Functional diversification and molecular mechanisms of **FLOWERING LOCUS T/TERMINAL FLOWER 1** family genes in horticultural plants

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**Abstract**

Flowering is an important process in higher plants and is regulated by a variety of factors, including light, temperature, and phytohormones. Flowering restriction has a considerable impact on the commodity value and production cost of many horticultural crops. In *Arabidopsis*, the **FT/TFL1** gene family has been shown to integrate signals from various flowering pathways and to play a key role in the transition from flower production to seed development. Studies in several plant species of the **FT/TFL1** gene family have revealed it harbors functional diversity in the regulation of flowering. Here, we review the functional evolution of the **FT/TFL1** gene family in horticulture plants and its unique regulatory mechanisms; in addition, the **FT/TFL1** family of genes as an important potential breeding target is explored.

**Keywords:** FLOWERING LOCUS T (FT), TERMINAL FLOWER 1 (TFL1), Flowering, Functional evolution, Horticultural plant

**Introduction**

Flowering is an important stage in the life history of higher plants that includes the processes of flower bud differentiation, development, and the opening of flowers (Parmar et al. 2017; Xu et al. 2019). An optimal flowering is of great significance for plants to complete their life cycle under suitable environmental conditions (Su et al. 2019). Horticultural plants are critical components of agricultural production; they include fruits, flowers, vegetables, spices, medicinal, and aromatic plants (Karikwe et al. 2017). Understanding how environmental factors influence the flowering transition of horticultural plants, as well as the underlying mechanisms involved, can help to improve the commercial value, lower production costs, and augment the annual production and seasonal supply of horticultural products (Higuchi 2018; Matsoukas et al. 2012).

Flowering time in the model plant *Arabidopsis* is regulated by integrating vernalization, temperature, photoperiod, hormones, age, autonomic pathways, and other floral transition signal transduction pathways (Srikanth and Schmid 2011; Cho et al. 2017). In 1936, M.K. Chailakhyan observed a type of flowering stimulator in *Chrysanthemum* that is produced in its leaves and transported to the shoot apex meristem (SAM) after photoperiod induction; it was designated ‘florigen’ (Chailakhyan and Krikorian 1975). This flowering element was later identified in *Arabidopsis* as a product of the **FLOWERING LOCUS T** (FT) gene (Kardailsky et al. 1999; Tsuji and Taoka 2014; Tsuji 2017). In *Arabidopsis*, TERMINAL FLOWER 1 (TFL1) of the FT/TFL1 family of proteins has been identified as a local floral inhibitor expressed in the SAM (Shannon and Meeks-Wagner 1991; Bradley et al. 1997). FT/TFL1 encodes a pair of flowering regulators that are homologous to phosphatidylethanolamine-binding proteins (PEBPs) (Ahn et al. 2006; Karlgren et al. 2011).

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PEBP gene family in *Arabidopsis* includes six members: FT (Kim et al. 2013; Xu et al. 2012), TWIN SISTER OF FT (TSF) (Yamaguchi et al. 2005; Michaels et al. 2005; D’Aloia et al. 2011; Song et al. 2015), and MOTHER OF FT AND TFL1 (MFT) (Xi et al. 2010; Yoo et al. 2004) all promote flowering, whereas TFL1 (Kim et al. 2013), *Arabidopsis Thaliana CENTRORADIALIS HOMOLOG* (ATC) (Yoo et al. 2010; Huang et al. 2012) and BROTHER OF FT AND TFL1 (BFT) (Yoo et al. 2010) have function that differ from flowering.

FT protein was induced in *Arabidopsis* leaf vascular tissue phloem companion cells and transferred to the SAM by interacting with FT-INTERACTING PROTEIN 1 (FTIP1), QUIRKY (QKY), and SYNTAXIN OF PLANTS121 (SYP121) (Mathieu et al. 2007; Liu et al. 2012; Putterill and Varkonyi-Gasic 2016; Liu et al. 2019). Long-distance transmission of the FT protein is blocked by its interaction with negatively-charged phosphatidylglycerol (PG) at low temperatures (Liu et al. 2020; Susila et al. 2021). After being transported to the SAM, the FT protein forms a complex with the bZIP transcription factor FD and induces the expression of the floral meristem-identity genes *APETALA1* (*AP1*) and *FRUIT-FULL* (*FUL*) (Abe et al. 2005; Wellmer and Riechmann 2010; Taoka et al. 2013). The interaction of environmental, endogenous, and hormonal signals precisely regulates the spatiotemporal expression of the FT gene in leaf phloem companion cells and the flowering in *Arabidopsis* (Fig. 1A). CONSTANS (CO) reflects the correspondence between external light signals and endogenous biological
circadian clock, to activate the expression of FT at the right time to induce flowering (Imaizumi and Kay 2006; Song et al. 2015; Goralogia et al. 2017). Moreover, CYCLING DOF FACTORS (CDFs) directly bind to the proximal Block A region of the FT promoter to inhibit the transcription of FT (Imaizumi et al. 2005; Goralogia et al. 2017). Genes related to the circadian clock, temperature, and blue-light signals, such as GIGANTEA (GI) (Sawa and Kay 2011), BR ENHANCED Production 1 (BEE1) (Wang et al. 2019), PHYTOCHROME INTERACTING FACTOR 4 (PIF4) (Kumar et al. 2012), and CIB (cryptochrome-interacting basic-helix-loop-helix) (Liu et al. 2008), bind upstream from the transcription start site (TSS) of the FT gene, triggering its expression. TEMPERATURE, ETHYLENE RESPONSE FACTOR (TZR) (Castillejo and Pelaz 2008), TARGET OF EAT 1 (TOE1), TOE2, SCHAFFMUTZE (SMZ), CURLY LEAF (CLF), MULTICOPY SUPPRESSOR OF APETALA1 (TOE2) (Castillejo and Pelaz 2008), TAR-PANILLO (TEM) (Mathieu et al. 2009), and SHORT VEGETATIVE PHASE (SVP) (Lee et al. 2007) respond to ambient temperature or photoperiod to directly repress FT expression. Further, several MADS transcription factors, namely FLOWERING LOCUS C (FLC), SVP, FLOWERING LOCUS M (FLM), and MADS AFFECTING FLOWERING (MAF), can inhibit transcription by binding to the first intron of FT at low temperatures or before vernalization (Luo et al. 2021). Other hormone signals also play a role in controlling the initiation of flowering. For example, ERF1, a key member of the ethylene signal transduction pathway, binds directly to the FT’s promoter and inhibits its transcription (Chen et al. 2021). Furthermore, polycomb group (Pc-G) proteins reportedly mediate epigenetic gene regulation, which maintains the identity of the inflorescence and floral meristems after floral induction (Müller-Xing et al. 2014). The simultaneous occurrence of H3K27me3 at FT has also been demonstrated, using a sequential ChIP analysis (Jiang et al. 2008). The genes of Pc-G subunits, including EMBRYONIC FLOWER 2 (EMF2), EMF1, CURLY LEAF (CLF), MULTICOPY SUPPRESSOR OF IRA 1 (MSI1) and LIKE HETEROCHROMATIN PROTEIN 1 (LHP1), deposit H3K27me3 in the chromatin of FT to repress its expression (Jiang et al. 2008; Schatlowski et al. 2008; Mozgova and Hennig 2015; Merini and Calonje 2015). Unlike other Pc-G target genes in Arabidopsis, modification by H3K27me3 occurs in the promoter, coding region, and downstream region of the FT gene (Turck et al. 2007).

In Arabidopsis, the antagonism of TFL1 and floral meristem-specific genes controls flower initiation and the ensuing inflorescence structure. TFL1, which is expressed in the central region of the apical meristem but can move to the meristem layer L1, is required for movement into the SAM to regulate floral transition (Conti and Bradley 2007; Goretti et al. 2020). Once in the SAM, TFL1 interacts with the bZIP transcription factor FD via the 14–3–3 protein, and FT and TFL1 compete for binding FT to regulate the downstream floral meristem identification genes LEAFY (FLY), APETALA1 (API), and CAULIFLOWER (CAL), which maintains meristem indeterminacy (Zhu et al. 2020; Goretti et al. 2020) (Fig. 1B). Under long day (LD) conditions, SOC1 and AGL24 bind to TFL1’s chromatin regions and directly activate its transcription in the SAM (Azpeitia et al. 2021). LFY binds to the TFL1 promoter and directly activates TFL1 transcription, a regulatory loop which ensures that flower formation occurs only when API/CAL levels are sufficiently high to repress TFL1 expression and trigger the genetic program required for flower development (Serrano-Mislata et al. 2017). The proteins encoded by the FT/TFL1 family of genes have small differences in conformation, giving them opposite functions in plants. Hanzawa et al. (2005) showed that changing only a single amino acid in the Arabidopsis TFL1 protein can render TFL1 to function as a floral activator, and vice versa.

Recent reports in gymnosperms indicate that the ancestor of FT functioned in a TFL1-like manner (Karlgren et al. 2011). For example, PaFTL1 and PaFTL2 in Norway spruce (Picea abies) both repress this conifer tree’s growth, and their heterologous expression in Arabidopsis also delays the onset of flowering (Karlgren et al. 2011; Klintenäs et al. 2012). The data to date suggests that the function of FT and TFL1 diverged after the evolutionary separation in different plant species. Moreover, FT/TFL1 family genes are reportedly involved in other developmental processes and feature functional diversification in regulating flowering time in several species (Karlgren et al. 2011; Klintenäs et al. 2012). This review summarizes the functional diversification and molecular mechanisms of the FT/TFL1 family members in horticultural plants, to provide a timely reference for further research on these pivotal genes in horticultural plants.

**FT/TFL1 family genes regulate flowering time in horticultural plants**

In horticultural plants, the number of FT/TFL1 family genes varies yet they have conserved functions in the process of floral transition (Table 1). For example, in ornamental plants of the Asteraceae—the largest flowering plant family contains the greatest number of species—three FT-like genes have been identified in Chrysanthemum seticuspe: CsFTL1, CsFTL2, and CsFTL3, which are flowering inducers (Oda et al. 2012; Mao et al. 2016; Sun et al. 2017; Wang et al. 2020a). Mao et al. (2016) found that the archetypal and alternative splicing (AS) forms of CmFTL1 (C. morifolium cultivar ‘Jimba’) has the function of complementing the late-flowering phenotype of the Arabidopsis ft-10 mutant, and CmFTL1 can induce
Table 1 Diverse functions of the *FT/TFL1* gene family in horticultural plants

| Gene name | Effect on flowering | Other function | Regulatory input | References |
|-----------|---------------------|----------------|-----------------|------------|
| **Arabidopsis** *(Arabidopsis thaliana)* |                      |                |                 |            |
| AtFT      | Induction           | Plant growth; Dormancy | LD              | Shannan and Meeks-Wagner, 1991; Yoo et al., 2004; Yamaguchi et al., 2005; Michaels et al., 2005; Xi et al., 2010; Yoo et al., 2010; D’Alloia et al., 2011; Huang et al., 2012; Kim et al., 2013; Moraes et al., 2019; Azpeitia et al., 2021; Chen et al., 2021 |
| AtTFL1    | Inhibition          | Inflorescence development | LD              |            |
| AtBFT     | Inhibition          | Inflorescence development | LD              |            |
| AtATC     | Inhibition          |                |                 |            |
| AtMFT     | Induction           | Seed germination |                 |            |
| **Chrysanthemum** *(Chrysanthemum spp.)* |                      |                |                 |            |
| CsFTL1    | Induction           |                | LD, NB          | Oda et al., 2012; Higuchi et al., 2013; Higuchi and Hisamatsu, 2015; Mao et al., 2016; Sun et al., 2017; Gao et al., 2019; Wang et al., 2020a, b; Haider et al., 2020 |
| CsFTL2    | Induction           |                | LD, Sucrose     |            |
| CsFTL3    | Induction           |                | LD, Sucrose     |            |
| CsTFL1b   | Inhibition          |                |                 |            |
| CmTFL1a   | Inhibition          |                |                 |            |
| CmTFL1c   | Inhibition          |                |                 |            |
| CsAFT     | Inhibition          |                | LD, NB          |            |
| **Phalaenopsis** *(Phalaenopsis* hybrid) |                      |                |                 |            |
| PhFT1     | Induction           |                |                 | Li et al., 2014; Zhou et al., 2018; Jiang et al., 2022 |
| PhFT3     | Induction           |                |                 |            |
| PhFT5     | Induction           |                |                 |            |
| PhFT6     | Inhibition          |                |                 |            |
| **Orchid** *(Oncidium Gower Ramsey)* |                      |                |                 | Hou and Yang, 2009 |
| OnFT      | Induction           |                |                 |            |
| OnTFL1    | Inhibition          |                |                 |            |
| **Dendrobium** *(Dendrobium huoshanense)* |                      |                |                 |            |
| DhFT3     | Induction           |                | Gibberellin     | Song et al., 2021 |
| DhFT1     | Induction           |                | Gibberellin     |            |
| DhFT2     | Induction           |                | Gibberellin     |            |
| DhTFL1a   | Inhibition          |                |                 |            |
| DhTFL1b   | Inhibition          |                |                 |            |
| **Tomato** *(Solanum lycopersicum)* |                      |                |                 |            |
| SP        | Inhibition          | Indeterminate growth |                 | Molinero-Rosales et al., 2004; Lifschitz et al., 2006; Shalit et al., 2009; Jiang et al., 2013; Lifschitz et al., 2014; Cao et al., 2016; Song, 2020 |
| SFT       | Induction           | Inflorescence development | SD              |            |
| FTL1      | Induction           |                |                 |            |
| SP5G      | Inhibition          |                |                 |            |
| SP5G2     | Inhibition          |                |                 |            |
| SP5G3     | Inhibition          |                |                 |            |
| **Strawberry** *(Fragaria × ananassa)* |                      |                |                 |            |
| FvFT1     | Induction           |                | LD              | Koskela et al., 2012; Nakano et al., 2015 |
| FvTFL1    | Inhibition          |                | LD, Cool temperature | Iwata et al., 2012; Randoux et al., 2014, b; Otagaki et al., 2015 |
| **Rose** *(Rosa spp.)* |                      |                |                 |            |
| RoKSN     | Inhibition          |                |                 |            |
| RoFT      | Induction           |                |                 |            |
flowering in *C. morifolium ‘Yuuka’* (Wang et al. 2020a). Sucrose induces the transcriptional upregulation of *CmFTL2* (*C. morifolium ‘Yuuka’*) in chrysanthemum leaves and promotes flowering (Sun et al. 2017). However, changing a single amino acid in *CmFTL3* of chrysanthemum results in the loss of its flowering function (Sun et al. 2018). Moreover, there are three *TFL1* homologs in chrysanthemum that act as flowering inhibitors (Higuchi and Hisamatsu 2015; Gao et al. 2019; Haider et al. 2020).

The orchid family (Orchidaceae) is the second largest family of flowering plants, for which three *FT-like* genes were identified in *Phalaenopsis*: *PhFT1*, *PhFT3*, and *PhFT5*, heterologous expression of which in *Arabidopsis* cause early flowering phenotype (Zhou et al. 2018; Li et al. 2014). Ectopic expression of *OnFT* could not fully complement the late-flowering phenotype of the *Arabidopsis ft-1* mutant, and it was not regulated by photoperiod but did inhibit flowering in *Oncidium* (Hou and Yang 2009). Six PEBP family genes (i.e., *DhFT3*, *DhFT1*, *DhMFT*, *DhTFL1b*, *DhFT2*, and *DhTFL1a*) were isolated and characterized from the *Dendrobium huoshanense* genome (Song et al. 2021). Gibberellin (GA) treatment increased the expression of all those *DhFTs* and promoted flowering, while inhibiting the expression of *DhTFL1s* (Song et al. 2021). A year-round tropical orchid, *Arundina graminifolia*, lacks any *TFL1-like* gene, but does have two *FT-like* genes: *AgFT1* and *AgFT2*. The functions of *AgFT1* and *AgFT2* in regulating flowering have not been verified, however (Auberon et al. 2016; Ahmad et al. 2021).

In vegetable crops, the FT-like protein StSP3D is essential for flowering in potato (*Solanum tuberosum*) (Navarro et al. 2011). Tomato (*Lycopersicon esculentum*) is the second most globally important vegetable crop (after potato), whose flowering time is jointly controlled by the flowering inducer *SINGLE FLOWER*

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**Table 1** (continued)

| Gene name (non-FT) | Effect on flowering | Other function | Regulatory input | References |
|--------------------|---------------------|----------------|-----------------|-----------|
| Poplar (*Populus* spp.) |                      |                |                 |           |
| *PtFT1*            | Induction           |                |                 |           |
| *PtFT2*            | Inhibition          | Vegetative growth; Shoot dormancy | LD, High temperature | Mohamed et al., 2010; Hsu et al., 2011; Gómez-Soto et al., 2022 |
| *PopCEN1*          | Inhibition          |                |                 |           |
| *PopCEN2*          | Inhibition          |                |                 |           |
| Sugar beet (*Beta vulgaris*) |                 |                |                 |           |
| *BvFT1*            | Inhibition          |                | SD, Non-vernalized | Pin et al., 2010 |
| *BvFT2*            | Induction           |                |                 |           |
| Cucumber (*Cucumis sativus*) |                 |                |                 |           |
| ‘short-1’ UR *CfF*  | Induction           |                |                 | Wen et al., 2019; Wang et al., 2020b |
| ‘short-2’ UR *CfF*  | Induction           |                |                 |           |
| ‘long’ UR *CsFT*    | Inhibition          |                |                 |           |
| *CsTFL1*           | Inhibition          | Determinate growth |               |           |
| Tulip (*Tulipa gesneriana*) |              |                |                 | Leeggangers et al., 2018 |
| *TgFT1*            | Inhibition          |                |                 |           |
| *TgFT2*            | Induction           |                |                 |           |
| *TgFT3*            | Inhibition          |                |                 |           |
| Potato (*Solanum tuberosum*) |                |                |                 |           |
| *StSP5G*           | Inhibition          |                |                 | Navarro et al., 2011; Lee et al., 2013 |
| *StSP5G-like*      | Inhibition          |                |                 |           |
| *StSP6A*           | Tuber formation     |                |                 |           |
| Onion (*Allium cepa*) |                   |                |                 |           |
| *AcFT1*            | Bulb formation      |                | LD              | Blackman et al., 2010; Lee et al., 2013 |
| *AcFT2*            | Induction           |                | Vernalization   |           |
| *AcFT4*            | Inhibition          | Bulb formation |                |           |
| Kiwifruit (*Actinidia spp.*) |            |                |                 |           |
| *Kiwfruit FT*      | Induction           | Dormancy release | Cool temperature | Varkonyi-Gasic et al., 2013 |
| *Kiwfruit CEN*     | Inhibition          |                |                 |           |
| Pineapple (*Ananas comosus*) |             |                |                 |           |
| *AcFTL2*           | Induction           | Ethylene        |                 | Liu and Fan, 2016; Liu et al., 2018 |
TRUSS (SFT) and suppressor SELF PRUNING (SP) 
(Molinero-Rosales et al. 2004; Jiang et al. 2013). SFT 
is an ortholog of FT-like that is expressed in mature 
leaves and systematically promotes flowering, while SP 
is the ortholog of TFL1-like that is instead expressed 
in young leaves and shoot tips, and inhibits flowering 
(Shalit et al. 2009). Recently, FTL1, which regulates 
flowering time in tomatoes, was located and sequenced 
through map-based cloning. FTL1 is only specifically 
expressed under short day (SD) conditions and regu-
lates tomato flowering by promoting the expression of 
SFT (Song 2020). Among fruit crops, in strawberry 
(Fragaria × ananassa) FvFT1 and FvTFL1 have antago-
nistic functions for inducing flowering. Interestingly, 
owing to a base deletion in FvTFL1, strawberry has 
become a permanent flowering plant (Koskela et al. 2012; Nakano et al. 2015).

Moreover, perennial woody plants possess flower-
ing-inductive FT genes and flowering-inhibitory TFL1 
genes. Poplar (Populus species) contains two FT-like 
genes (PtFT1/PtFT2) (Hsu et al. 2011) and two CEN/ 
TFL1-like genes (PopCEN1/PopCEN2) (Mohamed et al. 2010). Overexpression of PtFT1 in poplar caused 
its flowering in the tissue culture stage at 6 weeks; 
whereas, PtFT1 promotes flowering (Hsu et al. 2006; 
Hsu et al. 2011; Gómez-Soto et al. 2022). Both Pop-
CEN1 and PopCEN2 inhibited flowering, however. 
Downregulating the expression of PopCEN1 and Pop-
CEN2 can accelerate the time of first onset of flower-
ing and the maturity of poplar (Mohamed et al. 2010). 
In a Chinese continuous-flowering rose plant cultivar, 
the TFL1-like gene RoKSN is a flowering suppressor 
whereas RoFT is a floral inducer (Iwata et al. 2012; 
Otagaki et al. 2015). The insertion of a retrotranspo-
son in RoKSN inhibits RoKSN expression in roses, 
thereby facilitating their continuous flowering (Rand-
doux et al., 2014, b). Collectively, these reports sug-
ject the function of FT/TFL1 family genes is generally 
conserved in horticultural plants.

Functional diversification of FT/TFL1-like in horticultural 
plants
The functions of proteins encoded by homologous FT/ 
TFL1-like genes are not entirely conserved in horti-
cultural plants, in that they show functional diversifica-
tion in regulating flowering time (Table 1).

Homologous genes of FT could contribute to inhib-
itig flowering. In vegetable crops, the two FT-like 
homologous genes BvFT1 and BvFT2 in sugar beet (Beta 
vulgaris) function antagonistically in flowering. Under 
non-vernalized or SD conditions, the flowering inhibi-
tor BvFT1 inhibits flowering by limiting the expression of 
the flowering-inducing factor BvFT2 (Pin et al., 2010). In 
cucumber (Cucumis sativus), the structural types in the 
upstream region (UR) of CsFT1 have differential effects on 
flowering induction; the ‘short-1’ UR CsFT and ‘short-2’ 
UR CsFT accelerate the onset of flowering, whereas the 
‘long’ UR CsFT delays flowering (Wang et al., 2020b). Four FT-like homologous genes have been identified 
in tomato: SP3D/SFT1 has a florigen function, whereas 
SP5G, SP5G2, and SP5G3 are characterized by flower-
ing inhibitory activity (Cao et al., 2016). AcFT4 in onion 
(Allium cepa) and both StSP5G and StSP5G-like in potato 
are also able to inhibit flowering (Navarro et al., 2011; Lee 
et al., 2013). In ornamental plants, three PEBP genes were 
isolated in tulip (Tulipa gesneriana): TgFT1, TgFT2, and 
TgFT3. Overexpression of TgFT2 in Arabidopsis resulted 
in an early-flowering phenotype, while TgFT1 and TgFT3 
overexpression resulted in a late-flowering phenotype 
(Leeggangers et al., 2018). The PtFT6 in Phalaenopsis 
and HaFT1 in sunflower (Helianthus annuus) can also 
repress their flowering (Li et al., 2014; Blackman et al., 
2010). The two FT-like genes PtFT1/PtFT2 in poplar, a 
woody perennial species, also have opposing flowering 
regulatory functions (Hsu et al. 2011; Mohamed et al., 
2010). PtFT1 has a florigen function, whereas PtFT2, it 
induced by LDs and high temperature, reduces the level 
of GA via the GA 13-hydroxylation pathway and main-
tains the vegetative growth of poplar to preclude flower-
ing (Gómez-Soto et al., 2022).

In addition to regulating flowering time, members of 
FT/TFL1-like genes are involved in a variety of other pro-
cesses in horticultural plants. CsTFL1 inhibits determi-
nate growth and terminal flower formation in cucumbers 
(Zhao et al., 2018; Wen et al., 2019; Njogu et al., 2020). 
Navarro et al. (2011) reported that overexpressing the 
FT homologous gene Hdl3a in potato enabled it to grow 
two tubers than the wild type, and that the endogenous 
gene StSP6A also had a similar function, thus indicating 
that FT promotes tuber formation. In onion, LDs induced 
the downregulation of AcFT4 expression but the upregu-
lation of AcFT1 expression, which promoted the forma-
tion of bulbs and increased the yield (Lee et al., 2013). In 
tomato sft mutants, the inflorescence differentiated into 
only one flower, the sepals were enlarged, and leaves have 
excess intercalary leaflets; however, the leaves became 
smaller blades and lack folioles after the overexpression 
of SFT (Shalit et al., 2009; Lifschitz et al., 2014). In 
Dendrobium Chao Praya Smile, DoFT-RNAi transgenic 
lines also displayed abnormal inflorescence develop-
ment and delayed pseudobulb formation, suggesting that 
DOFT may have evolved with unknown functions related 
to the regulation of storage organs and flower develop-
ment (Wang et al., 2017). PtFT2 promotes vegetative 
growth and shoot dormancy in poplar trees (Mohamed 
et al., 2010); similarly, FT and CEN are involved in the
regulation of kiwifruit plant growth by integrating developmental and environmental signals (Varkonyi-Gasic et al., 2013). Taken together, these reports show that the functions of members of the FT/TFL1 gene family have evolved dynamically over the course of horticultural plants’ evolution.

**Regulation of FT/TFL1 family genes in horticultural plants**

The photoperiodic pathway is the most important and most conserved of the floral induction pathways, and some of the key loci and mechanisms are shared even among distantly related plant species, whereas others are not conserved and give rise to crucial species differences (Matsoukas et al., 2012). The autumn flowering chrysanthemum cultivars are short day plants that require a repeated SD photoperiod for successful flowering, because CsFTL3 expression increases with such repeated SDs before successful flowering occurs, but their vegetative growth can be strictly maintained under LD or night-break (NB) conditions. When SDs switch to LDs before the involucre-forming stage, those plants do not initiate florets on the apical receptacle, or their capitulum development is strongly suppressed (Higuchi, 2018; Nakano et al., 2019). Recent studies have revealed the transcriptional regulation mechanism of the FT/TFL1 family genes in chrysanthemum (Fig. 2). CICRY2 facilitates floral transition in *C. lavandulifolium* by fine-tuning the expression of circadian clock-related genes, such as the downregulation of LHY and overexpression of GI (Yang et al., 2018). By downregulating CsFTL3 and CsAFT, CsLHY-SRDX induced a photoperiod-insensitive floral transition (Oda et al., 2017). The transcription of another circadian-clock-related gene, CsGI, has been shown to increase the necessary night length for blooming, chiefly by maintaining lower levels of CsAFT (Oda et al., 2020). In chrysanthemums, CsPHYB-mediated light signaling upregulates CsFTL3 but downregulates CsAFT to determine their obligate photoperiodic blooming response (Higuchi et al., 2013). Furthermore, gibberellins function critically in floral induction in response to LDs (Porri et al., 2012). CmBBX24 inhibits the expression of CmFTL3, which regulates flowering primarily through effects on the GA pathway under LDs (Yang et al., 2014). Recently, the role of NF-Y proteins in the aging pathway in chrysanthemum was identified, in that CmNF-YB8 influences flowering time by directly upregulating the expression of *cmo-MIR156* in the aging pathway (Wei et al., 2017). More recently, the CO homologous protein CmBBX8 was discovered to target CmFTL1 for flowering regulation in chrysanthemum (Wang et al., 2020a).

Nevertheless, the functions of CO1 and CO2 in poplar do not overlap with those in *Arabidopsis*. The growth of CO2 RNAi transgenic poplar stopped when LDs transitioned to SDs, and its shoots formed earlier. Overexpression of CO1 and CO2 in poplar did not induce the upregulated expression of FT2 under SD conditions, and its timing of flowering and bud formation did not change (Hsu et al., 2012). Another SD-dependent FT2 inhibition pathway mediated by LHY2 was recently discovered in poplar. Under SD conditions, LHY2 is induced to express and directly bind to the homeopatric element at the 3′ end of FT2 to inhibit its expression, resulting in the arrested growth of poplar (Fig. 3A). But under LD

![Fig. 2 Flowering time regulation by florigen and anti-florigen in Chrysanthemum](image)
conditions, the expression of LHY2 is low, while CO and other activators induce the expression of FT2, thereby promoting the flowering of poplar (Ramos-Sánchez et al., 2019; André et al., 2022).

Some FT homologs regulate flowering and aspects of development in response to temperature except for photoperiod in horticultural plants. In sugar beet, the expression of the flowering inhibitor BvFT1 was inhibited by both vernalization and LD conditions and BvFT2 was induced under LDs (Pin et al., 2010) (Fig. 3B). In strawberry, FvFT1 was specifically upregulated in mature leaves and this promoted the upregulation of FvSOC1 in shoot tips, which activated FvTFL1 expression to inhibit flowering under LDs (Mouhu et al., 2013; Rantanen et al., 2014). Furthermore, FvTFL1 was regulated by a temperature-dependent pathway independent of photoperiod-dependent regulation (Rantanen et al., 2015). Floral transition of lily (Lilium longiflorum) is also induced by low-temperature conditions and is not regulated by photoperiod. In lily, LIFT, as a flowering activator, is significantly induced by a period of low-temperature treatment and this promoted flowering; however, without the vernalization treatment, overexpression of LIFT also led to a bloom, indicating that LIFT is the main regulatory factor controlling flowering in the vernalization pathway (Lazare and Zaccai et al., 2016). After switching from vegetative to reproductive growth, LIFT expression was further reduced in floral meristems and small flower buds. Therefore, LIFT is thought to be involved in switching the meristem to a flowering state during vernalization, but it does not act as a flowering inducer (Leeggangers et al., 2018). Further, the flowering regulation of Narcissus tazetta and tulip is induced by high temperature and does not depend on the photoperiod and vernalization pathways. In narcissus, high temperature induces the transcription of Narcissus FLOWERING LOCUS T1 (NFT1), which promotes the expression of the downstream LFY homolog gene NLF and induces flowering (Li et al., 2013; Noy-Porat et al., 2013). The floral transition of tulip occurs in the bulb, for which high temperature induces the expression of TgFT2 and inhibits the expression of TgTFL1, which then induces the floral transition (Leeggangers et al., 2018) (Fig. 3C). On the contrary, the chrysanthemum flowering is severely delayed by high temperature during the summer, when the reduction of CsFTL3 expression at high temperatures are involved in flowering’s retardation in C. seticuspe (Higuchi, 2018). Interestingly, exogenous ethylene induces the upregulated expression of FT-like and AP1-like genes, which promotes transition to flower formation in pineapple (Liu and Fan, 2016; Liu et al., 2018) (Fig. 3D), this starkly differing from their inhibitory effect on Arabidopsis flowering (Chen et al., 2021). These findings indicate that not only the functions of members of the FT/TFL1 family of genes, but also their upstream regulators, have evolved drastically and in cases also divergently in horticultural plants.

The transport of florigens in horticultural plants has also been studied. In Cucurbita moschata, LD-induced transport of FT proteins from its leaves to shoot tips promoted the transition into flowering (Lin et al., 2007). Moreover, floral promotion via the graft transmission of FT has been demonstrated in woody plants. For a recent example, when the scion of JcFT-RNAi transgenic Jatropha curcas was grafted onto SUC2:JcFT rootstock, FT protein was transported into the scion which promoted the transition into flowering, whose efficacy depended on the length of the scion (Tang et al., 2022). In trifoliate orange, its early flowering was induced in the transgenic tomato as well as trifoliate orange plants transformed with ToFT. However, the rootstocks of transgenic trifoliate orange could not induce flowering of grafted wild-type (WT) juvenile scions because of their low accumulation of total FT protein (Wu et al., 2022). That finings suggests the expression of FT must reach a certain threshold to induce flowering. A TFL1 homolog (RoKSN)
in rose was found to be immobile, precluding its transmission via grafting experiments (Randoux et al., 2014, b). Yet when a WT chrysanthemum plant was grafted onto the CsFTL1-ox stock, the flowering of the WT scion was delayed vis-à-vis the WT/WT grafting (Higuchi and Hisamatsu, 2015). Spatial expression patterns of CsFTL1 showed that it was mainly expressed in shoot tips, with low expression levels in leaves (Higuchi and Hisamatsu, 2015; Gao et al., 2019; Haider et al., 2020). These results suggest that CsFTL1 probably can move long distances through a grafting union as a floral repressor, to systemically regulate an indeterminate apical meristem. Because FT participates in vesicle trafficking (Liu et al., 2020), whether the transport of TFL1 occurs via a similar way awaits investigation.

**Outlook**

In summary, many studies of diverse horticultural plants have revealed the conserved functioning of members of the FT/TTFL1 gene family, which have evolved dynamically over the course of horticultural plant evolution. Moreover, amino acid substitutions in FT/TTFL1 family genes in Arabidopsis and horticultural plants such as sugar beet could cause a conversion in functionality, from having repressor activity to becoming a floral activator and vice versa (Ho and Weigel, 2014; Pin et al., 2010). A single base deletion or the products of a premature stop codon in TFL1 gene in strawberry facilitates their continuous flowering (Koskela et al., 2012). In cucumber and domesticated tomato, the short upstream region of CsFT and mutations in the cis-regulatory region of antiflorigen SP5G hasten their onset of flowering, respectively (Soyk et al., 2017; Wang et al., 2020b). These results suggest FT/TTFL1 family genes are elite editing targets for manipulating gene structure, to change key flowering characteristics of horticultural plants, using genome editing technology, which is a powerful and precision-breeding approach, although there are legal/ethical concerns (Gao, 2021).

Because FT/TTFL1 family genes integrate multiple regulatory pathways, such as photoperiod, vernalization, and ambient temperature pathway, to govern flowering, not only the functions of their members but also their upstream regulators have drastically evolved in horticultural plants. With ongoing global warming, the rise in ambient temperature is often accompanied by a greater concentration of carbon dioxide (CO₂), which is conducive to the accumulation of photosynthetic products (sugar and starch) in plants. This increase in CO₂ is apt to cause changes in tissues’ sugar status or directly drives FT/TTFL1 to regulate flowering (Jagadish et al., 2016). Although studies have found that FT can mediate nitrogen’s control of flowering, its regulatory mechanism is still not well understood (Gras et al., 2018; Zhang et al., 2021). Therefore, elucidating in detail how the regulation mechanisms of FT/TTFL1 family genes may respond to various environmental and endogenous stimuli would promote the development of an efficient and energy-saving approach to regulate flowering. Due to the rapid adoption and spread of genomic sequencing technology applied to horticultural plants, genomic resources are becoming increasingly available. This combined with other techniques, namely high-throughput phenotyping, genomic selection, and gene function analysis, will enable us to obtain detailed knowledge of the FT/TTFL1 gene family, so as to modify their action to meet the increasing demand for horticultural products in the future.

**Abbreviations**

SAM: Shoot apical meristem; FT: FLOWERING LOCUS T; AP1: APETALA1; FUL: FRUITFULL; SD: Short-day; DN: Day-neutral; TSS: Transcription start site; TF1: TERMINAL FLOWER 1; LD: Long-day; PEBPs: Phosphatidyethanolamine-binding proteins; MFT: MOTHER OF FT AND TFL1; TSF: TWIN SISTER OF FT; ATC: Arabidopsis thaliana CENTRORADIALES homolog; BFT: BROTHER OF FT AND TFL1; NB: Night-break; GA: Gibberellin; SFT: SINGLE FLOWER TRUSS; SP: SELF PRUNING; UR: Upstream region; NF-Y: Nuclear Factor Y; AS1: ASYMMETRIC LEAVES 1; TEM: TRAVELLUCC; TDE1: TARGET OF EAT 1; SM2: SCHAFMUTZEN; SNZ: SCHNARCHZAPFEN; BEE1: BR ENHANCED EXPRESSION 1; SVP: SHORT VEGETATIVE PHASE; PIF4: PHYTOCHROME INTERACTING FACTOR 4; FLC: FLOWERING LOCUS C; FLM: FLOWERING LOCUS M; MAE: MAES AFFECTING FLOWERING; IM: inflorescence meristem; LFY: LEAFY; CAL: CALIFLOWER; FM: floral meristem; SOCT: SUPPRESSOR OF OVEREXPRESSION OF CO 1; AGL24: AGAMOUS LIKE 24; NFT1: FLOWERING LOCUS T1; FTIP1: FT-INTERACTING PROTEIN 1; NaKP1: SODIUM POTASSIUM ROOT DETECTIVE 1; PCG: Phosphatidylglycerol; Pol: Polycarp group; LHP1: LIKE HETEROCROMATIN PROTEIN 1; CBF: CURLY LEAF; NAC2: EMBRYONIC FLOWER 2; MSI1: MULTICOPY SUPPRESSOR OF IRA 1.

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**Authors’ contributions**

SW and JJ conceptualized the paper, wrote the draft, SW, JJ and FC reviewed and comments on the manuscript. YY prepared the figures. All authors read and approved the final manuscript.

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References

Abe M, Kobayashi Y, Yamamoto S, Daimon Y, Yamaguchi A, Ikeda Y, et al. FD, a BZIP protein mediating signals from the floral pathway integrator FT at the shoot apex. Plant Science. 2005;309(5737):1052–6. https://doi.org/10.1016/j.plantsci.2005.04.106.

Ahmad S, Lu C, Gao J, Ren R, Wei Y, Wu Y, et al. Genetic insights into the regulatory pathways for continuous flowering in a unique orchid Anurandra graminifolia. BMC Plant Biol. 2021;21(1):587. https://doi.org/10.1186/s12870-021-03350-6.

Ahn JH, Miller D, Winter BJ, Banfield MJ, Lee JH, Yoo SY, et al. A divergent external loop confers antagonistic activity on floral regulators FT and TFL1. EMBO J. 2006;25(3):605–14. https://doi.org/10.1038/sj.emboj.6006950.

Andrè D, Zambrano JA, Zhang B, Lee KC, Rühl M, Marcon A, et al. Populus SVL acts in leaves to modulate the timing of growth cessation and bud set. Front Plant Sci. 2022;13:823019. https://doi.org/10.3389/fpls.2022.823019.

Auberon F, Olutunji OJ, Krisa S, Antheaume C, Herbette G, Bonté F, et al. Two new Stilbenoids from the aerial parts of Arundina graminifolia (Oidioideae). Molecules. 2016;21(11):1430. https://doi.org/10.3390/molecules21111430.

Azpeitia E, Tichtinsky G, Le Masson M, Serrano-Mislata A, Lucas J, Gregis V, et al. Cauliflower fractal forms arise from perturbations of floral gene networks. Science. 2021;373(6551):192–7. https://doi.org/10.1126/science.abg5999.

Blackman RK, Strasburg JL, Raduski AR, Michaels SD, Rieseberg LH. The role of FKF1 homologs CmTFL1a gene from Chrysanthemum cv. ‘Jinba’ with TERMINAL FLOWER 1 homolog CmTFL1a. Genes (Basel). 2020;11(10):860. https://doi.org/10.3390/genes11080860.

Hanzawa Y, Money T, Bradley D. A single amino acid converts a repressor to an activator of flowering. Proc Natl Acad Sci U S A. 2005;102(21):7748–53. https://doi.org/10.1073/pnas.0503992102.

Higuichi Y, Florigen and anti-florigen: flowering regulation in horticultural crops. Breed Sci. 2018;68(1):109–18. https://doi.org/10.1270/jsbbs.17084.

Higuichi Y, Hsiamsat T, CmTFL1, a constitutive local repressor of flowering, modulates floral initiation by antagonising florigen complex activity in chrysanthemums. Plant Sci. 2015;237:1–7. https://doi.org/10.1016/j.plantsci.2015.04.011.

Higuichi Y, Namami T, Oda A, Nakano Y, Sumitomo K, Fukui S, et al. The gated induction system of a systemic floral inhibitor, anti-florigen, determines obligate short-day flowering in chrysanthemums. Proc Natl Acad Sci U S A. 2013;110(42):17137–42. https://doi.org/10.1073/pnas.1307617110.

Ho WW, Weigel D. Structural features determining flower-promoting activity of Arabidopsis FLOWERING LOCUS T LOCUS. Plant Cell. 2014;26(2):552–64. https://doi.org/10.1105/tpc.113.115220.

Hou CJ, Yang CH. Functional analysis of FT and TFL1 orthologs from orchid (Oncidium Gower Ramsey) that regulate the vegetative to reproductive transition. Plant Cell Physiol. 2009;50(8):1544–57. https://doi.org/10.1093/pcp/pcp099.

Hsu CY, Adams JP, Kim H, No K, Ma C, Strauss SH, et al. FLOWERING LOCUS T duplication coordinates reproductive and vegetative growth in perennial poplar. Proc Natl Acad Sci U S A. 2011;108(26):10756–61. https://doi.org/10.1073/pnas.1104713108.

Hsu CY, Adams JP, No K, Liang H, Mellan R, Rechanova O, et al. Overexpression of CONSTANS homolog CO1 and CO2 fails to alter normal reproductive onset and fall bud set in woody perennial poplar. PLoS One. 2012;7(9):e45448. https://doi.org/10.1371/journal.pone.0045448.

Hsu CY, Liu Y, Luthe DS, Yuece C. Poplar FT2 shortens the juvenile phase and promotes seasonal flowering. Plant Cell. 2006;18(6):1846–61. https://doi.org/10.1105/tpc.106.049038.

Huynh NC, Jane WN, Chen J, Yu TS. Arabidopsis thaliana CENTRORADIALIS homologue (ATC) acts systemically to inhibit floral initiation in Arabidopsis. J Integr Plant Biol. 2021;63(10):1712–23. https://doi.org/10.1111/jipb.13144.

Iwata H, Gaston A, Remay A, Thouroude T, Jausserf J, Kawamura K, et al. The TFL1 homologue KSN is a regulator of continuous flowering in rose and promotes seasonal flowering. Plant Cell. 2012;69(3):619–31. https://doi.org/10.1093/jxb/erx423.

Jiang L, Jiang X, Li Y, Gao Y, Wang S, Ma Y, et al. FT-like paralogs are repressed by a bZIP protein mediating signals from the floral pathway integrator FT, and promotes seasonal flowering. Plant Physiol. 2019;182(4):2081–95. https://doi.org/10.1104/pp.19.00867.

Gras DE, Vidal EA, Undurraga SF, Rivers E, Moreno S, Dominguez-Figueroa J, et al. SMZ/SNZ and gibberellin signaling are required for nitrate-elicited delay of flowering time in Arabidopsis thaliana. J Exp Bot. 2018;69(6):619–31. https://doi.org/10.1093/jxb/ery423.

Haider S, Gao Y, Gao Y. Standardized genetic transformation protocol for Chrysanthemum cv. ‘Jinba’ with TERMINAL FLOWER 1 homolog CmTFL1a. Genes (Basel). 2020;11(8):860. https://doi.org/10.3390/genes11080860.

Jiang D, Wang Y, Wang Y, He Y. Repression of FLOWERING LOCUS C and FLOWERING LOCUS T by the Arabidopsis Polycomb repressive complex 2 components. PLoS One. 2008;3(10):e3404. https://doi.org/10.1371/journal.pone.0003404.

Jiang K, Liberatore KL, Park SJ, Alvarez JP, Lippman ZB. Tomato yield heterosis is triggered by a dosage sensitivity of the florigen pathway that fine-tunes shoot architecture. PLoS Genet. 2013;9(12):e1004043. https://doi.org/10.1371/journal.pgen.1004043.

Jiang L, Jiang X, Li Y, Gao Y, Wang S, Ma Y, et al. FT-like paralogs are repressed by an SWP protein during the floral transition in Phalaenopsis orchid. Plant Cell Rep. 2022;41(1):1–13. https://doi.org/10.1007/s00299-021-02805-2.

Kardaliyska I, Shukla VK, Ahn JH, Dagenais N, Christensen SK, Nguyen JT, et al. Activation tagging of the floral inducer FT. Science. 1999;286(5446):1962–5. https://doi.org/10.1126/science.286.5446.1962.
Liu L, Liu C, Hou X, Xi W, Shen L, Tao Z, et al. FTIP1 is an essential regulator required for florigen transport. PLoS Biol. 2012;10(4):e1001313. https://doi.org/10.1371/journal.pbio.1001313.

Liu L, Zhang Y, Yu H. Florigen trafficking integrates photoperiod and temperature signals in Arabidopsis. J Integr Plant Biol. 2020;62(9):1385–98. https://doi.org/10.1111/jipb.13000.

Luo X, Yin M, He Y. Molecular genetic understanding of photoperiodic regulation of flowering time in Arabidopsis and soybean. Int J Mol Sci. 2021;23(1):466. https://doi.org/10.3390/ijms23010466.

Mao T, Sun J, Cao P, Zhang R, Fu Q, Chen S, et al. Functional analysis of alternative splicing of the FLOWERING LOCUS T orthologous gene in Chrysanthemum morifolium. Hort Res. 2016;3:16058. https://doi.org/10.1038/hortres.2016.58.

Matheiu J, Wirthmann N, Kütter F, Schmid M. Export of FT protein from phloem companion cells is sufficient for floral induction in Arabidopsis. Curr Biol. 2007;17(12):1055–60. https://doi.org/10.1016/j.cub.2007.05.009.

Matheiu J, Yant LJ, Murdter F, Kütter F, Schmid M. Repression of flowering by the miR172 target SMZ. PLoS Biol. 2009;7(7):e1000148. https://doi.org/10.1371/journal.pbio.0010148.

Matsoukas KG, Massiah AJ, Thomas B. Florigenic and anti-florigenic signaling in plants. Plant Cell Physiol. 2012;53(1):1827–42. https://doi.org/10.1093/pcp/pcs150.

Merini W, Calionge M. PRC1 is taking the lead in PRC repression. Plant J. 2014;78(1):110–20. https://doi.org/10.1111/tpj.12181.

Michaels SD, Himelblau E, Kim SY, Schomburg FM, Amasino RM. Integration of flowering signals in winter-annual Arabidopsis. Plant Physiol. 2005;137(1):149–56. https://doi.org/10.1104/pp.104.052811.

Mohamed R, Wang CT, Ma C, Shevchenko O, Dye SJ, Puzey JR, et al. Populus CEN/TFL1 regulates first onset of flowering, auxín meristem identity and dormancy release in Populus. Plant J. 2010;62(4):674–88. https://doi.org/10.1111/j.1365-313X.2010.04185.x.

Molino-Rosas N, Latorre A, Jamilena M, Lozano R. SINGLE FLOWER TRUSS regulates the transition and maintenance of flowering in tomato. Planta. 2004;218(3):427–34. https://doi.org/10.1007/s00425-003-1109-1.

Moraes TS, Dornelas MC, Martinelli AP. FT/TFL1: Calibrating Plant Architecture. Plant Sci. 2014;259:86–93. https://doi.org/10.1016/j.plantsci.2014.02.007.

Molinero-Rosales N, Latorre A, Jamilena M, Lozano R. SINGLE FLOWER TRUSS regulates the transition and maintenance of flowering in tomato. Plant Physiol. 2017;170(3):1235–48. https://doi.org/10.1104/pp.17.00379.

Mozgovoi I, Hennig L. The polycorm group protein regulatory network. Annu Rev Plant Biol. 2015;66:269–96. https://doi.org/10.1146/annurev-arpl-040314-115627.

Muller-Ring X, Clarens O, Pekorny L, Goodrich J, Schubert D. Polycorm-group proteins and FLOWERING LOCUS T maintain commitment to flowering in Arabidopsis thaliana. Plant Cell. 2014;26(6):2475–71. https://doi.org/10.1105/tpc.114.123323.

Nakano T, Higuchi Y, Yoshida Y, Hisamatsu T. Environmental responses of the FT/TFL1 gene family and their involvement in flower induction in Fragaria × ananassa. J Plant Physiol. 2015;171(6):60–7. https://doi.org/10.1016/j.jplph.2015.01.007.

Nakano Y, Takase T, Takahashi S, Sumimoto K, Higuchi Y, Hisamatsu T. Chrysanthemeum requires short-day repeats for anthesis: gradual CsFTL3 induction through a feedback loop under short-day conditions. Plant Sci. 2019;283:247–55. https://doi.org/10.1016/j.plantsci.2019.01.023.

Navarro C, Abelenda JA, Cruz-Oró E, Cuéllar CA, Tamaki S, Silva J, et al. Control of flowering and storage organ formation in potato by FLOWERING LOCUS T. Nature. 2011;478(7367):119–22 https://www.nature.com/articles/ncomms3884.

Nguyen MA, Yang Y, Niu W, Zhang B, Niu Z, et al. Molecular characterization of flowering time and substitution for diverse environmental stimuli. Proc Natl Acad Sci. 2014;111(6):2335–40. https://doi.org/10.1073/pnas.1316590111.

Oda A, Higuchi Y, Hisamatsu T. Photoperiod-insensitive floral transition in Arabidopsis. Plant Cell Physiol. 2019;31(10):2475–90. https://doi.org/10.1093/pcp/pcz036.
Oda A, Higuchi Y, Hisamatsu T. Constitutive expression of CsGAI alters critical night length for flowering by changing the photo-sensitive phase of anti-florigen induction in chrysanthemum. Plant Sci. 2020;293:110417. https://doi.org/10.1016/j.plantsci.2020.110417.

Oda A, Narumi T, Li T, Kandot T, Higuchi Y, Sumitomo K, et al. CsFTL3, a chrysanthemum FLOWERING LOCUS-T-like gene, is a key regulator of photo-periodic flowering in chrysanthemums. J Exp Bot. 2012;63(3):1461–77. https://doi.org/10.1038/jxb.2011.387.

Otogaki S, Ogawa Y, Hibrand-Saint-Oyant L, Fouther F, Kawamura K, Horibe T, et al. Genotype of FLOWERING LOCUS T homologue contributes to flower initiation differences in wild and cultivated rose. Plant Biol (Stuttgart). 2015;17(4):808–15. https://doi.org/10.1111/pbl.12299.

Parmar N, Singh KH, Sharma D, Singh L, Kumar P, Nanjundan J, et al. Genetic engineering strategies for biotic and abiotic stress tolerance and quality enhancement in horticultural crops: a comprehensive review. 3. Biotech. 2017;7(4):239. https://doi.org/10.1007/s40060-017-0380-y.

Pin PA, Beniloch R, Bonnet D, Wremelsn-Weich E, Kraft T, Gienel JJ, et al. An antagonistic pair of FT homologs mediates the control of flowering time in sugar beet. Science. 2010;330(6009):1397–400. https://doi.org/10.1126/science.1197004.

Porri A, Torti S, Romero-Branchat M, Coupland G. Spatially distinct regulatory roles for gibberellins in the promotion of flowering of Arabidopsis under long photoperiods. Development. 2012;139(12):2198–209. https://doi.org/10.1242/dev.077164.

Putterill J, Varkonyi-Gasic ET, FT and florigen long-distance flowering control in plants. Curr Opin Plant Biol. 2016;33:77–82. https://doi.org/10.1016/j.pbi.2016.06.008.

Ramos-Sánchez JM, Tirozzi PM, Alieque D, Geng F, Gao M, Jaeger KE, et al. LHY2 integrates night-length information to determine timing of poplar photoperiodic growth. Curr Biol. 2019;29(14):2402–2406.e4. https://doi.org/10.1016/j.cub.2019.06.003.

Randoux M, Davière JM, Jeuffrée J, Thouroude T, Pierre S, Toualbia Y, et al. SAWA M, Kay SA. GIAGANTEA directly activates flowering locus T in Arabidopsis. Plant Cell. 2010;22(6):1733–48. https://doi.org/10.1105/tpc.109.071108.

Sawata M, Ogawa Y, Hibrand-Saint-Oyant L, Fouther F, Kawamura K, Horibe T, et al. Genotype of FLOWERING LOCUS T homologue contributes to flower initiation differences in wild and cultivated rose. Plant Biol (Stuttgart). 2015;17(4):808–15. https://doi.org/10.1111/pbl.12299.

Sawata M, Kay SA. GIAGANTEA directly activates flowering locus T in Arabidopsis thaliana. Proc Natl Acad Sci U S A. 2011;108(28):11698–703. https://doi.org/10.1073/pnas.1102271.

Sawata M, Kay SA. GIAGANTEA directly activates flowering locus T in Arabidopsis thaliana. Proc Natl Acad Sci U S A. 2011;108(28):11698–703. https://doi.org/10.1073/pnas.1102271.

Scatolini N, Creasy K, Goodrich J, Schubert D. Keeping plants in shape: a comprehensive review. 3. Bio- tech. 2017;7(4):239. https://doi.org/10.1007/s40060-017-0380-y.

Shalit A, Rozman A, Goldshmidt A, Alvarez JP, Bowman JL, Eshed Y, et al. Serrano-Mislata A, Goslin K, Zheng B, Rae L, Wellmer F, Graciet E, et al. Regulation of terminal flower1 integrates photoperiod and temperature signals to regulate vegetative and reproductive development in rose. New Phytol. 2017;215(2):531–42. https://doi.org/10.1111/nph.14726.

Song YH, Shim JS, Kwon YJ, Hwang J, Hwang YS, Park JH, et al. Spatially distinct regulatory roles for gibberellins in the promotion of flowering of Arabidopsis under long photoperiods. Development. 2012;139(12):2198–209. https://doi.org/10.1242/dev.077164.

Song J, Map-based cloning and functional analysis of the flowering gene FTL1 in tomato. Master thesis, Chinese Academy of Agricultural Sciences 2010. https://doi.org/10.1105/1588.15866.

Song J, Map-based cloning and functional analysis of the flowering gene FTL1 in tomato. Master thesis, Chinese Academy of Agricultural Sciences 2010. https://doi.org/10.1105/1588.15866.

Song Y, Liu Y, Wang J, Chen T, Meng X, Deng H, et al. Efficiency of graft-transmitted JtFT for floral induction in woody perennial species of the Jatropha genus depends on transport distance. Tree Physiol. 2022;42(1):189–201. https://doi.org/10.1093/treephys/tpab116.

Taoka K, Ohki I, Tsuji H, Kojima C, Shimamoto K. Structure and function of florigen and the receptor complex. Trends Plant Sci. 2013;18(5):287–94. https://doi.org/10.1016/j.tplants.2013.02.002.

Tsuji H. Molecular function of florigen. Breed Sci. 2017;67(4):327–32. https://doi.org/10.1270/jsbsb.17026.

Tsuji H, Taoka K. Florigen signaling Enzymes. 2014;35:113–44. https://doi.org/10.1016/j.flr.2014.07.002.

Tuck F, Roudier F, Farrona S, Martin-Magniette ML, Guillaume E, Buisine N, et al. Arabidopsis TFL2/LHP1 specifically associates with genes marked by trimethylation of histone H3 lysine 27. PLoS Genet. 2007;3(6):e86. https://doi.org/10.1371/journal.pgen.0030086.

Varkonyi-Gasic E, Moss SMA, Voogd C, Wang T, Putterill J, Hellens RP. Homologs of FT, CEN and FD respond to developmental and environmental signals affecting growth and flowering in the perennial vine kwifruit. New Phytol. 2013;198(3):732–46. https://doi.org/10.1111/nph.12166.

Wang F, Gao Y, Liu Y, Zhang X, Xu G, Ma D, et al. BES1-regulated BEET1 controls photoperiodic flowering downstream of blue light signaling pathway in Arabidopsis. New Phytol. 2019;233(3):1407–19. https://doi.org/10.1111/nph.15866.

Wang L, Sun J, Ren L, Zhou M, Han X, Ding L, et al. CmBKBX accelerates flowering by targeting CmFTL1 directly in summer chrysanthemum. Plant Biotechnol J. 2020a;18(7):1562–72. https://doi.org/10.1111/pbj.13322.

Wang S, Li H, Li Y, Li Z, Qi J, Lin T, et al. FLOWERING LOCUS T improves cucumber adaption to higher latitudes. Plant Physiol. 2020b;182(2):908–18. https://doi.org/10.1093/plphys/kiab015.

Wang Y, Liu L, Song S, Li Y, Shen L, Yu H. DOFT and DOFTP1 affect reproductive development in the orchid Dendrobium Chao Praya smile. J Exp Bot. 2017;68(21–22):5759–72. https://doi.org/10.1093/jxb/erx400.

Wei Q, Ma C, Xu Y, Wang T, Chen Y, Lu J, et al. Control of chrysanthemum flowering through integration with an aging pathway. Nat Commun. 2017;8(1):829.https://doi.org/10.1038/s41467-017-00812-0.

Wellmer F, Reichmann JL. Gene networks controlling the initiation of flower development. Trends Genet. 2010;26(12):519–27. https://doi.org/10.1016/j.tig.2010.09.001.

Wen C, Zhao W, Liu Y, Wang L, Yang Y, Liu X, et al. CsFTL1 inhibits determinate growth and terminal flower formation through interaction with CsNO2A in cucumber. Development. 2019;146(4):dev180166. https://doi.org/10.1242/dev.180166.

Wu YM, Ma YJ, Wang Y, Zhou H, Gan ZM, Zeng RF, et al. Mobility of FLOWERING LOCUS T protein as a systemic signal in trifoliate orange and its low accumulation in grafted juvenile scions. Hortic Res. 2022;9:uhac056. https://doi.org/10.1093/hortres/uhac056.

Xu L, Liu Y, Cao P, Hou X, Yu H. MOTHER OF FT AND TFL1 regulates seed germination through a negative feedback loop modulating ABA signaling in Arabidopsis. Plant Cell. 2010;22(6):1733–48. https://doi.org/10.1105/tpc.109.073072.
Xu F, Rong X, Huang X, Cheng S. Recent advances of flowering locus T gene in higher plants. Int J Mol Sci. 2012;13(3):773–81. https://doi.org/10.3390/ijms1303773.

Xu J, Hua K, Lang Z. Genome editing for horticultural crop improvement. Hortic Res. 2019;6:113. https://doi.org/10.1038/s41438-019-0196-5.

Yamaguchi A, Kobayashi Y, Goto K, Abe M, Araki T. TWIN SISTER OF FT (TSF) acts as a floral pathway integrator redundantly with FT. Plant Cell Physiol. 2005;46(8):1175–89. https://doi.org/10.1093/pcp/pci151.

Yang LW, Wen XH, Fu JX, Dai SL. CICRY2 facilitates floral transition in Chrysanthemum lavandulifolium by affecting the transcription of circadian clock-related genes under short-day photoperiods. Hortic Res. 2018;5:58. https://doi.org/10.1038/s41438-018-0063-9.

Yang Y, Ma C, Xu Y, Wei Q, Imtiaz M, Lan H, et al. A zinc finger protein regulates flowering time and abiotic stress tolerance in Chrysanthemum by modulating gibberellin biosynthesis. Plant Cell. 2014;26(5):2038–54. https://doi.org/10.1105/tpc.114.124867.

Yoo SJ, Chung KS, Jung SH, Yoo SY, Lee JS, Ahn JH. BROTHER OF FT AND TFL1 (BFT) has TFL1-like activity and functions redundantly with TFL1 in inflorescence meristem development in Arabidopsis. Plant J. 2010;63(2):241–53. https://doi.org/10.1111/j.1365-313X.2010.04234.x.

Yoo SY, Kardailsky I, Lee JS, Weigel D, Ahn JH. Acceleration of flowering by overexpression of MFT (MOTHER OF FT AND TFL1). Mol Cells. 2004;17(1):95–101 http://europepmc.org/article/MED/15055534.

Zhang S, Zhang Y, Li K, Yan M, Zhang J, Yu M, et al. Nitrogen mediates flowering time and nitrogen use efficiency via floral regulators in Rice. Curr Biol. 2021;31(4):671–683.e5 https://doi.org/10.1016/j.cub.2020.10.095.

Zhao W, Gu R, Che G, Cheng Z, Zhang X. CsfTFL1b may regulate the flowering time and inflorescence architecture in cucumber (Cucumis sativus L.). Biochem Biophys Res Commun. 2018;499(2):307–13. https://doi.org/10.1016/j.bbrc.2018.03.153.

Zhou S, Jiang L, Guan S, Gao Y, Gao Q, Wang G, et al. Expression profiles of five FT-like genes and functional analysis of PhFT-1 in a Phalaenopsis hybrid. Electron J Biotechnol. 2018;31:75–83. https://doi.org/10.1016/j.ejbt.2017.11.003.

Zhu Y, Klasfeld S, Jeong CW, Jin R, Goto K, Yamaguchi N, et al. TERMINAL FLOWER 1-FD complex target genes and competition with FLOWER-ING LOCUS T. Nat Commun. 2020;11(1):5118. https://doi.org/10.1038/s41467-020-18782-1.

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