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Review

Genetic and epigenetic regulation of flowering in rice

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Abstract The timing of floral transition, which is directly related to reproductive fitness, is regulated by many environmental factors. Transduction of these environmental signals is sensed in several tissues as the primary adaptive signal for flowering, integrated into the plant's florigenic signaling pathway, and transmitted to the shoot apex, where the transition to reproductive organ development is initiated. Recent studies have identified the mobile signal, florigen, for photoperiod-dependent flowering, which is conserved between long-day plants (*Arabidopsis*) and short-day plants (rice). Vernalization also controls the flowering time of *Arabidopsis* by modifying the chromatin of the flowering repressor gene. Here, we review the molecular mechanisms that control photoperiodic flowering associated with the *FT-like* gene family, including epigenetic regulation in rice.

Key words: Photoperiod flowering, *FT-like* gene, epigenetic regulation, rice.

The developmental pathway leading to flowering consists of a vegetative stage, a transitional period, and a reproductive stage. The triggering of the transition from vegetative growth to the reproductive stage requires both endogenous and environmental signals including day length, temperature and water supply. Among the various environmental signals, photoperiod provides plants with an indisputable signal for the most suitable season for flowering (Yanovsky and Kay 2003; Baurle and Dean 2006). Plants generally fall into one of three photoperiod-sensing classes. Long-day plants (LDP) promote flowering by sensing long-day (LD) photoperiods, short-day plants (SDP) promote flowering by sensing short-day (SD), and day-neutral plants, which are not regulated by photoperiod. Recent studies suggest that *FT/Hd3a*, which is a common floral inducer in *Arabidopsis thaliana* (LDP) and rice (*Oryza sativa* L.; SDP), encodes florigen, the mobile flowering signal (Tamaki et al. 2007; Corbesier et al. 2007; Jaeger and Wigge 2007; Mathieu et al. 2007; Lin et al. 2007). Although the FT/Hd3a florigen signal is conserved between these two types of plants, the regulation of *FT/Hd3a* expression differs with the day length in order for the plants to respond appropriately to seasonal light differences. In this review, the recent developments in understanding the molecular mechanisms of photoperiodic flowering are discussed, using the long day plant *Arabidopsis* and the short day plant rice as model systems.

Vernalization is a well-known example of the effect of temperature on flowering time. Recently it was discovered that epigenetic regulation through histone modification affects flowering regulation in the vernalization pathway in winter annual accessions (He and Amasino 2005). Two environmental signals, photoperiod and vernalization, are integrated to affect many floral initiation genes in *Arabidopsis*, but rice does not require vernalization for flowering. Photoperiodic flowering is thus the key pathway in rice (Figure 1). Recently we have introduced evidence that rice flowering is regulated by histone modifications of the *FT-like* genes (Komiya et al. 2008).

The photoperiodic flowering pathways of rice and *Arabidopsis*

The signaling cascades of photoperiodic flowering have been studied in *Arabidopsis*. *CONSTANS* (*CO*) encodes a zinc-finger transcriptional activator, and induces expression of the floral integrator *FLOWERING LOCUS T* (*FT*) under LD conditions (Kardailsky et al. 1999; Kobayashi et al. 1999; Yanovsky and Kay 2002). The *CO-FT* pathway is conserved in rice, which is an SDP (*Heading date1* (*Hd1*)→*Heading date 3a* (*Hd3a*)) (Yano et al. 2000; Hayama et al. 2003). *Hd3a*, which was identified as a quantitative trait locus (QTL) for flowering time, is a key activator of flowering in rice (Kojima et al. 2002). *Hd3a* expression is regulated by *Hd1*, which suppresses *Hd3a* under LD conditions (Hayama et al. 2003), and by *Ehd1*, a B-type response regulator which functions independently of *Hd1* (Yano et al. 2000; Hayama et al. 2003; Doi et al. 2004). *Hd3a* is

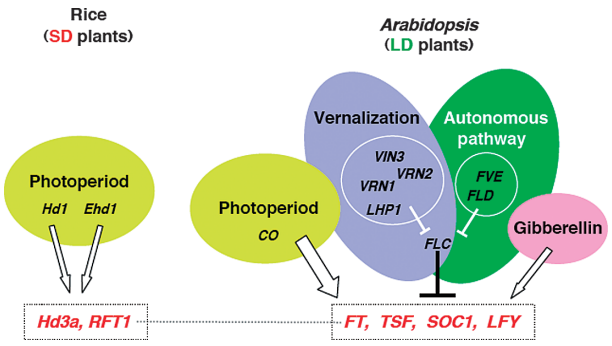

Figure 1. Comparison of flowering regulation in Rice and *Arabidopsis*. Rice is a short day plant, and *Arabidopsis* is a long day plant. Rice does not require vernalization for flowering. Rice flowering is regulated by *Hd3a* and *RFT1* of the photoperiodic pathway. In *Arabidopsis*, flowering is regulated by the floral activators *FT*, *TSF*, *SOC1* and *LFY* through the photoperiod, vernalization, autonomous and gibberellin pathways.

also regulated by light *via* the phytochrome B sensory system. These two functional pathways merge at *Hd3a* (Izawa et al. 2002; Ishikawa et al. 2005). The key regulators of photoperiodic flowering in rice and *Arabidopsis* are conserved, but differences in their regulation result in either SDP or LDP (Hayama et al. 2003).

Florigen, mobile flowering signal, in *Arabidopsis* and rice

The shoot apical meristem (SAM) gives rise to vegetative structures, eventually transitioning to the reproductive stage that produces flowers. Because photoperiod is measured in the leaf, signals must be transmitted from the leaf to the shoot apex. This mobile flowering signal, or florigen, has been proposed as the messenger between photoreception in leaves and floral initiation in the shoot apex.

In *Arabidopsis*, *FT*, which encodes phosphatidil ethanol binding protein (PEBP), is expressed in leaf phloem under LD conditions (Kardailsky et al. 1999; Kobayashi et al. 1999; Yanovsky and Kay 2002). *FT* mRNA is not expressed in the SAM. *FD*, a bZIP transcriptional factor, is expressed at the SAM and interacts with *FT*. *FD* which is required for the function of *FT* within the SAM, up-regulates the floral meristem identity gene *APETALA1* (*AP1*). Moreover, ectopic expression of *FT* in the SAM rescues the *ft* mutant phenotype (Abe et al. 2005; Wigge et al. 2005). These results suggest the possibility that one or both of the products of *FT* (mRNA or protein) are translocated through the phloem to the meristem prior to the transition to flowering (Abe et al. 2005; Wigge et al. 2005).

Under inducible SD conditions, rice *Hd3a* mRNA is expressed in the vascular tissues of leaf blades, and is barely detected in the SAM of wild-type plants. In *Hd3a* promoter::*GUS* plants, *Hd3a* is also expressed in vascular tissues (Tamaki et al. 2007). To detect where Hd3a protein is produced or accumulates, our group made *Hd3a* promoter::*Hd3a*:*GFP* transgenic plants. These transgenic plants flower earlier than wild-type, indicating that Hd3a protein fused to GFP retains its function for flowering. Using confocal laser scanning microscopy, GFP signal was detected in the SAM and stem vascular tissue, but not in the other tested tissues. These studies in rice and *Arabidopsis* suggest that it is the Hd3a protein in rice, and *FT* in *Arabidopsis*, rather than mRNA that acts as the mobile flowering signal (Tamaki et al. 2007; Corbesier et al. 2007; Jaeger and Wigge 2007; Mathieu et al. 2007; Lin et al. 2007).

Hd3a and *RFT1* are essential for photoperiodic flowering in rice

In *Arabidopsis*, the *FT* homologue *TSF* acts redundantly with *FT* to promote floral transition, because *tsf ft* double mutants delay flowering longer than *ft* mutants under LD conditions. (Michaels et al. 2005; Yamaguchi et al. 2005). The rice genome contains thirteen members of the *Hd3a* gene family (Chardon and Damerval 2005; Faure et al. 2007). *RFT1*/*FT-L3* is the closest homologue of *Hd3a*, and *FTL*/*FT-L1* is the second closest. Transgenic rice plants that over-express *RFT1* or *FTL* flower early, much like *Hd3a*-overexpressing plants (Izawa et al. 2002; Kojima et al. 2002).

In rice, *RFT1* lies adjacent to *Hd3a*, separated by only 11.5 kb on chromosome 6, with 91% identity in the deduced amino acid sequence (Kojima et al. 2002; Chardon and Damerval 2005; Faure et al. 2007). However, there are no null mutants of *FT-like* genes, including *Hd3a*. To determine whether *RFT1*, or *FT-like* genes other than *Hd3a* function as floral activators, we studied the developmental expression and phenotypic consequences of losing *RFT1* and *Hd3a* function by RNAi.

Under SD conditions, levels of *RFT1* and *Hd3a* transcripts were highest 30 days before flowering, which is concurrent with floral transition, though absolute transcript levels of *RFT1* are much lower than *Hd3a*. *RFT1* acts downstream of *Hd1* in the photoperiodic pathway and *RFT1* expression is diurnal with peaks at dawn. An RFT1::GUS reporter fusion protein, like Hd3a::GUS, can be detected in leaf blade vascular tissues 35 days after sowing (DAS) under SD conditions. On the other hand, under LD conditions, expression of *Hd3a* and *RFT1* is much lower at any developmental stage in wild-type plants than under SD conditions. The similarity of *Hd3a* and *RFT1* expression patterns under SD and LD conditions, and in vascular tissues suggests that *RFT1* could function redundantly with *Hd3a* in promoting floral transition under SD conditions (Komiya et al. 2008).

This was tested by producing transgenic plants that

Table 1. Flowering time of RNAi plants under SD conditions

Genotype	Days to flowering	n
	SD (10h light 14h dark)	
Wild type (cv. Norin8)	59±3.5	9
Hd3a RNAi plants	95±6.4	9
RFT1 RNAi plants	61.9±8.3	18
double *RFT1-Hd3a* RNAi plants	>300	10

suppress *RFT1*, *Hd3a*, or both (Table 1). The flowering time of *RFT1* RNAi plants (T_1) is essentially the same as wild-type (59±3.5 DAS, days after sowing, n=9 for wild type v. 61±8.3 DAS, n=18 for *RFT1* RNAi plants) under SD conditions (Table 1). In contrast, *Hd3a* RNAi plants (T_1) flower 95±6.4 DAS (n=9) under SD conditions, about 30 days later than wild-type plants (Table 1). These results suggest that *Hd3a* thus acts as the primary activator of flowering in *RFT1* RNAi plants, with *RFT1* playing only a minor, if any, role in floral transition under SD conditions. Double *RFT1-Hd3a* RNAi plants do not flower at all (n=10) under SD conditions (Table 1). These plants continue vegetative growth throughout the 300 days of the experiment and reach a height of 110–130 cm, about double the height of wild-type plants. The absence of flowering in double *RFT1-Hd3a* RNAi plants is apparently due to a complete defect in floral transition. These results suggest that *RFT1* is a novel floral activator whose expression advances flowering under SD conditions. *Hd3a* and *RFT1* are thus both required for flowering under SD conditions in rice (Komiya et al. 2008).

Epigenetic regulation of flowering

In addition to the photoperiodic pathway, the vernalization, autonomous and gibberellin pathways are integrated into the transcriptional regulation of downstream target genes such as *FT*, *TWIN SISTER OF FT* (*TSF*), *SUPPRESSOR OF OVEREXPRESSION OF CONSTANS 1* (*SOC1*) and *LEAFY* (*LFY*) in *Arabidopsis* (Figure 1) (Boss et al. 2004; Imaizumi and Kay 2006). Prolonged exposure to cold, a process known as vernalization, promotes flowering in winter annual *Arabidopsis*. *FLOWERING LOCUS C* (*FLC*), a MADS-box transcription factor, suppresses floral transition by repressing the expression of floral activators (Figure 1) (Michaels and Amasino 1999). *FLC* expression is repressed by the vernalization pathway through epigenetic mechanisms at the *FLC* locus (Sung and Amasino 2004a; He and Amasino 2005). Vernalization requires at least three genes: *VERNALIZATION INSENSITIVE 3* (*VIN3*), a member of a plant-specific protein family with plant homeodomain and fibronectin domains; *VERNALIZATION 2* (*VRN2*), a homologue of polycomb group protein; and *VERNALIZATION 1* (*VRN1*), a protein containing a DNA-binding domain (Levy et al. 2002; Bastow et al. 2004; Sung and Amasino 2004b). These genes are involved in H3K9-mediated deacetylation, and H3K9- and H3K27-mediated chromatin dimethylation modifications at the first intron of *FLC*, and promote flowering by suppressing *FLC*. Furthermore, *HETEROCHROMATIN PROTEIN 1* (*LHP1*)/*TERMINAL FLOWER II* (*TFLII*) is required to maintain the increased level of H3K9 dimethylation at the *FLC* locus (Sung et al. 2006). In rapid-cycling accessions of *Arabidopsis*, *FLC* expression is also regulated by the autonomous pathway, which constitutively represses flowering. In this pathway, *FLOWERING LOCUS D* (*FLD*) and *FVE*, plant homologues of a protein found in the histone deacetylase (HDAC) complex of mammals, partly regulate flowering by histone deacetylation at the *FLC* locus (Figure 1) (He et al. 2003; Ausin et al. 2004). Chromatin modifications at the *SOC1* locus have also been observed (Bouveret et al. 2006). However, no chromatin modifications at the *FT* locus have been reported (Sung et al. 2006), even though *FT* expression is regulated by *FLC*. In *Arabidopsis*, flowering is regulated by many floral activators through multiple pathways, but there is no *FLC* orthologue in the rice genome (Goff et al. 2002; Doi et al. 2004), and rice does not require vernalization for flowering. Photoperiodic flowering is thus the determinative pathway in rice. No other confirming report of floral regulation through chromatin modification has as yet been published.

Interestingly, *RFT1* expression is much higher in *Hd3a* RNAi plants at later developmental stages, but transcript levels of *RFT1* were very low in wild-type plants throughout development (Komiya et al. 2008). Because *RFT1* RNAi plants did not appreciably affect the timing of floral transition (Table 1), *RFT1* does not play a significant role in flower induction under SD conditions in wild-type plants. However, the marked increase of *RFT1* expression at a later stage in the absence of *Hd3a* expression, as in *Hd3a* RNAi plants, is highly correlated with the induction of flowering, suggesting that *RFT1* can act as a floral activator as in *Hd3a* RNAi plants. Moreover, in *Hd3a* RNAi plants, H3K9 acetylation in the region around the *RFT1* transcriptional start site increase from wild type levels at 70 DAS, when *RFT1* expression is highly activated in *Hd3a* RNAi plants (Komiya et al. 2008). In contrast, there was no increase in H3K9 acetylation 35 DAS in *Hd3a* RNAi plants, a stage at which *RFT1* expression is low. Increased H3K9 acetylation at the *RFT1* locus is thus correlated with the activation of *RFT1* transcription. Together, these results suggest that *RFT1* functions as a floral activator in the absence of *Hd3a* expression under SD conditions, and that *RFT1* is regulated by chromatin modification. The molecular mechanism for *RFT1* expression in *Hd3a* RNAi plants through histone modifications remains to be identified. Because the study of epigenetic regulation of flowering

has barely begun in rice, the extent to which epigenetic regulation affects the timing of flowering, which is regulated mainly by the photoperiodic pathway, is an intriguing future topic of research.

Downstream factors of *Hd3a* and *RFT1*

In *Arabidopsis*, *APETALA1* (*AP1*), *SEPALLATA3* (*SEP3*), *FRUITFULL* (*FUL*) and *SOC1* are induced by *FT* in leaves and/or in the SAM (Abe et al. 2005; Michaels et al. 2005; Teper-Bamnolker and Samach 2005). In rice, *OsMADS1*, *OsMADS14* and *OsMADS15* are up-regulated in the floral meristem as it begins to differentiate into primary panicle branch primordia (Furutani et al. 2006).

OsMADS14 and *OsMADS15* are rice orthologues of *AP1*, and *OsMADS50* is a rice orthologue of *SOC1* (Jeon et al. 2000; Lee et al. 2004). *OsMADS14* and *OsMADS15* are suppressed in *Hd3a* RNAi plants 35 DAS, but their expression is higher at 70 DAS, when *RFT1* expression is also higher in *Hd3a* RNAi plants. Moreover, expression of *OsMADS14* and *OsMADS15* is suppressed at all stages in double *RFT1-Hd3a* RNAi plants. Because their expression is dependent on *RFT1*, *OsMADS14* and *OsMADS15* apparently act downstream of *Hd3a* and *RFT1* (Komiya et al. 2008). The expression of *OsMADS50* in *Hd3a* RNAi and double *RFT1-Hd3a* RNAi plants was similar to that of wild-type plants. These results show that under SD conditions, *Hd3a* and *RFT1* promote floral transition and induce expression of *OsMADS14* and *OsMADS15*, but not *OsMADS50*.

A model for the regulation of photoperiodic flowering in rice

Enough information is now available to propose a model with three flowering pathways in rice (Figure 2). Under SD conditions, *Hd3a*, which is the main promoter of floral transition, is activated by *Hd1* and *Ehd1*, *Hd3a* then induces expression of two rice *AP1* orthologues, *OsMADS14* and *OsMADS15*. Under SD conditions, flowering takes place at about 60 DAS in wild-type plants *via* the *Hd1-Hd3a-OsMADS14*, *OsMADS15* pathway. This pathway, Short-Day Activation pathway, is mainly activated early in development under SD conditions. However, when *Hd3a* expression is suppressed, as in *Hd3a* RNAi plants, *RFT1* expression increases at a later stage, and promotes flowering, though expression of *RFT1* in wild-type plants is very low. The presence of an auxiliary floral activator that is normally repressed marks this as a *de novo* adaptive pathway, which arises during the extended vegetative stage presumably from a lack of *Hd3a*. This pathway is activated late in development under SD conditions (Figure 2). On the other hand, the *Hd1-Hd3a* pathway is entirely suppressed at all developmental stages under LD

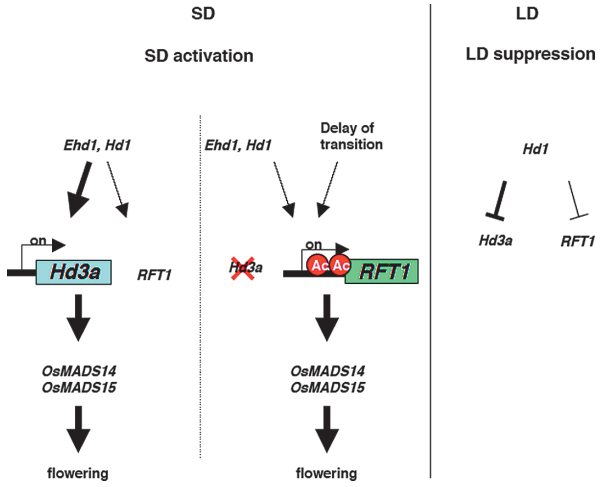

Figure 2. A model for photoperiodic flowering in rice. In wild-type plants, *Hd3a* promotes transition to the reproductive stage, and induces expression of *OsMADS14* and *OsMADS15*. Wild type rice flowers about 60 DAS under SD conditions. This pathway is activated early in development under SD conditions. However, in *Hd3a* RNAi plants, *RFT1* expression increases during later stages, and induces *OsMADS14* and *OsMADS15* expression. *Hd3a* RNAi plants flower 30 days later than wild-type plants under SD conditions. *RFT1* expression is correlated with high H3K9 acetylation levels at the 5′UTR of *RFT1*. *RFT1* thus represents an auxiliary, late activating pathway that is only expressed with the loss of the main activator, *Hd3a*. Under LD conditions, *Hd1-Hd3a* is the Long-Day Suppression pathway in rice. Double *RFT1-Hd3a* RNAi plants did not flower up to 300 DAS under SD conditions, suggesting that *RFT1* and *Hd3a* are the key and possibly only, regulators of photoperiodic flowering under SD conditions.

conditions (Hayama et al. 2003), making it a Long-Day Suppression pathway in rice (Figure 2).

Suppression of both *Hd3a* and *RFT1* resulted in no flowering even 300 DAS under SD conditions (Table 1), indicating that *Hd3a* and *RFT1* are the major floral activators in rice, and one or the other is essential for photoperiodic flowering under SD conditions. Regulation by two members of the *FT/Hd3a* gene family involved in flowering may be a rice-specific mechanism, or an as-yet undiscovered auxiliary mechanism in other plants. There may be an adaptive mechanism to adjust to changes in gene expression of a major regulator of flowering to secure flowering for the production of offspring, or *Hd3a*/*RFT1* could reflect the evolution of rice from a late season to an early season flowering plant.

It remains to be determined whether Long-Day Activation, the gibberellin pathway, or epigenetic regulation is required for flowering in rice. In the future, it may be that finding other interactors with *Hd1* or *Hd3a*, and new flowering factors will clarify the molecular mechanisms for flowering in many plants and will contribute to significantly to basic plant sciences and agriculture.

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