JIPB Journal of Integrative Plant Biology

Review Article
https://doi.org/10.1111/jipb.70304

# Mineral nutrients as regulators of plant flowering time: A molecular perspective[oo]

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## ABSTRACT

Flowering time is a key agronomic trait that influences plant reproductive success and crop yield, and its regulation is closely associated with soil nutrient availability. This review summarizes recent advances in understanding the molecular mechanisms through which macronutrients and micronutrients regulate flowering time in plants. An emerging central theme is that nutrient-derived signaling integrates with core flowering regulatory pathways, including the photoperiodic, gibberellin, vernalization, autonomous, and sugar pathways, with nitrogen and phosphorus being the most extensively studied. However, major knowledge gaps remain regarding the regulatory roles of potassium, sulfur, and micronutrients, as well as species-specific nutrient responses and the molecular basis of nutrient–nutrient and nutrient–environment interactions in flowering regulation. In addition, the role of nutrient-derived metabolites and rhizosphere microorganisms in flowering control remains largely unexplored. Addressing these challenges is essential for the rational development of crop varieties with optimized flowering time and enhanced nutrient use efficiency through targeted genetic engineering, molecular breeding, and innovative nutrient management strategies, thereby supporting sustainable agricultural development.

Keywords: flowering regulation, gene expression, macronutrient, micronutrient, signaling pathway, transcription factor

**Zeng, H., Wang, Y., Xu, J., Zhang, S., Ali, S., Qin, C., Lei, M., and Xu, G.** (2026). Mineral nutrients as regulators of plant flowering time: A molecular perspective. J. Integr. Plant Biol. **00:** 1–24.

## INTRODUCTION

Flowering represents a crucial developmental transition in higher plants, marking the shift from vegetative to reproductive growth. The precise timing of flowering is essential for successful reproduction, enabling fertilization and seed development under favorable environmental conditions. As an important agronomic trait, flowering time governs the trade-off between vegetative growth and reproduction under limited resource availability (Obeso, 2002). Optimal flowering timing ensures a balanced source–sink relationship, facilitating the efficient translocation of photosynthates to developing grains (Wingler et al., 2025). In agricultural production, synchronizing flowering at an appropriate stage is crucial for achieving high yields. A shortened vegetative phase may limit resource accumulation and reduce grain yield (Gol et al., 2017), whereas delayed flowering can shorten the grain-filling period, thereby compromising grain development and yield potential (Wingler et al., 2025).

Plant flowering time is regulated by a combination of internal cues, such as hormones, sugars, and plant age, and external environmental factors, including photoperiod, temperature, water availability, salinity, and nutrient status (Kazan and Lyons, 2016; Cao et al., 2021; Maple et al., 2024). Among these factors, mineral nutrients have emerged as critical modulators of flowering time. The essential mineral nutrients required for plant growth and development include six macronutrients: nitrogen (N), phosphorus (P), potassium (K), sulfur (S), calcium (Ca), and magnesium (Mg); and eight micronutrients: iron (Fe), manganese (Mn), copper (Cu), zinc (Zn), nickel (Ni), boron (B), molybdenum (Mo), and chlorine (Cl) (de Bang et al., 2021; Zeng et al., 2024). Beyond their fundamental roles in metabolism and cellular processes, these nutrients also function as signaling molecules that profoundly influence flowering time.

It has long been recognized that fertilizer application, particularly N, P, and K, as well as nutrient deficiency, can alter flowering time in plants. For example, excessive N fertilization commonly delays flowering and maturity in rice and wheat (Hall et al., 2014; Ye et al., 2019), whereas appropriate N application promotes flowering in apple (Grasmanis and Edwards, 1974) and white birch (Wang et al., 2011). Similarly, the application of P and K fertilizers promotes heading in rice (Ye et al., 2019), while P deficiency delays flowering in Arabidopsis (Nord and Lynch, 2008; Dai et al., 2024), maize (Ren et al., 2019), *Trifolium subterraneum* (Rossiter, 1978), and rice (Jin et al., 2025). Identifying the key factors involved in nutrient-mediated flowering regulation could provide valuable targets for breeding programs aimed at fine-tuning flowering time, improving nutrient use efficiency, and maintaining high crop productivity.

Soil nutrient availability significantly influences crop yield and quality. In modern agriculture, large amounts of fertilizers are frequently applied to meet crop nutrient demands. Although this practice can alleviate nutrient deficiencies, fertilizer nutrients are often utilized inefficiently, increasing the risks of environmental pollution, ecological degradation, and crop susceptibility to diseases and pests. Therefore, improving fertilizer use efficiency and enhancing nutrient utilization in crops are crucial for sustainable agricultural production (Fageria et al., 2008; Liu et al., 2022).

In recent years, considerable progress has been made in elucidating the molecular basis of nutrient-mediated regulation of flowering time. This review systematically summarizes the effects and underlying mechanisms of macro-nutrients (N, P, K, and S) and micro-nutrients (Fe, Zn, Cu, Mn, and Mo) on flowering time. The roles of other mineral nutrients, including Ca, Mg, B, and Cl, remain insufficiently understood and therefore not discussed in detail. Finally, this review highlights future research directions and potential agricultural applications of nutrient-mediated flowering regulation.

## MOLECULAR MECHANISMS REGULATING FLOWERING TIME

The major flowering regulatory pathways include the photoperiodic, vernalization, temperature, autonomous, gibberellin (GA), and age pathways (Figure 1). These pathways integrate diverse endogenous and environmental signals and converge on key floral integrators, FLOWERING LOCUS T (FT), TWIN SISTER OF FT (TSF), SUPPRESSOR OF OVEREXPRESSION OF CONSTANS 1 (SOC1), CONSTANS (CO), and FLOWERING LOCUS C (FLC). These integrators subsequently activate floral meristem identity genes, such as *APETALA1* (*AP1*), *AP2*, *FRUITFULL* (*FUL*), *LEAFY* (*LFY*), and *CAULIFLOWER* (*CAL*), thereby initiating flower development (Yamaguchi et al., 2009; Chen et al., 2020). LFY directly activates *AP1*, while AP1 in turn positively regulates *LFY*, forming a feedback loop (Liljegren et al., 1999; Wagner et al., 1999; Kaufmann et al., 2010). Once activated in floral meristems, LFY and AP1 repress C2H2 ZINC FINGER PROTEIN (ZFP) transcription factors such as *ZP1* and *ZFP8*, thereby derepressing *AP3*, *PISTILLATA*, and *AGAMOUS* to promote stamen and carpel specification (Hu et al., 2023). SOC1 can directly regulate *LFY* through interaction with AGAMOUS-LIKE 24 (AGL24) (Lee et al., 2008) and repress *TERMINAL FLOWER 1* (*TFL1*) expression via interaction with AGL79 (Yang et al., 2023). In addition, AGL16 represses *SOC1* expression and forms a protein complex with SOC1 to regulate flowering genes (Dong et al., 2023).

*FT* is widely recognized as a florigen gene. In Arabidopsis, *FT* belongs to a phosphatidylcholine-binding protein (PEBP) gene family, which also includes *TSF*, *MOTHER OF FT* (*MFT*), and *TFL1* (Yamaguchi et al., 2005). In the shoot apical meristem (SAM), FT forms a complex with the bZIP transcription factor FD and 14-3-3 proteins to activate *AP1* and *SOC1* expression, thereby promoting floral transition (Wigge et al., 2005; Martignago et al., 2023; Gao et al., 2025). The interaction between the FT tail and the DNA-bound FD–14-3-3 complex plays a pivotal role in the assembly of the florigen activation complex (FAC) and floral induction (Gao et al., 2025). *FT* is expressed in leaf companion cells (Chen et al., 2018a), and the FT protein is transported to sieve elements and subsequently to the SAM via long-distance translocation (Corbesier et al., 2007; Tamaki et al., 2007; Chen et al., 2018a). In contrast to FT, TFL1 acts antagonistically by competing for FD binding in the SAM and repressing flowering (Goretti et al., 2020; Zhu et al., 2020). *TFL1* expression is suppressed by AP1 but is promoted by LFY (Goslin et al., 2017).

CO, a B-box transcription factor, acts as a key regulator in the photoperiodic flowering pathway (Yu et al., 2025), and its functional conservation and divergence are clearly manifested in plants. In Arabidopsis, under long-day conditions, CO activates *FT* expression by binding to specific motifs in the *FT* promoter (Zeng et al., 2022). In rice, the Heading date 1 (Hd1), a homolog of Arabidopsis CO, functions as a bifunctional regulator that promotes flowering under short-day conditions but represses it under long-day conditions through interaction with other flowering regulators, including Hd2, Grain number, plant height and heading-date7 (Ghd7, also named Hd4), and Days-to-heading on chromosome 8 (DTH8, also named Ghd8/Hd5) (Nemoto et al., 2016; Zong et al., 2021). Rice also harbors an Hd1-independent flowering pathway centered on Early heading date 1 (Ehd1), which promotes the expression of

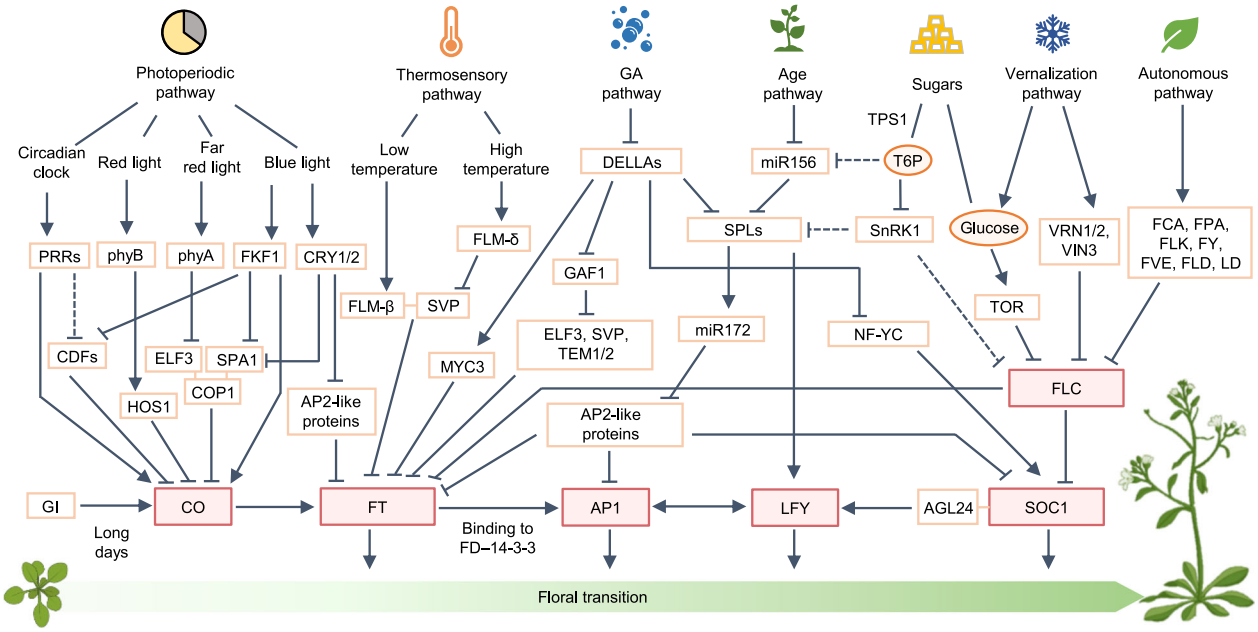


**Figure 1. Flowering regulatory pathways in Arabidopsis**

The floral transition in plants is mainly regulated by the photoperiod, thermosensory, gibberellic acid (GA), age, vernalization, and autonomous pathways, which are extensively interconnected. Sugars also contribute to the regulation of flowering. Key flowering integrators are highlighted in red boxes. Signals from different pathways converge on major integrators such as FT, SOC1, and FLC, which subsequently regulate the expression of floral meristem identity genes, including *AP1*, *LFY*, and *FUL*, thereby initiating flower development. Straight lines refer to a situation or category to which different pathways belong. Arrows indicate positive regulation, while bars represent negative regulation. Dashed lines designate putative regulation. AP1, APETALA 1; AP2-like proteins, Apetala2-like proteins; CDFs, Cyclin DOF factors; CO, CONSTANS; COP1, Constitutive photomorphogenic 1; CRY1/2, Cryptochrome 1/2; ELF3, Early flowering 3; FCA, Flowering locus CA; FKF1, Flavin-binding, kelch repeat, f-box 1; FLC, Flowering locus C; FLD, Flowering locus D; FLK, Flowering locus K homology domain; FLM, Flowering locus M; FPA, Flowering locus PA; FT, Flowering locus T; FVE, Flowering locus VE; FY, Flowering locus Y; GAF1, GAI associated factor 1; GI, GIGANTEA; HOS1, High expression of osmotically responsive genes 1; LD, Luminidependens; LFY, Leafy; NF-YC, Nuclear factor Y-C; phyA/B, phytochrome A/B; PRRs, Pseudo response regulators; SnRK1, Sucrose non-fermenting-1 related kinase 1; SOC1, Suppressor of overexpression of CONSTANS 1; SPA1, Suppressor of phyA-105s; SPL, Squamosa promoter binding protein-like; SVP, Short vegetative phase; TEM1/2, Tempranillo 1/2; T6P, Trehalose-6-phosphate; TOR, Target of rapamycin; VIN3, Vernalization insensitive 3; VRN1/2, Vernalization 1/2. The Arabidopsis plant in the schematic was acquired from BioGDP (https://biogdp.com/).

florigen genes *Hd3a* and *RICE FLOWERING LOCUS T 1* (*RFT1*) (Doi et al., 2004). *Ehd1* itself is positively regulated by Rice Indeterminate1 (RID1, also named Ehd2 or OsID1) (Park et al., 2008; Wu et al., 2008), while it is negatively regulated by Ghd7 (Xue et al., 2008), as well as the cooperative interaction between OsRE1 (regulator of *Ehd1*) and OsRIP1 (OsRE1-interacting protein) (Chai et al., 2021). Furthermore, the flowering suppressor Heading Date Repressor1 (HDR1) and its interacting kinase OsK4 coordinately regulate rice photoperiodic flowering under long-day conditions. HDR1 and OsK4 upregulate *Hd1* and downregulate *Ehd1*, thereby repressing *Hd3a* and *RFT1*. In addition, OsK4 phosphorylates Hd1 in the presence of HDR1 (Sun et al., 2016).

The proper execution of CO function is dependent on the tight regulation of its expression and protein stability by the circadian clock and light signaling (Suárez-López et al., 2001; Takagi et al., 2023). *CO* mRNA levels display distinct diurnal oscillations: morning repression is mediated by CYCLIN DOF FACTORs (CDFs), which recruit the TOPLESS corepressor (Goralogia et al., 2017), whereas activation in the evening is driven by the GIGANTEA (GI)-FLAVIN-BINDING, KELCH REPEAT, F-BOX 1 (FKF1) complex (Imaizumi et al., 2005; Sawa et al., 2007; Fornara et al., 2009; Song et al., 2012). Photoperiod-responsive FLOWERING BHLH (FBH) transcription factors form an activation complex with microRNA319-sensitive TEOSINTE BRANCHED/CYCLOIDEA/PCF (TCP) transcription factors, and this complex directly targets the *CO* promoter and regulates its expression (Ito et al., 2012; Liu et al., 2017). CO protein stability is modulated by multiple photoreceptors and regulatory proteins: blue light photoreceptors CRYPTOCHROME 1 (CRY1) and CRY2, as well as the far-red light receptor PHYTOCHROME A (phyA), promote CO stability, whereas the red-light receptor phyB promotes CO degradation (Valverde et al., 2004). In the dark, CO proteins are phosphorylated and degraded through the E3 ubiquitin ligase complex of CONSTITUTIVE PHOTOMORPHOGENIC 1 (COP1) and SUPPRESSOR OF *phyA-105s* (SPAs) (Jang et al., 2008; Sarid-Krebs et al., 2015). Upon light activation, phyA disrupts the COP1-SPA interaction by directly binding to SPA1 and other SPA proteins (Sheerin et al., 2015). The circadian clock component EARLY FLOWERING 3 (ELF3) can directly interact with CO to promote its degradation (Song et al., 2018) and forms a protein complex with COP1, SPAs, and phyA *in vivo* (Huang et al., 2016), suggesting that phyA may affect the ubiquitin ligase activity of

COP1–SPA through interaction with the ELF3 complex. Rice contains two orthologs of ELF3 (OsELF3-1 and OsELF3-2); OsELF3-1 (also named Hd17 or Ef7) plays a more dominant role than OsELF3-2 in promoting rice heading (Zhao et al., 2012) and functions as a floral activator under long-day conditions by negatively regulating the expression of *Ghd7* and *OsGI*, thereby derepressing the expression of *Ehd1* and the downstream florigen genes *Hd3a* and *RFT1* (Matsubara et al., 2012; Saito et al., 2012; Yang et al., 2013). Moreover, the E3 ubiquitin ligase HIGH EXPRESSION OF OSMOTICALLY RESPONSIVE GENES 1 (HOS1) specifically ubiquitinates CO under red light and is responsible for CO degradation from morning to afternoon under long-day conditions (Lazaro et al., 2012, 2015); phyB is involved in this process by physically interacting with HOS1 and CO and may be required for HOS1-mediated CO degradation (Lazaro et al., 2015). CRY2 physically impairs the COP1–SPA complex (Zuo et al., 2011; Holtkotte et al., 2017; Ponnu et al., 2019) and AP2-like proteins TARGET OF EAT1/2 (TOE1/2) (Du et al., 2020) in a blue light-dependent manner, which further promotes the stability of CO and the expression of *FT*. Blue light photoreceptor FKF1 directly interacts with CO to enhance its stability (Song et al., 2012), while ZEITLUPE (ZTL), another blue light photoreceptor highly homologous to FKF1, physically interacts with CO and triggers its degradation (Song et al., 2014). Similar to CRY2, FKF1 directly interacts with COP1, leading to the attenuation of COP1-dependent CO degradation (Lee et al., 2017). Additionally, the circadian clock components PSEUDO RESPONSE REGULATOR (PRR) proteins, including TIMING OF CAB EXPRESSION 1 (TOC1, also named PRR1), PRR3, PRR5, PRR7, and PRR9, also directly stabilize CO proteins (Hayama et al., 2017). Interestingly, PRRs can repress the expression of *CDFs* (Nakamichi et al., 2012; Toda et al., 2019), thus potentially further relieving the inhibition of *CO* and *FT* (Figure 1).

FLC is a MADS-box transcription factor that acts as a major floral repressor in the vernalization and autonomous pathways (Figure 1). FLC suppresses *FT* expression in leaves and inhibits *FD* and *SOC1* in the SAM (Searle et al., 2006). The vernalization pathway involves prolonged cold exposure to downregulate *FLC*, thereby promoting flowering. In Arabidopsis, FRIGIDA (FRI) is a positive regulator of *FLC* (Johanson et al., 2000), while VERNALIZATION1 (VRN1), VRN2, VERNALIZATION INSENSITIVE3 (VIN3), and VRN5 are negative regulators of *FLC* (Greb et al., 2007). Cold exposure induces the accumulation of VIN3, which then associates with the nucleation region of *FLC* (Wood et al., 2006). VIN3 interacts with VRN5 and collaborates with the VRN2-Polycomb Repressive Complex 2 (PRC2) complex to mediate the epigenetic repression of *FLC* (Yang et al., 2017; Franco-Echevarría et al., 2023). In cereal crops such as wheat and barley, vernalization also promotes flowering, although FLC homologs have not been identified. Instead, cereal VRN2 (not the same protein as Arabidopsis VRN2) represses *FT-like1* (*FT1*) under long-day conditions before winter (Hemming et al., 2008; Deng et al., 2015). During winter, VRN1, a MADS-box family transcription factor homologous to Arabidopsis AP1, is activated by low temperatures and binds to the promoter of *VRN2* to repress its expression, thereby allowing *FT1* induction in the spring (Trevaskis et al., 2006; Hemming et al., 2008; Deng et al., 2015). In temperate cereals such as wheat and barley, vernalization-induced *VRN1* expression is tightly governed by epigenetic modifications (Oliver et al., 2009; Niu et al., 2024). Before vernalization, the repressive histone mark histone 3 lysine 27 trimethylation (H3K27me3) is enriched at the *VRN1* locus to repress its transcription in both species. During vernalization, the active histone marks H3K4me3 gradually accumulate at *VRN1*, while H3K27me3 levels decline (Oliver et al., 2009). In wheat, *Heading-time Locus1* (*HtL1*) encodes a fructose-1,6-bisphosphate aldolase that is involved in sugar metabolism. The enzymatic activity of HtL1 is enhanced by vernalization, thus promoting *VRN1* expression to induce flowering (Yang et al., 2025). SHORT VEGETATIVE PHASE (SVP), another MADS-box protein, plays a crucial role in temperature-mediated flowering regulation (Lee et al., 2013). SVP binds to the *FT* promoter and inhibits its expression. Although *SVP* transcript levels remain relatively stable across temperature, its protein abundance and stability are temperature-sensitive (Lee et al., 2013). At low temperature, SVP forms a heterodimer with the FLM-β isoforms of FLOWERING LOCUS M (FLM), inhibiting the expression of *FT*. At high temperature, SVP preferentially binds FLM-δ in the cytoplasm and is subsequently degraded via the proteasome pathway, suggesting that SVP protein stability is critical to temperature-responsive flowering (Lee et al., 2013; Jin et al., 2022).

The autonomous, age, and GA pathways regulate flowering through internal developmental and hormonal signals and are generally independent of external environmental conditions. The autonomous pathway promotes flowering primarily by inhibiting *FLC* expression. In Arabidopsis, seven genes, namely *FCA* (*Flower locus CA*) (Liu et al., 2010), *FY* (*Flower locus Y*) (Simpson et al., 2003), *FPA* (*Flower locus PA*) (Hornyik et al., 2010), *FVE* (*Flower locus VE*) (Ausín et al., 2004), *FLD* (*Flower locus D*) (He et al., 2003; Fang et al., 2020; Inagaki et al., 2021), *FLK* (*Flower locus K Homology domain*) (Lim et al., 2004; Amara et al., 2023), and *LD* (*Luminidependens*) (Kim et al., 2006), regulate the expression of *FLC* in different ways through the autonomous flowering pathway (Figure 1).

The age pathway is associated with plant developmental stages. As plants mature, flowering is initiated through a regulatory cascade involving microRNAs miR156 and miR172 (Wang et al., 2009; Wu et al., 2009). miR156 levels decline over developmental age instead of chronological age, and the initiation of cell division within the SAM acts as an inducer of miR156 downregulation (Cheng et al., 2021), leading to increased expression of its target genes encoding SQUAMOSA promoter binding protein-like (SPL) transcription factors, which promote flowering by activating downstream floral identity genes, including *SOC1*, *AP1*, *LFY*, and *FUL* (Wang et al., 2009; Yamaguchi et al., 2009). miR156-targeted SPLs, such as SPL9, SPL10, and SPL15, also upregulate the expression of *MIR172A* and *MIR172D* to promote floral transition by suppressing the expression of several AP2-like transcription factors (e.g., *AP2*, *TOE1*, *TOE2*, *TOE3*, *SMZ,* and *SNZ*) and further relieving the inhibition of *FT* in leaves and *SOC1* and *AP1* in the SAM

(Wu et al., 2009; Lian et al., 2021; O'Maoileidigh et al., 2021; Figure 1). The accumulation of bioactive GAs increases before plants initiate flowering, and this upsurge promotes floral transition through the activation of *SOC1* and *LFY* expression in the shoot apex (Eriksson et al., 2006). In the GA-mediated pathway, GAs bind to the receptor Gibberellin insensitive dwarf 1 (GID1), promoting the degradation of negative regulator DELLA proteins via the ubiquitin-proteasome system. This degradation lifts DELLA-mediated repression of flowering activators like SPL9 (Yu et al., 2012), as well as modulating regulators such as MYC3 (Bao et al., 2019), thereby enhancing the expression of downstream genes such as *FT*, *SOC1*, and *LFY* (Figure 1). Several transcription factors, including FLC, CO, MYC3, nuclear factor Y (NF-Y), GAI ASSOCIATED FACTOR 1 (GAF1), and WRKY75, physically interact with DELLA proteins and participate in GA-mediated flowering regulation (Hou et al., 2014; Li et al., 2016; Wang et al., 2016; Zhang et al., 2018b; Bao et al., 2019; Fukazawa et al., 2021). GAF1 forms a transcriptional repressor complex and promotes the expression of *FT* and *SOC1* by repressing genes encoding negative regulators of flowering, such as *ELF3*, *SVP*, *TEMPRANILLO 1* (*TEM1*) and *TEM2* (Fukazawa et al., 2021).

Sugars, particularly sucrose and trehalose-6-phosphate, also influence flowering time. TREHALOSE-6-PHOSPHATE SYNTHASE 1 (TPS1), which catalyzes the formation of trehalose-6-phosphate (T6P), is essential for the induction of *FT* and floral transition (Wahl et al., 2013). T6P controls the expression of *SPL3*, *SPL4*, and *SPL5* in the SAM, partially via regulating miR156 (Wahl et al., 2013; Figure 1). T6P-mediated regulation of plant development is associated with the inhibition of protein kinase activity of SUCROSE NON-FERMENTING1 RELATED KINASE1 (SnRK1); disruption of the SnRK1 α-subunit (SnRK1α1/KIN10) or regulatory βγ-subunit SNF4 effectively ameliorates the characteristic developmental defects of *tps1* mutants, such as embryonic lethality and flowering disorders (Zacharaki et al., 2022). SnRK1 mutation rescues the flowering defect of *tps1* mutants through the spatiotemporal activation of both the photoperiod-responsive CO–FT module and the age-dependent miR156–SPL regulatory pathway (Zacharaki et al., 2022). Moreover, the T6P-SnRK1 module regulates flowering time by affecting the expression of *FLC* (Gramma et al., 2025). In addition, glucose–TARGET OF RAPAMYCIN (TOR) signaling regulates vernalization-dependent flowering via modulation of H3K27me3 enrichment at *FLC* (Ye et al., 2022).

## EXPRESSION OF FLOWERING-RELATED GENES CHANGES UNDER VARIOUS NUTRIENT DEFICIENCY CONDITIONS

Consistent with the observation that deficiencies of diverse nutrients significantly influence plant flowering time, the expression of multiple flowering-related genes is largely changed under nutrient limitation. By analyzing the transcriptome data from Arabidopsis subjected to various nutrient deficiency stresses, such as low N (Luo et al., 2020), P deficiency (Bustos et al., 2010; Chen et al., 2025), low S (Luo et al., 2020), low Ca (Shikanai et al., 2020), Mg deficiency (Hermans et al., 2010), Fe deficiency (Mai et al., 2016), Cu deficiency (Bernal et al., 2012), and Zn deficiency (Chen et al., 2018b), we found that 117 out of 304 flowering-related genes (Kinoshita and Richter, 2020) were significantly changed under various conditions (Figure 2A; Tables S1–S10). At least 15 and 33 flowering-related genes were differentially expressed under low N and P deficiency, respectively, and the number of flowering-related genes reached 59 under low S conditions. Among these genes, *WRKY75*, *TEMPRANILLO 1* (*TEM1*), *GA2OX2*, *GID1B*, and *JAZ1* were significantly upregulated, whereas *PCNA1* and *SPL5* were downregulated by diverse nutrient deficiency stresses (Figure 2B). Several flowering-related genes, such as *RGL3*, *FBH3*, *COL5*, and *GRP7*, showed distinct responses to different nutrient stresses (Figure 2B). These transcriptomic responses suggest potential roles for flowering-related genes in nutrient-mediated flowering regulation.

## NITROGEN REGULATION OF FLOWERING TIME

Plants primarily absorb nitrogen (N) in the form of ammonium ($NH_4^+$) and nitrate ($NO_3^-$), which are transported by nitrate transporters (NRTs) and ammonium transporters (AMTs), respectively (Xu et al., 2012). Once inside the plant, $NO_3^-$ is reduced to $NH_4^+$ by nitrate reductase (NR) and nitrite reductase (NiR) and then assimilated into amino acids via the glutamine (Gln) synthetase/glutamate synthase (GS/GOGAT) pathway in both roots and shoots. Beyond its nutritional role, nitrate also acts as a signaling molecule that regulates gene expression and development, including flowering (Grasmanis and Edwards, 1974; Zhang et al., 2022; Figure 3). In Arabidopsis, Nitrate transporter 1.1 (NRT1.1) plays a central role in linking nitrate signaling to flowering. Loss-of-function mutants of *nrt1.1* show late-flowering (Guo et al., 2001; Teng et al., 2019), whereas overexpression of its rice homolog *OsNRT1.1A* promotes flowering in both Arabidopsis and rice (Wang et al., 2018).

Flowering time often follows a U-shape response to N, with both low and high N levels delaying flowering in both Arabidopsis (Lin and Tsay, 2017) and rice (Zhang et al., 2022, 2025). N-mediated flowering regulation is closely related to the photoperiodic pathway. Low N enhances the expression of *CO*, a key photoperiod regulator (Liu et al., 2013). Long-day conditions promote the expression of *NRT1.1* and *NRT2.1*, and the *nrt1.1*/*nrt2.1* double mutant flowers late, likely due to reduced *CO* and *FT* expression (Ye et al., 2021). Several N-responsive regulators connect nutrient status to the photoperiodic pathway. Low N induces expression of *FNR1* (*Ferredoxin-NADP*$^+$*-oxidoreductase 1*), which promotes NADPH/ATP accumulation and suppresses

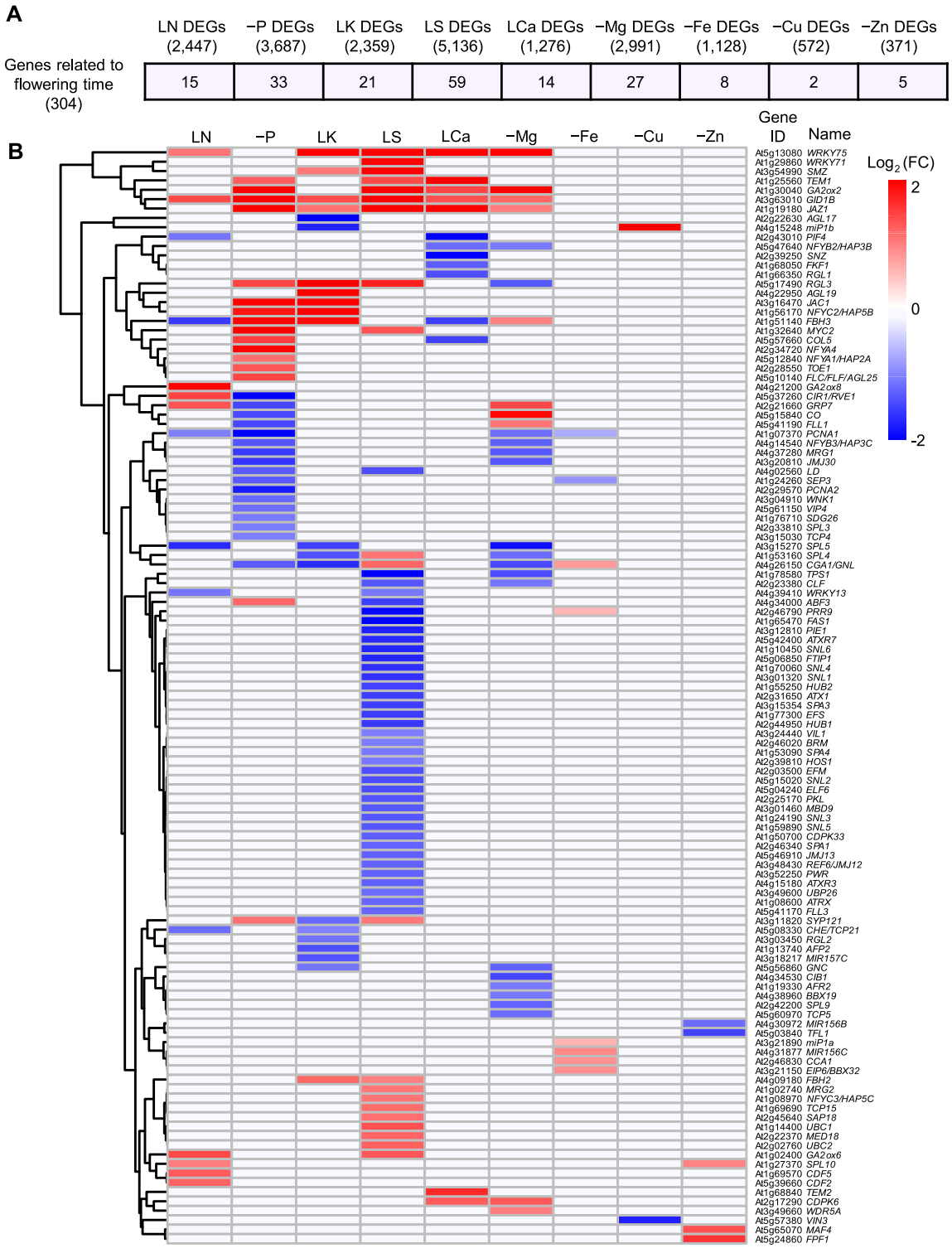


**Figure 2. Differentially expressed flowering-related genes in Arabidopsis under various nutrient-deficiency conditions**

**(A)** Integrated flowering-related genes (Kinoshita and Richter, 2020) were compared with transcriptomic datasets containing genes responsive to low nitrogen (LN; Luo et al., 2020), phosphorus deficiency (−P; Chen et al., 2025), low potassium (LK), sulfur deficiency (−S; Luo et al., 2020), low calcium (LCa; Shikanai et al., 2020), magnesium deficiency (−Mg; Hermans et al., 2010), iron deficiency (−Fe; Mai et al., 2016), copper deficiency(−Cu; Bernal et al., 2012), and zinc deficiency (−Zn; Chen et al., 2018b). The figure shows the overlap between flowering-related genes and differentially expressed genes (DEGs) identified under each nutrient-deficiency condition. DEGs were defined according to the criteria used in the respective studies, with thresholds of fold change ≥ 2 and adjusted *P*-value (or false discovery rate) ≤ 0.05, except for −Fe, where a fold change ≥ 1.5 was applied. The number of DEGs per treatment is indicated in parentheses. **(B)** A total of 117 flowering-related genes were identified across nutrient-deficiency treatments; their expression patterns are shown in the heatmap.

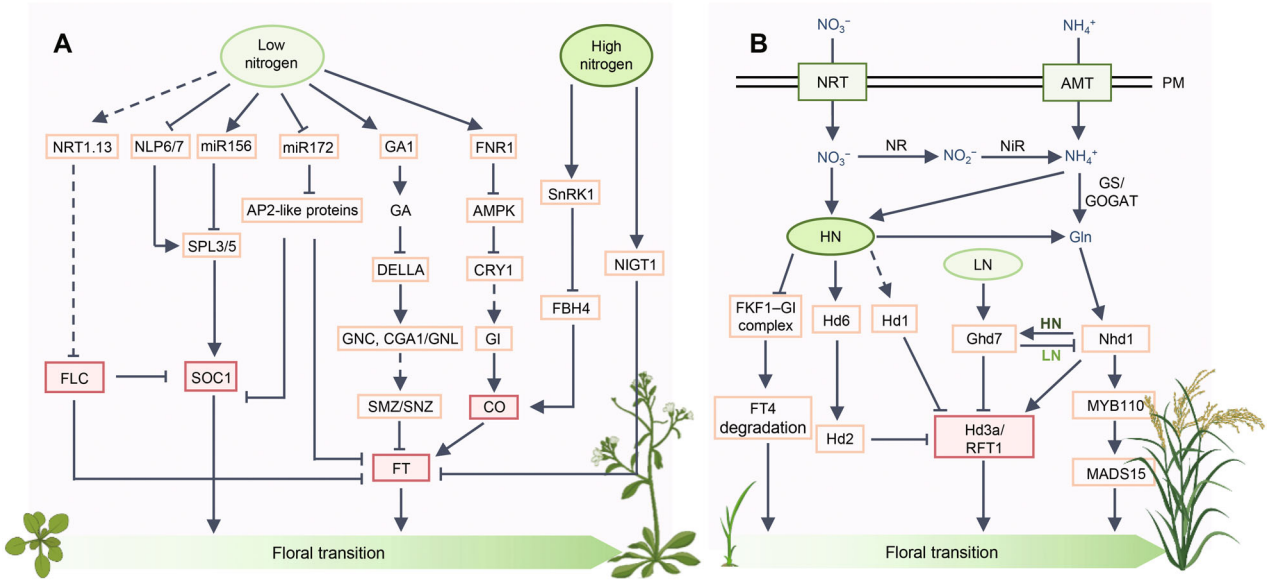


**Figure 3. Nitrogen-mediated regulation of flowering**

**(A)** N availability regulates flowering time by modulating the photoperiod, gibberellin (GA), age, vernalization, and autonomous flowering regulatory pathways, as well as the expression of associated genes. Under low nitrogen (LN) conditions, *FNR1* and *CRY1* are induced, leading to enhanced expression of key photoperiod pathway genes such as *CO* and *GI*. By contrast, high nitrogen (HN) activates SnRK1, which phosphorylates FBH4 and delays flowering by negatively regulating *CO* expression. High N-induced NIGT1 transcription factors repress *FT* expression and negatively regulate flowering time. Low N promotes GA biosynthesis, thereby influencing the downstream regulators GNC and CGA1/GNL, which modulate the expression of the flowering repressors *SMZ* and *SNZ*, ultimately delaying flowering. In the age pathway, low N upregulates miR156 while downregulating miR172. The nitrate signaling transcription factors NLP6 and NLP7 may indirectly regulate the flowering integrator *SOC1* by binding to the NREs in the promoters of *SPL3* and *SPL5*. In addition, under low N-conditions, NRT1.13 indirectly inhibits the flowering repressor *FLC*, thereby increasing *FT* expression and promoting flowering in Arabidopsis. **(B)** In rice, Nhd1 is regulated by N assimilation products such as glutamine (Gln), which activates *Hd3a* and *RFT1* (homologs of *FT*) and the MYB transcription factor OsMYB110, thereby promoting flowering. Under high N conditions, Hd6 accumulation enhances the phosphorylation and stability of Hd2, which acts together with Hd1 to suppress *Hd3a* and *RFT1* expression. N deficiency delays heading by inhibiting *Nhd1* expression through Ghd7, whereas excess N also delays heading by activating *Ghd7* via Gln-induced Nhd1, resulting in a U-shaped response of flowering time to N availability under long-day conditions. In *Brachypodium distachyon* and rice, high N inhibits flowering by impairing the interaction between GI and FKF1. These proteins assemble into biomolecular condensates and promote the degradation of FT4, which functions as an anti-florigen. Arrows indicate positive regulation, while bars represent negative regulation. Dashed lines designate putative regulation. AMPK, Adenosine monophosphate-activated protein kinase; AMT, Ammonium transporter; AP2-like protein, Apetala2-like protein; CGA1/GNL, Cytokinin-responsive GATA factor 1/GNC-like; CO, CONSTANS; CRY1, Cryptochrome 1; FBH4, Flowering bHLH 4; FKF1, Flavin-binding, kelch repeat, f-box 1; FLC, Flowering locus C; FNR1, Ferredoxin-NADP⁺-oxidoreductase 1; FT, Flowering locus T; FT4, Flowering locus T 4; GA, Gibberellic acid; GA1, GA requiring 1; Ghd7, Grain number, plant height and heading-date 7; GI, GIGANTEA; GNC, GATA, nitrate-inducible, carbon-metabolism involved; GS/GOGAT, Glutamine synthetase/glutamate synthase; Hd1/2/6, Heading date 1/2/6; Hd3a, Heading date 3a; NF-Y, Nuclear factor Y; Nhd1, N-mediated heading date 1; NIGT1, Nitrate-inducible GARP-type transcriptional repressor 1; NiR, Nitrite reductase; NLP6/7, NIN-like protein 6/7; NR, Nitrate reductase; NRT, Nitrate transporters; PM, plasma membrane; RFT1, Rice flowering locus T 1; SMZ/SNZ, Schlafmutze/schnarchzapfen; SnRK1, Sucrose non-fermenting-1 related kinase 1; SOC1, Suppressor of overexpression of CONSTANS 1; SPL3/5, Squamosa promoter binding protein-like 3/5. The Arabidopsis and rice plants in the schematic were acquired from BioGDP (https://biogdp.com/).

adenosine monophosphate-activated protein kinase (AMPK) activity. This suppression relieves phosphorylation of CRY1, enhancing the expression of *CO* and *GI* and promoting flowering (Yuan et al., 2016; Figure 3). The transcription factor FLOWERING BHLH 4 (FBH4) and SNF1-RELATED KINASE 1 (SnRK1) are also involved in this process. Under low N conditions, decreased FBH4 phosphorylation favors its nuclear localization and activation of *CO*, increasing *FT* expression and promoting flowering (Sanagi et al., 2021; Figure 3). Conversely, high N activates SnRK1, which phosphorylates FBH4 and delays flowering by negatively regulating *CO* expression (Sanagi et al., 2021; Figure 3). Arabidopsis NITRATE-INDUCIBLE GARP-TYPE TRANSCRIPTIONAL REPRESSOR1 (NIGT1) homologs, which are directly regulated by nitrate signaling-related NIN-LIKE PROTEIN (NLP) transcription factors, negatively regulate N starvation-responsive genes such as *NRT2.1* and *NRT2.4* under high N conditions (Kiba et al., 2018; Maeda et al., 2018). Recently, the binding motif of NIGT1 was found to be significantly enriched in the promoters of *FT* and *FT* co-expressed genes in the phloem companion cells (Takagi et al., 2025). In addition, ectopic overexpression of *NIGT1.2* and *NIGT1.4* represses *FT* expression and delays flowering under N-replete conditions, suggesting the role of NIGT1 in N-dependent flowering regulation (Takagi et al., 2025).

In rice, *N-mediated heading date1* (*Nhd1*), also known as *OsCCA1/OsLHY* (Wang et al., 2020; Sun et al., 2021), directly regulates N-dependent flowering by promoting *Hd3a*

expression. It also regulates N use efficiency by down-regulating Fd-GOGAT activity (Zhang et al., 2021). A reciprocal feedback loop between Nhd1 and Ghd7 forms a regulatory module that controls the U-shaped flowering response to N in rice (Zhang et al., 2025). N deficiency delays flowering by suppressing *Nhd1* via Ghd7, whereas excess N delays flowering by activating *Ghd7* through Gln-induced Nhd1, thereby coordinating the U-shaped response under long-day conditions (Zhang et al., 2025). In addition, high N conditions induce Hd6 protein accumulation, which promotes Hd2 phosphorylation and enhances its stability. The increased Hd2 protein, together with Hd1, inhibits the expression of flowering-inducing genes such as *Hd3a* (Yoshida et al., 2025). In model grass *Brachypodium distachyon* and in rice, the florigen homolog FLOWERING LOCUS T 4 (FT4) negatively regulates flowering and is more stable under high N conditions than under moderate N conditions (Lyu et al., 2026). High N impairs FT4 degradation by weakening the interaction between GI and FKF1, which normally form biomolecular condensates that promote FT4 degradation (Lyu et al., 2026). Rice OsFKF1 also contributes to high N-induced flowering delay, and natural variations in the *OsFKF1* locus underlie fine-tuning of flowering time under different soil N concentrations (Lyu et al., 2026).

The regulation of flowering time by N is also linked to the GA pathway. Low nitrate increases the expression of the GA biosynthesis gene *GA1* (Liu et al., 2013), which may promote flowering. GNC (GATA, NITRATE-INDUCIBLE, CARBON-METABOLISM INVOLVED) and GNL/CGA1 (GNC-LIKE/CYTOKININ-RESPONSIVE GATA FACTOR1) are GATA-type transcription factors acting downstream of DELLA proteins. They participate in GA signaling and regulate flowering genes such as *SMZ* (*SCHLAFMUTZE*) and *SNZ* (*SCHNARCHZAPFEN*) (Richter et al., 2010; Gras et al., 2018). Both SMZ and SNZ are AP2-type transcription factors responsive to nitrate. Under high nitrate conditions (10 mM), *GNC* and *GNL/CGA1* expression increases, which enhances *SMZ* and *SNZ* expression and delays flowering (Gras et al., 2018; Figure 3). High nitrate also represses positive regulators of flowering, including *FT*, *AP1*, and the GA receptor *GID1B*, while inducing negative regulators of GA signaling (Kant et al., 2011; Richter et al., 2010; Figure 3). Thus, nitrate availability can control flowering time through the GA biosynthesis and GA signaling.

N nutrition also influences flowering through the age pathway. In Arabidopsis, miR156 expression is upregulated under N deficiency (Pant et al., 2009; Liang et al., 2012), whereas miR172 expression is downregulated (Liang et al., 2012; Figure 3). Eight SPL family members (SPL2, SPL3, SPL4, SPL5, SPL9, SPL10, SPL11, and SPL15) promote the transition to flowering (Quiroz et al., 2021). Nitrate signaling transcription factors NLP6 and NLP7 bind to nitrate-responsive elements (NREs) in target genes' promoters and are expressed in the SAM, where they regulate *SPL3/5* and the downstream integrator gene *SOC1* (Olas et al., 2019). Low N significantly reduces the expression of *SPL3*, *SPL4*, *SPL5*, and *SOC1*, leading to delayed flowering. Consistently, the *nlp6/7* double mutant shows a strong late-flowering phenotype under both long- and short-day conditions (Olas et al., 2019; Figure 3).

Arabidopsis NRT1.13 is localized to the plasma membrane (PM) and expressed in parenchyma cells of petioles and stem nodes (Chen et al., 2021a). The *nrt1.13* mutant shows delayed flowering, especially under low nitrate conditions. *FLC* expression is increased in this mutant. Genetic analysis shows that the flowering phenotype of the *nrt1.13 flc* double mutant resembles that of *flc*, indicating that FLC is required for the late flowering of *nrt1.13* (Chen et al., 2021a). These results indicate that NRT1.13 is required to repress *FLC* expression to facilitate flowering under low-nitrate conditions (Chen et al., 2021a). Similarly, the *nrt1.1* mutant also shows increased *FLC* expression, and the *nrt1.1 flc* double mutant resembles the *flc* mutant, suggesting that NRT1.1 regulates flowering through an FLC-dependent pathway (Teng et al., 2019). A recent study further showed that N-signals (likely involving NLP7) and sucrose converge on *FLC* to regulate flowering time (Gramma et al., 2025). These findings suggest that N status can influence flowering time through the FLC-dependent vernalization and autonomous pathways.

Even when the photoperiodic, autonomous, and GA pathways are disrupted, flowering can still respond to nitrate. In the *fca-1 co2 ga1-3* triple mutant, low nitrate accelerates flowering (Castro Marin et al., 2011), suggesting the existence of an additional pathway. Similarly, low nitrate promoted flowering in the *ft-7 soc1-1* double mutant (Castro Marin et al., 2011), indicating that nitrate can act downstream of major flowering integrators. In addition to nitrate, Gln, a preliminary assimilation product of inorganic N, also regulates flowering. In rice, Gln promotes the expression of *Nhd1*, which in turn activates *Hd3a* (*Heading date 3a*) (Zhang et al., 2021; Figure 3) and OsMYB110, which further induces the expression of *MADS15* in the SAM (Jin et al., 2025) to promote flowering (Figure 3).

Plants' responses to N vary depending on genotypes and environmental conditions. In Arabidopsis, the flowering time of Col-0 is more sensitive to nitrate supply levels than that of the Ws or Ler genotypes under short-day conditions (Yan et al., 2021). In rice, the effect of N supply on flowering time (heading date) varies across accessions and N levels. Four flowering patterns in response to N supplies were found, including high N induction, high N inhibition, the U-shape (postponed flowering by both high and low N), and insensitivity to N (Zhang et al., 2022). However, the mechanisms underlying these patterns and their evolutionary significance remain unclear.

## PHOSPHORUS REGULATION OF FLOWERING TIME

Inorganic phosphate (Pi) available for plant uptake is mainly present in the forms of $H_2PO_4^-$ and $HPO_4^{2-}$. Insufficient phosphorus (P) supply slows growth, reduces leaf size,

decreases branching or tillering, lowers flower production, and leads to poor yield or fruit development (de Bang et al., 2021). Since Pi availability in natural soils is very limited, plants have evolved multiple adaptive strategies, including modification of root system architecture, enhanced Pi uptake, secretion of organic acids and acid phosphatases, and coordinated transport, distribution, and recycling of Pi across tissues (Madison et al., 2023). Many genes involved in Pi deficiency responses and homeostasis have been identified (Yang et al., 2024). Among them, the MYB-CC (MYB-coiled-coil) transcription factor PHR1 (Phosphate starvation response 1) and its homologous protein PHL1 (PHR1-like 1) play central roles in activating Pi starvation-responsive genes (Bustos et al., 2010). Inositol polyphosphate (InsP) functions as a key intracellular Pi signaling molecule. Cellular Pi status regulates the levels and ratios of $InsP_6$, $InsP_7$, and $InsP_8$, which in turn control the Pi signaling (Jia et al., 2021). When Pi is sufficient, intracellular Pi and $InsP_8$ levels rise, facilitating the formation of InsP8–SPX complex (named after yeast Syg1 and Pho81 and mammalian XPR1 protein). This complex binds to the CC domain of PHR1/PHL1 and suppresses transcription of Pi starvation-responsive genes (Dong et al., 2019; Zhou et al., 2021; Figure 4). Under Pi deficiency, $InsP_8$ is converted to $InsP_7$ or $InsP_6$, leading to dissociation of the SPX–PHR1 complex. PHR1 is then released and binds to the P1BS (PHR1 binding site) in the promoter region of Pi starvation-responsive genes, activating their expression (Figure 4). Representative Pi starvation-responsive genes regulated by PHR1/PHL1 include *PHT* (*phosphate transporters*), the long non-coding RNA *IPS1*, miR399, and acid phosphatases, all of which contribute to Pi homeostasis and stress responses (Bari et al., 2006; Chang et al., 2019; Gu et al., 2016; Figure 4).

Both excessive and insufficient Pi availability affect flowering time. External Pi supply strongly influences flowering. Pi fertilizers promote flowering in rice (Ye et al., 2019; Jin et al., 2025) and *Gnaphalium supinum* (Petraglia et al., 2014), whereas low P delays flowering in tomato (Menary and Staden, 1976), Arabidopsis (Nord and Lynch, 2008; Dai et al., 2024), and *Trifolium subterraneum* (Rossiter, 1978). In Arabidopsis, the *nla* mutant accumulates excessive Pi due to the overaccumulation of downstream PHT1 and flowers early, whereas the *phf1* (*phosphate transporter facilitator 1*) mutant, which is defective in the trafficking of Pi transporters from the endoplasmic reticulum to the PM, shows reduced Pi levels and delayed flowering (Kant et al., 2011). PHO1 (PHOSPHATE 1), a SPX-EXS protein, mediates Pi transport from roots to shoots (Poirier et al., 1991). The *pho1* mutant has low shoot Pi levels and displays dwarfism and delayed flowering. Loss-of-function mutants of *PHO1* in Arabidopsis and its homolog *OsPHO1;2* in rice both show pronounced late flowering (Dai et al., 2024). Supplying Pi to rosette leaves or shoot apices partially rescues the late-flowering phenotype of *pho1*, and grafting the root of the wild type (Col-0) with the shoot of *pho1* results in a normal flowering phenotype, indicating that the late flowering of *pho1* is caused by the

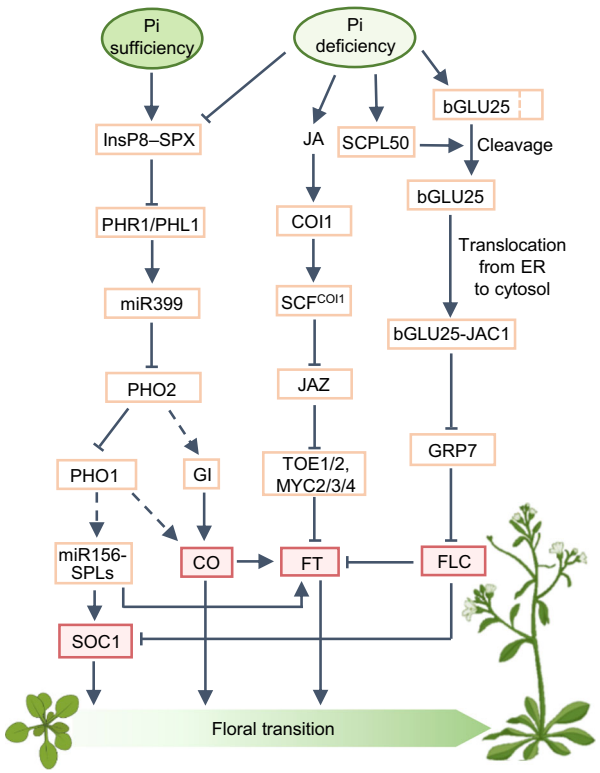


**Figure 4. Phosphate (Pi)-mediated regulation of flowering**

Under Pi-sufficient conditions, intracellular Pi and InsP8 levels are high, promoting the formation of the InsP8-SPX complex. This complex binds to PHR1/PHL1 and prevents them from binding to the cis-element P1BS in the promoters of numerous PSR genes and activating their transcription. Under Pi-deficient conditions, InsP8 levels decrease, and the InsP8–SPX complex fails to bind to PHR1/PHL1, thereby activating the expression of downstream PSR genes, such as the gene encoding the small RNA miR399, which targets *PHO2* to inhibit its expression, in turn leading to the accumulation of PHT1 and PHO1. The PHR1/PHL1–miR399–PHO2–PHO1 regulatory module regulates flowering by integrating with diverse flowering pathways. Pi deficiency delays flowering by inducing jasmonic acid (JA) biosynthesis and activating the JA signaling pathway, thus inhibiting the expression of flowering genes such as *FT* by releasing transcription factors that interact with JAZ, such as TOE1, TOE2, and MYC2/3/4. Under low Pi conditions, Arabidopsis bGLU25 inhibits the nuclear translocation of GRP7, thereby increasing *FLC* expression and delaying flowering. Arrows indicate positive regulation, while bars represent negative regulation. Dashed lines designate putative regulation. bGLU25, β-Glucosidase 25; CO, CONSTANS; COI1, Coronatine insensitive 1; FLC, Flowering locus C; FT, Flowering locus T; GI, GIGANTEA; GRP7, Glycine-rich RNA-binding protein 7; InsP8, Inositol polyphosphate 8; JAC1, Jacalin-lectin like 1; JA, Jasmonic acid; JAZ, Jasmonate zim-domain; PHO1, Phosphate 1; PHO2, Phosphate 2; PHL1, PHR1-like 1; PHR1, Phosphate starvation response 1; SCPL50, Serine carboxypeptidase-like 50; SOC1, Suppressor of overexpression of CONSTANS 1; SPL, Squamosa promoter binding protein-like; SPX, SPX domain-containing protein; TOE1/2, Target of EAT 1/2. The Arabidopsis plant in the schematic was acquired from BioGDP (https://biogdp.com/).

impaired transport of Pi from roots to shoots (Dai et al., 2024). In rice plants, *OsMYB110* is a direct target of OsPHR2 and regulates OsPHR2-mediated inhibition of rice height (Wang et al., 2024). Genetic epistasis places OsMYB110 downstream of Nhd1 but upstream of OsMADS15 in the regulatory hierarchy for promoting flowering time (Jin et al., 2025). While elevated Pi accelerates flowering, this response is abolished

in *osmyb110* and *osmads15* mutants but maintained in *nhd1* mutants, indicating the OsMYB110–OsMADS15 module functions in regulating Pi-mediated flowering time (Jin et al., 2025).

Pi status also interacts with hormone signaling. Pi deficiency induces jasmonic acid (JA) biosynthesis in Arabidopsis and other plants, linking Pi nutrition to defense (Khan et al., 2016; Luo et al., 2021; Figure 4). JA levels were also increased in *pho1* (Khan et al., 2016). In JA signaling, the F-box protein COI1 (Coronatine insensitive 1) can sense JA and form the E3 ubiquitin ligase $SCF^{COI1}$, which promotes the degradation of the transcriptional repressor Jasmonate ZIM domain (JAZ) proteins through the 26S proteasome and releases transcription factors that interact with JAZ, such as TOE1 (TARGET OF EAT 1), TOE2, and MYC2/3/4 (Chini et al., 2007; Yan et al., 2009; Figure 4). TOE1, TOE2, and MYC2/3/4 can inhibit the expression of flowering genes such as *FT* (Wang et al., 2017; Zhai et al., 2015; Figure 4). Therefore, JA negatively regulates plant flowering (Zhai et al., 2015; Zhao et al., 2022). Genetic analysis showed that late flowering in *pho1* is associated with the JA signaling pathway (Dai et al., 2024). The expression of *FT* in the *pho1* mutant is lower than that in the wild type, while the expression level of *FT* in the *pho1 coi1* double mutant is significantly higher than that in *pho1*. Knocking out the JA receptor protein COI1 or JAR1 (JA-resistance 1), which is responsible for the synthesis of bioactive JA-Ile (the conjugate of JA and isoleucine), partially rescues the late-flowering phenotype of *pho1* (Dai et al., 2024). Thus, JA plays an important role in the regulation of flowering time by P nutrition (Figure 4). Interestingly, InsP can bind to COI1 and stabilize the COI1–JAZ complex (Laha et al., 2015; Wu et al., 2023). The role of the interaction between InsP and JA signals in P-mediated regulation of flowering time remains to be further explored.

In Arabidopsis, overexpression of *miR399b* or loss of its target gene *PHO2* (*PHOSPHATE 2*) both cause excessive Pi accumulation in shoots and lead to early flowering under normal growth temperature (around 22°C). Interestingly, this early-flowering phenotype disappears at a lower temperature (16°C), suggesting that the miR399–PHO2 regulatory module is integrated with the temperature-mediated flowering pathway (Kim et al., 2011; Figure 4). Lower temperature also reduces Pi uptake and transport, but whether the altered flowering phenotypes are directly linked to temperature effects on Pi absorption remains unclear. In rice, the loss of functional *PHO2* also leads to excessive Pi accumulation, but the rice *pho2* mutant showed a late-flowering phenotype (Li et al., 2017). Interestingly, rice PHO2 interacts with GI, which is involved in the photoperiodic flowering pathway (Figure 4). Both the *pho2* and *gi* mutants exhibit P accumulation and late-flowering phenotypes, and the expression levels of *Hd3a* and *RFT1*, the homologs of Arabidopsis *FT*, are significantly decreased (Li et al., 2017). These results suggest that rice PHO2 may be involved in the photoperiodic flowering pathway. However, it is still unclear why the flowering phenotypes of the *pho2* mutants are opposite in rice and Arabidopsis. Whether it is related to their growth habits (rice is a short-day plant, while Arabidopsis is a long-day plant) remains to be studied. Under low Pi conditions, Arabidopsis SCPL50 (SERINE CARBOXY PEPTIDASE-LIKE 50) interacts with bGLU25 (β-GLUCOSIDASE 25) and cleaves bGLU25 at the C terminus, then mediates its translocation to the cytosol from the endoplasmic reticulum and binds to JAC1 (JACALIN-LECTIN LIKE1) to prevent the nuclear translocation of GRP7 (GLYCINE-RICH RNA-BINDING PROTEIN 7), thus elevating *FLC* expression and delaying flowering (Cho et al., 2026). These results suggest that Pi nutrition-mediated flowering regulation is possibly interconnected with the FLC-dependent vernalization and autonomous flowering pathways. Transcriptome analysis also supports the connection between Pi nutrition and multiple flowering pathways (Figure 2). In Arabidopsis, loss of *PHO1* suppresses expression of *SPL3*/4/5 (miR156 targets), which enhances the expression of *SMZ* (a target gene of miR172) (Dai et al., 2024), linking Pi availability to the age pathway (Figure 4). Genetic studies also suggest that late flowering of *pho1* involves the CO-mediated photoperiodic pathway and the SVP-mediated temperature pathway (Dai et al., 2024).

Together, these findings indicate that Pi nutrition intersects with several major flowering-time pathways, including vernalization, age, temperature, and photoperiod. However, the molecular basis of these interactions and the reasons for species-specific differences, such as the contrasting *pho2* phenotypes in rice and Arabidopsis, remain unclear (He and Shou, 2024). In addition to JA, it remains to be determined whether Pi influences flowering through other hormones, such as GA and brassinosteroids.

## POTASSIUM REGULATION OF FLOWERING TIME

Unlike N and P, potassium (K) does not directly form biological macromolecules but is essential for osmotic regulation, maintenance of membrane potential, and enzyme activation (Cui and Tcherkez, 2021; Wang et al., 2021). $K^+$ uptake in roots is mediated by channel proteins, such as Arabidopsis $K^+$ Transporter (AKT), as well as transporters including High-Affinity $K^+$ Transporter (HAK), $K^+$ Uptake Transporter (KUP), and $K^+$ Transporter (KT) (Figure 5). The calcium sensor CBL4 (calcineurin B-like protein 4) and its interacting protein kinase CIPK6 regulate the trafficking and activity of AKT2. Mutants of *cbl4* and *cipk6* display a similar late-flowering phenotype under short-day conditions, highlighting the role of $K^+$ transport in flowering time regulation (Held et al., 2011).

Another component, *SODIUM POTASSIUM ROOT DEFECTIVE 1* (*NaKR1*), encodes a heavy metal-associated domain protein whose expression is promoted by CO under long-day conditions. NaKR1 facilitates FT transport from leaves to the SAM, and *nakr1* mutants flower late due to impaired FT movement (Zhu et al., 2016). NaKR1 may also positively regulate *FT* expression through the miR156–SPL3 module (Negishi et al., 2018; Figure 5). Notably, *nakr1* mutants show excessive accumulation of $K^+$ and $Na^+$, and their

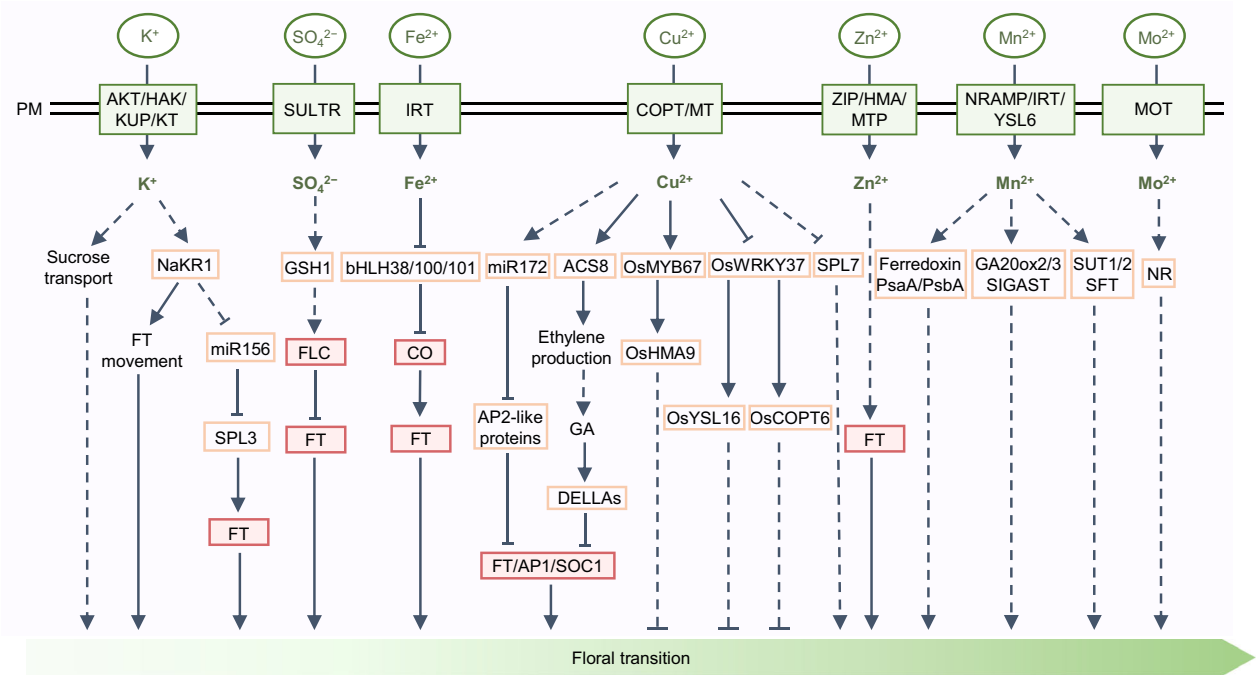


**Figure 5. Regulation of flowering by other plant nutrients**

Potassium (K), sulfur (S), iron (Fe), copper (Cu), zinc (Zn), manganese (Mn), and molybdenum (Mo) are absorbed by specific transporters and activate downstream signaling and metabolic pathways involving transcription factors, microRNAs, and phytohormone-mediated regulation. Their nutrient-dependent signals converge on key flowering regulators, including *FT*, *FLC*, *CO*, and *SPL3*, thereby modulating the timing of flowering. Arrows indicate positive regulation, while bars represent negative regulation. Dashed lines designate putative regulation. ACS, 1-Aminocyclopropane-1-carboxylate synthase; AKT, Arabidopsis $K^+$ transporter; AP1, Apetala 1; AP2-like proteins, Apetala2-like proteins; bHLH28/100/101, basic helix-loop-helix 28/100/101; CO, CONSTANS; COPT, Copper transporter; FT, Flowering locus T; GA, Gibberellic acid; GA20ox2/3, GA 20-oxidase 2/3; GSH1, γ-Glutamylcysteine synthetase; HAK, High-affinity $K^+$ transporter; HMA, Heavy metal ATPase; IRT, Iron-regulated transporter; KT, $K^+$ transporter; KUP, $K^+$ uptake transporter; MAT, S-Adenosylmethionine synthetase; MOT, Molybdate transporter; MT, Cysteine-rich metallothionein; NaKR1, Sodium potassium root defective 1; NR, Nitrate reductase; NRAMP, Natural resistance associated macrophage protein; OsHMA9, *Oryza sativa* P-type heavy metal ATPase 9; OsYSL16, *Oryza sativa* yellow stripe-like protein 16; PM, plasma membrane; PsaA, Photosystem I P700 chlorophyll A apoprotein A1; PsbA, Photosystem II reaction center protein A; SFT, Single flower truss; SlGAST, *Solanum lycopersicum* GA-stimulated transcript; SOC1, Suppressor of overexpression of CONSTANS 1; SPL3, Squamosa promoter binding protein-like 3; SPL7, Squamosa promoter binding protein-like 7; SULTR, Sulfate transporter; SUT1/2, Sucrose transporter 1/2; YSL6, Yellow stripe-like protein 6; ZIP, Zinc-regulated transporter (ZRT)/iron-regulated transporter (IRT)-related protein.

late-flowering phenotype is inhibited by low K (Negishi et al., 2018). However, it remains unclear whether K nutrition directly affects FT transport via proteins such as NaKR1.

In addition, K plays a key role in carbohydrate transport, particularly sucrose. K deficiency impairs photosynthesis and reduces the transport of soluble sugars from leaves to the SAM (Hermans et al., 2006; Tighe-Neira et al., 2018). In Arabidopsis, AKT2 regulates sugar transport through sucrose/$H^+$ symporter. Loss-of-function mutants of *AKT2* have a delayed flowering phenotype, likely caused by the impaired sugar loading and long-distance transport (Deeken et al., 2002; Held et al., 2011; Figure 5). Nevertheless, the effects of K status and K fertilizer application on flowering time, as well as the mechanistic links between K-mediated regulation of flowering time and sugar transport, remain to be investigated.

## REGULATION OF FLOWERING TIME BY SULFUR AND MICRONUTRIENTS

Sulfur (S) is mainly absorbed by plants in the form of sulfate ($SO_4^{2-}$) and assimilated into S-containing amino acids, such as cysteine, cystine, and methionine. It plays essential roles in proteins, coenzymes, vitamins, and antioxidants (Kopriva et al., 2019). Overexpression of *γ-glutamylcysteine synthetase* (*GSH1*), which is related to tripeptide glutathione biosynthesis, delays flowering in Arabidopsis by enhancing *FLC* expression and reducing *FT* expression, whereas *gsh1* mutants flower earlier than the wild type (Cheng et al., 2015; Figure 5). However, it remains unclear whether S nutrition regulates flowering time through GSH1. Sulfate uptake, transport, and storage are mediated by a specialized group of integral membrane proteins known as sulfate transporters (SULTRs) (Singh et al., 2025). Recent studies have shown that the low-affinity sulfate transporter SULTR2;1 promotes long-distance transport of sulfate in Arabidopsis. The levels of sulfate, cysteine, glutathione (GSH), and total S are reduced in knockout mutant *sultr2;1*, although GSH levels are increased in leaves (Soudthedlath et al., 2024). Interestingly, the *sultr2;1* mutant exhibited early flowering (Soudthedlath et al., 2024), but the underlying mechanism remains to be elucidated.

Fe, an essential micronutrient, functions as a cofactor for many enzymes and is a key component of the electron

transport chain. It plays critical roles in metabolic processes such as photosynthesis, respiration, chlorophyll biosynthesis, and nitrate/sulfate reduction (Briat et al., 2015). Fe deficiency, often manifested by leaf chlorosis, impairs photosynthesis, leading to stunted growth and yield loss (Krohling et al., 2016; Huang and Suen, 2021). In addition, Fe deficiency delays flowering in Arabidopsis (Chen et al., 2021b). Basic helix-loop-helix (bHLH) transcription factors are key components of the Fe deficiency-induced transcriptional regulatory network (Gao et al., 2021). For example, bHLH38, bHLH100, and bHLH101 regulate the expression of Fe uptake-related genes in Arabidopsis. The *bhlh38/100/101* triple mutant shows chlorosis, reduced Fe content, and an early-flowering phenotype, along with increased *FT* expression (Chen et al., 2021b). Moreover, these transcription factors interact with CO and inhibit its transcriptional activity. Thus, the delayed flowering caused by Fe deficiency is linked to the bHLH38/100/101-CO-FT signaling cascade (Figure 5). It has also been indicated that the circadian rhythm regulates genes responsible for Fe absorption and transport and that the circadian period is prolonged under Fe deficiency (Hong et al., 2013). However, it remains unclear whether Fe nutrition influences flowering time directly via the circadian clock pathway.

Plant roots mainly absorb Zn in the form of divalent cations ($Zn^{2+}$). Three main transporter families are involved in Zn uptake and transport: ZIP (zinc-regulated transporter (ZRT)/iron-regulated transporter (IRT)-related protein), $P_{1B}$-type ATPase HMA (heavy metal ATPase), and MTP (metal tolerance protein) (Zeng et al., 2021). Zn deficiency negatively affects plant development, inhibits stem elongation, and reduces the yield. Interestingly, high concentrations of Zn (within non-toxic ranges) can promote flowering (Przedpelska-Wasowicz and Wasowicz, 2012), whereas Zn deficiency delays flowering and represses the expression of *FT* and *SOC1* in Arabidopsis (Chen and Ludewig, 2018). However, the underlying molecular mechanism remains unclear.

Cu participates in diverse biological processes, including photosynthesis, respiration, ethylene signaling, reactive oxygen species metabolism, and cell wall remodeling (Burkhead et al., 2009). Both Cu deficiency and Cu excess disrupt plant physiology: Deficiency impairs photosynthesis, respiration, and reproduction, while excess causes toxicity. Homeostasis of Cu is mainly controlled by Cu transporter (COPT) and cysteine-rich metallothionein (MT) proteins (Burkhead et al., 2009). The transcription factor SPL7 is a central regulator of Cu homeostasis (Schulten et al., 2022). Under Cu deficiency, SPL7 binds to the Cu response element (CuRE, GTAC) in the promoter region of target genes, activating Cu transport-related genes (Yamasaki et al., 2009). The *spl7* mutant shows a mild flowering delay under both Cu-deficiency and normal conditions (Schulten et al., 2022). In Arabidopsis, Cu deficiency delays flowering and reduces the expression of miR172 and *FT* (Rahmati Ishka and Vatamaniuk, 2020; Figure 5). In rice, the transcription factor OsWRKY37, induced by Cu deficiency, enhances Cu uptake and root-to-shoot transport by positively regulating *OsCOPT6* and *OsYSL16* (*Yellow stripe-like protein 16*) (Ji et al., 2024; Figure 5). Knockout mutants of *OsWRKY37* or *OsCOPT6* exhibited delayed flowering under Cu deficiency (Ji et al., 2024). Similarly, OsMYB67, a Cu-induced R2R3-MYB transcription factor, binds directly to the *OsHMA9* promoter to activate its expression. Loss of OsMYB67 reduced *OsHMA9* expression and increased *OsATX1* (*Antioxidant protein 1*) and *OsYSL16* expression, resulting in higher Cu allocation to panicles, earlier heading, and improved grain yield (Ding et al., 2025; Figure 5). Excess Cu also influences hormone signaling (Mattoo et al., 1992). High Cu levels induce the expression of ethylene biosynthesis genes, such as *ACS8* (*1-aminocyclopropane-1-carboxylate synthase 8*), thereby enhancing ethylene production (Zhang et al., 2018a). Ethylene activation reduced bioactive GA levels, causing DELLA accumulation and delayed flowering (Achard et al., 2007). Although the influence of Cu on flowering is well established across higher plants, the precise molecular mechanism remains to be clarified. In particular, whether and how Cu-mediated flowering regulation is directly linked to age, GA, and other flowering pathways such as ethylene warrants further investigation.

Mn plays a vital role in photosynthesis because it is an indispensable constituent of the metalloenzyme cluster in the oxygen-evolving complex of photosystem II (PSII). In Arabidopsis, Mn uptake in roots is facilitated by the NRAMP1 (Natural Resistance Associated Macrophage Protein 1) metal transporter localized at the PM, with additional involvement of IRT1, an iron/zinc-regulated transporter (Alejandro et al., 2020). Rice OsYSL6 was considered to transport Mn-nicotianamine complexes from the leaf apoplast to the symplast (Sasaki et al., 2011). The foliar application of $MnFe_2O_4$ in tomato increased the leaf chlorophyll content by up to 20% and enhanced photosynthesis efficiency. This was accompanied by higher expression of genes associated with the photosynthetic electron transport chain, such as *ferredoxin*, *PsaA* (*photosystem I P700 chlorophyll A apoprotein A1*), and *PsbA* (*photosystem II reaction center protein A*) in leaves (Hakala et al., 2005). Genes related to GA biosynthesis, such as *GA20ox2* (*GA 20-oxidase 2*), *GA20ox3*, and *GAST* (*GA-stimulated transcript*), the *SUT1* (*Sucrose Transporter 1*) and *SUT2*, and flowering-related gene *SFT* (*Single Flower Truss*), were significantly upregulated in $MnFe_2O_4$-treated leaves and meristems; the expression of these genes may contribute to the promotion of flowering time (Yue et al., 2022; Figure 5). Thus, $Mn^{2+}$ may induce flowering by promoting photosynthesis and sugar accumulation, activating hormone signal transduction, and upregulating flowering gene expression.

In addition, Mo is a component of enzymes involved in redox reactions and is essential for the activity of NR, xanthine dehydrogenase, aldehyde oxidase, and sulfite oxidase (Kaiser et al., 2005). Legumes have evolved a specialized molybdate uptake system featuring multiple Molybdate Transporter 1 (MOT1)-family transporters to ensure adequate molybdate supply for nitrogenase activity in their symbiotic rhizobia (Vatansever et al., 2016). Unlike legumes, Arabidopsis possesses well-characterized molybdate transporters for

micro-compartmentation, storage, and allocation of this essential micronutrient (Weber et al., 2023). Previous studies indicated that Mo application exclusively during the vegetative stage accelerates flowering in *Nicotiana rustica*, concomitant with enhanced NR activity and elevated root nitrate content (Martin et al., 2008; Figure 5). Consistent with this, Mo deficiency leads to impaired N metabolism, which in turn results in delayed flowering (Martin et al., 2008). Despite these advances, the molecular mechanisms underlying Mo-mediated regulation of flowering time remain poorly understood and warrant further investigation.

## CONCLUSION AND PERSPECTIVE

Appropriate flowering time is pivotal for plant environmental adaptation and reproductive success, with nutrient availability exerting a profound impact on flowering time and subsequent fruit set or grain filling, thus linking nutrient metabolism closely to crop yield formation. Current insights into nutrient-mediated flowering regulation are predominantly derived from studies on N and P in the model plant Arabidopsis, while the regulatory mechanisms of other macronutrients (e.g., K and S) and micronutrients (e.g., Fe, Zn, Cu, Mn, and Mo) remain largely elusive (Table 1). The conservation and divergence of these regulatory mechanisms in horticultural, cereal, and legume crops are yet to be clarified, which restricts the translational application of basic research to agricultural production. N regulates flowering time through different forms, such as $NO_3^-$, $NH_4^+$, and Gln. Among these, nitrate-mediated flowering regulation is best characterized and involves interactions with photoperiodic, GA, age, and vernalization pathways (Table 1), although potential links with other pathways cannot be excluded. P deficiency delays flowering, partly through JA signaling, and may also interact with photoperiodic, GA, and age pathways (Table 1), although the precise mechanisms remain unclear. K affects flowering time possibly by influencing sucrose transport and FT movement. Other nutrients, such as S, Fe, Zn, Cu, Mn, and Mo, can also regulate plant flowering, possibly by affecting hormones, carbohydrates, and other metabolites, although their precise molecular mechanisms remain unclear. Notably, nutrient signals (such as N, P, K, and Fe) are intricately interconnected with flowering-related signaling pathways (such as auxin, GA, JA, brassinosteroids, strigolactones, nitric oxide, and sucrose). The roles and underlying mechanisms of these nutrient-related signaling molecules in flowering time regulation warrant further investigation, with newly developed technologies, such as gene editing, single-cell transcriptomics, live imaging, and multi-omics approaches, providing powerful tools for deciphering these complex regulatory networks.

In natural and agricultural ecosystems, plants rarely encounter single nutrient stress but often face combined stresses such as N/P/K co-deficiency or the coexistence of nutrient deficiencies and metal ion toxicity (Dai et al., 2023; DeLoose et al., 2024). Existing studies have revealed the interactive regulation of flowering by N and P. For instance, low N promotes flowering, while low P delays it in Arabidopsis, with low N-induced early flowering potentially associated with Pi accumulation (Kant et al., 2011; Cho et al., 2025). The roles and underlying mechanisms of other nutrient interactions in flowering time regulation remain unclear and need to be elucidated. Studying the role of nutrient interactions in regulating flowering time can provide a theoretical basis for optimized fertilization strategies in agricultural production. Furthermore, soil nutrient stress is frequently accompanied by abiotic and biotic stresses, including salinity, drought, ion toxicity, pathogen infection, and pest infestation (Gong et al., 2020; Zeng et al., 2025; Zhang et al., 2026). The availability of soil nutrients and plant nutrient signaling pathways are also affected by environmental factors (e.g., water availability, temperature, light intensity, $CO_2/O_2$ concentration in the air, and soil characteristics), as well as global climate change (such as the increase in $CO_2$ concentration and temperature) (Figure 6), but how nutrient signals crosstalk with environmental cues to coordinately regulate flowering remains largely unclear. Identification of the shared molecular nodes (e.g., transcription factors) that integrate nutrient signals and environmental stimuli to modulate flowering is vital for improving crop adaptability. It is notable that most current research is conducted in model organisms grown under controlled conditions, which fails to reproduce the complexity of natural and agricultural environments. Exploring the molecular regulatory mechanisms of flowering time under multiple nutrient stresses and combined nutrient and environmental stresses can provide a knowledge base for improving crop adaptability to multiple stresses and global climate change.

In agricultural production, synchronizing flowering at an optimal stage is crucial for improving yield. Nutrient availability strongly influences flowering time, thereby affecting fruit setting or grain filling. In rice, the application of chemical N fertilizer delays flowering and prolongs the flowering duration, while P and K fertilizers promote flowering (Ye et al., 2019). In addition to traditional soil fertilizers, innovative fertilizer forms can be applied to regulate plant growth and flowering time. Foliar spraying has attracted significant attention due to its advantages over soil fertilization, including high efficiency, reduced fertilizer use, and environmental protection. For example, Ca and B are widely used in Brazil (Domingos et al., 2021) due to soil Ca deficiency in some regions and the high B nutritional requirements of crops (Lopes and Guimarães Guilherme, 2016). With advances in nanotechnology, engineered nanomaterials have shown great potential for enhancing agricultural productivity (Lowry et al., 2019). Some macronutrients and micronutrients, such as N, P, Zn, and Mn, combined with nanomaterials, have been shown to supplement crop nutrition and promote growth (Liu and Lal, 2014; Kottegoda et al., 2017; Venkatachalam et al., 2017; Yue et al., 2022). Biological fertilizers are also effective for agricultural production. Rhizosphere microorganisms that increase and prolong N bioavailability by mediating nitrification have been suggested to delay flowering by converting tryptophan into the

**Table 1. Genes associated with nutrients influencing flowering time in plants**

| Nutrient | Species | Nutrient-related gene | Gene ID | Response to nutrient | Downstream flowering regulator | Integrated flowering pathway | Reference |
|---|---|---|---|---|---|---|---|
| Nitrogen (N) | *Arabidopsis thaliana* | *NRT1.1* | At1g12110 | Nitrate transceptor | FLC; CO; FT | Vernalization; autonomous; photoperiod | Teng et al. (2019), Ye et al. (2021) |
| | *Arabidopsis thaliana* | *NRT1.13* | At1g33440 | Nitrate transporter | FLC | Vernalization; autonomous | Chen et al. (2021a) |
| | *Arabidopsis thaliana* | *NRT2.1* | At1g08090 | Nitrate transporter reduced by high N | CO; FT | Photoperiod | Ye et al. (2021) |
| | *Arabidopsis thaliana* | *NIGT1.2* | At1g68670 | Induced by high N | FT | Unknown | Takagi et al. (2025) |
| | *Arabidopsis thaliana* | *NIGT1.4* | At1g13300 | Induced by high N | FT | Unknown | Takagi et al. (2025) |
| | *Arabidopsis thaliana* | *NLP6* | At1g64530 | Transcription factor in nitrate signaling | SPL3/5; SOC1 | Age; vernalization; autonomous | Olas et al. (2019) |
| | *Arabidopsis thaliana* | *NLP7* | At4g24020 | Nitrate sensor and transcription factor | SPL3/5; SOC1; FLC | Age; vernalization; autonomous | Gramma et al. (2025) |
| | *Arabidopsis thaliana* | *FNR1* | At5g66190 | Induced by low N | CO; GI | Photoperiod | Yuan et al. (2016) |
| | *Arabidopsis thaliana* | *FBH4* | At2g42280 | Protein phosphorylation reduced by low N | CO; FT | Photoperiod | Sanagi et al. (2021) |
| | *Arabidopsis thaliana* | *SnRK1* | At3g01090 | Induced by high N | CO | Photoperiod | Sanagi et al. (2021) |
| | *Arabidopsis thaliana* | *GA1* | At5g57380 | Induced by low N | GA | GA | Liu et al. (2013) |
| | *Arabidopsis thaliana* | *GNC* | At5g56860 | Induced by low N | SMZ; SNZ | GA | Gras et al. (2018) |
| | *Arabidopsis thaliana* | *GNL/CGA1* | At4g26150 | Induced by low N | SMZ; SNZ | GA | Gras et al. (2018) |
| | *Arabidopsis thaliana* | *GID1B* | At3g63010 | Reduced by high N | GA | GA | Richter et al. (2010) |
| | *Arabidopsis thaliana* | *miR156* | — | Induced under N deficiency | SPLs | Age | Pant et al. (2009), Liang et al. (2012) |
| | *Arabidopsis thaliana* | *miR172* | — | Reduced under N deficiency | AP2-like proteins | Age | Liang et al. (2012) |
| | *Oryza sativa* | *OsNRT1.1A* | LOC_Os08g05910 | Nitrate transporter | OsHd3a; OsEhd1; OsRFT1 | Photoperiod | Wang et al. (2018) |
| | *Oryza sativa* | *OsNhd1* | LOC_Os08g06110 | Suppressed by low N | OsHd3a | Photoperiod | Zhang et al. (2021, 2025) |
| | *Oryza sativa* | *OsHd6* | LOC_Os03g55389 | Induced by high N | OsHd3a | Photoperiod | Yoshida et al. (2025) |
| | *Oryza sativa* | *OsFT4* | — | Protein stabilization promoted by high N | OsGI; OsFKF1 | Photoperiod | Lyu et al. (2026) |
| | *Brachypodium distachyon* | *BdFKF1* | — | Interaction with GI weakened by high N | BdGI; BdFT4 | Phototperiod | Lyu et al. (2026) |
| | *Brachypodium distachyon* | *BdFT4* | — | Protein degradation impaired by high N | BdGI; BdFT4 | Phototperiod | Lyu et al. (2026) |

Continued

**Table 1. Continued**

| Nutrient | Species | Nutrient-related gene | Gene ID | Response to nutrient | Downstream flowering regulator | Integrated flowering pathway | Reference |
|---|---|---|---|---|---|---|---|
| Phosphorus (P) | *Arabidopsis thaliana* | *PHO1* | At3g23430 | Induced by low P | JA; SPL3/4/5; SMZ; CO; SVP | Age; photoperiod; thermo-sensory | Dai et al. (2024) |
| | *Arabidopsis thaliana* | *miR399* | — | Induced by low P | Unknown | Thermosensory | Kim et al. (2011) |
| | *Arabidopsis thaliana* | *PHO2* | At2g33770 | Reduced by low P | Unknown | Thermosensory | Kim et al. (2011) |
| | *Arabidopsis thaliana* | *NLA* | At1g02860 | Reduced by low P | Unknown | Unknown | Kant et al. (2011) |
| | *Arabidopsis thaliana* | *PHF1* | At3g52190 | Unknown | Unknown | Unknown | Kant et al. (2011) |
| | *Arabidopsis thaliana* | *SCPL50* | At1g15000 | Induced by low P | FLC | Vernalization; autonomous | Cho et al. (2026) |
| | *Arabidopsis thaliana* | *bGLU25* | At3g03640 | Induced by low P | FLC | Vernalization; autonomous | Cho et al. (2026) |
| | *Oryza sativa* | *OsPHO1;2* | LOC_Os02g56510 | Unknown | OsHd3a; RFT1 | Unknown | Dai et al. (2024) |
| | *Oryza sativa* | *OsPHO2* | LOC_Os05g48390 | Reduced by low P | OsGI | Photoperiod | Li et al. (2017) |
| | *Oryza sativa* | *OsMYB110* | LOC_Os10g33810 | Unknown | OsMADS15 | Unknown | Jin et al. (2025) |
| | *Oryza sativa* | *OsMADS15* | LOC_Os07g01820 | Induced by high Pi | OsHd3a; RFT1 | Unknown | Jin et al. (2025) |
| Potassium (K) | *Arabidopsis thaliana* | *NaKR1* | At5g02600 | Unknown | FT; miR156-SPL3 | Photoperiod; age | Zhu et al. (2016), Negishi et al. (2018) |
| | *Arabidopsis thaliana* | *AKT2* | At4g22200 | Unknown | Sugar transport | Sugar | Deeken et al. (2002), Held et al. (2011) |
| | *Arabidopsis thaliana* | *CBL4* | At5g24270 | Unknown | Promote the activity of AKT2 | Unknown | Held et al. (2011) |
| | *Arabidopsis thaliana* | *CIPK6* | At4g30960 | Unknown | Promote the activity of AKT2 | Unknown | Held et al. (2011) |
| Sulfur (S) | *Arabidopsis thaliana* | *SULTR2;1* | At5g10180 | Repressed by low S | Unknown | Unknown | Soudthedlath et al. (2024) |
| | *Arabidopsis thaliana* | *GSH1* | At4g23100 | Unknown | FLC, FT | Vernalization; autonomous | Cheng et al. (2015) |
| Iron (Fe) | *Arabidopsis thaliana* | *bHLH38* | At3g56970 | Possibly induced by Fe deficiency | CO, FT | Photoperiod | Chen et al. (2021b) |
| | *Arabidopsis thaliana* | *bHLH100* | At2g41240 | Possibly induced by Fe deficiency | CO, FT | Photoperiod | Chen et al. (2021b) |
| | *Arabidopsis thaliana* | *bHLH101* | At5g04150 | Possibly induced by Fe deficiency | CO, FT | Photoperiod | Chen et al. (2021b) |
| Zinc (Zn) | *Arabidopsis thaliana* | *FT* | At1g65480 | Reduced by Zn deficiency | FT | Unknown | Chen and Ludewig (2018) |
| | *Arabidopsis thaliana* | *SOC1* | At2g45660 | Reduced by Zn deficiency | SOC1 | Unknown | Chen and Ludewig (2018) |
| Copper (Cu) | *Arabidopsis thaliana* | *SPL7* | At5g18830 | Unknown | SPL7 | Unknown | Yamasaki et al. (2009), Schulten et al. (2022) |

Continued

**Table 1. Continued**

| Nutrient | Species | Nutrient-related gene | Gene ID | Response to nutrient | Downstream flowering regulator | Integrated flowering pathway | Reference |
|---|---|---|---|---|---|---|---|
| | *Arabidopsis thaliana* | *miR172* | — | Reduced by Cu deficiency | AP2-like proteins, FT | Age | Rahmati Ishka and Vatamaniuk (2020) |
| | *Arabidopsis thaliana* | *ACS8* | At4g37770 | Induced by high Cu | GA | GA | Achard et al. (2007), Zhang et al. (2018a) |
| | *Oryza sativa* | *OsWRKY37* | LOC_Os04g50920 | Unknown | Unknown | Unknown | Ji et al. (2024) |
| | *Oryza sativa* | *OsCOPT6* | LOC_Os08g35490 | Unknown | Unknown | Unknown | Ji et al. (2024) |
| | *Oryza sativa* | *OsMYB67* | LOC_Os05g37060 | Induced by Cu | Unknown | Unknown | Ding et al. (2025) |

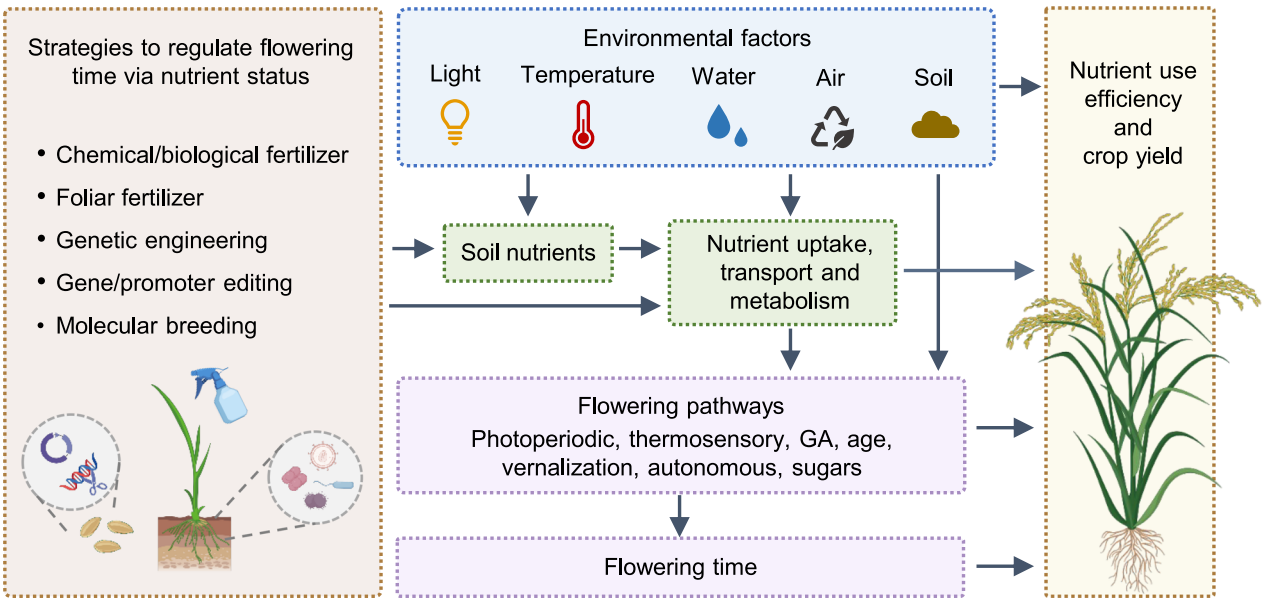


**Figure 6. Strategies to simultaneously improve flowering time, nutrient use efficiency, and crop yield by altering soil nutrient composition as well as plant nutrient uptake, transport, and metabolic processes**
The rice plant in the schematic was acquired from BioGDP (https://biogdp.com/).

phytohormone indole acetic acid, consistent with downregulation of genes that trigger flowering (Lu et al., 2018). Volatile compounds emitted by phytopathogenic microorganisms can promote plant growth and flowering by enhancing photosynthesis and increasing cytokinin and sugar accumulation (Sánchez-López et al., 2016). These findings suggest that regulating plant flowering time using biological fertilizers is a promising strategy (Figure 6).

We expect that integrating multiple technologies will lead to more environmentally friendly and cost-effective nutrient fertilizers for sustainable agricultural development. Moreover, targeting nutrient-mediated flowering regulation mechanisms through natural allelic variation analysis, molecular breeding, genetic engineering, and gene/promoter editing strategies can facilitate the development of crops with optimal flowering time and improved nutrient use efficiency (Figure 6). Currently, several genes have been identified that can coordinately regulate nutrient utilization and flowering time. For example, overexpression of *OsNRT1.1A* in rice can increase the N utilization rate, shorten the growth period, but does not affect the yield (Wang et al., 2018); overexpression of the *OsDREB1C* transcription factor in rice can improve N absorption and utilization, shorten the growth period, and increase the yield (Wei et al., 2022). Expanding our understanding of nutrient-mediated flowering regulation will yield additional target genes and strategies to improve nutrient use efficiency and crop yields, thereby promoting the development of eco-friendly agriculture.

## ACKNOWLEDGEMENTS

This study was supported by the National Natural Science Foundation of China (32372802), National Key Research and

Development Program of China (2021YFF1000400), and Jiangsu Seed Industry Revitalization Project (JBGS [2021] 011).

## CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

## AUTHOR CONTRIBUTIONS

H.Z. and G.X. conceived the manuscript. H.Z., Y.W., J.X., and S.A. wrote the manuscript. H.Z. and Y.W. prepared the figures and tables. H.Z., Y.W., S.Z., S.A., C.Q., M.L., and G.X. revised the article. All authors have read and approved the final version of the manuscript.

**Edited by:** Young Hun Song, Seoul National University, Korea

**Received** Dec. 30, 2025; **Accepted** May 6, 2026

**OO:** OnlineOpen

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article: http://onlinelibrary.wiley.com/doi/10.1111/jipb.70304/suppinfo

**Table S1.** The list of genes that regulate flowering time in Arabidopsis
**Table S2.** DEGs responsive to low N in shoots of Arabidopsis
**Table S3.** DEGs responsive to P deficiency in shoots of Arabidopsis
**Table S4.** DEGs responsive to low S in shoots of Arabidopsis
**Table S5.** DEGs responsive to low Ca conditions in shoots of Arabidopsis
**Table S6.** DEGs responsive to Mg deficiency in shoots of Arabidopsis
**Table S7.** DEGs responsive to Fe deficiency in shoots of Arabidopsis
**Table S8.** DEGs responsive to Cu deficiency in shoots of Arabidopsis
**Table S9.** DEGs responsive to Zn deficiency in shoots of Arabidopsis
**Table S10.** A total of 117 overlapped flowering genes across diverse nutrient stresses

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