FLOWERING LOCUS T (FT) CONTROLS FLOWER DEVELOPMENT IN PLANTS

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May 5, 2020

Abstract

Flower development is a crucial trait of higher-plant and is controlled by the action of central genetic regulator, *FLOWERING LOCUS T (FT)*; one of the most crucial promoters of the floral transition that encodes the phloem-mobile florigen protein which is an essential plants flowering signal. *FT* has a conserved PHOSPHATIDYL-ETHANOLAMINE BINDING PROTEIN (PEBP) domain, but its biochemical properties remain uncharacterized. *FT* transcriptional regulation is the most competent route to control the flowering period in plants. The expression level of *FT* can be modified by various TFs of different families such as; *MYB, MADS-box, NF-Y, SPL* etc which can bind to the promoter region of *FT*. In temperate grasses microRNA (miRNA) and alternative splicing (AS) can cause modulation in *FT* expression. Determination of the endogenous levels of *FTs* in plant is a challenging task because it is difficult to raise antibodies which can be used for the mentioned purpose due to more amino acid resemblance of *FT* homologs. The facts and findings reviewed in this study incorporate the information and progress regarding the role of *FT* in controlling flower induction. In this review article, we have summarized the general introduction of *FT* and discussed its molecular mechanism in regulating flower development in plants.

Keywords: Flower Development, *FLOWERING LOCUS T*(*FT*), Transcriptional regulation, Post-transcriptional regulation, Post-translational regulation

1. Introduction

In the life cycle of plant, the flower development is a vital checkpoint at which shoot apical meristem (SAM) stops producing vegetative growth and starts to produce reproductive growth. The devotion to this developmental step transition is prevailing irremediable for a used meristem, plants develop different pathways to incorporate environmental and endogenous stimuli to assure flowering at right time. There are so many factors like hormones, sugars, temperature and photoperiod which are responsible for flowering time regulation (Branchat et al., 2014; Song et al., 2015; Srikanth and Schmid, 2011). In many species flowering time has been regulated by photoperiod. Depending on the requirements of light, plant have been divided into categories like short day, long day and day neutral.

In day-length sensitive plants, inducing light period is mainly sense in leaves where it causes the formation of florigen which is a long distance signal that moves to the shoot apical meristem and results into flowering (An et al., 2004; Corbesier et al., 2007; Mathieu et al., 2007). The molecular complexion of florigen clarifies evidence for the better part of the century. Nowadays *FLOWERING LOCUS T*(*FT*) and its related genes have been identified as evolutionary conserved campaigner, which are encoded as phosphatidylethanolamine-binding proteins (PEBP) (Corbesier et al., 2007; Mathieu et al., 2007). A lots of studies have nowadays substantiated that the evolution of *FLOWERING LOCUS T*(*FT*)-like proteins play a crucial function in plant portfolio and adaptianisms. A mobile protein; *FT* transmission from leaf to shoot apex promotes flowering (Chen et al., 2018). Addition to their crucial roles in flowering time, FT proteins serve as sovereign

proteins that intervening multiple developmental proceeding like, growth, plant structural control, fruit and tuber formation. Under inductive photoperiod, *FT* protein transports into the phloem sieve elements and translocate to shoot apical meristem which is a good evidence that*FT* is expressed in leaf phloem companion cells (PCC) (Chen et al., 2018). At shoot apical meristem, *FT* interacts with *FD*and *14-3-3* proteins making flowering-activation complex (FAC), which controls the exact expression of flowering time and flowering homeotic genes to raise the transition of the vegetative part into a reproductive inflorescence meristem (Taoka et al., 2011; Wigge et al., 2005; Abe et al., 2005).

In the blooming of plants, the *FT* protein considers as a flowering mobile signal in the shape of a key component of florigen (Nakamura et al., 2019). In all angiosperms examined to date,*FT* -like genes are responsible in regulating the floral transition. The study of molecular evolution shows that the occurrence of *FT* -like genes coexist with the progression of the flowering spices. Therefore the part of *FT* in flower advancement is well-preserved but look like to be limited to the angiosperms (P. A. Pin and O. Nilsson 2012). These polygonal roles of *FT* -like proteins have produced from extensive gene duplication actions, which happened independently in all modern angiosperm lineages, followed by sub- or neo functionalization. Recently, several experimental studies have been conducted on the documentation of the mobile signal acting downstream of leaf stimulation and activating flowering at the SAM. Based on molecular and genetic proof, a product of the *FLOWERING LOCUS T* (*FT*) gene, mainly the mRNA has been concerned as this signal and these advances are reviewed in this study.

2. Transcription regulation of *FT*

Structure, development and homeostasis of all organisms cannot be considered without the mechanism of transcriptional regulation because the initiation step from genome to proteome of biological information flow is transcription (Polouliakh, 2019). *FT* transcriptional regulation is the most competent route to control the flowering period in plants. The expression level of *FT* can be modified by various TFs of different families such as; *MYB* , *MADS* -box,*NF-Y* , *SPL* etc which can bind to the promoter region of*FT* (Figure 1). The chromatin loops produced at different sites of*FT* *cis* -elements by various TF complexes have been reported as the key determinants for floral transitions initiation. (Cao et al., 2014; Liu et al., 2014). The interaction of TFs with the introns of*FT* as well as the 30-downstream region of the coding sequence has also been reported (Figure 1). Furthermore, for different pathways (e.g. photoperiod and thermo-sensory) the vigorous accumulation of H3K4me3, H3K27me3 and H2A.Z are important to transcribe *FT* (He, 2012). These studies suggest that both TFs and epigenetic regulators are crucial for the transcriptional regulation of *FT* . However, transcriptional regulation of *FT* has been studied but very less is known about *FT* regulation at the protein level.

3. Post-Transcription Regulation of *FT*

Post-transcriptional regulation is one the crucial mechanisms responsible for the control of gene expression. It is cleared from the previous studies that TF; MYB, WEREWOLF are the reasons behind the*FT* mRNA stabilization whereas, at the molecular level the mode of action still need to be described in detail (Seo et al., 2011). It has been reported recently from the study on temperate grasses that microRNA (miRNA) and alternative splicing (AS) can cause modulation in *FT*expression.

MicroRNAs (miRNAs) constitute an enormous family of small non-coding RNAs (approx. 21-24 nucleotides) that have emerged an important post-transcriptional regulators of gene expression in plants. Most of the miRNAs have perfectly complementary sequences to that of the targets due to which they become the reason for digestion of mRNA because of their involvement in gene silencing. Taking miR5200 as an example; detected in *Brachypodium distachyon* for the first time, cleaves the transcripts of two *FT* orthologs, *FT1* and *FT2*(Figure 2) (Wu et al., 2013). Under different day lengths the study on miR5200 expression patterns and its targets showed that they are specifically identical but temporally different in *Brachypodium distachyon* . During long days the flowering delays in B. distachyon because of the overexpression of miR5200 (Wu et al., 2013).

In *B. distachyon* , under short day-conditions (SDs) and long-day conditions (LDs) the accumulation of

miR5200 increases and decreases, respectively, because of the vigorous changes in the levels of H3K27 and H3K4me3 at its originator loci. Through a target mimicry strategy, knockdown of miR5200 activity accelerates flowering in *B. distachyon* under SDs; suggested that there is a negative effect of miR5200 on blooming in the photoperiod pathway (Wu et al., 2013). Due to the absence of miR5200 in maize, rice and other monocots, it was assumed that miR5200 may be a new miRNA with particular functions in Pooideae plants (Wu et al., 2013). In the experimental study on temperate grasses the non-inductive condition-dependent accumulation of mature miR5200 has been observed. Whereas, the involvement of photoperiod mediated regulation of its precursor has been reported in Brachypodium lineage which proposed that in different grasses, transcription or mRNA regulation could be a factor for miR5200 accumulation. (McKeown et al., 2017; Wu et al., 2013).

Alternative splicing (AS) is the reason which expands the diversity of the transcriptome which may result in main consequences in eukaryotes. It has been suggested that for *FT* regulation, the *FT* AS may be a common machinery because of the observation of a number of*FT* events in various plants (Figure 2). The gene expression mostly regulates with the introduction of non-functional mRNA isoforms with a pre-mature stop codon by AS, which results into the degradation of mRNA. The two functional proteins; *ΦT2a* and *ΦT2β* , produce in the result of B. distachyon-*FT2* AS. Surprisingly, delay of flowering occurs with the ectopic production of *ΦT2β,*which is totally opposite to the remarkably bloomed flowering with the overproduction of *FT2a,* suggesting that *ΦT2a* is a normal florigen protein whereas *ΦT2β* seems to be a repressor for flowering. The interesting part is that, both the *FT2a* and*ΦT2β* are identical except the absence of some amino acids (Qin et al., 2017). The opposite functions of *ΦT2a* and *ΦT2β* · accelerated and delayed flowering respectively, have proved by an experimental study on transgenic plants of *B. distachyon* (Qin et al., 2017). Molecular analyses showed that *ΦT2β* cannot form a homodimer with itself though it form a heterodimer with *ΦT2a,*which inhibits florigen activation complex activities by restricting the ability of *ΦT2a* to bind 14-3-3s and FDs. The expression ratio of*ΦT2a / ΦT2β* decreases with the passage of plant age in wheat, barley and *B. distachyon* (Qin et al., 2017), the blooming during juvenile stage has prevented by the presence of *ΦT2β* . Hence, premature flowering resulted in the absence of *ΦT2β* which may cause antagonistic effect on plant growth and development. It will be a remarkable study to analyze the expression of *FT* genes in temperate grasses; that wither they are regulated by these processes, as there is the involvement of 5' capping and 3' polyadenylation in post transcriptional modification of mRNAs.

4. Post-translational regulation of *FT*

Determination of the endogenous levels of *FT* s in plant is a challenging task because it is difficult to raise antibodies which can be used for the mentioned purpose due to the high amino acid resemblance of *FT* homologs. Recently in a study, Ahn's group has reported an antibody which has been generated against a very short peptide of*FT* in *Arabidopsis thaliana* . This antibody enabled them to find out that the abundance of *FT* increases before the blooming of plants begin and gradually decreases then, although continuous transcription of *FT* mRNA in a short period may lead to an uncoupling of mRNA level and protein. According to these findings, much faster transcription of *FT* has been observed than its degradation after the variation in photoperiod (Kim et al., 2016). Even though, it has not been appear that there is some effect of ubiquitination pathway on *FT* degradation, an unknown serine/cysteine protease has been attached between E167 and S168 in the cleavage of *FT* (Figure 2) (Kim et al., 2016). Along with these evidences that the cleavage of seven amino acids from C-terminus is essential for the transport of*FT* , these results proposed that the proteolytic truncation of*FT* is significant in *A. thaliana.* The in-depth knowledge about the appropriate protease may be helpful to explain *FT*hydrolysis in detail.

Keeping in mind the post-transcriptional modification of animal PEBPs signaling activities with the binding of phosphatidylethanolamine (PE), Nakamura along with colleagues suggested that binding of small lipids may modulate plant *FT* functions. They observed in their in vitro experimental study that phosphatidylcholine (PC) binds to *FT* in A. thaliana, instead of PE (Figure 2) (Nakamura et al., 2014). It has been reported with a transgenic analyses that flowering has been promoted with the increased abundance of PC in shoot meristem but this may be mitigated with the compromised activity of *FT* . Additional study demon-

strated that diurnal oscillation of PC content was crucial for the activity of *FT* , as day-dominant PC species bind by*FT* to promote flowering (Nakamura et al., 2014). Thus, small molecules binding by *FT* may be a superfluous way to specifically control blooming time.

5. Conclusions and Perspectives

The facts and findings discussed in the study not only show clearly the key involvement of *FLOWERING LOCUS T* (*FT*) in flowering induction but also provide crucial information on flower development mechanism. A product of the *FLOWERING LOCUS T* (*FT*) gene; mRNA has been reported as a downstream signal of leaf induction which promotes flowering at SAM. Both TFs and epigenetic regulators are important for the transcriptional regulation of *FT* , whereas, very less is known about *FT* regulation at protein level. A detailed and comprehensive study is needed to elucidate *FT* regulation at protein level. Recent studies regarding the production of *FT*post-transcriptional regulation has provided new perceptions for examinations of the multifaceted regulation of flower development in plant. During breeding of crops, modulation of *FT* production at RNA and protein levels should be considered.

Acknowledgement

The research was funded by National Natural Science Foundation of China (Grant No. 31529001; 31570183).

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