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Review Article

Modulating Flowering for Breeding Efficiency and Biomass Optimization: A Molecular and Biotechnological Review

Aqwin Polosoro

Research Center for Genetic Engineering, National Research and Innovation Agency, Cibinong, Bogor 16911, West Java, Indonesia

*Corresponding author: aqwi001@brin.go.id

ABSTRACT

Regulation of flowering time is a critical determinant of plant reproductive success and a key trait for optimizing crop adaptation, yield stability, and breeding efficiency. This review highlights recent advances in the molecular pathways controlling flowering, including photoperiod sensing, vernalization and temperature response, autonomous and hormonal regulation, and floral integrator networks. Key genes such as *FT*, *SOC1*, *FLC*, *TFL1*, and *Ghd7* serve as central nodes within these interconnected pathways. The application of genetic engineering tools—including gene overexpression, CRISPR/Cas-mediated knockouts, promoter editing, and transient expression systems—has enabled precise manipulation of flowering phenology across a wide range of crops. These strategies have accelerated fast-track breeding in temperate and tropical perennials and facilitated the enhancement of vegetative biomass in forage and industrial crops through delayed flowering. However, the deployment of flowering-modified genotypes presents challenges, including environmental interactions, phenological trade-offs, biosafety regulation, and potential ecological impacts. Future directions should emphasize the integration of flowering time control with speed breeding platforms, genomic selection, and climate-adaptive trait design, tailored to species—and region—specific requirements. Such multidisciplinary approaches will be vital to advancing crop resilience, productivity, and sustainability under changing environmental conditions.

Keywords: flowering time regulation, genetic engineering, *FT* gene, fast-track breeding, biomass optimization

Introduction

Flowering represents a pivotal developmental transition in plants, marking the onset of reproductive competence and playing a central role in plant fitness, yield potential, and breeding success. This process is tightly coordinated by the shoot apical meristem (SAM), which transitions from vegetative to reproductive development in response to a combination of internal cues and environmental signals such as photoperiod, temperature, vernalization, and various abiotic stresses (Amasino, 2010; Fornara et al., 2010).

Over the past two decades, model plants like *Arabidopsis thaliana* and *Oryza sativa* (rice) have been instrumental in elucidating the genetic framework that controls flowering. In both species, the gene *FLOWERING LOCUS T* (*FT*) acts as a systemic floral inducer, produced in leaves and translocated to the SAM to initiate floral development (Turck et al., 2008; Xu et al., 2012). The timing of flowering is further modulated by floral

repressors, such as *FLOWERING LOCUS C* (*FLC*) in *Arabidopsis* and *Ghd7*/*VRN2* in cereals, which act as integrators of environmental and endogenous signals to delay flowering until favorable conditions are met (Castaings et al., 2014; Deng et al., 2011; Weng et al., 2014; Zhao et al., 2005).

In the context of agriculture, flowering time is a key trait that affects crop adaptation, stress resilience, yield stability, and harvest synchronization (Ionescu et al., 2016; Mallik, 2018). Fine-tuning flowering responses enables breeders to align reproductive development with local agroclimatic conditions, a need that is increasingly urgent under climate change (Deva et al., 2023; Wang et al., 2023). However, optimizing flowering time is complicated by polyploidy, genotype × environment interactions, and physiological trade-offs, such as early flowering at the expense of biomass accumulation or seed filling (Schiessl & Schiessl, 2020; Teklemariam et al., 2024). Recent tools like CRISPR/Cas9 genome editing, phenomic selection, and computational modeling have empowered breeders to more precisely regulate flowering traits across diverse environments (Deva et al., 2023; Hodaei & Werbrouck, 2023).

Perennial crops such as apple, citrus, and oil palm present additional challenges due to prolonged juvenile phases and seasonal flowering patterns. These temporal constraints significantly delay breeding timelines. Biotechnological interventions—particularly the overexpression of floral activators like *FT* and MADS-box genes—have shown strong potential to shorten juvenile phases and induce precocious flowering, thereby enhancing breeding efficiency (Endo et al., 2020; Tränkner et al., 2010; Yamagishi et al., 2011).

A broad range of genetic engineering strategies has now been applied to modulate flowering time, including gene overexpression, knockout, silencing, and promoter editing (Chen et al., 2019; Nakashima & Miyazaki, 2014). While overexpression of genes such as *FT* and *SUPPRESSOR OF OVEREXPRESSION OF CONSTANS1* (*SOC1*) promotes early flowering, downregulation or knockout of repressors such as *TFL1*, *PHYB*, and *Ghd7* has similarly been used to reduce the flowering delay (Hu & Xing, 2019; Reed et al., 1994; Shannon & Meeks-Wagner, 1991). These tools offer remarkable flexibility to customize flowering phenotypes for specific agronomic purposes—ranging from synchronizing flowering in hybrids to extending vegetative growth in biomass crops.

Among the most impactful applications of flowering time modulation is the development of fast-track breeding systems. These approaches combine rapid generation advancement (RGA), speed breeding, and genetic engineering to dramatically accelerate breeding cycles. RGA strategies include single seed descent and doubled haploidy, while speed breeding leverages-controlled environments to enable multiple generations per year (Ghosh et al., 2024; Watson et al., 2017). Marker-assisted selection (MAS) and transgenic tools have been effectively integrated to enhance key traits, for example, incorporating citrus tristeza virus (CTV) resistance in citrus or improving micronutrient density in pearl millet (Endo et al., 2020).

Despite their promise, fast-track systems also present technical and logistical hurdles, such as the need for precise environmental control, high input costs, and potential unintended effects on flowering architecture or yield components (Gaurha et al., 2024). Nonetheless, successful demonstrations in perennial species, such as apple and poplar, have validated the utility of *FT*-based transgenic strategies to reduce generation time and accelerate varietal release (Tränkner et al., 2010).

This review synthesizes current advances in molecular flowering pathways, functional gene studies, and engineering strategies across model and crop systems.

Special emphasis is placed on the application of flowering time regulation in fast-track breeding platforms and its role in enabling climate-smart, high-yielding, and resource-efficient agricultural systems.

Molecular Pathways and Key Regulators of Flowering Time

Flowering represents a critical developmental transition in plants and is orchestrated by a complex regulatory network that integrates external environmental cues with internal physiological signals. This network comprises four principal pathways: photoperiod and light signaling, vernalization and temperature sensing, autonomous and hormonal signaling, and floral integrator pathways. These pathways converge on a conserved set of floral activators and repressors that determine the timing of reproductive development. The molecular components and gene interactions of these pathways are schematically illustrated in Figure 1 for *A. thaliana* and Figure 2 for *O. sativa* (rice), offering comparative insights into flowering regulation in dicot and monocot model systems.

Photoperiod and Light Signaling Pathways

Photoperiodism enables plants to measure day length and align flowering with favorable seasonal conditions. In the facultative long-day plant *A. thaliana*, flowering is promoted under extended daylight through stabilization of the *CONSTANS* (*CO*) protein, which activates *FT*—a mobile florigen that moves from the leaves to the shoot apical meristem (SAM) to induce flowering (Turck et al., 2008; Xu et al., 2012).

CO expression is tightly regulated by the circadian clock and light signaling pathways. In darkness, *CO* is targeted for degradation by the E3 ubiquitin ligase *COP1*, whereas in long-day conditions, the blue-light photoreceptor *FKF1* and circadian protein *GIGANTEA* (*GI*) form a complex that degrades *CO* repressors (CDFs), allowing *CO* to accumulate (Fornara et al., 2010; Zhang et al., 2015). Red light, perceived by *PHYTOCHROME B* (*PHYB*), suppresses *CO* during the morning, contributing to day-length sensitivity (Reed et al., 1994).

In contrast, short-day plants like rice utilize a divergent mechanism. The *CO* ortholog *Heading date 1* (*Hd1*) promotes flowering under short days by inducing *Hd3a* (an *FT* ortholog), but suppresses flowering under long days through interaction with *Ghd7*, which represses *Early heading date 1* (*Ehd1*) and its downstream targets (Shim & Jang, 2020). This inversion highlights the evolutionary adaptation of photoperiodic regulation between dicots and monocots. The photoperiodic pathway serves as a prime target for breeding efforts to adjust flowering across latitudes. Key regulatory genes such as *CO*, *FT*, *Hd1*, and *Hd3a* have been successfully used to modify photoperiod sensitivity and extend crop adaptability.

Vernalization and Temperature Sensing Pathways

Vernalization—the acquisition of flowering competence after prolonged exposure to cold—is essential in many temperate species to prevent premature flowering before winter ends. In *Arabidopsis*, cold exposure represses *FLC*, a potent floral repressor, via epigenetic mechanisms. This repression permits the expression of *FT* and *SOC1*, leading to floral initiation (Boss et al., 2004; Greb et al., 2007).

The silencing of *FLC* is mediated by *Polycomb Repressive Complex 2* (*PRC2*), which is recruited to the FLC locus by *VERNALIZATION INSENSITIVE 3* (*VIN3*) and maintained by *VERNALIZATION 1* (*VRN1*) even after the cold period (Greb et al., 2007; Sheldon et al., 2000). In cereals like wheat and barley, vernalization response involves *VRN1* (a MADS-box activator), *VRN2* (a flowering repressor), and *VRN3* (a florigen orthologous to *FT*). Cold exposure leads to activation of *VRN1*

and suppression of *VRN2*, coordinating the transition to reproductive development (Asp et al., 2011; Sasani et al., 2009).

Although rice does not require vernalization, the gene *Ghd7*, a *VRN2* analog, suppresses *Ehd1* and flowering under long-day and cool conditions. *Ghd7* expression is also responsive to abiotic stress signals such as drought and abscisic acid (ABA), demonstrating its broader role in environmental adaptation (Hu & Xing, 2019; Zhao et al., 2012). Phylogenetic analyses suggest that *FLC*-mediated vernalization is largely restricted to the Brassicaceae, while monocots and other dicots employ alternative regulators. This lineage-specific divergence underscores the need for crop-specific strategies when engineering vernalization responses.

Autonomous and Hormonal Pathways

Unlike photoperiodic or vernalization pathways, the autonomous pathway promotes flowering based on intrinsic developmental cues. In *Arabidopsis*, this pathway acts through suppression of *FLC*, enabling the activation of *FT* and *SOC1*. Core autonomous pathway genes such as *Flowering Control A* (*FCA*), *Flowering Promoting A* (*FPA*), *Flowering Locus Y* (*FY*), *Flowering Locus D* (*FLD*), and *Flowering Locus VE* (*FVE*) are involved in RNA processing and chromatin remodeling (Boss et al., 2004). Plant hormones, particularly gibberellins (GAs), add another regulatory layer. GAs stimulate floral transition by promoting the expression of *SOC1* and *LEAFY* (*LFY*), especially under non-inductive short-day conditions. GA-deficient mutants exhibit delayed flowering, validating its floral-promoting role (Kim, 2020). Abscisic acid (ABA) generally functions as a negative regulator, delaying flowering in response to environmental stress by modulating repressors like Ghd7 (Zhao et al., 2012). Additional hormones, such as auxins and cytokinins, also influence meristem identity and flowering indirectly.

Aging-related microRNAs, particularly miR156 and miR172, serve as internal developmental timers. High miR156 levels repress *SPL* transcription factors, delaying flowering. As plants mature, miR156 decreases and miR172 rises, promoting SPL-mediated activation of downstream floral genes (Kim, 2020). Together, the autonomous and hormonal pathways ensure that flowering occurs at an appropriate developmental stage, regardless of external conditions.

Floral Integrators and Meristem Identity Genes

All upstream flowering pathways ultimately converge on a small set of floral integrator genes that orchestrate the reproductive transition. The key integrators—*FT*, *SOC1*, and *AGAMOUS-LIKE 24* (*AGL24*)—act in the shoot meristem to activate meristem identity genes such as *APETALA1* (*AP1*), *CAULIFLOWER* (*CAL*), and *LEAFY* (*LFY*) (Boss et al., 2004; Kim, 2020). FT protein, produced in the leaves in response to inductive cues, travels to the SAM where it forms a complex with the bZIP transcription factor FD to activate AP1 and trigger floral development. SOC1 integrates diverse inputs—photoperiodic, vernalization, autonomous, and hormonal—and acts as a molecular hub to promote floral transition.

Manipulation of integrators and meristem genes offers a versatile strategy for engineering flowering time and inflorescence structure. These genes are central targets in both transgenic and genome editing approaches to accelerate breeding and modify plant architecture.

Genetic Engineering Strategies to Modulate Flowering Time

Advancements in plant biotechnology have enabled precise genetic manipulation of flowering time, a trait critical for optimizing breeding efficiency, geographical adaptation, and biomass accumulation. Key strategies involve either accelerating flowering—typically to

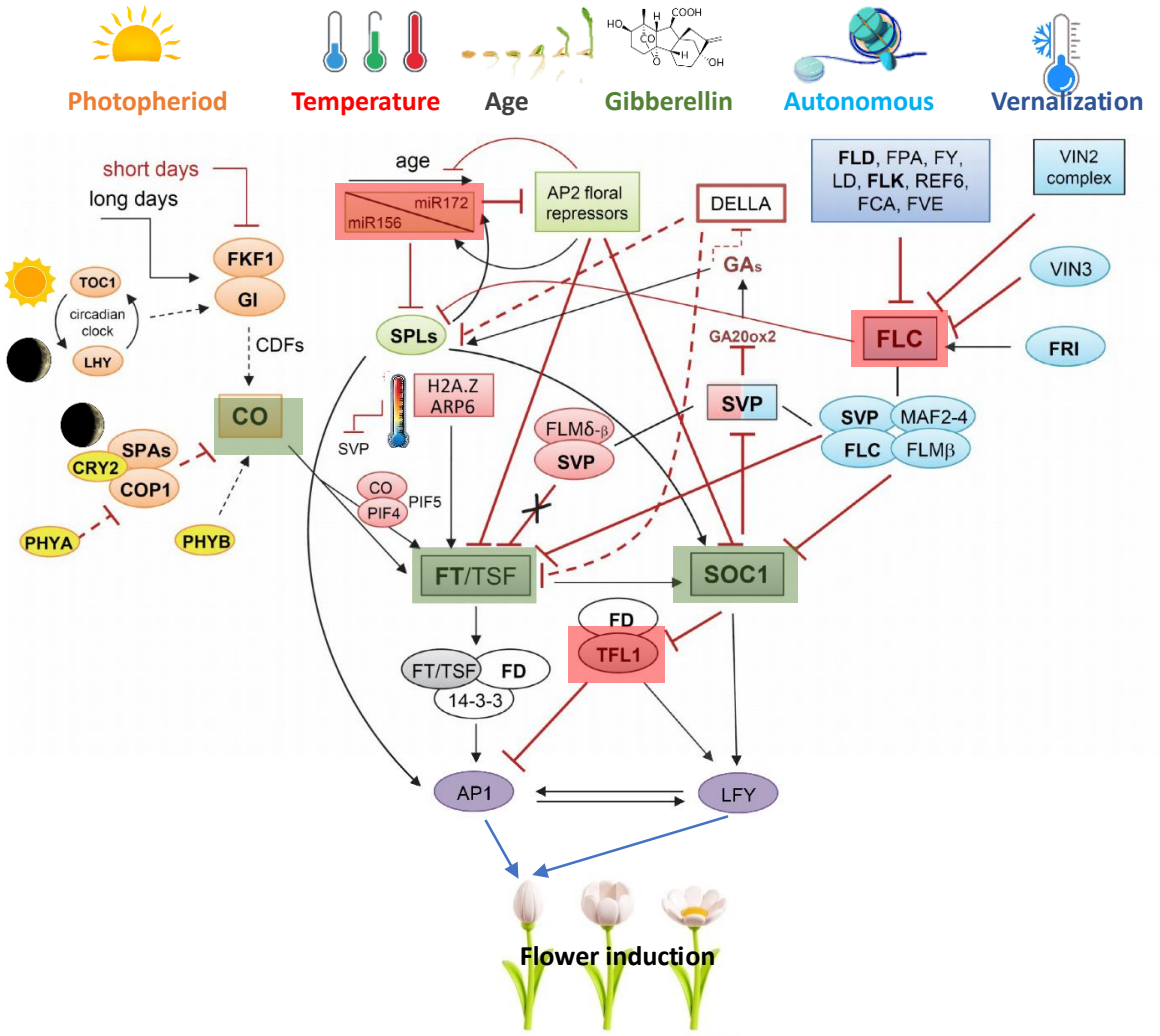

Fig. 1. Gene regulatory network of flowering induction integrating environmental signals and endogenous pathways in *Arabidopsis thaliana* (modified from Leijten et al., 2018). Floral activator genes are highlighted with green outer boxes, while floral repressors are marked in red.

shorten generation cycles—or delaying it to extend vegetative growth and enhance yield components in certain crops. This section outlines two principal approaches: overexpression of flowering regulators and gene silencing or knockout of flowering repressors. These strategies have been applied in both annual and perennial species, using tools ranging from transgenic expression to CRISPR/Cas-mediated genome editing.

Overexpression Approaches

Overexpression of flowering activator genes is a well-established method to promote early flowering and shorten juvenile phases, particularly in long-lived perennial crops. The most commonly targeted gene for this purpose is *FT*—a mobile florigen that triggers floral transition across many plant species. In *Arabidopsis*, rice, and tomato, constitutive or inducible overexpression of *FT* or its homologs has been shown to accelerate flowering (Table 1), reduce generation time, and facilitate rapid breeding (Kotoda et al., 2010; Turck et al., 2008). For example, overexpression of *Hd3a* under a strong promoter induces precocious flowering in rice. Similarly, downstream

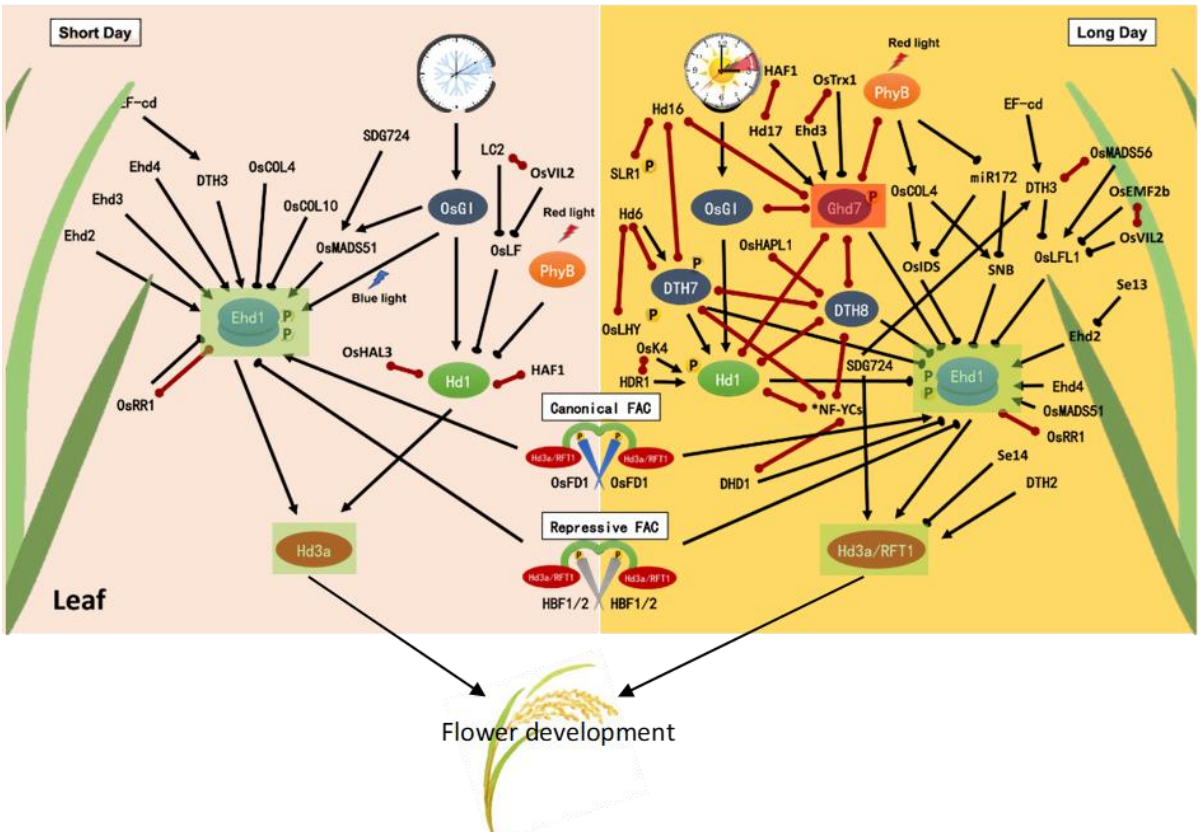

Fig. 2. Photoperiod-dependent gene regulatory network controlling flowering under short-day and long-day conditions in *Oryza sativa* (rice) (modified from Zhou et al., 2020). Floral activator genes are highlighted with green outer boxes, while floral repressors are marked in red.

MADS-box genes such as *OsMADS14* and *OsMADS15* also promote heading when overexpressed (Komiya et al., 2008).

In cassava (*Manihot esculenta*), which exhibits asynchronous and genotype-dependent flowering, transgenic lines overexpressing *FT* have shown earlier and more uniform flowering (Odipio et al., 2020). In perennial fruit trees such as apple, overexpression of *MdFT1* leads to flowering within the first year—drastically reducing the breeding cycle from 5–8 years to just a few months (Tränkner et al., 2010). Citrus transgenic lines overexpressing *AtFT* or *CiFT* have also achieved rapid flowering and have been incorporated into trait introgression systems (Endo et al., 2020).

In addition to *FT*, other flowering integrators such as *SOC1* and *LFY* are effective overexpression targets (Table 1). *SOC1* enhances the expression of floral meristem identity genes and has been used in *Arabidopsis* and *Brassica* crops to synchronize flowering and reduce time to maturity (Li et al., 2023; Tao et al., 2012). *LFY* overexpression can induce floral structures even under non-inductive conditions, though its pleiotropic effects on inflorescence architecture may be more suitable for ornamental breeding.

On the opposite end, delayed flowering can also be achieved by overexpressing floral repressors such as *TERMINAL FLOWER1* (*TFL1*). This strategy extends the vegetative phase, which is advantageous in crops grown for biomass or vegetative organs. For instance, overexpression of *TFL1* in alfalfa (*Medicago sativa*) increases forage yield, while in basil and mint, prolonged leaf production correlates with higher essential oil content (Hanano & Goto, 2011). To mitigate unwanted side effects of constitutive overexpression, modern

approaches employ inducible promoters (e.g., heat-shock, dexamethasone, ethanol-inducible systems) and tissue-specific expression strategies. These methods offer spatiotemporal control over flowering, enabling more precise phenotypic modulation (Wenzel et al., 2013).

Gene Silencing and Knockout Techniques

Gene silencing and knockout methods provide complementary tools to overexpression by suppressing floral repressors, thereby promoting early flowering or adjusting phenology for adaptation. These approaches have benefited from RNA interference **(**RNAi**)** and more recently, CRISPR/Cas9-based genome editing, which allows for precise and heritable gene disruption. In *Arabidopsis*, *FLC* knockdown through RNAi or null mutation removes repression on *FT* and *SOC1*, resulting in accelerated flowering. Similarly, *TFL1* silencing (Table 1) shortens the vegetative phase but may alter inflorescence determinacy (Shannon & Meeks-Wagner, 1991). In rice, knockout of *Ghd7* using CRISPR/Cas9 enhances heading under long-day conditions and improves adaptability to temperate environments (Hu & Xing, 2019; Wang et al., 2020).

Gene editing has also been applied in crops with erratic flowering habits. In *Camelina sativa*, multiplexed edits of flowering repressors resulted in early and stable phenotypes (Bellec et al., 2022), while in tomato, mutations in the *FANTASTIC FOUR* gene family and SP5G induced rapid flowering without yield penalties (Shang et al., 2023; Soyk et al., 2017). Chinese cabbage lines edited at FLC homologs flowered early without vernalization (Jeong et al., 2019), and mini-citrus (*Fortunella hindsii*) further reduced juvenile phases with targeted mutagenesis (Zhu et al., 2019). In rapeseed, BnaSVP quadruple mutants showed the shortest flowering times among edited lines (Ahmar et al., 2021). These examples underscore the promise of gene editing in promoting early flowering to meet modern agricultural demands.

A major advantage of CRISPR over RNAi is its high specificity and stable inheritance, making it more applicable for breeding programs. Furthermore, multiplex genome editing enables simultaneous targeting of multiple genes—an approach increasingly used to fine-tune complex flowering networks.

Opportunities and Challenges in Engineering Flowering Time

The ability to manipulate flowering time through genetic engineering offers transformative opportunities for modern

Table 1. Genetic engineered flowering regulator genes in crops and their potential applications.

Gene	Species/example	Strategy	Effect	Application/ potential applications	References
FT	Arabidopsis, apple, cassava, citrus	Overexpression	Accelerates flowering	Fast-track breeding	Endo et al., 2020; Kotoda et al., 2010; Odipio et al., 2020; Turck et al., 2008
SOC1	Arabidopsis and Brassica	Overexpression	Accelerates flowering	Fast-track breeding	Li et al., 2023; Tao et al., 2012
TFL1	*Medicago sativa*	Overexpression	Delays flowering	Forage/biomass	Hanano & Goto, 2011
TFL1	Arabidopsis, Chinese cabbage	RNAi/knockout	Promotes flowering	Early flowering	Jeong et al., 2019; Shannon & Meeks-Wagner, 1991
Ghd7	Rice	CRISPR knockout	Early heading	Tropical adaptation	Hu & Xing, 2019
PHYB	Arabidopsis	Mutation	Early flowering	Photoperiod modulation	Reed et al., 1994

FT: *Flowering Locus T, SOC*: *Suppressor of Overexpression of Constans 1, TFL1*: *Terminal Flower 1, Ghd7*: *Grain number, heading date and plant height 7, and PHYB*: *Phytochrome B*

agriculture, particularly in the face of climate change, evolving market demands, and resource constraints. However, the practical deployment of these technologies must carefully navigate several biological, environmental, regulatory, and socio-economic challenges. This section highlights key considerations and trade-offs associated with flowering time manipulation in crop breeding programs.

Agronomic Trade-Offs and Phenological Balance

Accelerating flowering through the overexpression of florigen genes such as *FT* or *SOC1* can significantly reduce breeding cycles, enhance generation turnover, and align reproductive development with optimal growing seasons (Table 1). These benefits are particularly valuable in long-cycle crops like fruit trees and perennials, as demonstrated in apple, citrus, and poplar (Endo et al., 2020; Tränkner et al., 2010). However, early flowering can introduce trade-offs. In crops where yield is linked to vegetative growth duration—such as cereals, root tubers, and leafy vegetables—early flowering may reduce total biomass, seed size, or sink strength. Conversely, delaying flowering to enhance vegetative yield, as done in forage crops or bioenergy grasses, may compromise reproductive success or extend the growing period beyond seasonal limits.

Therefore, flowering time engineering must be context-dependent, considering species-specific developmental requirements, regional agroecology, and target traits. Phenological modeling tools and trait optimization platforms can assist in balancing these trade-offs to meet both breeding and agronomic goals.

Environmental and Ecological Considerations

Flowering phenology is tightly coupled with ecological interactions such as pollinator activity, seed dispersal, and abiotic stress exposure. Shifts in flowering time—whether early or late—can disrupt synchrony with pollinators, alter pathogen susceptibility windows, or expose reproductive structures to frost or drought. For instance, transgenic lines that flower out of season may experience reproductive failure or disrupt local ecological rhythms. Moreover, in perennial systems, repeated annual modulation of flowering time may affect perennial reserves, altering long-term plant fitness or yield stability. To mitigate these concerns, flowering time interventions should be combined with ecological modeling, field validation, and environmental monitoring, particularly in genetically engineered or edited cultivars intended for open-field use.

Regulatory and Public Acceptance Issues

The implementation of flowering-related genetic modifications is subject to regulatory frameworks, which vary across countries and depend on the technology used. While transgenic constructs involving foreign DNA typically fall under strict GMO regulations, CRISPR/Cas-mediated edits that do not introduce foreign sequences may be exempt in jurisdictions such as the U.S., Argentina, and Japan. Nevertheless, even non-transgenic technologies such as viral vectors or graft-transmissible RNAs may face biosafety scrutiny. Public perception and market acceptance also pose significant challenges, especially when flowering control involves visible phenotypic changes or is linked to controversial species. To promote responsible deployment, developers should engage in transparent communication, provide trait-specific labeling, and collaborate with local communities and regulatory bodies. Participatory breeding models and co-design approaches can also help align flowering innovations with end-user needs.

Integration with Modern Breeding Platforms

The full potential of flowering time engineering is realized when integrated with modern breeding technologies, including speed breeding and rapid generation advancement (RGA), high-

throughput phenotyping, genomic selection (GS) and machine learning-assisted trait prediction, digital agriculture and climate-smart decision support systems. For example, *FT*-based transgenics combined with controlled-environment speed breeding can enable up to six generations per year in some crops, dramatically accelerating varietal development. Coupling this with genomic selection allows breeders to rapidly introgress complex traits such as stress tolerance or nutrient efficiency alongside optimized flowering. Emerging innovations, such as tissue-specific promoters, epigenetic editing, and florigen transport modification, offer new avenues to spatially and temporally regulate flowering with greater precision. These tools are particularly promising in fine-tuning floral induction without compromising vegetative vigor or reproductive quality.

Conclusions and Future Perspectives

The precise regulation of flowering time is central to plant reproductive success and crop productivity. Over the past two decades, advances in molecular biology and biotechnology have greatly expanded our understanding of the genetic pathways underlying floral induction. These include well-characterized regulatory modules such as photoperiod sensing**,** vernalization, autonomous control, hormonal signaling, and floral integrator networks, as exemplified in model species like *A. thaliana* and *O. sativa*.

Harnessing this knowledge, plant scientists have developed a diverse toolkit for flowering time manipulation. Strategies such as overexpression of florigen genes (e.g., *FT* and *SOC1*), silencing of floral repressors (e.g., *FLC*, *TFL1*, and *Ghd7*), and CRISPR/Cas-based genome editing have enabled tailored control of flowering across a wide range of crop species. These interventions have proven highly effective in shortening breeding cycles, synchronizing flowering events, and optimizing biomass accumulation in both annuals and perennials. Particularly impactful has been the integration of flowering time engineering into fast-track breeding platforms. By combining genetic modification with speed breeding, marker-assisted selection, and digital phenotyping, breeders can now accelerate varietal development while preserving agronomic performance. Such tools are instrumental for achieving climate-resilient, high-yielding, and regionally adapted crops in the face of growing environmental challenges.

Nonetheless, the deployment of flowering-modified genotypes must account for several important considerations. These include potential agronomic trade-offs, such as altered yield dynamics or inflorescence architecture; ecological risks, such as disrupted pollination or seasonality mismatch; regulatory uncertainties, especially in the context of transgenic versus gene-edited products. Transparent stakeholder engagement and robust risk assessments will be essential for navigating these complexities.

Looking ahead, the next frontier lies in precision flowering control—achieved through inducible promoters, tissue-specific expression, epigenome editing, and mobile signal engineering. Additionally, expanding flowering research into underutilized, tropical, and orphan crops will enhance global food system resilience. Future studies should also explore the crosstalk between flowering genes and other regulatory networks involved in stress responses, nutrient use efficiency, and metabolic output, enabling multifaceted crop improvement. Ultimately, flowering time remains a prime leverage point in plant developmental biology and agricultural innovation. Continued collaboration among molecular geneticists, breeders, ecologists, and policy experts will be vital to translate this knowledge into sustainable, equitable, and globally scalable outcomes.

Conflict of Interest

We confirm that we have no conflict of interest regarding any financial, personal, or other affiliations with individuals or organizations related to the subject matter discussed in the manuscript.

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