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Review

Floral Regulation: The Significant Virtue of Horticultural Flowering Plants

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Abstract: Flowering is a complex developmental mechanism and is essential for successful reproduction in plants. Complex regulatory networks transform vegetative shoot apical meristems into inflorescence meristems. Further, floral meristems transition to floral bud outgrowth and flowering. Floral regulatory pathways are independently involved in flowering, and most of what we know about genetic regulation comes from model plants. Despite the advancements in plant development biology, the understanding of molecular mechanisms and floral signals in horticultural plants is complex. Studies on gene regulatory mechanisms provide a global view of flowering in horticultural plants. In this paper, we discuss the flowering pathways converging on complex gene regulatory mechanisms and summarize the recent findings in horticultural plants in order to help us understand how they regulate flowering and provide an update for future research.

Keywords: *Arabidopsis thaliana*; bud; citrus; floral meristem identity; *FLOWERING LOCUS T*; gene regulation; grapevine; tomato

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1. Introduction

Floral induction is a crucial switch in the plant life cycle that results in the production of seeds for successive generations. Floral induction involves the transcriptional regulation of several genes and their regulatory pathways, including numerous environmental cues that transform vegetative meristems into inflorescence meristems, which leads to floral meristem identity, floral bud outgrowth, and flowering [1–3]. In model plants such as *Arabidopsis thaliana*, flowering is triggered by molecular regulatory pathways, including vernalization, age-dependent, autonomous, and photoperiod pathways (Figure 1) [4]. Morphological flowering signs are qualitative and visible only after the complex signals have already induced flowering. This is also because direct measurements of the internal developmental state of plants during floral induction are lacking [5]. Considerable advances have been made in understanding the molecular genetic mechanisms that result in reproductive phase transition [6].

This progress in flowering-related genes has been precisely studied in model plants such as *Arabidopsis* and rice (*Oryza sativa*). One of the prime reasons for this is that large amounts of genetic and genomic resources are required to identify the regulatory mechanisms. As the number of identified genes in model plants has increased, molecular biology techniques, including genetic transformation, in vitro regeneration, and gene expression patterns, have enabled the knowledge of these genes to be applied to other plants, especially perennial plants growing in the natural environment; these genes are linked to flowering regulatory pathways [7,8]. These regulatory pathways consist of *FLOWERING LOCUS T* (*FT*), *FLOWERING LOCUS C* (*FLC*), *SUPPRESSOR OF OVEREXPRESSION OF CONSTANS 1* (*SOC1*), *CONSTANS* (*CO*), *LEAFY* (*LFY*), *AGAMOUS-LIKE20* (*AGL20*), *APETALA1* (*AP1*), and *WUSCHEL-related homeobox* (*WUS*) genes [7,9–12]. Other floral regulators, such as *SUPPRESSOR OF OVEREXPRESSION OF CONSTANS 1-like*, *FLOWERING LOCUS T* (*FT*)*-like*, and *FRIGIDA* (*FD*)-like genes, as well as upregulation, also trigger flowering [13–15]. The orthologs of *Arabidopsis*, such as *FT*, *SOCI*, *LFY*, *TERMINAL FLOWER1* (*TFL1*), and *MADS*-box, have been identified in *Citrus* (*Citrus sinensis*, *Poncirus trifoliata*, and *Fortunella hindsii*) [16–18], apple (*Malus domestica* Borkh.) [19], longan (*Dimocarpus longan* Lour.) [20], avocado (*Persea americana* Mill.) [21], kiwifruit vine (*Actinidia deliciosa*) [22], pomegranate (*Punica granatum* L.) [23], loquat (*Eriobotrya japonica*) [24], and tomato (*Solanum lycopersicum* L.) [25].

The FT protein is the most famous florigen (a systemic signal that promotes flowering); it is synthesized in the leaf vasculature and moves through the phloem to the shoot apical meristem [26,27]. In *Citrus* species, *FT* (*CiFT*, *CsFT*, *PtFT*, *ToFT*, *CiFT*, *CiFT2*, and *CiFT3*) has been found to functionally characterize and promote early flowering [28–33]. Carrizo citrange (*Citrus triptera x Citrus sinensis*) *CcFT1*, *CcFT2*, and *CcFT3* genes overexpression induced non-inductive flowering in transgenic *Carrizo* rootstocks and grafted juvenile scions [32]. Grapevine (*Vitis vinifera* L.) *VvFT* overexpression in *Arabidopsis* promotes early flowering [34]. Apple *MdFT1* overexpression induced early flowering in annual and perennial plants [19]. The transcript abundance of *FT* is increased by the transcriptional activator, the CO protein, which strongly influences floral regulation [35]. In tomatoes, six *FT-like* genes, namely, *SlSP3D*, *SlSP6A*, *SlSP5G*, *SlSP5G1*, *SlSP5G2*, and *SlSP5G3*, have been identified [25]. Mango (*Mangifera indica*) *MiTFL1-1*, *MiTFL1-2*, *MiTFL1-3*, and *MiTFL1-4* overexpression in *Arabidopsis* repressed flowering [36]. *MdTFL1-1* gene virus-induced gene silencing promotes early flowering in apple [37]. Overexpression and CRISPR/Cas9 base editing of *CiMADS43* induce leaf curling and early flowering in lemon (*Citrus limon*) [38]. In sweet cherry (*Prunus avium*), *PavMADS1*, and *PavMADS2*, RNAi-based silencing enhances *FT* expression during dormancy [39]. Overexpression of the silver birch (*Betula pendula*) *BpMADS4* gene in apple induced early flowering [40]. *SOCI-like* genes, *AcSOC1e*, *AcSOC1f*, and *AcSOC1i* overexpression promote flowering in kiwifruit vines [41]. *Arabidopsis LFY* (*AtLFY*), a floral meristem identity gene, has been reported to be the first transgene to accelerate flowering in perennial plants [42]. The *AtLFY* ortholog has also been reported in grapevine *VFL* [43]. *VFL* is highly expressed in the floral meristem that develops the following spring. This expression pattern indicates the significance of *VFL* in floral meristem initiation and organization, similar to other *LFY-like* genes in different species [44]. *MdLFY* overexpression in apple increases shoot diameter [45].

Other floral meristem identity genes, such as *API* and *FRUITFUL* [23], have also been characterized and named in grapevine *VAP1* and *VFUL-L*. *VFUL-L* and *VAPI* are expressed in the very early stages of uncommitted lateral meristems, and their expression is sustained in other initiative organs, such as inflorescences or tendrils [46,47]. In tomatoes, *FALSIFLORA* (*FA*) encodes a similar protein to *AtLFY*. A mutation in *FA* causes a delay in flowering. Further, *fa* mutants replace flowering with leaves and inflorescence with a similar phenotype to *lfy Arabidopsis* [48]. *FUL-like* genes regulate inflorescence development and flowering in tomatoes [49].

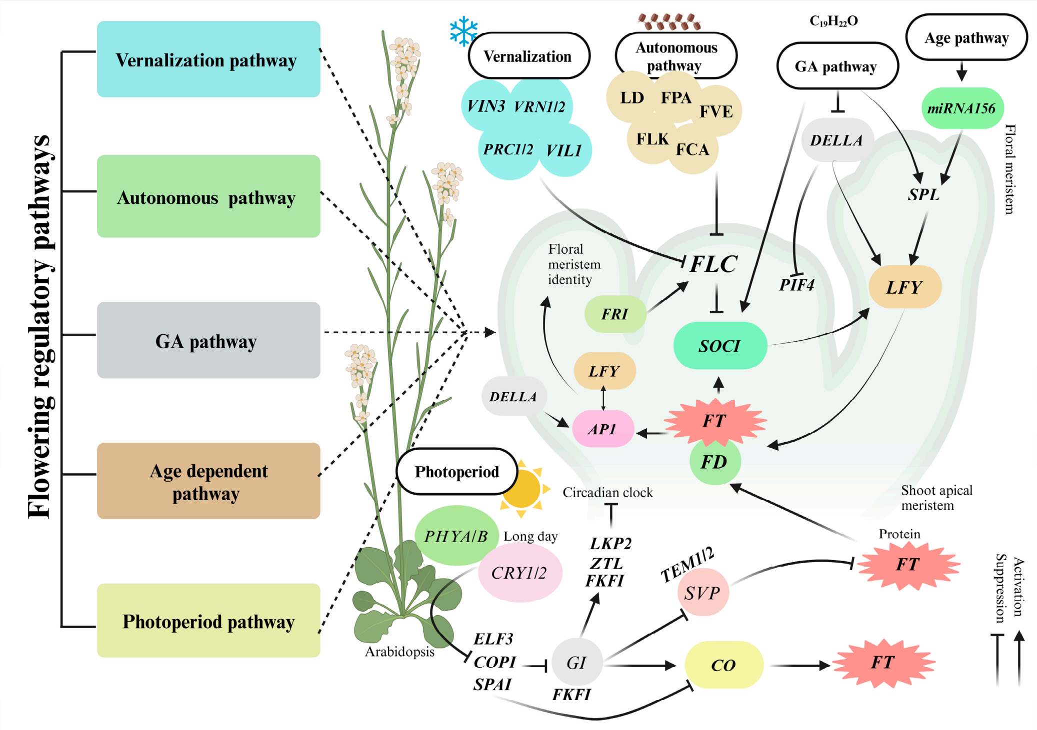

Figure 1. Schematic representation of *Arabidopsis* flowering regulatory pathways [26,50–57], including floral regulators and suppressors. The black solid arrows indicate gene regulation, and the black straight lines indicate gene suppression.

The mechanism by which the meristem terminates involves the interaction between the meristem identity gene and the machinery that maintains the undifferentiation of the meristem, represented by the *CLAVATA* (*CLV*) and *WUS* pathway [58]. *C. sinensis CsWUS* overexpression in tobacco plays a role in floral organ development [12]. In contrast, virus-induced gene silencing causes thorn development in lemon [12]. A mutation in *COMPOUND INFLORESCENCE*, a homolog of *WOX9* (*S*); the F-box gene, a homolog of *UNUSUAL FLORAL ORGAN*, *UFO* (*AN*); and its partner *FALSIFLORA*, a homolog of *LFY* (*FA*), play an essential role in inflorescence determination in tomato [59]. The tomato *MADS-box* gene *JOINTLESS* (*J*) is involved in flower development and pedicel differentiation, whereas *jointless* mutants affect the inflorescence meristem [60]. Additionally, *the TOMATO MADS-box 8* gene (*TM8*) is highly expressed in tomato reproductive organs and plays an essential role in flower development [61]. The *TOMATO MADS*-Box 6 (*TM6*) gene acts as a transcriptional regulator during floral development [62]. A loss of function of the *TOMATO AP3* (*TAP3*) gene results in the homeotic development of stamens and petals. *TM6* and *AP3* play significant roles in flower development in tomato (Figure 2) [63]. Grapevine *VvMADS9* (*VvPI*), *VvAP3*, and *VvTM6* have been identified. *VvMADS9* shows a low-expression pattern in the latent bud, and *VvTM6* is vastly expressed in reproductive organs [34].

Over the past three decades, molecular and genetic analyses have led to the identification of various genes and transcription factors (TFs) and provided insights into how they control floral development and floral meristem identity in plants. In this review, we highlight the current knowledge of floral regulation and the mechanisms of floral regulatory pathways.

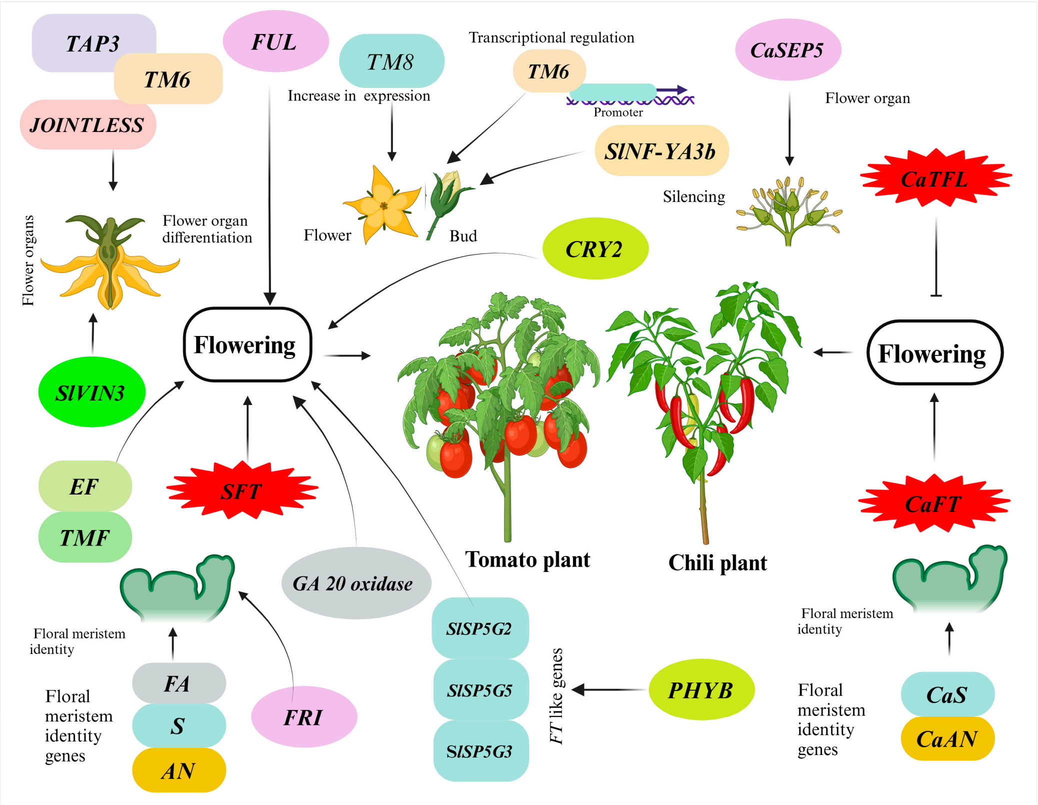

Figure 2. Overview of floral regulation and development in tomato plant (*Solanum lycopersicum*) [25,48,59–66] and chili plant (*Capsicum annuum*) [67–69]. The black solid arrows indicate gene regulation, and the black straight lines indicate gene suppression.

2. The Vernalization Pathway: Low-Temperature-Induced Flowering

Plants tend to flower when exposed to changing climatic conditions [70]. A period of chilling or cold exposure from −1 °C to 10 °C activates the vernalization pathway. Chilling acts as an external factor for shoot apical meristem dormancy release and promotes floral transition in plants [71,72]. *FT* movement via the phloem to the shoot apex is affected at low temperatures, and plants exhibit late flowering [73]. However, in many horticultural plants, such as orange (*C. sinensis*), olive (*Olea europaea* L.), litchi (*Litchi chinensis* Sonn.), mango, and apple, flowering can be induced by exposure to cold or chilling [74–76]. Low temperatures also influence the timing of bud bursts and flowering in grapevines [77].

The flowering response to low temperatures has also been reported in Satsuma mandarin (*Citrus unshiu* Mar.) [78]. The overexpression of *Citrus CiFT* induces early flowering in pear (*Pyrus communis*) [79]. Vernalization works by inhibiting the expression of *FLC*, a robust floral repressor of flowering encoded by the MADS-box protein in the shoot apical meristem [80]. The *SEPALLATA-like MADS-Box* gene (*CaSEP5*) is highly expressed in flower organs in peppers (*C. annuum*). *CaSEP5* silencing results in leaf-like sepals and rigid, straight pedicels (Figure 2) [67]. *FD* acts as a floral repressor by stimulating the expression of *FLC*. However, it acts as an inhibitor in the independent pathway [80]. Cold exposure degrades the FRI protein and downregulates *FLC* [81]. Furthermore, *FLC* suppresses the expression of *SOC1* and inhibits the upregulation of *FD* in the shoot apical meristem [57]. *FLC* binds to the promoter of *SOC1* and *SQUAMOSA PROMOTER BINDING-LIKE 15* (*SPL15*) and suppresses their expression. Floral transition in mango occurs during late autumn and early winter. Mango floral induction requires a higher temperature (10 °C to 15 °C) than vernalization [82,83]. However, *M. indica cv.* Dashehari promotes flowering under leaf-bearing conditions during vernalization. The expression patterns of the *FRI*, *SUPPRESSOR OF FRIGIDA 4* (*SUF4*), and *FLC EXPRESSOR* (*FLX*) genes are upregulated in bearing mango leaves.

Other floral regulators such as *AG*, *FUL*, *FPA*, *FCA*, and *FLD* are also upregulated in bearing mango leaves [84]. The *MdFLC3-like* gene was functionally characterized to understand how chilling mediates flowering in apples. *MdTFL1* overexpression delays flowering in *Arabidopsis* and maintains the juvenile phase in apple [85]. *PcTFL1* RNAi-based silencing induces early flowering in transgenic pears [86]. In *Citrus*, *FLC* homolog (*PtFLC*) overexpression delays flowering in *Arabidopsis* [87]. Cold treatment upregulates *CiFT* and *CiLFY* expression before flower development in Satsuma mandarin buds and leaves [16,88]. Similarly, *CsFT*, *CsLFY*, and *CsAP1* are upregulated in the leaves, floral meristem, and buds of sweet orange under cold treatment (Figure 3) [88,89]. In *Citrus*, *Nuclear Factor YA* (*CiNF-YA*) activates *CiFT* expression under low temperatures and drought conditions by binding to the *CiFT* promoter. Further, CiFT forms a complex with GOLDEN2−LIKE protein (CiFE) and stimulates *CiLFY* to promote flowering [90]. The *Arabidopsis HD-ZIP* (*AtHB13*) homolog *PtHB13* binds to the *PtFLC* promoter and regulates its expression during citrus floral induction. Low temperatures affect the ectopic expression patterns of *PtFLC* and *PtHB13* and regulate floral induction (Figure 3). In contrast, the overexpression of *PtFLC* and *PtHB13* inhibits flowering in *Arabidopsis* [87]. *VIN3* expression positively increases in bearing mango leaves and flowers [82].

The *FT* ortholog in tomato *SFT* plays a vital role in the primary shoot flowering time and flower morphology [65]. In tomatoes, *Nuclear Factor YA3b* (*SlNF-YA3b*) plays an essential role in floral regulation. The knockout of *SlNF-YA3b* results in an early flowering phenotype, whereas the overexpression of *SlNF-YA3b* delays flowering in tomato plants. Further study indicates that *NF-YA3b* binds to the CCAAT motif of the *SFT* promoter and represses its expression [91]. In tomatoes, the *SlVIN3* gene protein is closely related to the *VvVIN3* gene. The *SlVIN3* gene shows high expression during floral organ differentiation and low expression during fruit development [66]. The *Capsicum annuum FT/TFL* orthologs *CaFT* and *CaTFL1* show conserved functioning in floral regulation and plant development (Figure 2) [68].

The genes involved in the vernalization pathway also act on the florigen marker *FT*, inducing downregulation via *FLC* but upregulation via *VRN1*. *TFL1* represses *FT* activity, which maintains an indeterminate meristem [92]. *TFL1* represses the floral meristem identity genes (*LFY* and *AP1*) and is expressed only on the edges of meristem-developing primordia [93]. During the early stages of inflorescence development, latent buds exhibit a high expression of *VvFT/TFL1*. Still, this expression pattern is not displayed during flower development in the following season in grapevines [94]. The overexpression of *VvTFL1*, named *VvTFL1A* in *Arabidopsis*, causes delays in flowering time and the initiation of the floral meristem, and it yields a phenotype of complex inflorescence with multiple co-inflorescences [55,94]. In tomatoes, *TERMINATING FLOWER* (*TMF*) mutants cause early flowering and replace multi-flower inflorescence with a single flower. *ANANTHA* (*AN*) and *FALSIFLORA* (*FA*) encode the flowering specification complex and promote early flowering [64]. Tomato *TMF* synchronizes flower development with a slow reproductive phase transition [64]. However, *SINGLE FLOWER TRUSS* (*SFT*) regulates floral meristem identity during floral development [95]. In peppers, the *fa* mutant causes a reduction in flowering time, whereas *CaAN* is essential for floral meristem differentiation, and *CaS* is involved in an earlier stage of the transition to floral meristem differentiation [69].

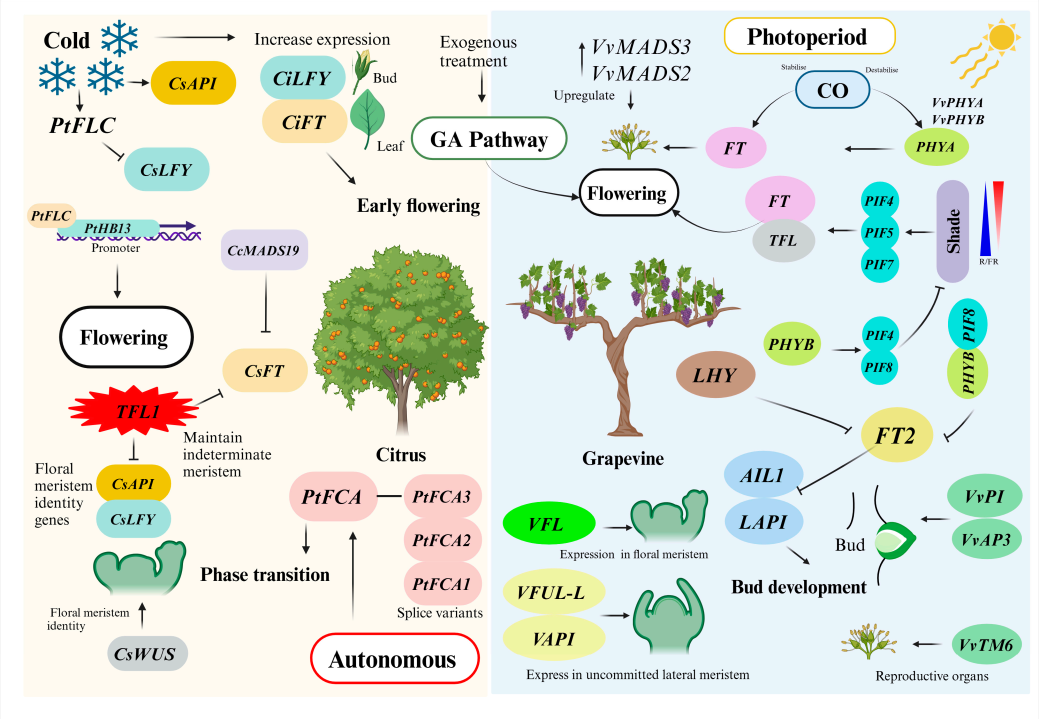

Figure 3. The flowering regulatory pathways in horticultural perennials (*Citrus*, grapevine). In *Citrus*, *PtHB13* binds to the *PtFLC* promoter and induces early flowering [87]. A low temperature or cold enhances the expression of *CiLFY* and *CiFT* in leaves/buds and promotes early flowering [16,88]. In contrast, *PtFLC* represses the expression of *CsLFY*, *CsFT*, and *CsAP1* [88,89]. The citrus *CsWUS* gene is involved in meristem maintenance [11]. *TFL1* represses *FT* activity, which maintains an indeterminate meristem [92]. *TFL1* represses the floral meristem identity (*LFY* and *AP1*) genes [93]. The black solid arrows indicate gene regulation, and the black straight lines indicate gene suppression. The induction of *CcMADS19* (*FLC* ortholog) represses the *Citrus FT* ortholog [96]. In grapevine, *VFL* is highly expressed in the floral meristem and involved in floral meristem initiation [44]. *VAP1* and *VFUL-L are* expressed in the uncommitted lateral meristem [46,47]. Short-day (SD) conditions negatively regulate *VvFT* and *PHYTOCHROME A* (*VvPHY A*) and positively control *VvPHY B* in buds [97]. *VvFT* regulates floral induction in latent buds with the development of inflorescence, flowers, and fruits [94]. SD conditions negatively control *VvFT* and *VvPHY A* and positively control *VvPHY B* in grapevine buds [98]. *PIF4*, *PIF5*, and *PIF7* stimulate shade (low R–FR ratio)-induced flowering through *FT* [99,100]. The *PHY B* gene negatively regulates the SAS through PIF genes; PIF4 and PIF8 act downstream of *PHY B*. Under SD conditions, the *PHY B-PIF8* module inhibits growth by repressing the expression of the *FT2* gene [97]. The *PHY B/PIF8* module mediates SD-induced growth cessation [97]. *VvMADS8* shows a high-expression pattern during the early stage of inflorescence development [101]. *VvMADS3* is involved in vegetative organs and flower development [102,103]. The black solid arrows indicate gene regulation, and the black straight lines indicate gene suppression.

3. Autonomous Pathway of Flower Induction

Vernalization and autonomous pathways act opposite to each other (Figure 3). The autonomous pathway induces flowering independently under day-length conditions by repressing the central floral repressor and vernalization regulatory gene *FLC* [104–106]. *FLC* inhibits the expression of flowering-related genes, such as *FT*, *SOC1*, *AGL20*, *LFY*, *AG*, and *APL3*, and it delays floral transition [9,107,108]. *FLOWERING LOCUS K* (*FLK*), *FY*, *FLOWERING LOCUS VE* (*FVE*), *LUMINIDEPENDENS* (*LD*), *FCA*, and *FLOWERING LOCUS D* (*FLD*) are redundant genes that ensure the developmental turning of flowering by inhibiting *FLC* [55,109]. Mutations inserted in *FLC* did not promote plant flowering [110]. Meanwhile, mutations in autonomous pathways related to *FCA*, *LD*, *FVE*, *FLD*, *FLK*, and

FY prolonged floral induction under LD and SD conditions. In contrast, vernalization treatment recovered the phenotype [105].

In star fruit (*Averrhoa carambola* L.), *FCA* and *FVE* suppress *SVP*. However, they promote *FT* and *FD* expression under low temperatures and regulate flowering [111]. Several previous studies have demonstrated that the *EARLY IN SHORT DAYS 4* (*ESD4*), *Developmentally Retarded Mutant1* (*DRM1*), *Casein kinase II* (*CK2*), *RELATIVE OF EARLY FLOWERING 6* (*REF6*), *ARABIDOPSIS THALIANA SYNTAXIN OF PLANTS 22* (*SYP22*), *PCF11P-SIMILAR PROTEIN 4* (*PCFS4*), *AGL28*, *DNA-binding protein phosphatase* gene 1 (*DBP1*), *HISTONE DEACETYLASE 5* (*HDA5*), and *HISTONE DEACETYLASE 6* (*HDA6*) genes are also involved in autonomous flowering regulatory pathways [50]. In tomatoes, autonomous pathway-related genes, such as FRI-like protein 3, show a high-expression pattern at the initial stage of flower bud differentiation and then during flower development. Thus, *FRI* may be involved in meristem development at the initial stage of flowering and may act downstream of the gene to inhibit early flowering [112].

4. Light-Dependent Pathway/Photoperiod Pathway of Flower Induction

Photoperiod is a crucial external factor in the vegetative-to-reproductive phase transition. Photoperiod is sensed through the leaves in long-day (LD) and short-day (SD) plants. The role of light intensity in inflorescence formation has been studied in vineyards regarding the hours of sunshine [113] or shading treatment [114]. Applying high light intensities under controlled environmental conditions affects the development of inflorescence primordia depending on the conditions that depend on the photoperiod [115]. In grapevines, floral initiation and floral development are delayed by SD conditions. Previous studies have reported that growth cessation may be SD obligate and SD facultative depending on the genotype in the grapevine [116]. Flowering-related genes such as *FT*, *G1*, *FD*, *AP1*, *CRY2* (*CRYPTOCHROME2/FHA*), *ELF3* (*EARLYFLOWERING3*), and *CO* play a central role in the photoperiod pathway [117–119]. The flowering time regulators *FD* and *FT* control photoperiodic seasonal growth. For example, the *FD-like 1* (*FDL1*)/*FT2* complex controls the downstream target *LAP1* and regulates photoperiodic growth. *FLD1* triggers SD-induced transcriptional regulations in these two pathways' adaptive responses and bud maturation [120]. *ELONGATED HYPOCOTYL 5* (*HY5*), *ATHB7*, and *PRR7* are expressed in grapevine buds under different photoperiod treatments and in floral meristem development, suggesting a vital role in floral and dormancy induction [121]. Grapevine *VvFT* is involved in floral induction in latent buds with the development of inflorescence, flowers, and fruits [34,94]. SD conditions negatively control *VvFT* and *PHYTOCHROME A* (*VvPHY A*) and positively control *VvPHY B* in grapevine buds [98]. *PHYTOCHROME B* (*PHY B*) acts as a thermal and light sensor. *PHY B* (*PHY B1*, *PHY B2*, and *PHY B3*) genes act as suppressors of shoot elongation, and their downstream targets, *PHYTOCHROME INTERACTING FACTOR* (*PIF*) genes (*PIF4* and *PIF8*), are involved in shade avoidance syndrome, and *PIF8* plays a central role in the inhibition of seasonal growth in plants [97]. In *V. vinifera. cv*. Thompson seedless, photoperiod drives the transition of buds into endodormancy. It modifies the expression of the *VvPHY A* and *VvPHY B* transcripts in grapevine leaves [122]. *PIF4*, *PIF5*, and *PIF7* stimulate shade (low R–FR ratio)-induced flowering through a positive expression of *FT* and *TWIN SISTER OF FT* (*TSF*) [99,100]. The *PHY B* gene negatively regulates the SAS through PIF genes; PIF4 and PIF8 act downstream of *PHY B*. Under SD conditions, *PHY B* acts as a negative regulator of growth cessation, and the *PHY B-PIF8* module inhibits growth by repressing the expression of the *FT2* gene [97]. The *PHY B/PIF8* module mediates SD-induced growth cessation in autumn and temperature-regulated bud break in spring [97].

Photoreceptors (*CRY1* and *CRY2*) and *PHY A* act antagonistically to *PHY B* in order to stabilize the CO protein and trigger it to upregulate *FT* [123]. *FT* and *FWA* act downstream of *CO* and other pathways, whereas *GI* and *CRY2* act upstream [124]. *CRY2* interacts with the *CIB1* TF in response to blue light in order to stimulate the transcription of *FT*, whereas *CIB3* interacts with *CIB1*, acts synergistically with CIB1, and promotes *GI* transcription [125]. In tomatoes, *CRY2* is significantly involved in flowering time. The *PHYB* gene regulates the expression patterns of the *FT-like* genes *SlSP5G2*, *SlSP5G3*, and *SlSP5G5* and regulates flowering [126]. Further, the FT-like gene *SlSPD3* encodes mobile florigen signals and promotes flowering [95].

Clock resetting genes such as *FLAVIN-BINDING*, *KELCH REPEAT*, *F-BOX1* (*FKF1*), *CONSTITUTIVEPHOTOMORPHOGENIC1* (*COP1*), *KELCHPROTEIN2* (*LKP2*), and *ZEITLUPE* (*ZTL*) play essential roles in the photoperiod pathway. *FKF1* is involved in CO protein stabilization and directly binds to CO via the LOV domain, which triggers CO accumulation [127]. Recent studies have revealed that *CRY1* stabilizes the DELLA protein through direct interactions, whereas FKF1 degrades the DELLA protein to control diurnal changes in DELLA protein stability through ubiquitination [128]. DELLA also participates in several repressor actions. For example, *MYC3* not only binds to the *FT* promoter but also inhibits the DNA-binding activity of CO through interactions with DELLA proteins [129]. Moreover, DELLA protein expression levels become low during the night because of GA-dependent degradation [130]. *ZTL* and genes also act as blue light receptors that interact with *G1* and regulate flowering [56,131,132]. These results indicate the crucial role of photoperiod and light in floral regulation. In tomatoes, *EF* (*EARLY FLOWERING*) is involved in early floral induction, and *ef* mutants cause early flowering. The EF-dominant gain-of-function allele elevates the *SlFAF1/2c* transcript. The overexpression of *SlFAF1/2c* also shows a similar phenotype of early flowering to *ef* mutants. Moreover, FAF1/2c interacts with CONSTITUTIVEPHOTOMORPHOGENIC9 (COP9) and reduces its protein stability and accumulation [133].

5. Gibberellic Acid Pathway: Hormonal Control of Flowering

The gibberellin (GA) pathway is actively involved in floral transition in plants because the endogenous GA level acts as an inhibitor in floral meristem development under SD conditions [134]. The GA pathway also participates in floral transition under LD conditions [135]. However, GA-deficient *ga1-3* mutants promote timely flowering under LD and cause delayed flowering in SD [136]. *FT* and GA express seasonal cues to the shoot apical meristem. GA acts downstream of *FT* in seasonal growth regulation and control [137]. The antagonistic factors *TFL1* and *LAP1* of *FT* act as promoters or repressors of seasonal growth [137]. GA_3 and 1-amino cyclopropane carboxylic acid [138] treatment delays flowering in *Citrus* [139]. Before floral induction, the level of bioactive GAs increases in the shoot apex via the activation of *GA2oox1*, encoding the GA biosynthetic enzyme GA20 oxidase, which promotes the expression of the floral integrators *LFY* and *SOC1*. Under SD conditions, GA_4 is produced in leaves, transported to the meristem, upregulates *LFY* and *SOC1*, and induces flowering [140]. GA acts as a floral repressor in apples without disturbing shoot elongation—the exogenous treatment of GA results in the downregulation of GA biosynthesis. The GA transporter, GA receptor, and GA catabolic *GA oxidase*-related genes depend on GA feedback and feedforward regulation. Moreover, *TFL1*-like genes induce a swift response to GA, while the upregulation of *MdTFL1* inhibits flowering in apples [141]. *GA 20 oxidase* genes also play a significant role in flower development in tomatoes [142].

In *Arabidopsis* GA receptors, *GIBBERELLIN INSENSITIVE DWARF1* (*GID1*) plays a positive role in GA signaling [143]. GID (Cs3g13110, Cs8g05670, and Cs5g32180) and

DELLA proteins (Cs6g09040 and Cs6g17530) show differential expression patterns during citrus-induced floral induction in sweet orange [1]. GA binds to GID1, which then binds to DELLA in order to form a unique GA-GID1-DELLA complex. DELLA is then recruited to the SCF$^{SLY1/GID2}$ E3 ubiquitin ligase for polyubiquitination and subsequent degradation by 26 proteosomes. This results in the plant exhibiting a GA response [144]. DELLA proteins are negative regulators in the GA signaling pathway [145,146]. DELLAs are abruptly degraded in the presence of GA [147]. *DELLA* mutants in *Arabidopsis* flower early under SD conditions. To date, five DELLA proteins have been identified in *Arabidopsis*, including *GIBBERELLIN INSENSITIVE* (*GAI*), *REPRESSOR OF GA1-3*, and *RGA-LIKE 1* (*RGL1*) [148,149].

A previous study demonstrated that the *DELLA-interacting factor GAI-ASSOCIATED FACTOR1* (*GAF1*) explained the role of *DELLA* as a transcriptional co-activator [150]. *GAF1* also interacts with the co-repressor *TOPLESS-RELATED* (*TPR*), whereas *DELLA* and *TPR* are co-repressors and co-activators of GAF1. GAs alter the *GAF1* complex from a transcriptional activator to a repressor and promote the expression of *FT* and *SOC1* [145]. The *GAFI* TF contains a zinc finger motif and belongs to *INDETERMINATE1* (*ID1*). In *Arabidopsis*, *IDD* members are closely related to *DELLA. Arabidopsis gaf1* and *idd1* mutants show a late-flowering phenotype compared to the wild type under SD conditions [150]. The *PpIDD* family has been identified in peach. The *PpIDD* family members *PpIDD4*, *PpIDD12*, and *PpDD13* interact with *PpDELLA1* proteins. This interaction activates *PpGA20ox1* promoter transcription. This transcriptional regulation indicates that *PpIDD-PpDELLA1* is involved in GA-mediated feedback regulation in peaches [151].

6. Conclusions and Perspectives

Reproductive phase transition is a critical adaptive developmental switch in plants. In-depth studies of the floral regulators or repressors will help to understand the conditions of horticultural plants' adaptability in the near future. Various studies suggest that a plant's genetic mechanism for flowering is highly conserved. Floral promoters or repressors, for example, the *FT/TFL* family and encoding proteins such as the phosphatidyl ethanolamine binding protein (PEBP), are the most promising factors for providing deep insights into floral regulation. Floral regulators and repressors are intensely studied in many horticultural plants. Biotechnology provides a significant approach to genetic improvement and speeds up efficient breeding in plants. The advancement in genetic transformation and gene editing in kumquat (*Fortunella hindsii*) resulted in short juvenility, with the process from explant to T_1 mutant taking 15 months [18]. The *PDS* gene was recently successfully edited in *F. hindsii*, with five months needed for regeneration from seed to T_0 plantlets and then ten months needed to obtain the T1 generation [18]. *F. hindsii* could be used as a model plant to understand the vegetative-to-reproductive phase transition in other citrus species.

In plants, virus-induced gene silencing is widely used to suppress the expression of endogenous genes [152]. For example, a virus-induced gene silencing vector based on TRV (tobacco rattle virus) was successfully used to silence the *CsWUS* gene in lemon [12]. This vector carries the *CsWUS* gene from *C. sinensis*, and it causes thorn development in gene-silenced plants [12]. A viral vector based on citrus leaf blotch virus (CLBV) carrying the *FT* gene predicted flowering in young citrus plants at four months post-infection, depending on the season and genotype [153,154]. Many researchers have also used the apple latent spherical virus vector ALSV for gene silencing. The inoculation of ALSV shortened the juvenile phase and induced early flowering in pears, apples, and grapevines [155,156]. RNA inference (RNAi) technology is extensively used to knock out gene function in order to promote early flowering in horticultural plants.

The RNAi-based knockdown of *TFL1* reduced the juvenile phase and induced early flowering in apple and pear trees [86,157]. However, expansion in floral development in transgenic perennial plants led to reduced vegetative growth, which reduced fruit and seed production in plants. Early-induced flowers require pollination via native pollinators (honey bees). In Longan, the early induction of flowering decreased fruit yield due to the absence of native pollinators [158]. Transgenic plants are often malformed, and fruit settings are shallow [40]. However, CRISPR/Cas9 has become a prominent and efficient biotechnology for genome editing in many plant species, and it has had various success stories in the past few years [159]. CRISPR/Cas system-based genome editing can also address the early floral induction of male sterility in vines such as the kiwi vine [160]. A CRISPR/Cas9-based mutant construction of *faf1/2b*, *faf3/4a*, and trfaf3/4b induced early flowering in tomato [161]. To sum up, determining the network regulation of flowering will help us understand how horticultural plants perceive developmental signals, regulate molecular mechanisms, and then accelerate flowering, ultimately boosting commercial production.

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