Review

Florigen and anti-florigen: flowering regulation in horticultural crops

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Flowering time regulation has significant effects on the agricultural and horticultural industries. Plants respond to changing environments and produce appropriate floral inducers (florigens) or inhibitors (anti-florigens) that determine flowering time. Recent studies have demonstrated that members of two homologous proteins, FLOWERING LOCUS T (FT) and TERMINAL FLOWER 1 (TFL1), act as florigen and anti-florigen, respectively. Studies in diverse plant species have revealed universal but diverse roles of the *FT/TFL1* gene family in many developmental processes. Recent studies in several crop species have revealed that modification of flowering responses, either due to mutations in the florigen/anti-florigen gene itself, or by modulation of the regulatory pathway, is crucial for crop domestication. The *FT/TFL1* gene family could be an important potential breeding target in many crop species.

Key Words: anti-florigen, chrysanthemum, florigen, FLOWERING LOCUS T (FT), photoperiod, TERMINAL FLOWER 1 (TFL1).

Introduction

Many plants utilize fluctuations in day-length (photoperiod) as the most reliable indicator of seasonal progression to determine when to initiate flowering. This phenomenon, called photoperiodism, enables plants to set seeds at favorable conditions and maximize their chance of survival. Photoperiodism was first described in detail by Garner and Allard (1920). They investigated the flowering response of a late-flowering tobacco cultivar 'Maryland Mammoth' and a soybean cultivar 'Biloxi', and found that these plants flower in response to changes in day-length, not light intensity, temperature, or nutrient availability. They categorized plants into three types based on their photoperiodic responses; short-day plants (SDPs), long-day plants (LDPs), and day-neutral plants (DNPs). Flowering in SDPs occurs or is accelerated when the night length is greater than a critical minimum, whereas flowering in LDP occurs or is promoted when the day becomes longer, and DNPs flower regardless of day-length. Chailakhyan (1936) proposed the concept of the flowering hormone "florigen", which is synthesized in the leaves and transmitted to the shoot apex to induce flowering. Recent molecular genetics approaches have demonstrated that homologs of the FLOWERING LOCUS T (FT) protein of *Arabidopsis* act as florigens in several plant spe-

cies (Corbesier *et al.* 2007, Lifschitz *et al.* 2006, Lin *et al.* 2007, Tamaki *et al.* 2007). In *Arabidopsis*, the FT protein is induced under flower-inductive long day (LD) photoperiod in leaves, whereas it forms a complex with a bZIP type transcription factor FD at the shoot apical meristem (SAM) to induce floral meristem-identity genes, such as *APETALA1* (*AP1*) and *FRUITFULL* (*FUL*) (Abe *et al.* 2005, Kardailsky *et al.* 1999, Kobayashi *et al.* 1999, Wigge *et al.* 2005). The long-distance transmission of the FT protein and its rice homolog Heading date 3a (Hd3a) from the leaves to the shoot apex via the phloem was further determined (Corbesier *et al.* 2007, Tamaki *et al.* 2007). The FT/Hd3a family protein acts as the universal flowering hormone "florigen" in many plant species (Matsoukas 2015, Wickland and Hanzawa 2015) (**Table 1**).

In addition to the floral inducer florigen, the systemic floral inhibitor produced in non-induced leaves inhibit flowering. The concept of a floral repressor (anti-florigen) was proposed almost at the same time with that of the florigen (Lang and Melchers 1943). Many physiological observations in *Hyoscyamus*, strawberry, *Lolium*, chrysanthemum, tobacco, and *Pharbitis* suggested the existence of the systemic floral inhibitor (Evans 1960, Guttridge 1959, Lang and Melchers 1943, Lang *et al.* 1977, Ogawa and King 1990, Tanaka 1967). A grafting experiment in tobacco plants with different photoperiodic responses strongly supported this hypothesis; a floral inhibitor produced in the leaves of LD tobacco under non-inductive short day (SD) systemically inhibited the flowering of the grafted day-neutral (DN) tobacco plants (Lang *et al.* 1977). Since the 1990s, molecular

Table 1. List of FT/TFL1 family genes in representative species

Species	Gene name	Effect on flowering	Other function	Regulatory input	Site of expression	References
Arabidopsis	FT	Induction		LD	Leaf	Bradley *et al.* 1997
	TSF	Induction		LD	Leaf	Kobayashi *et al.* 1999
	TFL1	Repression	Inflorescence development		Shoot apex Root	Kardailsky *et al.* 1999 Yamaguchi *et al.* 2005 Yoo *et al.* 2010
	BFT	Repression	Inflorescence development	LD, Salinity stress	Leaf	Xi *et al.* 2010 Huang *et al.* 2012
	ATC	Repression		SD	Vascular tissue	Ryu *et al.* 2014
	MFT	Induction	Seed germination		Seed	
Rice	Hd3a	Induction		SD	Leaf	Kojima *et al.* 2002
	RFT1	Induction		LD	Leaf	Izawa *et al.* 2002 Nakagawa *et al.* 2002
	RCN1	Repression			Shoot apex	Tamaki *et al.* 2007
	RCN2	Repression			Shoot apex	Komiya *et al.* 2009
Chrysanthemum	CsFTL1	Induction		LD, NB	Leaf	Oda *et al.* 2012
	CsFTL2	Induction		LD, Sucrose	Leaf	Higuchi *et al.* 2013 Nakano *et al.* 2013
	CsFTL3	Induction		SD, Heat	Leaf	Higuchi and Hisamatsu 2015
	CsTFL1	Repression			Shoot apex Root	Nakano *et al.* 2015a Sun *et al.* 2017
	CsAFT	Repression		LD, NB	Leaf	
Strawberry	FvTFL1	Repression		LD, Cool temperature	Shoot apex	Koskela *et al.* 2012 Mouhu *et al.* 2013
	FvFT1	Induction		LD	Leaf	Nakano *et al.* 2015b Rantanen *et al.* 2015
	FaFT3	–		SD	Shoot apex	Koskela *et al.* 2016
Tomato	SFT	Induction			Matured leaf	Lifschitz *et al.* 2006
	SP	Repression	Inflorescence development		Young leaf, Shoot apex	Shalit *et al.* 2009 Cao *et al.* 2016
	SP5G	Repression		LD	Cotyledon, Leaf	Soyk *et al.* 2017
	SP5G2	Repression		SD	Cotyledon, Leaf	
	SP5G3	Repression		SD	Cotyledon, Leaf	
Sugar beet	BvFT1	Repression		SD, Vernalization	Leaf	Pin *et al.* 2010
	BvFT2	Induction		LD, Vernalization	Leaf	
Rose	RoKSN	Repression			Shoot apex	Iwata *et al.* 2012
	RoFT	Induction			Shoot (reproductive)	Randoux *et al.* 2013 Otagaki *et al.* 2015
Morning glory	PnFT1	Induction		SD	Cotyledon, Leaf	Hayama *et al.* 2007
	PnFT2	–		SD, Stress	Cotyledon, Leaf	Wada *et al.* 2010
Sunflower	HaFT1	Repression			Shoot apex	Blackman *et al.* 2010
	HaFT4	Induction		LD	Leaf	
Potato	StSP3D	Induction			Leaf	Navarro *et al.* 2011
	StSP6A	Induction	Induction of tuberization	SD	Leaf, Stolon	Abelenda *et al.* 2016
	StSP5G	Repression	Inhibition of tuberization	LD	Leaf	
Onion	AcFT2	Induction		Vernalization	Central bud Leaf	Lee *et al.* 2013
	AcFT1	Induction	Induction of bulb formation	LD	Leaf	
	AcFT4	Repression	Inhibition of bulb formation	SD	Leaf	

genetic studies in *Arabidopsis* revealed that the TERMINAL FLOWER 1 (TFL1), a member of the phosphatidylethanol-amine-binding protein (PEBP) family protein, acts to suppress flowering (Bradley *et al.* 1997). The *TFL1* is expressed in the SAM and maintains an indeterminate inflorescence (Conti and Bradley 2007, Jaeger *et al.* 2013, Ratcliffe *et al.* 1999). TFL1 also forms a complex with FD, an interacting partner of FT, and acts to suppress flowering by antagonizing the florigenic activity of the FT-FD complex (Abe *et al.* 2005). Although the TFL1 acts as a floral inhibitor, it only moves over short distances within the meristematic zone (Conti and Bradley 2007). In *Arabidopsis*, it was reported that another *TFL1*-like gene, *Arabidopsis thaliana CENTRORADIALIS homolog* (*ATC*), is expressed in the vasculature tissues under non-inductive SD photoperiod, and acts systemically to suppress flowering (Huang *et al.* 2012). In sugar beet (*Beta vulgaris*), two *FT* homologs (*BvFT1* and *BvFT2*) with antagonistic function have been reported (Pin *et al.* 2010). BvFT1 suppresses flowering under SDs and before vernalization by repressing the expression of the floral promoter BvFT2. A recent study in a wild diploid chrysanthemum (*Chrysanthemum seticuspe*) identified a floral inhibitor, Anti-florigenic FT/TFL1 family protein (CsAFT), which moves over long distances (Higuchi *et al.* 2013). The *CsAFT* was induced in leaves under non-inductive LD or night-break (NB) photoperiods. CsAFT proteins move long distances from leaves to the shoot apex, and inhibit flowering by directly antagonizing the florigen complex activity. These findings suggest that the balance between floral inducers (florigens) and inhibitors (anti-florigens) determine flowering time variations in many plant species (**Fig. 1**).

Molecular mechanisms of the FT/TFL1 function

The *FT/TFL1* gene encodes a small protein similar to the PEBP. In *Arabidopsis*, there are six members of the PEBP gene family. *FT* and *TWIN SISTER OF FT* (*TSF*) act as floral activators, whereas *TFL1*, *ATC*, and *BROTHER OF FT AND TFL1* (*BFT*) act as floral repressors (Bradley *et al.* 1997, Kardailsky *et al.* 1999, Kobayashi *et al.* 1999, Mimida *et al.* 2001, Yamaguchi *et al.* 2005, Yoo *et al.* 2010). The *MOTHER OF FT AND TFL1* (*MFT*) has a weak floral-inducer activity and is involved in seed germination (Xi *et al.* 2010, Yoo *et al.* 2004). FT/TFL1-like proteins control flowering probably through transcriptional regulation of target genes, because these proteins form a complex with a transcription factor FD (Abe *et al.* 2005, Hanano and Goto 2011, Huang *et al.* 2012, Jang *et al.* 2009, Ryu *et al.* 2014, Wigge *et al.* 2005). In rice, the Hd3a forms a complex with the 14-3-3 adaptor proteins and OsFD1, known as the florigen activation complex (FAC), and then induces a rice *AP1* homolog *OsMADS15* (Taoka *et al.* 2011). Plant PEBP family proteins can be classified into three major clades, FT-like, TFL1-like, and MFT-like. FT-like and TFL1-like proteins have similar structures, but they have opposing roles in regulating flowering. A critical region or amino acid residues that convert a floral inducer into a repressor have been identified previously. In *Arabidopsis*, the segment B in the fourth exon encoding an external loop structure of PEBP is particularly important (Ahn *et al.* 2006). Specific mutations at Tyr-85, Glu-109, Tyr-134, Trp-138, Gln-140, and Asn-152 residues could convert FT into a TFL1-like repressor (Ahn *et al.* 2006, Hanzawa *et al.* 2005, Ho and Weigel 2014). In sugar beet, substitution of 3 amino acid residues in the external loop of BvFT1 (including Tyr-134 and Trp-138) was sufficient to convert its repressing activity to a promoting activity (Pin *et al.* 2010). The surface charges of FT and TFL1 are thought to be critical for recruitment of yet unidentified transcriptional coactivators or corepressors (Ho and Weigel 2014).

Fig. 1. Flowering time regulation by florigen and anti-florigen in Arabidopsis, rice, sugar beet, and chrysanthemums. The blue (solid) circles indicate systemic floral inducers, while red (dotted) circles indicate systemic floral inhibitors. TFL1 homologs suppress flowering at the shoot apex.

Photoperiodic flowering in Arabidopsis and rice

In *Arabidopsis*, induction of *FT* under LD photoperiod is dependent on the interaction of the endogenous biological clock and the external light inputs (Golembeski and Imaizumi 2015). The circadian rhythm entrained by light/dark cycles sets the expression of *CONSTANS* (*CO*), a positive regulator of *FT*, to occur in the evening. When high *CO* expression coincides with the light signal perceived by photoreceptors, a CO protein is stabilized and it induces *FT* (Valverde *et al.* 2004, Yanovsky and Kay 2002). In rice, a facultative SDP, expression of a *CO* homolog, *Heading date 1* (*Hd1*), is regulated by a circadian clock peaking in the
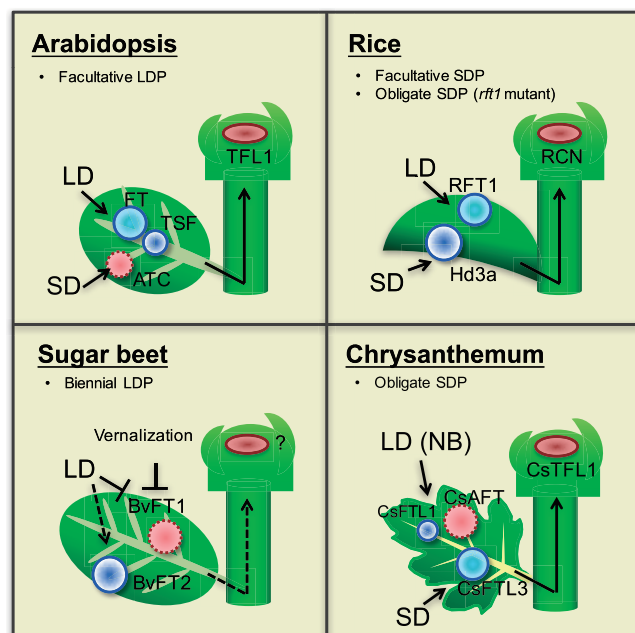
evening. The coincidence of Hd1 with the phytochrome signal under LD evenings suppresses flowering by negatively regulating the expression of *Hd3a* (Hayama *et al.* 2003, Izawa *et al.* 2002). Rice contains unique pathways that function independent of *CO* (*Hd1*). *Early heading date 1* (*Ehd1*), encoding a B-type response regulator, promotes flowering by up-regulating *Hd3a* expression independent of *Hd1* (Doi *et al.* 2004). Grain number, plant height, and heading date 7 (Ghd7), a CCT domain protein, is induced under LDs and suppresses flowering by down-regulating *Ehd1* expression (Xue *et al.* 2008). Interestingly, induction of both *Ehd1* and *Ghd7* by light is limited to a specific time of day (the photo-sensitive phase or the "gate") by a circadian clock action. The gate for *Ehd1* induction always opens around dawn, but the gate for *Ghd7* induction with red light opens at different times depending on day length. Acute induction of *Hd3a* in response to critical day-length is achieved by the interaction of these two gating mechanisms (Itoh *et al.* 2010). In addition to *Hd3a*, rice has another florigen gene, *RICE FLOWERING LOCUS T1* (*RFT1*), that functions under LD photoperiods (Komiya *et al.* 2009). Loss-of-function of *RFT1* results in extremely late flowering under LD, which is similar to the flowering response of absolute SDPs (Ogiso-Tanaka *et al.* 2013) (**Fig. 1**).

Flowering time regulation in chrysanthemum

Chrysanthemum (*C. morifolium*) is one of the most important floricultural crops around the world. The autumn-flowering chrysanthemum cultivars are categorized as absolute SDP that require repeated SD photoperiod for successful flowering, but their vegetative growth can be strictly maintained under LD or NB conditions. Soon after the discovery of photoperiodism by Garner and Allard, methods for day-length manipulation to control chrysanthemum flowering were established (Laurie 1930, Poesch 1936, Post 1931). Chrysanthemum growers use blackouts or artificial lighting (day-length extension or NB) to meet the demand for marketable flowers throughout the year. Thus, chrysanthemum is the most successful example of the use of day-length manipulation to benefit commercial crop production. Although the light sensitive flowering behavior made this plant a major floricultural crop, molecular mechanisms of photoperiodic flowering in chrysanthemums is largely unknown. The cultivated chrysanthemums are complex hybrids derived from several different species (Klie *et al.* 2014). The complex hybridity and polyploidy in this species make it difficult to conduct molecular-genetic modifications. To overcome this issue, a wild diploid species *C. seticuspe* has recently been used as an alternative model of chrysanthemum cultivars.

FT/TFL1-like genes in chrysanthemum

Oda *et al.* (2012) identified three *FT*-like genes from *C. seticuspe*: *CsFTL1*, *CsFTL2*, and *CsFTL3*. Among these, only *CsFTL3* is up-regulated in the leaves under flowering-

inducible SD photoperiod. *CsFTL1* is up-regulated under LD or NB photoperiods, inhibiting flowering, but has weak florigenic activity (Higuchi *et al.* 2013, Higuchi and Hisamatsu 2015). *CsFTL2* is expressed at very low levels in the leaves, but transient expression in protoplasts suggests that it also has weak florigenic activity (Higuchi and Hisamatsu 2015). More recently, *CmFTL2* was suggested to be involved in sucrose-induced promotion of flowering in a photo-insensitive *C. morifolium* cultivar (Sun *et al.* 2017). Constitutive expression of *CsFTL3* in *C. morifolium* resulted in photoperiod-insensitive flowering, and this flower-inducing effect was graft-transmissible. These results suggest that *CsFTL3* encodes a systemic floral inducer florigen in chrysanthemums (Oda *et al.* 2012). Unlike *Arabidopsis* and *Pharbitis*, chrysanthemums require repeated cycles of SD photoperiod for floral initiation and successful anthesis (Corbesier *et al.* 2007, Hayama *et al.* 2007, Oda *et al.* 2012). Consistent with this requirement, *CsFTL3* expression was not immediately induced by shifting plants from LD to SD photoperiod, but gradually increased with repetitive SD cycles (Nakano *et al.* 2013). Moreover, another floral inducer *CsFTL1* is expressed under non-inductive LD or NB, but flowering is strictly suppressed under those conditions. From the screening of highly expressed genes in leaves under NB compared to SD photoperiod, one *TFL1*-like gene (*CsAFT*) has been identified. *CsAFT* was induced in leaves under non-inductive LD or NB photoperiods and it rapidly decreased after a shift to SD photoperiod (Higuchi *et al.* 2013). Constitutive expression of *CsAFT* in *C. seticuspe* and *C. morifolium* (*CsAFT*-ox) resulted in extremely late flowering under SD conditions, indicating that CsAFT has a strong floral-repressor activity (**Fig. 2A**). Furthermore, the knockdown of *CsAFT* by RNAi resulted in reduced sensitivity to NB and promoted flowering. Grafting experiment using CsAFT-ox plants clearly demonstrated that CsAFT proteins can move long distances across the grafting union and act as a systemic floral inhibitor. Transient gene expression assay revealed that both CsFTL3 and CsAFT interact with the *C. seticuspe* homolog of FD (CsFDL1), suggesting that CsAFT suppresses flowering by directly antagonizing the flower inducibility of CsFTL3-CsFDL1 (Higuchi *et al.* 2013). In addition to a systemic floral inhibitor CsAFT, a *TFL1* homolog (*CsTFL1*) is constitutively expressed in shoot tips regardless of the photoperiods and shows strong floral inhibitor activity (Higuchi and Hisamatsu 2015). CsTFL1 also interacts with CsFDL1, suggesting that it suppresses flowering by directly interfering with the CsFTL3-CsFDL1 complex formation. Thus, in chrysanthemums, strict maintenance of a vegetative state under non-inducible photoperiod is achieved by a dual inhibitory system; one is a systemic floral inhibitor produced in non-inducible leaves (AFT), and another is a local inhibitor constitutively expressed at the shoot apex (TFL1) (Higuchi and Hisamatsu 2015) (**Fig. 2B**).

Photo-perception and light sensitive time of day

Light quality affects chrysanthemum flowering. NB with

Fig. 2. Photoperiodic regulation of flowering in chrysanthemums. (A) Over-expression of *AFT* in *Chrysanthemum morifolium* results in extremely late flowering under short day (SD) photoperiod. (B) Under SD, FTL3 is produced in leaves to systemically induce flowering. Under non-inductive long day (LD) or night-break (NB), AFT is induced in leaves to systemically inhibit flowering. The red light signal perceived by phyB induces *AFT* but suppresses *FTL3* expression. Induction of *AFT* by phyB is gated by the circadian clock. TFL1 acts as a constitutive local repressor of flowering. (C) Model for induction of *AFT* under LD, SD, and NB conditions. The gate for *AFT* induction opens at a constant time after dusk regardless of the photoperiod. Under LD, the photo-sensitive phase (dotted line) of *AFT* interacts with red light in the morning and induces *AFT* expression (solid line) to inhibit flowering. Under NB, illumination at midnight coincides with the photo-sensitive phase of *AFT*.

red light effectively inhibits flowering, which is partially reversed by subsequent exposure to far-red (FR) light, suggesting the involvement of phytochromes in this response (Cathey and Borthwick 1957, Sumitomo *et al.* 2012). Interestingly, NB with blue light and FR light are both effective in inhibiting flowering when the plants are grown under a daily photoperiod with monochromatic blue light, but not white (blue + red) light (Higuchi *et al.* 2012). This suggests that light quality during the daily photoperiod affects the sensitivity to NB at midnight, and at least two distinct phy-mediated regulation systems might exist. In rice, it has been reported that phyB acts as a primary photoreceptor mediating NB response (Ishikawa *et al.* 2005). In *C. seticuspe*, the knock-down of *CsPHYB* by RNAi resulted in reduced sensitivity to NB with red light and flowered extremely early. In *CsPHYB*-RNAi plants, *CsFTL3* was up-regulated, whereas *CsAFT* was down-regulated under NB conditions. These results indicated that CsPHYB acts as a primary photoreceptor mediating NB response and inhibits flowering by repressing *CsFTL3* and inducing *CsAFT* (Higuchi *et al.* 2013).

In *C. seticuspe*, the most sensitive time for NB occurs 8 to 11 h after dusk. Consistent with this, *CsAFT* expression

was strongly induced by red light from 8 to 10 h after dusk under both SD and LD conditions. Moreover, if long nights (14 h) were given, flowering was successfully induced, even under non-24-h light/dark cycles. Thus, induction of *CsAFT* by phy signaling is gated by an endogenous clock, and the gate for induction of *CsAFT* opens fully at a constant time after dusk, regardless of the photoperiod conditions provided (**Fig. 2C**). Therefore, day-length recognition by chrysanthemums is dependent on the absolute duration of darkness. Chrysanthemums detect the length of night by a time-keeping component, which is initiated by the dusk signal. Although the time-keeping mechanisms of chrysanthemums is still unclear, a recent study suggested the involvement of a core clock-component *LATE ELONGATED HYPOCOTYL* homolog of *C. seticuspe* (*CsLHY*). Constitutive expression of *CsLHY* fused with the transcriptional repressor domain (CsLHY-SRDX) showed photoperiod-insensitive floral transition, but further development of the capitulum was arrested (Oda *et al.* 2017). SRDX is a short transcriptional repression domain that turns a transcriptional activator into a strong repressor (Hiratsu *et al.* 2003). Thus, the plant expressing chimeric repressor shows phenotype similar to the loss-of-function mutation of the original transcription factor. In CsLHY-SRDX plants, diurnal and circadian expression of clock-related genes was not drastically attenuated, but expression of both *CsFTL3* and *CsAFT* was down-regulated. To date, homologs of circadian clock components and clock-controlled flowering time genes have been isolated in several species in the genus *Chrysanthemum* (Fu *et al.* 2014, 2015, Higuchi *et al.* 2012, Ren *et al.* 2016, Yang *et al.* 2014). It is of great interest to test whether these genes are involved in dark-time measurement and dark-dominant flowering of chrysanthemums.

Currently in Japan, chrysanthemum growers regulate flowering time by applying NB of 4–5 h at the middle of night. In *C. seticuspe*, systemic anti-florigen *CsAFT* was maximally induced by red light provided at a consistent time after dusk, but not during the middle of the darkness period (Higuchi *et al.* 2013). Consistent with this finding, the maximum sensitivity to NB (NB-max) appeared at a constant time after dusk in cultivated chrysanthemum varieties (Hakuzan and Kooriyama 2013). From these findings, by reconsidering the NB-max, which gradually changes depending on the season, it is possible to develop more efficient and energy-saving methods of artificial lighting.

Flowering retardation by high temperature

The growth temperature also affects chrysanthemum flowering. The flowering of autumn-flowering cultivars is severely delayed by high temperature during summer and early autumn in Japan. Recent studies have shown that heat-induced delay of flowering is mainly caused by inhibition of capitulum development (Nakano *et al.* 2013). Under optimum growth temperature, expression of *FTL3* continues to increase under repeated SD cycles, which leads to successful development of capitulum. However, up-regulation

of *FTL3* in leaves was inhibited under high temperature (Nakano *et al*. 2013). In contrast to *FTL3*, expression of *AFT* was not affected by high temperature. Interestingly, high temperature from midnight to dawn was the most effective condition delaying flowering (Nakano *et al*. 2015a), suggesting that some common time-keeping mechanisms may operate to set both heat-sensitive and light-sensitive time-of-day in chrysanthemums. Transcriptional regulation of *FTL3* is more sensitive to high temperature compared to that of *AFT*.

Regulation of flowering time and inflorescence architecture in tomato

Tomato (*Solanum lycopersicum*) is one of the most important vegetable crops around the world. The flowering time of tomato is regulated by the balance between the flowering inducer SINGLE FLOWER TRUSS (SFT) and the repressor SELF PRUNING (SP). *SFT*, a tomato ortholog of *FT*, is expressed in expanded mature leaves and systemically promotes flowering (Lifschitz *et al*. 2006, Shalit *et al*. 2009). In contrast, *SP*, a tomato homolog of *TFL1*, is expressed in young leaves and the shoot apex, and suppresses flowering (Shalit *et al*. 2009). The *sp* mutant flower earlier and gradually results in diminished sympodial growth, resulting in a more compact, determinate plant with nearly synchronized fruit ripening. Introduction of recessive *sp* mutation into modern tomato cultivars facilitated once-over mechanical harvesting, resulting in a major expansion of the tomato processing sector (Pnueli *et al*. 1998). The balance between SFT and SP regulates flowering and determinate or indeterminate shoot architecture. In the *sp* mutant background, the combination of weak alleles of *SFT* and mutations in *SUPPRESSOR OF SP* (*SSP*, *FD* homolog) weakened the activity of the florigen activation complex (FAC), resulting in a partially determinate architecture that provided maximum yield (Park *et al*. 2014).

A BLAST survey against tomato whole genome-database revealed the presence of at least 13 PEBP genes, of which six (*SP3D/SFT*, *SP6A*, *SP5G*, *SP5G1*, *SP5G2*, and *SP5G3*) were *FT*-like genes (Cao *et al*. 2016). Among these, only *SP3D/SFT* had floral inducer activities whereas *SP5G*, *SP5G2*, and *SP5G3* had floral inhibitor activities. The cultivated modern tomato species are categorized as DNPs, which do not respond to change in day-length, but the flowering of the wild species is promoted under SD conditions. A recent study reported that one of the *SFT* paralogs, *SELF PRUNING 5G* (*SP5G*), is highly induced in leaves grown under LD conditions in wild species, but not in cultivated species (Soyk *et al*. 2017). The loss-of-function mutation of *SP5G* induced by CRISPR/Cas9 system resulted in rapid flowering and early yield. Thus, SP5G acts as anti-florigen to suppress flowering under non-inductive LD photoperiod in a wild tomato species (Soyk *et al*. 2017). Mutations in the *cis*-regulatory region of cultivated tomato species reduced LD-induction of the floral repressor *SP5G*, resulting in early

(A) Tomato
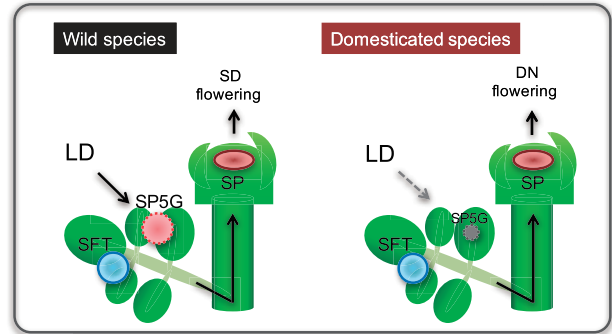
(B) Strawberry (*F. vesca*)
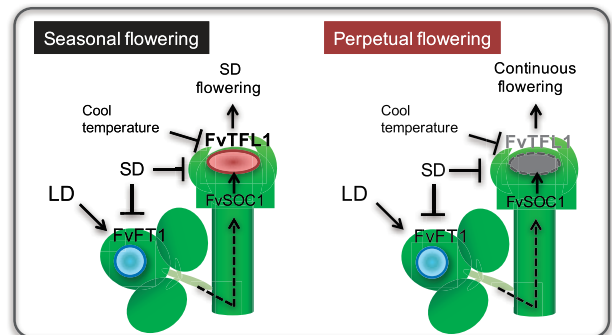
Fig. 3. The model for flowering time regulation in two major horticultural crops. (A) Flowering regulation in tomato. In wild species, a systemic anti-florigen SP5G is induced under long days (LD) to inhibit flowering. In day neutral (DN) domesticated species, the induction pathway of *SP5G* is attenuated. (B) Flowering regulation in wild strawberry (*F. vesca*). In seasonal flowering of short day (SD) cultivars, a strong floral repressor TFL1 suppresses flowering under LD. In perpetual flowering cultivars in which repressor activity of TFL1 is absent, FT1 and SOC1, act to promote flowering under LD.

flowering under LD photoperiod, which enabled cultivation of tomato in high latitude areas (**Fig. 3A**). Thus, day-length sensitivity is essentially lost in domesticated tomato. Recently, it has been reported that domesticated tomato cultivars show longer period lengths in circadian rhythms (Müller *et al*. 2016). In cultivated tomato, allelic variation in the homolog of *Arabidopsis, EMPFINDLICHER IM DUNKELROTEN LICHT 1* (*EID1*), which encodes the F-box protein, is responsible for the deceleration of the circadian clock. The *EID1* allele of cultivated tomato enhances photosynthetic performance specifically under LD photoperiod (Müller *et al*. 2016).

Flowering time regulation in strawberry

Strawberry (*Fragaria* × *ananassa*) is a perennial plant that belongs to the Rosaceae family, in which flowering is induced by low temperature and SD photoperiod (Heide *et al*. 2013). They normally initiate the flower bud in response to SD and cool temperature in autumn, but further development of the flower bud (blooming) is promoted under LD photoperiod in the following spring. Recent studies in rose

and diploid woodland strawberry (*F. vesca*) revealed that the loss-of-function mutation in *TFL1* homolog is the principal cause of the continuous flowering phenotype of ever bearing cultivars (Iwata *et al*. 2012, Koskela *et al*. 2012). In seasonal flowering *F. vesca*, *FvTFL1* mRNA expression is induced by LD photoperiod in shoot tips, but SD photoperiod suppresses it. However, in ever bearing (continuous flowering) cultivars, loss-of-function of a strong floral repressor, *FvTFL1*, resulted in the de-repression of flowering under LD photoperiod and reversed photoperiodic response (Koskela *et al*. 2012). Interestingly, a homolog of *FT* (*FvFT1*) is up-regulated in mature leaves specifically under LD conditions, and *SOC1* (*FvSOC1*) was similarly up-regulated under LD conditions in the shoot tips to activate expression of *FvTFL1* (Mouhu *et al*. 2013, Rantanen *et al*. 2014). Thus, *FvFT1* and *FvSOC1* act to suppress flowering under LD conditions through the activation of the strong floral repressor *FvTFL1*, but they act to promote flowering in continuous flowering accessions that lack functional *FvTFL1*. Moreover, *FvTFL1* was regulated by a temperature-dependent pathway, independent of the regulation of *FvFT1-FvSOC1* by photoperiod (Rantanen *et al*. 2015) (**Fig. 3B**). Molecular mechanisms of flowering regulation in cultivated octoploid species (*F. × ananassa*) are likely to be more complex. Genetic studies have suggested that continuous flowering of cultivated strawberry is controlled by a single dominant locus (Gaston *et al*. 2013, Morishita *et al*. 2012), whereas the continuous flowering trait of *F. vesca* is recessive. Recent studies have reported that flowering of *F. × ananassa* is strongly dependent on *FaTFL1* regulation by day-length and temperature (Koskela *et al*. 2016, Nakano *et al*. 2015b), but the factors involved in its promotion remain unclear. One of the *FT* paralogs, *FaFT3*, was up-regulated in the shoot tip under SD photoperiod and/or low temperature, in accordance with the promotion of flowering in *F. × ananassa* (Nakano *et al*. 2015b). It is of great interest to know whether the flowering of strawberry can be explained only by the reduced activity of a strong floral repressor or by the up-regulation of yet an unidentified floral promoter. Comparing the molecular mechanisms of flowering between *F. × ananassa* and *F. vesca* could provide further information.

Control of storage organ formation by florigens

The timing of vegetative reproduction events, such as the formation of the underground storage organ, is regulated by photoperiod. In potato (*Solanum tuberosum*), over-expression of the rice florigen gene *Hd3a* induced tuberization even under the non-inductive LD photoperiod (Navarro *et al*. 2011). One of the *FT* paralogs, *StSP6A*, is up-regulated in response to the inductive SD photoperiod in leaves, and acts systemically to induce tuberization. *StSP6A* expression is regulated by auto-regulatory mechanisms that amplify this signal in the stolons (Navarro *et al*. 2011). On the other hand, another *FT* paralog, *StSP5G*, is induced in leaves

under non-inductive LD photoperiod in a *StPHYB*- and *StCOL1*-dependent manner and acts as a repressor of tuberization by preventing *StSP6A* expression (Abelenda *et al*. 2016). In onion (*Allium cepa*), different *FT*-like genes were shown to be involved in flowering and bulb formation (Lee *et al*. 2013). Onion is a biennial crop that forms bulbs under LDs of late spring to summer, and the overwintered bulbs flower in the next season. *AcFT2* expression is correlated with flowering response, suggesting that this gene encodes a florigen. *AcFT1* is induced in leaves under LD photoperiod and promotes bulb formation. On the other hand, *AcFT4* is induced under SD photoperiod and inhibits bulb formation by preventing up-regulation of *AcFT1* (Lee *et al*. 2013).

Conclusions and future perspectives

Recent studies in diverse plant species have suggested that modifications in the floral inducer or inhibitor activity could lead to variations in flowering responses. As reported in *Arabidopsis* and sugar beet, a small number of amino acid substitutions could cause conversion of the floral inducer to repressor activity (Ho and Weigel 2014, Pin *et al*. 2010). Studies in rose and strawberry indicated that the loss-of-function of a single strong floral repressor, TFL1, can convert seasonal flowering to a perpetual flowering habit (Iwata *et al*. 2012, Koskela *et al*. 2012). In domesticated tomato, mutations in the *cis*-regulatory region of a systemic anti-florigen, SP5G, reduced its expression under non-inducible LD photoperiod, resulting in rapid flowering and early yield (Soyk *et al*. 2017) (**Fig. 3**). These results suggest that manipulating the gene structure or the expression levels of florigens/anti-florigens through conventional breeding or biotechnological approaches could greatly accelerate the development of new cultivars with desirable flowering characteristics. These findings suggest that the *FT/TFL1* gene family could be one of the most important breeding targets in many crop species. In addition to crop breeding, artificial control of flowering by manipulating the light and/or temperature conditions is particularly important for horticultural industries. Investigating the detailed expression profile of florigen/anti-florigen genes in response to various environmental stimuli could help us to develop efficient and energy-saving methods to control flowering. Due to the rapid spread of next generation sequencing technologies, it has become much easier to obtain genomic sequences of individual horticultural crops. By utilizing the various genetic resources and their genomic information, it will become possible to supply various marketable flowers, vegetables, and fruits year-round in the future.

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