum</i> race 1 (CCR1)	Lower susceptibility to infection	Marla et al. (2018)
		<i>Brassica juncea</i>	<i>Alternaria brassicicola</i>	Lower susceptibility to infection	Macioszek et al. (2021)
		<i>A. thaliana Col-0</i>	<i>Pyricularia oryzae</i> syn. <i>Magnaporthe oryzae</i>	Lower susceptibility to infection	Shimizu et al. (2021)

Of note, studies examining the impact of *Fusarium oxysporum* infection have revealed accelerated FTi alongside the modulation of key floral integrator genes, notably including *FLC*, *FT*, and *GI*. These findings underscore the multifaceted nature of plant–pathogen interactions, wherein the pathogenic infection elicits systemic responses influencing not only defense mechanisms but also developmental pathways, such as FTi regulation (Lyons et al., 2015). Similarly, investigations into the nematode *Meloidogyne incognita* infection have unveiled intriguing insights into the modulation of FTi in response to biotic stress. Specifically, the infection triggers enhanced expression of the 8D05 effector protein, thereby promoting a hastened flowering response (Xue et al., 2013). Moreover, a novel allele of the flowering regulatory gene *FLK*, which encodes a triple KH-repeat protein, has also been discovered. Mutants lacking *FLK* exhibited late flowering and reduced resistance to *Pseudomonas syringae* but enhanced resistance to *Botrytis cinerea* (Fabian et al., 2023). These findings suggest that regulatory genes such as *FLK* could play a key role in regulating plant flowering and immune response.

7 | CONVENTIONAL METHODS TO INDUCE EARLY FLOWERING

Conventional breeding techniques, such as intra-/inter-specific hybridization, have been the primary methods to enhance agronomical traits like early flowering and high yield. Another commonly used method for inducing early flowering is the manipulation of photoperiod, where the duration of light exposure is controlled to mimic shorter days, triggering the flowering response (Paradiso & Proietti, 2022). This can be achieved by using light-blocking covers or adjusting the duration of artificial light in controlled environments. The quantity and quality of light plants receive directly impact processes such as photosynthesis, photomorphogenesis, flowering, and fruiting (Ouzounis et al., 2015). Additionally, different wavelengths of light have specific effects on plant development and physiology. Red and blue light is highly efficient for photosynthesis, and blue light impacts stomatal opening and chlorophyll biosynthesis (Paradiso et al., 2011). Another approach is the application of plant hormones, such as GA, which can stimulate flowering and promote early maturity (Coelho et al., 2018). Additionally, temperature manipulation, such as cold or heat stress exposure, can accelerate flowering in some plant species (Khodorova & Boitel-Conti, 2013). These methods are often employed in breeding programs and agricultural practices to induce early flowering, allowing for shorter growth cycles and adaptation to specific environmental conditions. It is important to note that the effectiveness of these methods may vary depending on the plant species and specific environmental factors. These traditional methods of flowering induction in plants have cer-

tain limitations that make them less desirable as long-term solutions. These methods often rely on labor-intensive practices, requiring manual intervention such as pruning, light manipulation, or treatments such as vernalization. Such induction requires time and adds to the cost due to the need for a significant workforce and resources. To overcome these limitations, there is a growing need to explore alternative approaches, such as genomics or multi-omics approaches, that offer more efficient and cost-effective means of controlling flowering in plants.

8 | MULTI-OMICS INTERVENTIONS FOR REGULATING FLOWERING TIME

Multi-omics interventions have emerged as powerful approaches for unravelling and manipulating the complex regulatory networks involved in flowering control in plants (N. Liang, Cheng, et al., 2018; Tian et al., 2021; L. Wang, Fang, et al., 2020). By integrating multiple high-throughput omics techniques, such as genomics, transcriptomics, proteomics, and metabolomics, researchers can gain comprehensive insights into the molecular mechanisms underlying flowering and identify potential targets for intervention (Figure 1). Genomics studies have enabled the identification and characterizing of genes and genetic variants associated with FTi regulation. Quantitative trait loci (QTL) mapping, genome-wide association studies (GWAS), and genome editing have been extensively utilized for the manipulation and modification of various traits associated with yield, insect pests, and disease resistance in plants (Gangurde et al., 2022; Jha et al., 2023; Thudi et al., 2023). Similarly, for early-flowering traits, researchers have discovered numerous flowering-related genes and genetic markers in various crop species. This genomic information provides a foundation for understanding the genetic basis of FTi and facilitates targeted genetic modifications for manipulating this trait.

Transcriptomics studies have revealed dynamic changes in gene expression profiles during different flowering stages (V. K. Singh et al., 2013). Using RNA sequencing (RNA-seq) techniques, researchers could identify key regulatory genes and unravel the intricate transcriptional networks involved in flowering control (Z. Li, Zhang, et al., 2016). Comparative transcriptomics studies between early and late flowering genotypes or under different environmental conditions have shed light on the regulatory mechanisms underlying this trait (Kaashyap et al., 2022). Gene ontology analysis in a rice transcriptomics study revealed that drought-responsive genes impacted FTi by affecting flower development, reproduction, and pollen–pistil interaction. Furthermore, drought conditions significantly affected the expression levels of crucial FTi genes, such as *PRR37*, *CO*, and transcription factor *HY5* (K. Song et al., 2017). The study by K. Song et al. (2017)

emphasizes the complex interplay between drought stress and the regulation of FTi in rice. Another survey of gene expression analysis revealed higher expression of *Hd1*, *FT-1*, *OsFKF1*, *OsELF3-2*, and *OsGI* in the Yongyou-538 variety. *Os02g0771100* showed lower expression than the Ninggeng 4 variety in response to variations in temperature and light resources (M. Yin et al., 2021). These differences in gene expression may contribute to the distinct flowering responses observed between the two varieties.

Proteomics and metabolomics approaches complement genomics and transcriptomics studies by providing insights into the functional consequences of gene expression-related changes. The proteomic analysis allows for identifying and quantifying proteins involved in flowering regulation, providing an understanding of protein function and interaction networks. Similarly, metabolomic profiling enables identifying and quantifying small biomolecules, such as hormones and signaling compounds, which play critical roles in FTi (Arkhimandritova et al., 2020; Chakraborty et al., 2022).

9 | GENOMIC INTERVENTIONS FOR REGULATING FLOWERING TIME

Genomic interventions for regulating flowering involve applying genetic and molecular techniques to manipulate the genes and pathways responsible for the FTi in plants. These interventions optimize flowering and enhance crop productivity for specific agricultural needs. Genomic interventions regulating FTi have great potential in optimizing crop yields, adapting plants to changing environments, and ensuring sustainable agriculture (Varshney et al., 2018). However, carefully considering ecological and genetic impacts is necessary for their successful implementation.

9.1 | Targeting induced local lesions in genomes by sequencing

The targeting induced local lesions in genomes (TILLING) approach involves chemical-induced random mutagenesis and high-throughput screening to detect point mutations in specific genomic regions. It is a versatile and practical reverse genetic approach applicable to various types of genomes (L. Chen et al., 2014). In the context of mutation discovery in amplicons, NGS has become the preferred tool for mutation detection due to its ability to quickly analyze many amplicons (Fanelli et al., 2021). Ethyl methane sulfonate (EMS) as a chemical mutagen offers distinct advantages over alternative mutagens. EMS treatment generates diverse mutations, including missense and truncation mutations. This diversity provides greater flexibility compared to insertional mutagenesis (McCallum et al., 2000). Moreover, EMS exhibits high

efficiency in inducing random point mutations, even in polyploid plants, allowing for the acquisition of multiple alleles of a specific gene within a small population (Greene et al., 2003). Most TILLING populations have been established in predominantly autogamous (self-pollinated) species, including rice (Till et al., 2007), barley (Talame et al., 2008), and peanut (*Arachis hypogaea*; Guo et al., 2015). This characteristic simplifies the process of self-fertilization in M_1 plants to generate the M_2 population (Fanelli et al., 2021). Interestingly, the TILLING approach can identify mutants with early-flowering characteristics. In sunflower (*Helianthus annuus*), the TILLING by sequencing strategy was employed to identify multiple mutations in selected flowering-associated genes (Fanelli et al., 2021). This application of TILLING provides a powerful tool for uncovering genes involved in flowering control, facilitating the development of crop varieties with improved flowering traits and ultimately increasing agricultural productivity.

9.2 | QTL mapping

Genetic markers are integral components of modern plant breeding strategies. These markers are specific DNA sequences or variations in the genome that provide as genetic signposts, enabling researchers and breeders to identify and track desirable traits (Hasan et al., 2021). QTL mapping is primarily based on identifying associations between genetic markers and phenotypic traits in a population with genetic segregation. Advancements in high-throughput genotyping technologies, such as NGS and genotyping arrays, have significantly accelerated the molecular mapping process (Naik et al., 2024). These technologies enable the simultaneous genotyping of millions of SNP markers across a population, facilitating more precise and efficient identification of genetic loci associated with traits of interest. However, QTL mapping has emerged as a widely utilized method for studying various traits related to yield and other vital characteristics (Jha et al., 2021; S. B. Lee et al., 2018). In terms of FTi, numerous studies have been conducted across various crop species to investigate the genetic control, environmental factors, and molecular mechanisms underlying FTi regulation (see Table 3).

In soybean, various genomic regions were identified using different mapping populations. A mapping population was developed in soybean using well-known genotypes for early flowering, including ZK193, Suinong 14 and Dongnong 50 (Kong et al., 2018; F. Sun et al., 2019). Using bi-parental population, Kong et al. (2018) identified several QTLs specifically controlling either FTi or the reproductive period. For instance, the QTL *qRP-B1* on chromosome 11 influences reproductive period traits but does not affect FTi. Meanwhile, *qRI-J* on chromosome 16 and *qRI-L* on chromosome

TABLE 3 Summary genomic regions or genes responsible for flowering traits in major crops identified using quantitative trait loci (QTL) mapping.

Crop	Mapping population	QTL/genes	PVE (%)	References
Maize (<i>Zea mays</i>)	Huangzaosi × Mo17 ($n = 121$)	71 QTLs	7.9–21.3	Leng et al. (2022)
	Ye 478 × Qi 319	25 QTLs	3.97–23.68	L. Wang et al. (2021)
	Mutant F7p × Gaspe flint	<i>vgt1</i> and <i>vgt2</i>	–	Chardon et al. (2005)
Rice (<i>Oryza sativa</i>)	G23 × NG9108 ($n = 251$)	<i>qFOT6</i>	–	Hu et al. (2023)
	Milyang23 × H143	<i>OsPRR37/PRR37</i>	–	Koo et al. (2013)
	CO39 × Moroberekan	15 QTLs	7–40	Maheswaran et al. (2000)
	Nipponbare × Kasalath	<i>Hd1</i>	–	Yano et al. (2000)
Wheat (<i>Triticum aestivum</i>)	CDC Go × Attila, Cutler × AC Barrie and Peace × CDC Stanley ($n = 698$)	<i>Vrn-A1</i> , <i>Vrn-B1</i> , <i>Rht-A1</i> and <i>Rht-B1</i>	2.5–19.2	Semagn et al. (2021)
	Weimai 8 × Luohan 2, Weimai 8 × Yannong 19 and Weimai 8 × Jimai 20 ($n = 526$)	25 QTLs	6.6–32	Zhao et al. (2019)
	Japanese common wheat × synthetic hexaploids	2 QTLs	16 and 73	A. T. Nguyen et al. (2015)
Sorghum (<i>Sorghum bicolor</i>)	TX. 100 M × 80 M	<i>Ma2 QTL</i>	–	Casto et al. (2019)
	SC lines and exotic progenitor lines	<i>Ma1</i>	–	Higgins et al. (2014)
	Kikuchi Zairai × SC112	7 QTLs	3.4–9.4	El Mannai et al. (2012)
Barley (<i>Hordeum vulgare</i>)	Double round-robin population	<i>Ppd-H1</i> and 3 QTLs	–	Cosenza et al. (2024)
	Beka × Logan	5 QTLs	–	Casas et al. (2021)
	winter-type × spring-type	<i>qDHE.ak-1HS</i> , <i>Ppd-H1</i> , and <i>Ppd-H2</i>	6–39	Samari et al. (2011)
Soybean (<i>Glycine max</i>)	Apex × Prisma ($n = 94$)	21 QTLs	33–71	X. Yin et al. (2005)
	Noir × Archer and Noir × M336-1	4 QTLs	5.6–40.4	L. Wang, Fang, et al. (2020)
	AGS292 × K3 ($n = 75$)	<i>qDTF-10</i> , <i>qDTF-16-1</i> , and <i>qDTF-16-2</i>	23.9–56.1	F. Sun et al. (2019)
	Dongnong 50 × Williams 82 and Suinong 14 × Enrei ($n = 126, 140$)	17 QTLs	14.2–78.9	Kong et al. (2018)
	Toyomusume × Suinong 10	5 QTLs	5.6–46	Yang et al. (2017)
Pearl Millet (<i>Pennisetum glaucum</i>)	AGS292 × K3 ($n = 91$)	<i>qFT-B2-1</i> , <i>qFT-C1-1</i> , <i>qFT-K</i> , <i>qFT-D2</i> , and <i>qFT-F</i>	18.1–50.5	S. Lu et al. (2015)
	ICMS 8511-S1-17-2-1-1-B-P03 × AIMP 92901-S1-183-2-2-B-08	Single QTL	9.4	Kumar et al. (2021)
	ICMB 841-P3 × 863B-P2	6 QTLs	23–48	Kumar et al. (2017)
Chickpea (<i>Cicer arietinum</i>)	NAM populations (Gokce, <i>C. reticulatum</i> and <i>C. echinospermum</i>)	3 QTLs	–	Lakmes et al. (2022)
	(ICCV 96029 × CDC Frontier, ICC 5810 × CDC Frontier, BGD 132 × CDC Frontier and ICC 16641 × CDC Frontier)	<i>efl-1</i> , <i>efl-3</i> , and <i>efl-4</i>	5.66–88.14	Mallikarjuna et al. (2017)
	ICCV 96029 × CDC Frontier	7 QTLs	9–44	Daba et al. (2016)
	ICC 3996 × ILWC 184 ($n = 306$)	2 QTLs	90.2	Aryamanesh et al. (2009)
Lentil (<i>Lens culinaris</i>)	ILL 2601 × ILL 5588 ($n = 173$)	9 QTLs	–	Rajandran et al. (2022)

(Continues)

TABLE 3 (Continued)

Crop	Mapping population	QTL/genes	PVE (%)	References
	<i>Lens culinaris</i> cv. Lupa × <i>L. orientalis</i> accession BGE 016880	13 QTLs	1.7–62.9	H. Y. Yuan et al. (2021)
	Precoz × WA8649041	Single QTL	57	Kahriman et al. (2015)
	Lupa × BG16880 (<i>n</i> = 113)	3 QTLs	–	Fratini et al. (2007)
Pigeonpea (<i>Cajanus cajan</i>)	UAS Dwarf × HDM04-1	13 QTLs	3.18–51.4	Kumawat et al. (2012)
	Pusa Dwarf × H2001-4.	<i>qFL5.1</i> and <i>qMT5.1</i>	15.3 and 11.6	Geddam et al. (2014)
Faba bean (<i>Vicia faba</i>)	Vf6 × Vf27 (<i>n</i> = 124)	12 QTLs	5.3–17.9	Aguilar-Benitez et al. (2021)
	Icarus × Ascot	16 QTLs	7–38	Catt et al. (2017)
Peanut (<i>Arachis hypogaea</i>)	Silihong × Jinonghei 3	19 QTLs	1.15–21.82	W. Liang et al. (2020)
	Silihong × Jinonghei 3	15 QTLs	4.6–12.4	L. Wang, Yang, et al. (2020)
Rapeseed (<i>Brassica napus</i>)	SGDH284 × 158A	<i>cqDTF-C02</i> and <i>cqDTF-C06</i>	32.04 and 16	L. Chen et al. (2022)
	NO.2127 × ZY821	<i>qFTA2.1a</i> and <i>qFTA2.1b</i>	25.4 and 49.1	Cai et al. (2021)
	Spring type × Winter type	Single QTL	9	Scheben et al. (2020)
	GW × DZ	<i>qFTYL16-16</i> , <i>qFTYL16-2</i> , <i>qFTYL16-5</i> , <i>qFTYL17-6</i> , and <i>qFTSY17-7</i>	3.74–12.28	Y. Xu et al. (2020)
	F1 (Regent × Lagoda) and F1 (Lagoda × Regent)	<i>DTF1</i> and <i>DTF2</i>	21.7 and 15	ArifUzZaman et al. (2016)

Abbreviation: PVE, phenotypic variance explained.

19 are associated with FTi but not with reproductive period (Kong et al., 2018). In an F₂ mapping population in soybean, the major QTL *qFT12-1* for FTi was mapped to chromosome 12, with a phenotypic variance explained (PVE) of 20.5%. This QTL, initially located within a 567-kb region, was refined to 56.4 kb through recombinant plant analysis, identifying genes such as *Glyma.12G073900* (Y. Li, Dong, et al., 2019). These findings may indicate that FTi and reproductive period operate through relatively independent genetic mechanisms. In lentil, QTLs such as *DTF6a* and *DTF6b* were identified, and *DTF6a* alone conferring early flowering under short photoperiods (Rajandran et al., 2022). These QTL findings guide breeding strategies, enhancing legume resilience to environmental stress.

Many QTL studies have explored the genetic control of FTi in maize. Salvi et al. (2009) conducted a meta-QTL analysis from 29 independent across all chromosomes associated with FTi. QTL analysis has revealed loci influencing FTi in maize, with PVE from 7.9% to 21.3% across 71 QTLs in an RIL population (Leng et al., 2022). Because of the limited effect of individual QTLs, only a few QTLs for maize FTi have been fine-mapped and cloned despite the large number

identified. Vegetative to generative transition 1 (*Vgt1*) is the first FTi QTL cloned in maize. It has been narrowed down to an ~2 kb noncoding region, which functions as a cis-regulatory element for *ZmRap2.7*, an AP2 transcription factor located about 70 kb downstream (Salvi et al., 2007). Fine mapping of *qDTA3-2* QTL in maize led to the identification of MADS-box transcription factor and *ZmMADS69*. Functional studies revealed that mutants of *ZmMADS69* with reduced expression exhibited delayed flowering, while the overexpression of *ZmMADS69* resulted in accelerated flowering (Liang et al., 2018).

In rice, QTLs for early maturity and photoperiod insensitivity mitigate heat stress during anthesis. For instance, *qFOT6* on chromosome 6, identified via QTLseq and GradedPoolseq, has shown consistent results across multiple environments (Hu et al., 2023). Additionally, the *EH7-2* gene, also on chromosome 6, significantly affects heading date with a PVE up to 23.68% (Koo et al., 2013). Wheat's adaptability relies on flowering-related loci like *Vrn-A1*, *Rht-B1*, and QTLs on chromosomes 2DS and 5AL, contributing up to 73% in PVE (A. T. Nguyen et al., 2015). In barley, new QTLs for FTi have been identified, along with a novel functional allelic

variant of the primary regulatory gene *Ppd-H1* (Cosenza et al., 2024). These findings support breeding strategies to develop climate-resilient cereal varieties.

9.3 | QTL-seq approach

The QTL-seq approach has emerged as a highly effective strategy for rapidly identifying major QTLs that governs economically important traits in crop plants. QTL-seq involves whole-genome re-sequencing of two DNA bulks derived from progeny displaying extreme phenotypes. This method offers several advantages over traditional QTL mapping approaches. First, it allows for more efficient and precise localization of candidate genomic regions. Second, it avoids the necessity of the entire population's DNA marker development and genotyping, resulting in a more efficient and cost-effective procedure. This method has proven to be effective in unraveling the genetic basis of FTi in various crop plants, including pigeonpea (V. Singh et al., 2022), chickpea (Srivastava et al., 2017), lentil (Shivaprasad et al., 2024), rapeseed (*B. napus*) (Tang et al., 2023), cucumber (*Cucumis sativus*) (H. Lu et al., 2014) and cabbage (*Brassica oleracea*) (Shu et al., 2018). Using QTL-seq and gene expression profiling, a candidate QTL (*BnaC08cqDTF*) associated with early flowering in rapeseed was characterized. This analysis identified Cryptochrome 2 (*CRY2*), encoded by *BnaC08G0010400ZS*, within an 86-kb genomic region on chromosome 08 (Tang et al., 2023). This approach was also used to identify the candidate gene (*Efl.1*) from a major QTL on chromosome 1, associated with early flowering in cucumber (H. Lu et al., 2014). In lentil, this approach identified three important QTLs (*LcqDTF3.1*, *LcqDTF3.2* and *LcqDTF3.3*) for flowering time, along with 13 genes associated with the flowering pathway (Shivaprasad et al., 2024). Overall, the utilization of QTL-seq has brought about a revolution in exploring the genetic foundations of intricate traits such as FTi in crop plants.

9.4 | Genome-wide association studies

GWAS relies on linkage disequilibrium and has been widely applied to investigate the genetic basis of crucial traits in diverse plant species. This method explores the association between genetic variations across the entire genome and phenotypic variations in traits within a natural population. By analyzing numerous genetic markers distributed throughout the genome, GWAS facilitates the identification of candidate genes or genomic regions linked to quantitative traits (Gangurde et al., 2022; Thudi et al., 2023). Several studies have employed GWAS to investigate FTi. For instance, in soybean, GWAS identified the association of the *Dt1* gene with both maturity and plant height, while candidate genes homolo-

gous to *Arabidopsis* flowering genes were linked to days to flowering (J. Zhang et al., 2015). Another study with 278 soybean accessions identified 37 significant marker-trait associations (MTAs) with FTi and pod development traits across 14 chromosomes (M. Li, Liu, et al., 2019). In lentil, two loci, *DTF6a* and *DTF6b*, were identified, where dominant alleles led to early flowering (Rajandran et al., 2022). In wheat, a study identified 32 significant MTAs for days to heading, revealing important genes (*Ppd-A* and *Ppd-B*) for photoperiod and vernalization-associated genes (*Vrn-A1* and *VrnA7*) (Gupta et al., 2020). Additionally, in canola, significant MTAs were found with FT paralogs, indicating the regulatory role of FTi paralogs in influencing productivity traits (Raman et al., 2019). In *B. napus*, 10 main-effect associations were found with flowering-time-related climatic indices using association mapping. Five candidate genes, including *BnaFLCs*, *BnaFTs*, *BnaA02.VIN3* and *BnaC09.PRR7*, were validated through haplotype, selective sweep and co-expression analyses (X. Han et al., 2022). Additionally, GWAS identified 21 haplotypes with candidate genes linked to FTi in rapeseed, with structural variation in *BnVIN3-C03* on chromosome C03 showing a strong association with this trait (L. Huang et al., 2021). This report suggests that GWAS analysis can enhance our understanding of the genetic architecture of FTi, including the number of genes involved and their interactions.

9.5 | Gene editing

Gene editing technologies, such as CRISPR/Cas9, enable precise alterations in the plant genome, including the targeted alteration of specific FTi genes. By harnessing the knowledge gained from identifying key genes, researchers can utilize gene editing approaches to engineer plants with desired traits, such as FTi. For instance, researchers employed CRISPR/Cas9 in soybean to target the night light-inducible and clock-regulated 2 (*LNK2*) gene and revealed that mutations in *LNK2* led to a shortened FTi (Z. Li et al., 2021), which has important implications for soybean breeding, particularly in high-latitude regions. CRISPR/Cas9 was also used to modify the *E1* gene in soybean, resulting in two types of mutations that induced early flowering under extended daylight conditions (J. Han et al., 2019). On the other hand, scientists studied the *BnaSVP* (short vegetative phase) gene in rapeseed, which shares homology with the *Arabidopsis* *SVP* gene known to influence flowering. Mutation in four copies of *BnaSVP* with CRISPR/Cas9 resulted in mutant lines exhibiting early-flowering traits under both summer and winter conditions (Ahmar et al., 2022). This demonstrates potential benefits for fine-tuning FTi in oilseed crops to maximize productivity and adaptability.

In sorghum, *FT* gene was targeted, and a frame-shift mutation in the gene led to a significant delay of 10 days in

FTi, confirming the involvement of this gene in regulating the flowering process (Char et al., 2020). Similarly, it has been documented that *OsFLZ2* gene is a negative regulator of FTi in rice (Y. Ma et al., 2022). Y. Ma et al. (2022) showed that *OsFLZ2* destabilizes *OsMADS51*, reducing its activation of the downstream gene *Ehd1* and shedding light on rice flowering mechanisms. G. Wang, Wang, et al. (2020) identified a late-flowering gene in rice (*OsGhd7*), which delayed flowering when overexpressed. In contrast, CRISPR/Cas9 knockouts of *OsGhd7* accelerated flowering, with timing influenced by the field location. In another study, researchers edited rice's *uORFs* of the *Hd2* gene. These edited lines exhibited delayed flowering, ranging from 4 to 11 days compared to the wild type. Similarly, overexpression of *TFL1* in *Arabidopsis* caused late flowering, as it prevented the expression of *LFY* and *API* genes (Ratcliffe et al., 1999), while knockout of *TFL1* expression through CRISPR/Cas9 caused changes such as reduced growth and continuous flowering (Charrier et al., 2019). The delayed flowering was supported by decreased expression of pivotal flowering-related genes, specifically *Ehd1*, *Hd3a* and *RFT1*, compared to the wild type (Y. Liu et al., 2021). These studies together emphasize the versatility of CRISPR/Cas9 as a potent tool for modifying the genetic elements that influence FTi in different crop varieties. Such advancements hold immense promise for agricultural practices, enabling the development of crops with optimized flowering traits, improving adaptability to diverse environments, and ultimately contributing to global food security and sustainability.

10 | CURRENT CHALLENGES AND FUTURE PROSPECTS

In the context of climate change, unravelling the intricate interplay between the photoperiod pathway and environmental variables, notably temperature, has assumed paramount importance. Although plants demonstrate adaptability to changing temperatures in their developmental processes, there exists a notable gap in our understanding of how the photoperiod pathway precisely interacts with temperature cues (Jagadish et al., 2016). Equally crucial is the necessity for a diverse array of crop varieties with favorable agronomic traits to bolster the plasticity and resilience of crops amid these challenges. This diversity not only provides options for adaptation but also serves to mitigate potential losses in agricultural productivity. For instance, the identification of early morning flowering in rice as a potential trait to withstand heat stress highlights the significance of integrating traits like early morning flowering QTL (*qEMF3*) through introgression, thereby enhancing heat resilience and augmenting grain yield under heat stress conditions (Ishimaru et al., 2022). Moreover, deepening our

comprehension of the intricate connections between the photoperiod pathway and environmental conditions is critical to developing crop varieties that thrive under evolving climatic scenarios.

The landscape of plant research has been revolutionized by advancements in NGS and in vitro functional studies. The accessibility of technologies for efficiently generating large-scale population and functional genomic data facilitates the application of research findings across diverse systems. The utilization of gene-editing tools, notably CRISPR/Cas9, represents a potent avenue for advancing our insight into the pivotal roles played by photoreceptors and vernalization-related genes in plant development and the regulation of FTi. Through precise modifications using these tools, researchers can delineate the specific functions and interactions of these genes across various plant species. Furthermore, genome editing tools hold substantial promise for confirming gene functions across a broader taxonomic spectrum. Nevertheless, deciphering the genes and their regulatory mechanisms that determine FTi in conjunction with environmental factors such as temperature, photoperiod, CO₂, and various abiotic stresses and their interactions continues to be a focal point of research. Conversely, comparative studies on flowering pathways are indispensable for understanding the evolution of unique life histories, such as gregarious flowering or masting. Additionally, delving into the role of epigenetic modifications in FTi and their potential adaptive significance presents a promising avenue in evolutionary epigenetics, where the exploration of the occurrence and adaptive significance of natural epigenetic variations in FTi is still unfolding.

11 | CONCLUSION

The exploration of FTi in plants is an intricate and multifaceted domain, encompassing diverse environmental signals, genetic elements and regulatory pathways. While significant strides have been taken in identifying pivotal candidate genes, unraveling the precise functions and regulations governing genes associated with photoperiod and vernalization is crucial for a nuanced comprehension of FTi regulation. Notably, the advent of gene editing technologies, particularly CRISPR/Cas9, has ushered in novel avenues for elucidating gene functions and manipulating genes related to flowering. These technologies offer the potential to gain insights into the specific roles and interactions within the flowering modulation pathway. Furthermore, the progress in NGS technologies, functional studies, and omics technologies has broadened our molecular-level understanding of FTi. Nevertheless, there remains much to explore and comprehend, particularly concerning the intricate interplay between FTi and various environmental factors. Future research endeavors should employ diverse approaches, including comparative

analyses and evolutionary studies, to comprehensively understand FTi diversity and its adaptive significance.

AUTHOR CONTRIBUTIONS

Yogesh Dashrath Naik: Writing—original draft; writing—review and editing. **Rajeev N. Bahuguna:** Writing—original draft; writing—review and editing. **Pedro Garcia-Caparrós:** Writing—original draft; writing—review and editing. **Rebecca S. Zwart:** Writing—original draft; writing—review and editing. **M. S. Sai Reddy:** Writing—original draft; writing—review and editing. **Reyazul Rouf Mir:** Writing—original draft; writing—review and editing. **Uday Chand Jha:** Writing—original draft; writing—review and editing. **B. Fakrudin:** Writing—original draft; writing—review and editing. **Manish K. Pandey:** Writing—original draft; writing—review and editing. **Dinakar Challabathula:** Writing—original draft; writing—review and editing. **Vinay Kumar Sharma:** Writing—review and editing. **Umesh K. Reddy:** Writing—review and editing. **Chanda Venkata Sameer Kumar:** Writing—review and editing. **Venugopal Mendu:** Writing—review and editing. **P. V. Vara Prasad:** Writing—review and editing. **Somashekhar M. Punhuri:** Conceptualization; writing—original draft; writing—review and editing. **Rajeev K. Varshney:** Conceptualization; writing—original draft; writing—review and editing. **Mahendar Thudi:** Conceptualization; visualization; writing—original draft; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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There are no original data associated with this article.

ORCID

Yogesh Dashrath Naik  <https://orcid.org/0000-0002-4336-9364>

M. S. Sai Reddy  <https://orcid.org/0000-0002-7616-5210>

Manish K. Pandey  <https://orcid.org/0000-0002-4101-6530>

Rajeev K. Varshney  <https://orcid.org/0000-0002-4562-9131>

Mahendar Thudi  <https://orcid.org/0000-0003-2851-6837>

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