



Genetic and signaling pathways of flowering regulation in rice (*Oryza sativa* L.)

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Abstract

Flowering time is of great significance for crop reproduction, yield, and regional adaptability, which is intricately regulated by various environmental cues and endogenous signals. Photoperiod is a key flowering regulating factor due to its relatively high concern in the same geography, while other factors change year over year. Photoperiodic flowering time is controlled by a complex genetic network, which is regulated by florigen. RICE FLOWERING LOCUS T 1 (RFT1) is the closest homologue of Heading date 3a (Hd3a), which is thought to encode a mobile flowering signal and promote floral transition under short-day (SD) conditions in rice. Recent molecular genomic advancement revealed how to identify the molecular nature of florigen, its function, expression, and how to diversify its regulatory pathway. Here, we summarized the recent understanding of flowering time regulation mainly focused on rice Hd3a, its molecular function, expression, and diversified photoperiodic regulatory pathways under short-day and long-day (LD) conditions.

Keywords Florigen · Genetic architecture · Hd3a · Photoperiod · Rice

1 Introduction

Rice is one of the most important cereal crops and has wide adaptability in diverse climatic regions ranging from 44° N to 35° S and 6 ft below to 2700 ft above sea level (Molla 2022), which traits and mechanisms confer this adaptability is a major question in rice biology. Heading date (or flowering time) is a crucial trait for the regional and seasonal adaptation of rice and influences grain yield. Rice is a facultative short-day (SD) plant; SD conditions promote, and long-day (LD) conditions inhibit flowering (Sohail et al. 2022). Flowering time is a dramatic change from the vegetative stage to the reproductive stage and is predominantly controlled by genetic pathways, integrated with internal and external cues (Wu et al. 2018; Zhang et al. 2019). Most plant species can initiate flowering for reproduction mainly depending on environmental changes in photoperiod and temperature (Song et al. 2015; Tan et al. 2016). Flowering time is

vital for seasonal changes, regional adaptability, and often affluent to perceive (Zhang et al. 2017). Plants are generally classified into three categories regarding photoperiodic flowering initiation response; long-day plants (LDPs), initiate flowering when the day length becomes longer, short-day plants (SDPs), start flowering when the day length becomes shorter, while day-neutral plants (DNPs) are unaffected by photoperiodic fluctuations. The molecular mechanism of photoperiodic FT has been comprehensively examined in a model LDP (*Arabidopsis thaliana*) (Song et al. 2015) and a traditional SDP (*Oryza sativa* L.) (Tsuji et al. 2011; Shrestha et al. 2014). Flowering time regulation is controlled by several genes, which are suppressed/expressed in an association with environmental dynamics, i.e., photoperiod and temperature (Huan et al. 2018). Recent studies reported FLOWERING LOCUS T (FT) and Heading date 3a (Hd3a), as florigen in *Arabidopsis* and rice, respectively. These florigen moves in a form of mobile signals from the leaf to shoot apical meristem (SAM) and commence flowering (Goretti et al. 2017). More recently, the molecular mechanism of florigen function in shoot apical cells was revealed in rice. Hd3a florigen interacts with 14-3-3 proteins in the cytoplasm and forms a ternary complex with OsFD1 in the nucleus (Tsuji 2017). The ternary complex is known as the florigen activation complex (FAC), which activates *OsMADS15*,

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homologue of *A. thaliana* APETALA1 (AP1), which leads to flowering (Camoni et al. 2018). FD is a basic leucine zipper (bZIP)-containing transcription factor, and its loss-of-function mutants are late flowering (Taoka et al. 2011). These results indicate that 14-3-3 proteins act as intracellular receptors for florigen in shoot apical cells and offer new approaches to manipulate flowering in various crops and trees. Advancement in molecular genetics provides a clear concept of flowering time regulation mechanism in rice from molecular genetics, molecular biology, and comparative biology point of view. In this review article, we deliberate our understanding of flowering time, using the current findings of a strong candidate for rice mobile flowering signals, florigen, and incorporated the presence of complex layers of gene networks integrated with the synthesis of florigen protein and its subsequent transport and perception.

2 Rice florigen

Rice has two florigens, *Heading date 3a* (*Hd3a*) and *RICE FLOWERING LOCUS T 1* (*RFT1*), which are crucial for FT in rice. Regulations of these florigens involve a complex genetic network, which is discussed below.

3 Hd3a protein as rice florigen

Florigen, a mobile signal that moves from leaves to SAM and induces flowering, has been elucidating since it was identified 70 years ago. Understanding the nature of mobile

floral signals provides insight into the molecular mechanism of flowering induction (Brambilla and Fornara 2013). Recent research identified FT, encoding florigen in *Arabidopsis*, whereas *Hd3a*, an ortholog of FT, was reported in rice, which moves from leaves to SAM and causes flowering. These results showed that *Hd3a* is florigen in rice (Tamaki et al. 2007).

Hd3a was first identified as a quantity traits locus (QTL) that promotes flowering in rice under inductive short-day conditions (Yamamoto et al. 1998). The overexpression of *Hd3a* with cumulative promoter promoted flowering time, while RNA interference (RNAi) of *Hd3a* suppressed flowering in rice. (Monna et al. 2002).

The size of *Hd3a*/FT is about 22 kDa and their structures are similar to mammalian phosphatidylethanolamine-binding proteins (PEBPs) or Raf kinase inhibitor proteins (RKIP) (Ahn et al. 2006). However, it is not clear whether *Hd3a*/FT binds or not with phosphatidylethanolamine and kinase inhibitor. Recent molecular studies revealed that FT has a strong downstream effect on the flowering promotion of the known photoperiodic flowering pathway in *Arabidopsis* (Kobayashi and Weigel 2007; Guo et al. 2020; Zong et al. 2020). *Arabidopsis* and rice flowering time are assisted by LD and SD, respectively (Liu et al. 2020). FT mainly activates floral activity in *Arabidopsis* that expresses in leaves vascular tissue and transfers to SAM to induce flowering (Kobayashi et al. 1999; Shim and Jang 2020). The interaction of FT with the bZIP transcription activation factor results in full activation of FLOWERING LOCUS T (FD) in SAM, this activation is necessary for floral promotion in rice (Fig. 1) (Abe et al. 2008; Peng et al. 2021).

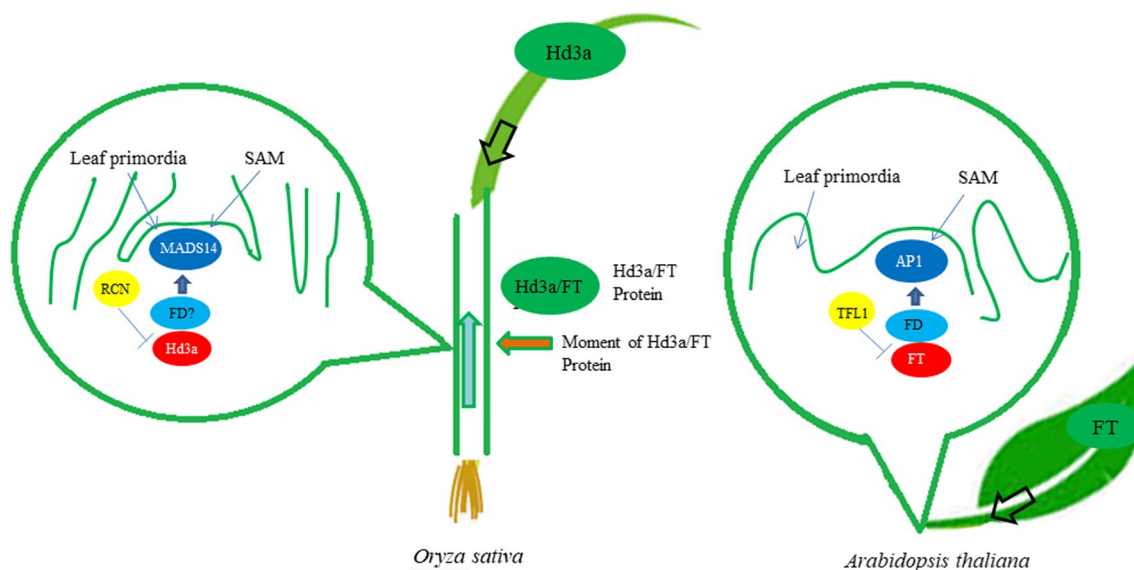


Fig. 1 The florigen (*Hd3a*/FT) model of rice and *Arabidopsis*. *Hd3a*/FT is induced in leaf vascular tissue and shifts through phloem tissue. These florigens are unloaded from vascular tissue and enter into SAM

Anatomical research showed that the product of FT is the main site for floral expression. If FT codes florigen and can act as a mobile floral agent via transcripts (mRNA) or protein, either of which interacts with FD in SAM. Now the question is whether mRNA or protein acts as a mobile agent for florigen activity (Zeevaert 2006). So the question was responded with rice as a model SD plant to elucidate the nature of florigen activity. Firstly, to determine the exact Hd3a transcription site and accumulation of mRNA. Using transgenic plants, the promoter activity of β -glucuronidase (GUS) was expressed in the presence of the Hd3a promoter in leaf blades with no expression in SAM. FT expression is tissue-specific in *Arabidopsis*, while this expression is promoted by FT in LD (*Arabidopsis*) and Hd3a in SD (rice) (Kobayashi and Weigel 2007). *Hd3a* mRNA stores more in leaf blade but lower in leaf sheet and much lower than $\frac{1}{4}$ in SAM under inductive SD conditions. *Hd3a* expression is specific to the vascular tissue of leaf blades. Hence, it is different from *Hd3a* mRNA, which transfers a significant amount from leaves to SAM (Fig. 1) (Jang et al. 2008).

Secondly, the tissue localization of Hd3a was studied from rice transgenic plants driven from the Hd3a promoter expressed as Hd3a-GFP fusion protein. Hd3a-GFP is located in the vascular tissue of leaf blades just below SAM where the node is localized. Thus, Hd3a-GFP protein is produced in the vascular tissue of the leaf blade and conveyed to the phloem where it is unloaded from vascular tissue into meristem tissue just below the SAM (Tamaki et al. 2007). Necessarily, the location of Hd3a-GFP was tested in other vascular tissues using different tissue-specific promoters conforming to the expression of Hd3a-GFP, revealing that Hd3a protein transmits from leaves and vasculature to SAM. This discussion revealed that Hd3a acts as a mobile flowering signal in rice and Hd3a/FT long-distance mobility is observed from rice proteome phloem sap (Aki et al. 2008). Hd3a mobility has probably not been detected because of photoperiod conditions, and sampling time was unsuitable for Hd3a detection. However, Hd3a/FT protein has been noticed in the phloem sap tissue of CmFTL2, an Hd3a/FT ortholog of *Cucurbita maxim*, which moves from graft union and induces flowering (Lin et al. 2007). Phloem sap acquired from the *Brassica napus* inflorescence also contains FT protein (Giavalisco et al. 2006). The above discussion provides additional information that Hd3a/FT is a florigen protein. *Arabidopsis* behavior also showed that FT is florigen. Phloem expresses FT-GFP and Hd3a-GFP transfer to SAM and promotes flowering but FT nuclear localization does not because of immobilization (Mathieu et al. 2007; Jaeger and Wigge 2007; Wu et al. 2020).

4 *RFT1* is essential for flowering in rice

RFT1 is also the second florigen and the closest homolog of *Hd3a* and 13 FT-like proteins in rice. *RFT1* is located on chromosome 6, 11.5 kb away from *Hd3a*. *RFT1* is 91% similar to *Hd3a* and most likely produced by tandem duplication (Sun et al. 2014; Hori et al. 2016). Tissue-specific expression of *RFT1* and *Hd3a* is the same under SD. Therefore, *RFT1* may function with *Hd3a* as the second florigen in rice. The *RFT1* involvement as florigen is examined from a detailed analysis of Hd3a suppression by RNAi rice plants. The flowering time of Hd3a RNAi plants was more than 30 days late, while *RFT1* RNAi flowering time was normal under SD conditions, indicating that *RFT1* did not promote flowering on its own. Both Hd3a and *RFT1* were suppressed in double RNAi plants and did not flower earlier than 300 days of germination. Thus, *RFT1*/Hd3a is involved completely in the regulation of rice flowering time. The expression level of *RFT1* is relatively low in wild rice as compared to Hd3a RNAi and is associated with the reproductive transition in SAM of rice plants. The upregulation of *RFT1* is associated with an abundance of histone-3-acetylation (H3A) near the transition induction site (Tan et al. 2016; Zhu et al. 2017). The above discussion suggests that the expression of *RFT1* enhances in the absence of *Hd3a*, and *RFT1* is *Hd3a* complementary in function. Therefore, *RFT1* acts as the second florigen in rice flowering time regulation under specific conditions (Nemoto et al. 2016).

5 Gene network of flowering regulation in rice

Recently, several flowering genes have been cloned, which play an important role in photoperiodic flowering regulation (Zhang et al. 2019). Rice photoperiodic flowering is monitored by two independent signaling pathways. The *GIGANTEA-Heading date-1-Heading date 3a* (*OsGI-Hd1-Hd3a*) pathway is evolutionarily associated with the *Arabidopsis* *GIGANTEA-CONSTANS-FLOWERING LOCUS T* (*GI-CO-FT*) pathway (Song et al. 2015). The evolutionarily unique pathway, *Early heading date 1-Hd3a/Rice FT1* (*Ehd1-Hd3a/RFT1*), controlled photoperiodic flowering in rice but does not function in *Arabidopsis* due to the lack of an *Ehd1* ortholog (Doi et al. 2004; Song et al. 2015). *Heading date 3a* (*Hd3a*) and *RICE FLOWERING LOCUS T1* (*RFT1*) are two florigens, which regulate flowering time under short-day (SD) and long-day (LD) conditions in rice (Tsuji et al. 2013). *Hd3a* and *RFT1* expression are activated under SD

and LD conditions, respectively (Chardon and Damer- val 2005; Komiya et al. 2009). Hd3a/RFT1 is mainly regulated by *Hd1* and *Ehd1* under both SD and LD conditions (Gao et al. 2013). *Ehd1* is upregulated by Early heading date 2 (*Ehd2*) (Matsubara et al. 2008), *Ehd3* (Matsubara et al. 2011), *Ehd4* (Gao et al. 2013), *Oryza sativa* GIGENTA (*OsGI*) (Park et al. 2008), *Ghd8* (Yan et al. 2011), *OsMADS51* (Ryu et al. 2009), *OsMFT1* (Song et al. 2018), and *OsMADS51* (Kim et al. 2007), while downregulated by CONSTANS-Like 4 (*OsCOL4*) (Lee et al. 2010), *OsCOL9* (Liu et al. 2016), and *OsCOL15* (Wu et al. 2018) under SD. In contrast, *Ehd1* is upregulated by *Ehd4* (Gao et al. 2013), *OsMADS56*, *OsMADS51* (Ryu et al. 2009), *Ghd8* (Yan et al. 2011), *LEC2*, and *FUSCA3-Like 1* (*OsLFL1*) (Peng et al. 2008), and *OsVIL2* (*O. Sativa* VIN3-LIKE 2) (Hori et al. 2013), while downregulated by *OsCOL4* (Wu et al. 2018), *OsCOL9* (Liu et al. 2016), *OsCOL10* (Tan et al. 2016), *OsCOL13* (Sheng et al. 2016), *OsCOL15* (Wu et al. 2018), *OsCOL16* (Wu et al. 2017), *DTH8* (Zhu et al. 2017), and *OsELF3* (Yang et al. 2013) (*Se13*, *OsTrx1* under LD conditions. Similarly, *Hd1* is upregulated by *OsGI* under both SD and LD conditions (Fig. 2) (Hori et al. 2013).

6 Photoperiods regulate the molecular genetic pathways of rice flowering

It is clear from the molecular study of Hd3a/FT protein that the induction of flowering is mainly measured from the expression level of Hd3a/FT genes that promote rice flowering. Recent studies provide the molecular understanding of *Hd3a* photoperiod regulation and the important features of this day-length regulation are LD suppression and SD promotion of *Hd3a* (Fig. 2).

7 *Hd3a* promotion under SD

Induction of *Hd3a* expression is at its peak about 30 days before the floral transition occurs under SD conditions in rice (Komiya et al. 2008). The circadian peak of *Hd3a* activity and mRNA production correspond at dawn, referring to an important unit of *Hd3a* transcriptional regulation (Ishikawa et al. 2005; Tamaki et al. 2007). *Hd3a* expression is mainly regulated by *Hd1* and *Ehd1* (Izawa 2007). *Hd1* was first reported as a major photoperiodic-sensitive QTL, it translates

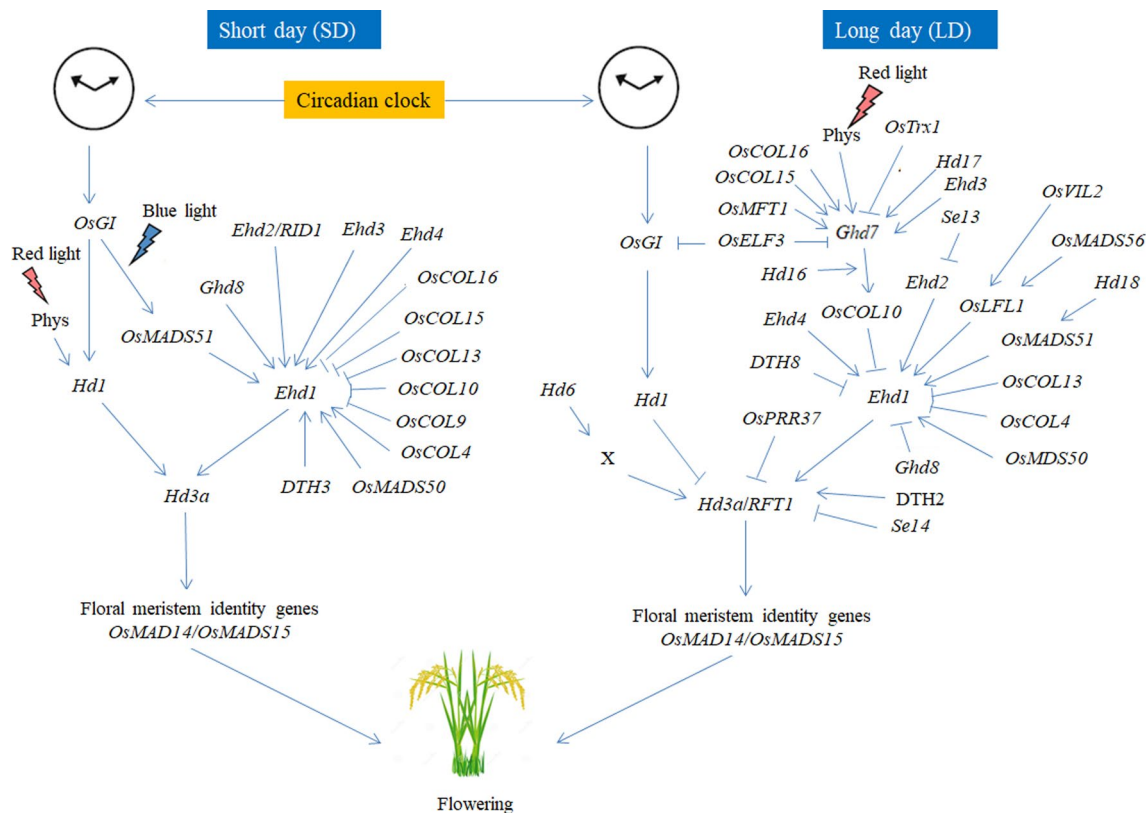


Fig. 2 Flowering regulatory genic web in rice. Rice florigen (Hd3a/RFT1) is mainly regulated by *Hd1* and *Ehd1* under both SD and LD conditions. The arrows and bar indicate up and downregulation, respectively

B-box zinc finger protein with C-terminal of CCT (CONSTANS, CONSTANS-LIKE, and TIMING OF CAB EXPRESSION1) Domain (Yano et al. 2000). During SD, the loss-of-function allele of *Hd1* results in suppression of flowering time and decreases *Hd3a* mRNA production (Izawa et al. 2002; Ishikawa et al. 2005). Phylogenetic studies revealed that *Hd1* is a CO ortholog of *Arabidopsis*, which is a key activator of FT (Izawa et al. 2003). *Hd1* involvement in *Hd3a* transcription is not so coherent, but the differences in spatiotemporal pattern of *Hd3a* and *Hd1* mRNA contribute to a more complex mechanism (Hayama et al. 2003). *Hd1* mRNA expression level is maximum at midnight, while *Hd3a* mRNA level peaks after 4–6 h of *Hd1* (Izawa et al. 2002; Shikawa et al. 2005).

OsGI is an ortholog of *Arabidopsis thaliana* GIGANTEA (GI) and a basic upstream regulator of *Hd1* expression (Hayama et al. 2002). *OsGI* is a big protein existing both in the nucleus and cytoplasmic matrix of cells in rice. Inhibition of *OsGI* expression by RNAi causes a delay in flowering, which reduces mRNA cumulating under SD conditions (Hayama et al. 2003; Kim et al. 2007). The *OsGI* expression is on peaks at dusk, while *Hd1* peaks at midnight, referring to the involvement of somewhat unknown mechanisms, which make the differences in the time of their expression (Sawa et al. 2007).

During circadian rhythm, the *OsGI* expression is regulated upstream of the circadian clock (Hayama et al. 2002; Mizoguchi et al. 2005). In *Arabidopsis*, circadian clock mutant GI has abnormal expression (Niwa et al. 2007), and GI itself is also considered a clock-associated protein (Locke et al. 2006; Zeilinger et al. 2006). *Ehd1* is another major gene that regulates the expression of *Hd3a*. *Ehd1* is identified from the cross of the T65 cultivar and Nipponbare (Doi et al. 2004). *Ehd1* encodes B-type regulation response, which reduces affinity for the target DNA sequence. Mutation suppresses the expression of *Ehd1*, which reduces the expression of *Hd3a* under SD, reflecting that *Ehd1* acts as an upstream regulator of *Hd3a* (Kim et al. 2007). *Ehd1* expression peaks before and after dawn under SD conditions, and the expression of *Hd3a* is like *Ehd1* in the absence of *Hd1* functional allele (Doi et al. 2004).

Ehd1 expression is controlled by two factors, *OsMADS51* and *Ghd7*. *OsMADS51* is the only activator of *Ehd1* under SD and LD conditions, while *Ghd7* suppresses *Ehd1* expression only under LD conditions (Fig. 2). *OsMADS51* activity is also suppressed by upregulation of *OsGI* because RNAi suppression of *OsGI* decreased *Ehd1* and *OsMADS51* expression (Fig. 2). *OsMADS51* and *OsGI* exhibited similar circadian rhythms, peaking at dusk under SD conditions (Lee and An 2015).

8 *Hd3a* suppression under LD

In many developmental stages, the *Hd3a* expression is low under LD conditions as compared to SD conditions. *Hd1* also plays a role in the suppression of *Hd3a* under LD, while promoting it under SD conditions. Prior to *Hd1* cloning, it was considered that mutant of *Hd3a* near-isogenic lines (NILs) delay flowering time under SD conditions and promote flowering under inductive LD, indicating that *Hd1* suppress the flowering time under SD condition and day-length modify the expression level of *Hd1* (Lin et al. 2000).

Photochromic signaling disturbs the day-length conversation of *Hd1* function because this action was not noted in phytochrome deficient plants; the flowering of rice double mutant *se5* and *Hd1* (which lack both phytochrome A and B and also *Hd1* gene), which is slightly later than single *se5* mutant (lacks only phytochromes) (Izawa et al. 2002). Furthermore, the *Hd3a* transcript production is low in *se5* and *Hd1* as compared to the *se5* mutant plant. The day length also modifies the function of *Hd1*, which was supported by manipulation of *OsGI* expression resulting in alteration in the expression of *Hd3* and *Hd1* expression (Hayama et al. 2003). Overexpression of *OsMTS1* and *OsGI* delay flowering under both SD and LD, indicating that *OsMTS1* and *OsGI* act as inhibitors of flowering under both conditions. In *OsGI* overexpression plants, the *Hd1* mRNA expression was increased under LD and SD conditions, while mRNA of *Hd3a* and *Hd1* is negatively associated with each other, revealing that *Hd1* suppresses *Hd3a* expression when it is extremely induced by *OsGI* overexpression line. *OsGI* overexpression also promotes *Hd3a* expression through upregulation of *Ehd1* of *OsGI*-*OsMADS51* pathway, but this expression is probably not observed due to strong inhibitor activity of *Hd1*. A diurnal temporal expression of *Hd3a* and *Hd1* showed a high level of *Hd3a* suppressed by *Hd1* during the light period. Under SD conditions, the *Hd1* expression probably increases at the start of dusk, thus maintaining *Hd1* as an activator. However, *OsGI* overexpression accumulates a high level of *Hd1* and converts into a repressor during the light period. Under LD conditions, *Hd1* expression is high during the day and converts *Hd1* into a suppressor (Hayama et al. 2003). Therefore, the external coincidence model can be applied to rice; a circadian clock regulates external light signals intermediated by phytochrome, and *Hd1* expression generate a specific response to day length (Izawa 2007).

The suppressor behavior of *Hd1* is not noted in association with *Arabidopsis thaliana* CO, showing that no different mechanisms that deliver this function. A

photoperiodic sensitive QTL *Hd2* may better explain this mechanism. *Hd2* was identified as QTL from crossing *indica* cultivar Kasalath and *japonica* cultivar Nipponbare (Yamamoto et al. 1998). *Hd2* required a functional allele of *Hd1* to delay flowering time under SD (Lin et al. 2000). Furthermore, *Hd2* is also necessary for *Hd6*, a photoperiodic sensitive QTL that delays flowering time under LD (Yamamoto et al. 2000).

Ehd1 expression suppresses under LD conditions, which results in low *Hd3a* expression. *Gh7* is also necessary for *Ehd1* suppression (Fig. 2). *Ghd7* contains a CCT domain, which is about 60% similar to *Hd1*, but *Hd7* does not have a zinc finger motif like *Hd1*. *Ghd7* does not affect *Ehd1* expression but intensely suppresses *Ehd1* expression. The expression of *Ghd7* is higher under inductive LD conditions in leaf vascular tissues and peaks significantly at dusk (Tsuji et al. 2013).

9 Genes contribute to Hd3a/FT signaling in SAM

The recognition of Hd3a/FT as florigen discloses the window for researchers to study the molecular mechanism of florigen in SAM. In this section, we will focus on FD, CEN/TFL1, MADS-box transcription factor (FUL/CAL/AP1), and MADS-box transcription factor (SOC1). The genes of above-mentioned categories are brief in below Table 1.

FD – In rice SAM, the interaction of *Hd3a* with bZIB transcription factor, which is orthologous of *Arabidopsis* FD results in the transformation of the vegetative phase into the reproductive phase. In *Arabidopsis thaliana*, FD accumulates on the edges of SAM where flower primordial produced. Its initiation starts in the vegetative stage before the arrival of FT. FD induces floral meristem identity gene *FRUIT-FULL* (*FUL*) and its paralog *APETALA1* (*AP1*) in the presence of the FT gene (Wigge et al. 2005; Abe et al. 2005). FD functions in not reported in rice. There are about seven FD orthologous (*OsbZIP24*, *OsbZIP27*, *OsbZIP54*,

Table 1 Flowering time genes involved in Hd3a/FT flowering signaling in SAM

Groups	Gene name	Locus	Specie	Domain	Note	References	
Hd3a/FT	<i>Hd3a</i>	<i>Os06g0157700</i>	Rice	Raf kinase inhibitor	Florigen; flowering promoter	Kojima et al. (2002)	
	<i>FT</i>	<i>At1g65480</i>	Arabidopsis		Florigen; flowering promoter	Kobayashi et al. (1999)	
	<i>FTL</i>	<i>Os01g0218500</i>	Rice		Flowering promoter	Izawa et al. (2002)	
	<i>RFT</i>	<i>Os06g0157500</i>	Rice		Flowering promoter	Izawa et al. (2002)	
CEN/TFL1	<i>RCN1</i>	<i>Os11g0152500</i>	Rice	Raf kinase inhibitor	Flowering inhibitor	Nakagawa et al. (2002)	
	<i>RCN2</i>	<i>Os02g0531600</i>	Rice		Flowering inhibitor	Nakagawa et al. (2002)	
	<i>RCN3</i>	<i>Os12g0152000</i>	Rice		Flowering inhibitor	Zhang et al. (2005)	
	<i>OsCEN3</i>	<i>Os04g0411400</i>	Rice		n.d	Zhang et al. (2005)	
	<i>TFL1</i>	<i>At5g03840</i>	Arabidopsis		Flowering inhibitor	Bradley et al. (1997)	
	<i>TSF</i>	<i>AT4g20370</i>	Arabidopsis		Flowering promoter	Yamaguchi et al. (2005)	
	FD	<i>FD</i>	<i>At4g35900</i>	Arabidopsis	bZIP	Flowering promoter	Wigge et al. (2005)
<i>OsbZIP27</i>		<i>Os03g0306700</i>	Rice		n.d	Nijhawan et al. (2008)	
<i>OsbZIP54</i>		<i>Os06g0719500</i>	Rice		n.d	Nijhawan et al. (2008)	
<i>OsbZIP55</i>		<i>Os06g0720900</i>	Rice		n.d	Nijhawan et al. (2008)	
<i>OsbZIP56</i>		<i>Os06g0724000</i>	Rice		n.d	Nijhawan et al. (2008)	
<i>OsbZIP69</i>		<i>Os08g0549600</i>	Rice		n.d	Nijhawan et al. (2008)	
<i>OsbZIP77</i>		<i>Os09g0540800</i>	Rice		n.d	Nijhawan et al. (2008)	
<i>OsbZIP24</i>		<i>Os02g0833600</i>	Rice		n.d	Nijhawan et al. (2008)	
MADS-box transcription factor (FUL/AP1/CAL)		<i>OsMADS14</i>	<i>Os03g0752800</i>	Rice	MADS-box	Flowering promoter	Kyozuka et al. (2000)
		<i>FUL</i>	<i>At5g60910</i>	Arabidopsis		Flowering promoter	Gu et al. (1998)
	<i>OsMADS15</i>	<i>Os07g0108900</i>	Rice		n.d	Kyozuka et al. (2000)	
	<i>AP1</i>	<i>At1g69120</i>	Arabidopsis		n.d	Mandel et al. (1992)	
MADS-box transcription factor (SOC1)	<i>OsMADS50</i>	<i>Os03g0122600</i>	Rice	MADS-box	Flowering promoter	Lee et al. (2004)	
	<i>SOC1</i>	<i>At2g45660</i>	Arabidopsis		Flowering promoter	Samach et al. (2000)	

n.d. not identified

OsZIP55, *OsZIP56*, *OsZIP69*, and *OsZIP77*) in rice whose function is not identified till now (Table 1). Among them, the *OsZIP24* mRNA level is comparatively more in SAM. *OsZIP54* mRNA distribute in the whole plant, especially SAM where the other FD-like bZIP factors is below the detection level (Nijhawan et al. 2008). Still, it is essential to study if there is any unclear functional differentiation among FD proteins.

10 MADS-box transcription factors

The genetic web acting downstream of FT in *Arabidopsis* involved *MADS-box* transcription factors. FT along with FD and LEAFY is essential for the induction of *FUL* and *API* in SAM. (Abe et al. 2005; Michaels et al. 2005; Teper-Bamnolker and Samach 2005). The regulation of FT-dependent gene has also been detected in *Arabidopsis* leaves. The expressions of *FUL* and *SEPALATA3* were promoted by overexpression of *FT* in leaves and decreased in *fd* and *ft* mutants (Teper-Bamnolker and Samach 2005). Therefore, both leaves and SAM share the same regulatory mechanisms. *OsMADS14/RAP1B*, an orthogonal of *API* and *OsMADS15* is upregulated by *Hd3a* in the leaves under SD (Komiya et al. 2008). This results shows that the similar regulatory mechanism involved in SAM and *OsMADS14* is expressed in apical meristem during a reproductive stage (Giavalisco et al. 2006; Furutani et al. 2006) and its ectopic behavior quickly endorses rice flowering (Jeon et al. 2000). API MADS-box proteins are serving as key mediators of Hd3a/FT activity in cereal crops flowering time. *OsMADS14* also acts as an activator of *Hd3a* in leaves (Kim et al. 2007; Lee et al. 2007). MADS-box protein suppresses the overexpression of Constants1 (SOC1) in *Arabidopsis*. The latest study showed that FT mediates SOC1 activation downstream of CO. SOC1 interacts directly with AGL24-MADS-box proteins in the SAM tips, and the direct attachment of AGL24-SOC1 forms a complex with the promoter of AGL24 and SOC1 and upregulates their expression level (Liu et al. 2008), whereas the regulatory mechanism and expression site is distinct in rice. Inserted T-DNA of *OsMADS50* reduces the transcription of *Hd3a* in the leaves, while RNAi inhibition of *Hd3a* or *Hd3a* and *RFT1* do not cause any modifications in the expression of *OsMADS50* (Table 1). Therefore, *OsMADS50* functions upstream of *Hd3a* in rice leaves (Lee et al. 2004; Komiya et al. 2008).

CEN/TFL1 – CENTORADIALIS (CEN)/TERMINAL FLOWER 1 (TFL1) protein provides an interesting understanding of Hd3a/FT signals in SAM. CEN/TFL1 is homologous of Hd3a/FT, which encodes RKIP proteins, however, the CEN/TFL1 protein inhibits flowering. The TFL1 mRNA

of *Arabidopsis* is restricted to the central inflorescence shoot meristem cells, and the TFL1 protein moves to the external cells. The suppression of flowering was comprehensively studied by *Arabidopsis* FT and TFL1 (Hanzawa et al. 2005; Ahn et al. 2006). Proteins carrying individual scums or alternatives to specific sections of FT and TFL1 are overexpressed in double *ft tfl1* mutants to draw residues or regions, that give the specific activity of both proteins. The crystal structure of TFL1 and FT were matched with specific map regions. These analyses showed that the consequent Tyr85 in His88 and FT in TFL1 are vital for the contrasting function of FT and TFL1 (Hanzawa et al. 2005), and the section liable for the difference is confined in 14 amino acid segments of the external loop of proteins at C-termini.

– There are about four CEN/TFL1-like genes in the rice genome (Chardon et al. 2005). *RICE CENTRORADIALS1 (RCN1)*, *RCN2*, and *RCN3* can suppress flowering initiation and affect panicle structure when overexpressed (Table 1) (Nakagawa et al. 2002; Zhang et al. 2005). The RCN3 protein can be observed in the phloem sap of rice, which suggests that the protein signals are linked between different parts (Aki et al. 2008). An attractive assumption that explains the differences between CEN/TFL1 and Hd3a/FT controlling activity is that the external loop introduces different partners to CEN/TFL1 or Hd3a/FT to define the capabilities of the complex. Screening analysis of protein interaction using a precise external loop provides a deeper understanding of Hd3a/FT signals and promotes flower promotion.

11 Conclusions and perspective

Decades of research on flowering time expand our understanding of the molecular mechanism of flowering time regulation in rice. A molecular control network is becoming complex day by day due to novel genes and their regulatory mechanisms. Florigen is also referred to as a mobile flowering hormone because of its mobility and flowering activation nature. For flowering time regulation in rice, it is necessary to explore Hd3a/FT synthesis, identification, transport, receptor activity, and cellular signaling pathway. Recent advances confirmed that still very less is known about Hd3a trafficking activity, the direction of Hd3a in the phloem, how Hd3a in companion cells is transported into the sieve element system, and how Hd3a targets SAM after unloading from the upper end of the phloem are all open questions for discussion. Flowering time research has also identified many important genes as a resources for breeding. Natural variation and artificial selection of flowering genes that are/were vanished through the domestication process should not only contribute to exploiting the mechanism

of flowering time gene regulation but also facilitate future breeding programs.

Data Availability The data that support this study cannot be publicly shared due to privacy reasons and may be shared upon reasonable request to the corresponding author if appropriate.

Declarations

Conflict of interest The authors declare no conflict of interest.

References

- Abe M, Kobayashi Y, Yamamoto S, Daimon Y, Yamaguchi A, Ikeda Y, Ichinoki H, Notaguchi M, Goto K, Araki T (2005) FD, a bZIP protein mediating signals from the floral pathway integrator FT at the shoot apex. *Sci* 309:1052–1056
- Abe M, Fujiwara M, Kurotani K, Yokoi S, Shimamoto K (2008) Identification of dynamin as an interactor of rice GIGANTEA by tandem affinity purification (TAP). *Plant Cell Physiol* 49:420–432
- Ahn JH, Miller D, Winter VJ, Banfield MJ, Lee JH, Yoo SY, Henz SR, Brady RL, Weigel D (2006) A divergent external loop confers antagonistic activity on floral regulators FT and TFL1. *EMBO J* 25:605–614
- Aki T, Shigyo M, Nakano R, Yoneyama T, Yanagisawa S (2008) Nano scale proteomics revealed the presence of regulatory proteins including three FT-like proteins in Phloem and Xylem saps from rice. *Plant Cell Physiol* 49:767–790
- Bradley D, Ratcliffe O, Vincent C, Carpenter R, Coen E (1997) Inflorescence commitment and architecture in *Arabidopsis*. *Science* 275:80–83
- Brambilla V, Fornara F (2013) Molecular control of flowering in response to day length in rice. *J Integr Plant Bio* 5:4–12
- Camoni L, Visconti S, Aducci P, Marra M (2018) 14-3-3 Proteins in plant hormone signaling: doing several things at once. *Front Plant Sci* 9:297
- Chardon F, Damerval C (2005) Phylogenomic analysis of the PEBP gene family in cereals. *J Mol Evol* 61:579–590
- Doi K, Izawa T, Fuse T, Yamanouchi U, Kubo T, Shimatani Z, Yano M, Yoshimura A (2004) *Ehd1*, a B-type response regulator in rice, confers short-day promotion of flowering and controls FT-like gene expression independently of *Hd1*. *Genes Dev* 18:926–936
- Gao H, Xiao MZ, Guilin F, Jun C, Mingna J, Yulong R, Weixun W, Zhou K, Sheng P, Zhou F, Jiang L, Wang J, Zhang X, Guo X, Wang J, Cheng Z, Wu C, Wang H, Wan JM (2013) *Ehd4* encodes a novel and Oryza-genus-specific regulator of photoperiodic flowering in rice. *PLoS Genet* 9:1–12
- Giavalisco P, Kapitza K, Kolasa A, Buhtz A, Kehr J (2006) Towards the proteome of *Brassica napus* phloem sap. *Proteom* 6:896–909
- Goretti D, Martignago D, Landini M, Brambilla V, Gomez AJ, Gnesutta N, Galbiati F, Collani S, Takagi H, Terauchi R, Mantovani R, Fornara F (2017) Transcriptional and post-transcriptional mechanisms limit Heading Date 1 (*Hd1*) function to adapt rice to high latitudes. *PLoS Genet* 13:1006530
- Gu Q, Ferrandiz C, Yanofsky MF, Martienssen R (1998) The FRUIT-FULL MADS-box gene mediates cell differentiation during *Arabidopsis* fruit development. *Dev* 125:1509–1517
- Guo T, Mu Q, Wang J, Vanous AE, Onogi A, Iwata H, Yu J (2020) Dynamic effects of interacting genes underlying rice flowering-time phenotypic plasticity and global adaptation. *Genome Res* 30:673–683
- Hayama R, Izawa T, Shimamoto K (2002) Isolation of rice genes possibly involved in the photoperiodic control of flowering by a fluorescent differential display method. *Plant Cell Physiol* 43:494–504
- Hayama R, Yokoi S, Tamaki S, Yano M, Shimamoto K (2003) Adaptation of photoperiodic control pathways produces short day flowering in rice. *Nature* 422:719–722
- Hori K, Matsubara K, Yano M (2016) Genetic control of flowering time in rice: integration of Mendelian genetics and genomics. *Theor Appl Genet* 129:2241–2252
- Huan Z, Shanshan Z, Tianzhen L, Chunming W, Zhijun C, Xin Z, Liping C, Peike S, Maohong C, Chaonan L, Jiachang W, Zhe Z, Juntao C, Liang Z, Cailin L, Xiuping GZ, Jiulin W, Jie W, Ling J, Chuanyin W, Jianmin W (2018) Delayed heading date1 interacts with OSHAP5C/D, delays flowering time and enhances yield in rice. *Plant Biotech J* 17:531–539
- Ishikawa R, Tamaki S, Yokoi S, Inagaki N, Shinomura T, Takano M, Shimamoto K (2005) Suppression of the floral activator *Hd3a* is the principal cause of the night break effect in rice. *Plant Cell* 17:3326–3336
- Izawa T (2007) Day length measurements by rice plants in photoperiodic short-day flowering. *Int Rev Cytol* 256:191–222
- Izawa T, Oikawa T, Sugiyama N, Tanisaka T, Yano M, Shimamoto K (2002) Phytochrome mediates the external light signal to repress *FT* orthologs in photoperiodic flowering of rice. *Genes Dev* 16:2006–2020
- Izawa T, Takahashi Y, Yano M (2003) Comparative biology comes into bloom: genomic and genetic comparison of flowering pathways in rice and *Arabidopsis*. *Curr Opin Plant Biol* 6:113–120
- Jaeger KE, Wigge PA (2007) FT protein acts as a long-range signal in *Arabidopsis*. *Cur Biol* 17:1050–1054
- Jang S, Marchal V, Panigrahi KCS, Wenkel S, Soppe W, Deng XW, Valverde F, Coupland G (2008) *Arabidopsis* COP1 shapes the temporal pattern of CO accumulation conferring a photoperiodic flowering response. *EMBO J* 27:1277–1288
- Kim SL, Lee S, Kim HJ, Nam HG, An G (2007) *OsMADS51* is a short day flowering promoter that functions upstream of *Ehd1*, *OsMADS14*, and *Hd3a*. *Plant Physiol* 145:1484–1494
- Kobayashi Y, Weigel D (2007) Move on up, it's time for change-mobile signals controlling photoperiod-dependent flowering. *Genes Dev* 21:2371–2384
- Kobayashi Y, Kaya H, Goto K, Iwabuchi M, Araki T (1999) A pair of related genes with antagonistic roles in mediating flowering signals. *Science* 286:1960–1972
- Kojima S, Takahashi Y, Kobayashi Y, Monna L, Sasaki T, Araki T, Yano M (2002) *Hd3a*, a rice ortholog of the *Arabidopsis* *FT* gene, promotes transition to flowering downstream of *Hd1* under short day conditions. *Plant Cell Physiol* 243:1096–1105
- Komiya R, Yokoi S, Shimamoto K (2009) A gene network for long-day flowering activates *RFT1* encoding a mobile flowering signal in rice. *Dev* 136:3443–3450
- Kyozuka J, Kobayashi T, Morita M, Shimamoto K (2000) Spatially and temporally regulated expression of rice MADS box genes with similarity to *Arabidopsis* class A, B and C genes. *Plant Cell Physiol* 41:710–718
- Lee, An (2015) Regulation of flowering time in rice. *J Plant Biol* 58:353–360
- Lee SY, Kim J, Han JJ, Han MJ, An GH (2004) Functional analyses of the flowering time gene *OsMADS50*, the putative *SUPPRESSOR OF OVEREXPRESSION OF CO 1/AGAMOUS-LIKE 20 (SOC1/AGL20)* ortholog in rice. *Plant J* 38:754–764
- Lee YS, Dong HJ, Dong YL, Jakyung Y, Gynheung A (2010) *OsCOL4* is a constitutive flowering repressor upstream of *Ehd1* and downstream of *OsphyB*. *Plant J* 63:18–30
- Lin HX, Yamamoto T, Sasaki T, Yano M (2000) Characterization and detection of epistatic interactions of 3 QTLs, *Hd1*, *Hd2*, and *Hd3*,

- controlling heading date in rice using nearly isogenic lines. *Theor Appl Genet* 101:1021–1028
- Lin MK, Belanger H, Lee YJ, Varkonyi GE, Taoka KI, Miura E, Xoconostle CB, Gendler K, Jorgensene RA, Phinney B, Lough TJ, Lucas WJ (2007) *FLOWERING LOCUS T* protein may act as the long-distance florigenic signal in the cucurbits. *Plant Cell* 19:1488–1506
- Liu H, Gu F, Dong S, Liu W, Wang H, Chen Z, Wang J (2016) Constans-like 9 (COL9) delays the flowering time in *Oryza sativa* by repressing the *ehd1* pathway. *Biochem Biophys Res Commun* 479:173–178
- Liu J, Gong J, Wei X, Yang S, Huang X, Li C, Zhou X (2020) Dominance complementation of *Hd1* and *Ghd8* contributes to extremely late flowering in two rice hybrids. *Mol Breed* 40:76
- Locke JCW, Kozma BL, Gould PD, Feher B, Kevei E, Nagy F, Turner MS, Hall A, Millar AJ (2006) Experimental validation of a predicted feedback loop in the multi-oscillator clock of *Arabidopsis thaliana*. *Mol Syst Biol* 2:59
- Mandel MA, Gustafson BC, Savidge B, Yanofsky MF (1992) Molecular characterization of the *Arabidopsis* floral homeotic gene *APETALA1*. *Nature* 360:273–277
- Mathieu J, Warthmann N, Küttner F, Schmid M (2007) Export of FT protein from phloem companion cells is sufficient for floral induction in *Arabidopsis*. *Cur Biol* 17:1055–1060
- Matsubara K, Yamanouchi U, Wang ZX, Minobe Y, Izawa T, Yano M (2008) *Ehd2*, a rice ortholog of the maize *INDETERMINATE1* gene, promotes flowering by up-regulating *Ehd1*. *Plant Physiol* 148:1425–1435
- Matsubara K, Yamanouchi U, Nonoue Y, Sugimoto K, Yano M (2011) *Ehd3*, encoding a plant homeodomain finger-containing protein, is a critical promoter of rice flowering. *Plant J* 66:603–612
- Michaels SD, Himelblau E, Kim SY, Schomburg FM, Amasino RM (2005) Integration of flowering signals in winter-annual *Arabidopsis*. *Plant Physiol* 137:149–156
- Mizoguchi T, Wright L, Fujiwara S, Cremer F, Lee K, Onouchi H, Mouradov A, Fowler S, Kamada H, Putterill J, Coupland G (2005) Distinct roles of *GIGANTEA* in promoting flowering and regulating circadian rhythms in *Arabidopsis*. *Plant Cell* 17:2255–2270
- Molla AK (2022) Flowering time and photoperiod sensitivity in rice: Key players and their interactions identified. *Plant Cell* 34:3489–3490
- Monna L, Lin HX, Kojima S, Sasaki T, Yano M (2002) Genetic dissection of a genomic region for a quantitative trait locus, *Hd3*, into two loci, *Hd3a* and *Hd3b*, controlling heading date in rice. *Theor Appl Genet* 104:772–780
- Nakagawa M, Shimamoto K, Kyojuka J (2002) Overexpression of *RCN1* and *RCN2*, rice *TERMINAL FLOWER 1/CENTRORADIALIS* homologs, confers delay of phase transition and altered panicle morphology in rice. *Plant J* 29:743–750
- Nemoto Y, Nonoue Y, Yano M, Izawa T (2016) *Hd1*, a *CONSTANS* ortholog in rice, functions as an *Ehd1* repressor through interaction with monocot-specific CCT-domain protein *Ghd7*. *Plant J* 86:221–233
- Nijhawan A, Jain M, Tyagi AK, Khurana JP (2008) Genomic survey and gene expression analysis of the basic leucine zipper transcription factor family in rice. *Plant Physiol* 146:333–350
- Niwa Y, Ito S, Nakamichi N, Mizoguchi T, Niinuma K, Yamashino T, Mizuno T (2007) Genetic linkages of the circadian clock-associated genes, *TOC1*, *CCA1* and *LHY*, in the photoperiodic control of flowering time in *Arabidopsis thaliana*. *Plant Cell Physiol* 48:925–937
- Park SJ, Song LK, Shinyoung L, Byoung IJ, Hai LP, Sung HP, Chu MK, Choong HR, Su HP, Yuan HX, Joseph C, Gynheung A, Chang DH (2008) Rice Indeterminate 1 (*OsId1*) is necessary for the expression of *Ehd1* (*Early heading date 1*) regardless of photoperiod. *Plant J* 56:1018–1029
- Peng LT, Shi ZY, Li L, Shen GZ, Zhang JL (2008) Overexpression of transcription factor *OsLFL1* delays flowering time in *Oryza sativa*. *J Plant Physiol* 165:876–885
- Peng Q, Zhu C, Liu T, Zhan S, Feng S, Wu C (2021) Phosphorylation of *OsFD1* by *OsCIPK3* promotes the formation of *RFT1*-containing florigen activation complex for long-day flowering in rice. *Mol Plant* 14:1135–1148
- Ryu CH, Lee S, Cho LH, Kim SL, Lee YS, Choi SC, Jeong HJ, Yi J, Park SJ, Han CD, An G (2009) *OsMADS50* and *OsMADS56* function antagonistically in regulating long day (LD)-dependent flowering in rice. *Plant Cell Environ* 32:1412–1427
- Samach A, Onouchi H, Gold SE, Ditta GS, Schwarz SZ, Yanofsky MF, Coupland G (2000) Distinct roles of *CONSTANS* target genes in reproductive development of *Arabidopsis*. *Science* 288:1613–1616
- Sawa M, Nusinow DA, Kay SA, Imaizumi T (2007) *FKF1* and *GIGANTEA* complex formation is required for day-length measurement in *Arabidopsis*. *Sci* 318:261–265
- Sheng P, Wu F, Tan J, Zhang H, Ma W, Chen L, Wang J, Wang J, Zhu S, Guo X, Wang J, Zhang X, Cheng Z, Bao Y, Wu C, Liu X, Wan J (2016) A *CONSTANS*-like transcriptional activator, *OsCOL13*, functions as a negative regulator of flowering downstream of *OsphyB* and upstream of *Ehd1* in rice. *Plant Mol Biol* 92:209–222
- Shikawa R, Tamaki S, Yokoi S, Inagaki N, Shinomura T, Takano M, Shimamoto K (2005) Suppression of the floral activator *Hd3a* is the principal cause of the night break effect in rice. *Plant Cell* 17:3326–3336
- Shim JS, Jang G (2020) Environmental signal-dependent regulation of flowering time in Rice. *Int J Mol Sci* 21:6155
- Shrestha R, Gomez AJ, Brambilla V, Fornara F (2014) Molecular control of seasonal flowering in rice, *Arabidopsis* and temperate cereals. *Ann Bot* 114:1445–1458
- Sohail A, Shah L, Liu L, Islam A, Yang Z, Yang Q, Anis GB, Xu P, Khan RM, Li J et al (2022) Mapping and validation of *qHD7b*: major heading-date QTL functions mainly under long-day conditions. *Plants* 11:2288
- Song YH, Shim JS, Kinmonth SHA, Imaizumi T (2015) Photoperiodic flowering: time measurement mechanisms in leaves. *Annu Rev Plant Biol* 66:441–464
- Song S, Wang G, Hu Y, Liu H, Bai X, Qin R (2018) *OsMFT1* is regulated by *Ghd7* and *OsLFL1* to increase spikelets per panicle and delay heading date in rice. *J Exp Bot* 69:4283–4293
- Sun C, Chen D, Fang J, Wang P, Deng X, Chu C (2014) Understanding the genetic and epigenetic architecture in complex network of rice flowering pathways. *Protein Cell* 5:889–898
- Tamaki S, Matsuo S, Wong HL, Yokoi S, Shimamoto K (2007) *Hd3a* protein is a mobile flowering signal in rice. *Science* 316:1033–1036
- Tan J, Jin M, Wang J, Wu F, Sheng P, Cheng Z, Wang J, Zheng X, Chen L, Wang M, Zhu S, Guo X, Zhang X, Liu X, Wang C, Wang H, Wu C, Wan J (2016) *OsCOL10*, a *CONSTANS*-like gene, functions as a flowering time repressor downstream of *Ghd7* in rice. *Plant Cell Physiol* 57:798–812
- Taoka KI, Izuru O, Tsuji H, Furuita K, Hayashi K, Yanase T, Yamaguchi M, Nakashima C, Purwestri YA, Tamaki S (2011) 14-3-3 proteins act as intracellular receptors for rice *Hd3a* florigen. *Nature* 476:332–335
- Teper-Bamnlolker P, Samach A (2005) The flowering integrator FT regulates *SEPALLATA3* and *FRUITFULL* accumulation in *Arabidopsis* leaves. *Plant Cell* 17:2661–2675
- Tsuji H (2017) Molecular function of florigen. *Breed Sci* 67:327–332
- Tsuji H, Taoka K, Shimamoto K (2011) Regulation of flowering in rice: two florigen genes, a complex gene network, and natural variation. *Curr Opin Plant Biol* 14:45–52

- Tsuji H, Taoka K, Shimamoto K (2013) Florigen in rice: complex gene network for florigen transcription, florigen activation complex, and multiple functions. *Curr Opin Plant Biol* 16:228–235
- Wu W, Zheng XM, Chen D, Zhang Y, Ma W, Zhang H, Sun L, Yang Z, Zhao C, Zhan X, Shen X, Yu P, Fu Y, Zhu S, Cao L, Chenga S (2017) *OsCOL16*, encoding a CONSTANS-like protein, represses flowering by upregulating *Ghd7* expression in rice. *Plant Sci* 260:60–69
- Wu W, Zhang Y, Zhang M, Zhan X, Cao L (2018) The rice constans-like protein *OsCOIL5* suppresses flowering by promoting *Ghd7* and repressing *RID1*. *Biochem Biophys Res Commun* 495:1349
- Wu CC, Wei FJ, Chiou WY, Tsai YC, Wu HP, Gotarkar D, Hsing YIC (2020) Studies of rice *Hd1* haplotypes worldwide reveal adaptation of flowering time to different environments. *PLoS ONE* 15:e0239028
- Yamaguchi A, Kobayashi Y, Goto K, Abe M, Araki T (2005) TWIN SISTER OF FT (TSF) acts as a floral pathway integrator redundantly with FT. *Plant Cell Physiol* 46:1175–1189
- Yamamoto T, Kuboki Y, Lin SY, Sasaki T, Yano M (1998) Fine mapping of quantitative trait loci *Hd-1*, *Hd-2* and *Hd-3*, controlling heading date of rice, as single Mendelian factors. *Theor Appl Genet* 97:37–44
- Yamamoto T, Lin HX, Sasaki T, Yano M (2000) Identification of heading date quantitative trait locus *Hd6* and characterization of its epistatic interactions with *Hd2* in rice using advanced backcross progeny. *Genetics* 154:885–891
- Yan WH, Wang P, Chen HX, Zhou HJ, Li QP, Wang CR, Ding ZH, Zhang YS, Yu SB, Xing YZ, Zhang QF (2011) A Major QTL, *Ghd8*, plays pleiotropic roles in regulating grain productivity, plant height, and heading date in rice. *Mol Plant* 4:319–330
- Yang Y, Peng Q, Chen GX, Li XH, Wu CY (2013) *OsELF3* is involved in circadian clock regulation for promoting flowering under long-day conditions in Rice. *Mol Plant* 1:202–215
- Yano M, Katayose Y, Ashikari M, Yamanouchi U, Monna L, Fuse T, Baba T, Yamamoto K, Umehara Y, Nagamura Y, Sasaki T (2000) *Hd1*, a major photoperiod sensitivity quantitative trait locus in rice, is closely related to the Arabidopsis flowering time gene CONSTANS. *Plant Cell* 12:2473–2483
- Zeevaart JAD (2006) Florigen coming of age after 70 years. *Plant Cell* 18:1783–1789
- Zeilinger MN, Farre EM, Taylor SR, Kay SA, Doyle FJ (2006) A novel computational model of the circadian clock in Arabidopsis that incorporates PRR7 and PRR9. *Mol Syst Biol* 2:58
- Zhang SH, Hu WJ, Wang LP, Lin CF, Cong B, Sun CR, Luo D (2005) *TFL1/CEN*-like genes control intercalary meristem activity and phase transition in rice. *Plant Sci* 168:1393–1408
- Zhang Z, Hu W, Shen G, Liu H, Hu Y, Zhou X, Liu T (2017) Alternative functions of *Hd1* in repressing or promoting heading are determined by *Ghd7* status under long-day conditions. *Sci Rep* 7:5388
- Zhang H, Zhu S, Liu T, Wang C, Cheng Z, Zhang X, Chen L, Sheng P, Cai M, Li C, Wang J, Zhang Z, Chai J, Zhou L, Lei C, Guo X, Wang J, Wang J, Jiang L, Wu C, Wan J (2019) *DELAYED HEADING DATE1* interacts with OsHAP5C/D, delays flowering time and enhances yield in rice. *Plant Biotechnol J* 17:531–539
- Zhu S, Wang J, Cai M, Zhang H, Wu F, Xu Y, Li C, Cheng Z, Zhang X, Guo X, Sheng P, Wu M, Wang J, Lei C, Wang J, Zhao Z, Wu C, Wang H, Wan J (2017) The OsHAPL1-DTH8-Hd1 complex functions as the transcription regulator to repress heading date in rice. *J Exp Bot* 68:553–568
- Zong W, Ren D, Huang M, Sun K, Feng J, Zhao J, Guo J (2020) Strong photoperiod sensitivity is controlled by cooperation and competition among *Hd1*, *Ghd7* and *DTH8* in rice heading. *New Phytol* 229:1635–1649

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